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The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa

HAROLD N. BRYANT AND ANTHONY P. RUSSELL

Department of Biological Sciences, University of Calgary, 2500 University Dr. N.W., Calgary, Alberta, Canada T2N 1N4

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SUMMARY

A research programme is proposed for the inference of unpreserved attributes of fossil taxa. The programme includes: (i) phylogenetic inference of attributes based on the cladistic distribution of known features in related taxa; and (ii) extrapolatory analyses that infer unpreserved features from the known attributes of the fossil. Phylogenetic inferences regarding the fossil taxon are based on the attributes of both the sister group of the fossil taxon and more distantly related clades. Unlike phylogenetic inferences that are based on a single related taxon, this broader phylogenetic context avoids unjustified assumptions regarding the occurrence of unpreserved features in particular fossil taxa. Phylogenetic inference is conservative; only features in related taxa can be inferred in the fossil. Extrapolatory analyses, such as form–function correlation and biomechanical design analysis, provide a means for choosing among equivocal phylogenetic inferences, and, on occasion, can provide a basis for rejecting a phylogenetic inference. Extrapolatory approaches provide the only means of inferring or interpreting autapomorphies in fossils. The results of phylogenetic and extrapolatory approaches to the reconstruction of the shoulder musculature of the ornithomimid *Struthiomimus* are compared. Results are congruent in most instances; however, many of the extrapolatory inferences are implicitly phylogenetic. The phylogenetic inferences constitute a null hypothesis regarding fossil attributes, and place constraints on the inferences generated by extrapolatory analyses. The potential uncertainty and untestability of many extrapolatory analyses suggests that the phylogenetic inference should be overturned only when the functional or other extrapolatory evidence is compelling. This procedure should identify and reduce speculation in fossil reconstruction.

1. INTRODUCTION

The relative incompleteness of information regarding extinct organisms, when compared with that for extant taxa, is manifest in two ways: (i) not all species or populations of extinct organisms are represented in the fossil record; and (ii) fossilized remains of extinct taxa preserve only a portion of the attributes that can be observed in extant organisms. The consequences of the first type of incompleteness have received consider-

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able recent attention (see, for example, Paul 1982; McKinney 1986; Schoch 1986; Hoffman 1989; Marshall 1990). The import of the second for the role of fossils in phylogenetic reconstruction has been debated (Crowson 1970; Lovtrup 1977; Patterson 1981; Gauthier *et al.* 1988*a*; Donoghue *et al.* 1989), whereas its significance for the study of fossils as intact functional entities has received less recent scrutiny. Thus, although 'the bringing of fossils to life' through the reconstruction of their unpreserved attributes has garnered much attention (see, for example, Paul 1987; Dodson *et al.* 1990), there is no clearly defined procedure that is consistent with modern phylogenetic theory and encompasses all relevant approaches. The need for extant models is acknowledged, but the justification for particular choices is often flawed or lacking. Consequently, reconstructions of *Archaeopteryx*, for example, as either a feathered 'reptile' (weak flier or glider, ectothermic) or as the archetype for extant birds (avian powered flight, endothermic) often lack the scientific rigor that a precise research programme could provide. Without the constraints of such a methodology the boundary between valid scientific inference and pure speculation in fossil reconstruction is too easily crossed.

Traditionally a limited number of extant taxa, often a single taxon, have provided the basis for inferences regarding unpreserved features of extinct taxa. The choice of extant models may be based on various rationales depending on the causal constraints governing attributes in particular fossils that are considered most important by the investigator. In many instances the rationale behind the choice of a particular model is uncertain. Cooper's (1981) reconstructions of muscle attachments in the sauropodomorph *Massospondylus* utilize birds as the primary model; it is unclear whether birds were chosen for phylogenetic reasons or because the two taxa were considered to have a functionally similar locomotory system.

In many instances a particular extant taxon is chosen because of an assumed close phylogenetic relationship to the fossil taxon. For example, Osborn (1929) based much of the anatomy of the brontothere *Palaeosyops* on that of *Equus*, Russell (1972) reconstructed the musculature of the thigh in ornithomimids from Romer's publications (1923, 1942) on 'reptiles', and Maglio (1973) reconstructed the skull musculature of the mammoth *Mammuthus* from that of the extant elephants (*Loxodonta* and *Elephas*). Such assumed relationships often lack a precise or complete phylogenetic framework. Thus, both crocodylians (see, for example, Coombs (1978) for ankylosaurs) and birds (see, for example, Paul (1988) for theropods) have been used as primary models for reconstructions of dinosaur anatomy. However, these single-taxon phylogenetic comparisons are problematic because there is no basis for determining if transfer of a feature from the extant to the fossil taxon is justified.

We herein propose a more formalized research programme for the inference of unpreserved attributes of fossil taxa that utilizes both phylogenetic information and extrapolations from the known features of the fossil. Proper phylogenetic inference involves a broader comparative context that is based on the outgroup algorithm of Maddison *et al.* (1984). Phylogenetic inferences regarding musculature in the ornithomimid *Struthiomimus* are compared with those generated by a previous analysis (Nicholls & Russell 1985) that adopted a functional (i.e. extrapolatory) approach to reconstruction. The roles of, and interactions between, different approaches to inferences in fossils are discussed. This paper focuses on the inference of attributes, such as soft anatomy, that are not normally preserved in the fossil record. Thus the comparative context in both the phylogenetic and extrapolatory approaches is provided primarily by extant taxa. The same approaches can be applied to the inference of unknown, but fossilizable, attributes; in this case, other extinct taxa may provide the most appropriate comparative context.

2. A RESEARCH PROGRAMME FOR THE INFERENCE OF ATTRIBUTES OF FOSSILS

The methodologies utilized in the inference of unpreserved attributes of fossil taxa are comparative; unpreserved features are inferred in the light of information provided, at least in part, by other taxa. Bock (1989) divided biological comparisons into two categories, historical and non-historical, which he related only roughly to evolutionary against functional explanations in biology (Mayr 1982; Bock 1988). He subdivided historical comparisons into those that elucidate phylogeny and those that use phylogeny as the basis for further analysis. Bock (1989) also divided non-historical comparisons into two categories: those that are used to infer biological generalizations, and those by which unknown properties of organisms are deduced. Bock's comparative framework is applicable to the methodology used in the inference of attributes in fossils.

Two separate approaches can provide valid inferences regarding the unpreserved attributes of extinct taxa: (i) transferral of known attributes in other taxa to the fossil taxon based upon an explicit statement of phylogenetic relationships; and (ii) extrapolatory analysis based on the preserved features of the fossil taxon. In the first approach, a phylogenetic hypothesis that includes the extinct taxon provides a basis for the inference of the fossil's unknown characteristics from the known distribution of characteristics in related taxa. This approach is a historical comparison (*sensu* Bock 1989) based on an established phylogeny. The second approach depends on established biological generalizations that allow the inference of unknown attributes of the fossil from its particular preserved features and is a deductive non-historical comparison (*sensu* Bock 1989).

The comparative contexts for phylogenetic and extrapolatory approaches differ. In phylogenetic inference, comparison is limited to a strict genealogical context; known features of related taxa that can be postulated to have characterized a mutual common ancestor are transferred to the fossil. The approach is conservative; unique features in the fossil cannot be postulated. Extrapolatory approaches depend on assumed nomological generalizations. These generalizations involve established law-like relationships between variables that are assumed to hold across a series of organisms (Bock 1989). The preservation of one variable in the fossil allows extrapolation of the second. The appropriate comparative context depends on the particular generalization. Certain generalizations will be restricted to particular monophyletic groups (e.g. skeletomuscular relationships in vertebrates) suggesting that Bock's designation of this as a non-historical approach is not entirely accurate. Other generalizations lack any strong phylogenetic context; these usually involve broadly applicable solutions to environmental constraints (e.g. modifications associated with streamlining in aquatic organisms). Unlike phylogenetic inference, extrapolatory approaches allow the inference of attributes in fossils that do not occur in genealogically related taxa.

(*a*) ***Theoretical basis for phylogenetic inference***

Phylogenetic inferences require a hypothesis of phylogenetic relationships between the fossil taxon (or taxa) and two or more extant taxa. Given the phylogeny, the character state that most parsimoniously fits the distribution of character states exhibited by the extant taxa is inferred to have been present in the fossil taxon. The basic evolutionary assumptions and their corollaries provide the justification for transferring the known features of organisms to closely related fossil taxa. Fossil taxa are predicted to share the synapomorphies that diagnose the clades to which they belong. In the absence of contradictory evidence, transferral of those attributes to the fossil is the most parsimonious inference. The strength of these inferences can be assessed by the degree of support that exists for the particular phylogenetic hypothesis used. This application of phylogenetic information exemplifies the increasing realization that corroborated phylogenetic hypotheses form the basis for various approaches in comparative biology (see, for example, Lauder 1981, 1982; Liem & Wake 1985; Pagel & Harvey 1988; Liem 1989; Lang 1990; Brooks & McLennan 1991; Harvey & Pagel 1991). Lauder (1981, pp. 431–432) stated that 'a phylogenetic hypothesis allows the reconstruction of the historical sequence of structural change through time and thus serves as a null hypothesis from which significant deviations may be detected and indicates the appropriate level of generality at which structure-environment correlations must be explained'. A fundamental role for phylogenetic relationships in fossil reconstruction is consistent with this view.

The extant sister group provides the single most appropriate comparison for the inference of character states in the fossil taxon. None the less, such single-taxon comparisons are problematic because they are based on the assumption that the feature was present in the common ancestor of the two taxa. There is no justification for this assumption based on the sister group relationship alone; the character state in the extant taxon could be an autapomorphy. Phylogenetic justification for inferring that the feature was present in the common ancestor of the extant and fossil taxa depends upon a broader comparative context that includes the extant sister group and at least one additional extant taxon that belongs to a more inclusive monophyletic group. For example, Bakker (1986) presented a series of arguments for gizzards in sauropod dinosaurs. Part of his argument is phylogenetic; extant crocodylians and most birds use gizzards in the mechanical digestion of food items. The occurrence of the same character state in the two most closely related extant clades provides a decisive phylogenetic inference of gizzards in dinosaurs. The association of probable gastroliths with some skeletons (Cooper 1981; Bakker 1986) supports the inferences provided by the phylogenetic relationships.

(*b*) ***Theoretical basis for extrapolatory analysis***

Alternatively, the reconstruction of unpreserved attributes in fossil taxa can be based on the known attributes of the fossil, which are analysed in light of assumed biological generalizations (i.e. law-like nomological statements (Bock 1989)) among variables that allow the inference of particular unknown morphologies, behaviour or other unfossilized attributes. For most features, especially soft anatomy and behaviour, these generalizations are formulated through the study of extant organisms. These deductions will be valid only if the nomological, or law-like, relationships exist. Most extrapolatory approaches fit one of two general categories, form–function correlation or biomechanical design analysis (Hopson & Radinsky 1980; Radinsky 1987). In form–function correlation, generalizations are based on observed associations among particular morphologies, functions and behaviours across groups of, usually extant, species. These taxa are used as analogues so that the occurrence of a particular feature in the fossil is used to predict the associated unpreserved attribute. Examples include the reconstruction of musculature from osteological features and inferences of diet from dentition. In vertebrates, established generalizations between superficial relief of skeletal elements and the morphology and functioning of joints, ligaments and muscles provide the justification for the reconstruction of posture and musculature from the skeleton in fossil taxa. These form–function correlations are often limited to a particular, if broad, phylogenetic context. In contrast, biomechanical design analysis infers function or other attributes from the interpretation of the fossil from a biomechanical or engineering perspective. Appropriate generalizations may concern the architectural properties of biological materials or typical responses of organisms to physical laws. The primary basis for comparison is usually environmental rather than phylogenetic; none the less, some broad historical context may apply. For example, similarities in body form among certain sharks, tunas and cetaceans have been correlated with optimal performance criteria for periodic body/caudal fin propulsion in an aquatic environment (Webb 1984). Such generalizations provide a basis for inferring similar behaviour in ichthyosaurs, which display the same basic design criteria (Massare 1988).

Extrapolatory inferences regarding fossil attributes suffer from potential uncertainty and untestability regarding the applicability of the necessary nomological statements. In extant organisms the existence of these nomological connections are often directly testable by experiment or observation (e.g. for muscle reconstruction from osteology (McGowan 1979, 1982, 1986; Bryant & Seymour 1990)). In extinct organisms, however, one must assume that these generalizations can be extended to particular fossils. Some nomological statements developed from the study of extant organisms can be assumed to apply equally to fossils. Examples include those related to structural properties of biological materials such as bone and ligaments, lever mechanics, and trophic energy flow in ecosystems. Others can be shown to hold for particular monophyletic groups, so that if the fossil belongs to the group the application of the nomological statement can be considered valid. However, when the nomological statement is applied across taxa for which equivalence in the functional or anatomical system has not, or cannot, be demonstrated, the justification for the extrapolation is suspect and the resulting inferences are necessarily uncertain.

(*c*) ***The research programme***

This difference in justification for phylogenetic and extrapolatory inferences provides a rationale for assigning primacy to the phylogenetic inferences and for allowing extrapolatory arguments to overturn the phylogenetic alternatives only when the evidence is compelling. It also supports the use of phylogeny in the choice of functional analogues. The framework of a smaller closed descent community (*sensu* Ax 1985, 1987) will increase the likelihood that the necessary nomological statements exist among the taxa being compared.

A complete research programme for the reconstruction of the unpreserved attributes of fossil taxa includes both phylogenetic and extrapolatory approaches. We propose a stepwise procedure (figure 1) beginning with the phylogenetic approach and proceeding to the evaluation of its results using extrapolatory approaches. The phylogenetic approach provides a 'null hypothesis', the most parsimonious inference or set of alternatives based on a corroborated hypothesis of phylogenetic relationships. The results can then be tested through analysis of the known attributes of the fossil, its depositional setting, or functional analyses, as appropriate for the attribute in question. Using a stepwise approach, phylogenetic inferences can be clearly separated from those based on extrapolatory arguments so that the contribution of each line of reasoning is evident. The phylogenetic approach tempers or places constraints on the inferences drawn from other analyses so that when the phylogenetic inference is decisive, strong arguments should be forwarded if alternative reconstructions are preferred.

The application of phylogenetic reasoning to the inference of attributes in fossils is outlined below. Subsequent comparison of the phylogenetic inferences of musculature in the ornithomimid *Struthiomimus* with inferences generated using an extrapolatory approach provides a basis for further discussion of the roles and independence of these approaches to fossil reconstruction.

3. THE PHYLOGENETIC METHOD FOR INFERENCES ABOUT EXTINCT TAXA

The method is conceptually predicated on the global method of outgroup comparison of Maddison *et al.* (1984) and is an application of their outgroup algorithm for multiple outgroups (figure 2). Maddison *et al.* (1984) demonstrated that, although use of a single outgroup can produce a decisive local inference regarding the character state at the outgroup node, this inference may not be the most parsimonious when more distant outgroups are considered. The outgroup algorithm determines the most parsimonious inference for the character state at the outgroup node based on the character distribution in a series of outgroups. The character states in terminal outgroup taxa are used to assign character states to internal nodes; two adjacent nodes or taxa are required in each instance. One proceeds from the terminal outgroup taxa towards the outgroup node (figure 2*a*, *b*). The assignment of a character state to the outgroup node may be decisive or equivocal.

The same reasoning can be used to assign a character state to the most recent common ancestor of the fossil taxon and its extant sister group (the fossil–extant node (figure 2*c*, *d*)); this character state is then transferred to the fossil. Use of the sister group alone cannot produce a decisive result regarding the fossil taxon because it is equally parsimonious to consider a character state to be unique to the extant taxon as it is to consider it a synapomorphy of the extant taxon and the fossil taxon. Inclusion of additional extant taxa allows one to use the outgroup algorithm to produce a more globally parsimonious inference for the fossil–extant node (figure 2*c*, *d*).

The assumptions of the approach are identical to those of Maddison *et al.* (1984) with the additional assumption that no autapomorphic character change occurred in the fossil taxon. This is a methodological requirement of the approach; although fossil taxa often have autapomorphies, those that are not preserved cannot be inferred using this method and thus cannot be considered.

(*a*) ***Generalizations of phylogenetic inference***

1. Minimally the character state in the extant sister group and in the next most closely related extant clade are required for phylogenetic inference; this provides the two necessary adjacent assigned nodes. If these two extant groups, or their basal nodes, share the same character state, an unequivocal decision is possible in the fossil taxon (first doublet rule for outgroup comparison of Maddison *et al.* (1984)). If the two extant groups have different character states the

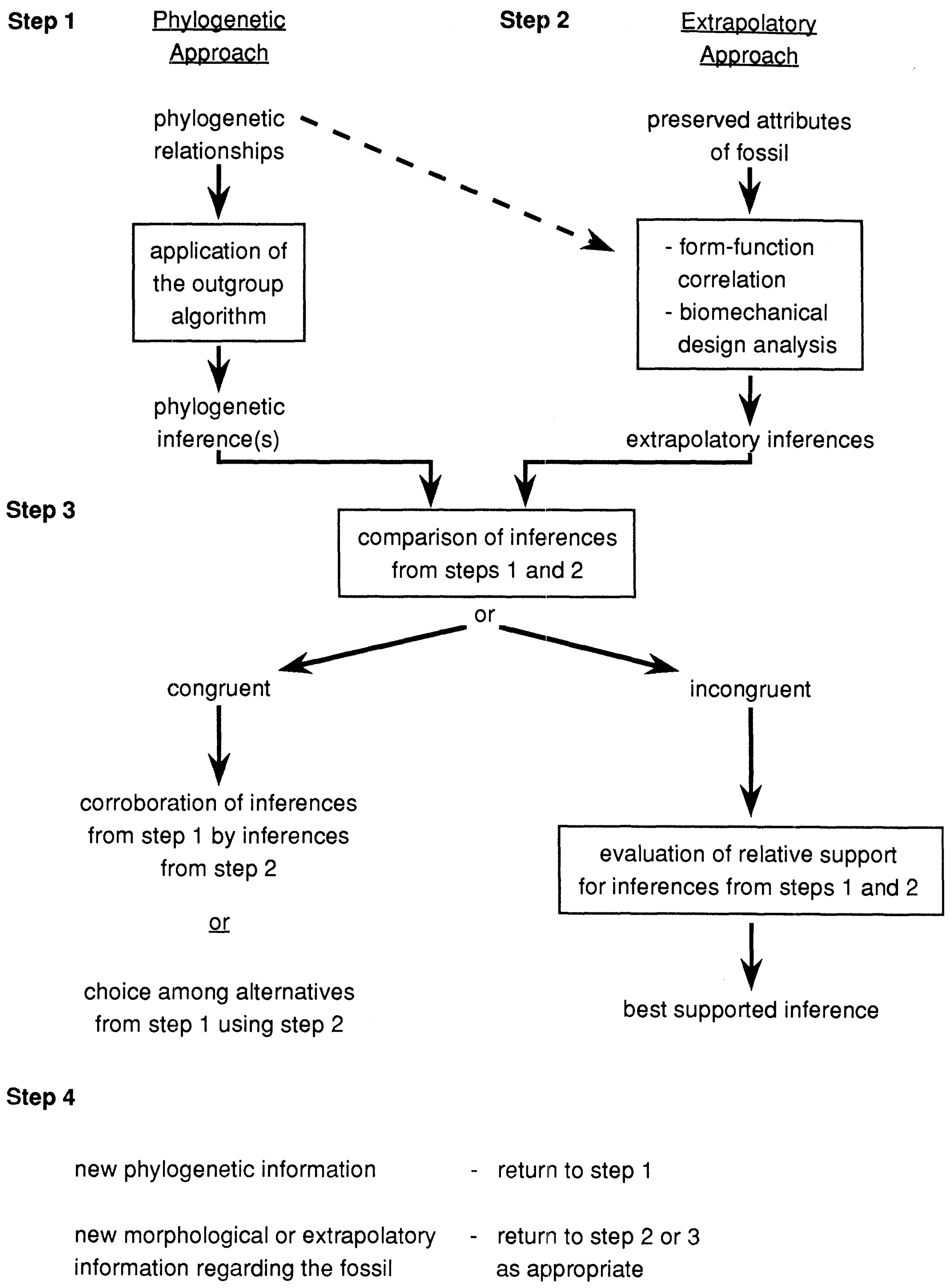

Figure 1. A flow chart for the proposed research programme for the inference of unknown attributes in fossil taxa. The dashed arrow denotes the role of phylogenetic relationships in the choice of appropriate models for extrapolatory approaches. See text for discussion.

situation may be resolvable by reference to one or more distantly related extant taxa. Some character-state distributions will not produce a decisive result regardless of the number of extant taxa surveyed. The method can accommodate situations in which the extant sister group or other pertinent clades are represented by a number of constituent clades (e.g. figure 3*b*). The basal character state for the more inclusive clade can be resolved before, or simultaneously with, inference in the fossil taxon (e.g. ancestral character states in Aves (figure 5)).

For example, consider a fossil taxon, X, and three extant taxa, A, B and C (figure 3). In figure 3*a*, if the same character state occurs in A and B, this character state is transferred to the fossil–extant node and to the fossil taxon, X. In this instance, the character state in C is irrelevant. If different character states occur in A and B, however, the character state in X cannot be determined unequivocally without reference to C or more distantly related taxa. For example, if A and C share the same character state, this state can be inferred in X; the most parsimonious inference is that the state in B is an autapomorphy for that taxon. However, if a more distant outgroup, D, was surveyed and agreed with B, the decision would become equivocal. In figure 3*b*, reference to all three extant taxa is necessary to provide information regarding the two adjacent nodes. If the character state in C is the

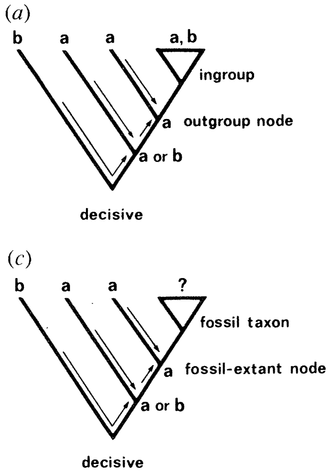

Figure 2. Comparison of the outgroup algorithm of Maddison *et al.* (1984) (*a*, *b*) with the phylogenetic method for inferring unpreserved attributes in fossil taxa (*c*, *d*). In using the outgroup algorithm, one proceeds from outgroup terminal taxa toward the outgroup node. An internal node is labelled 'a' if the two immediately adjacent nodes are labelled 'a' and 'a', or 'a' and 'a or b'. A node is labelled 'b' if the two adjacent nodes are labelled 'b' and 'b', or 'b' and 'a or b'. Nodes are labelled 'a or b' if the adjacent nodes are labelled 'a' and 'b', or 'a or b' and 'a or b'. In (*a*) the assignment to the outgroup node is decisive ('a'); in (*b*) the assignment is equivocal ('a or b'). The assignment at the outgroup node is used to polarize character transformations within the ingroup. See Maddison *et al.* (1984) for more details. In phylogenetic inference the same procedure is used to assign a character state to the fossil–extant node. As in the outgroup algorithm the assignment may be decisive or equivocal. The assignment at the fossil–extant node is transferred to the fossil as the most parsimonious phylogenetic inference regarding the unpreserved attribute.

same as that of at least one of A and B, that character state can be assigned unequivocally to X. If A and B differ, this 'local' decision could be affected by information regarding more distantly related taxa.

2. A character state other than that found in the extant sister group of the fossil taxon cannot be a decisive inference for the character state in the fossil. As in rule 3 of Maddison *et al.* (1984), more distantly related groups cannot overturn the character state implied by the sister group. Instead, more distantly related groups provide a basis of comparison that indicates when the condition in the sister group is the most parsimonious inference for the fossil taxon and when the character distribution is equivocal.

For example, in figure 3*a*, if the character state in B differs from that in A and agrees with that in C, the inference in X is equivocal. Although B and C form a doublet they cannot overrule the character state in A, the sister group to X. The most parsimonious inference for X is either the character state in the sister group or it is equivocal. In figure 3*c*, the identification of the sister group to X is unresolved. In this instance a decisive inference in X is possible only if the same character state occurs in A, B and C. In other instances the decision would depend on the particular resolution of the trichotomy.

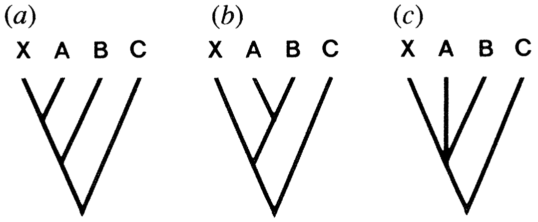

Figure 3. Three patterns of phylogenetic relationship among a fossil taxon, X, and three extant taxa, A, B, and C. See text for discussion.

3. Phylogenetic inference is conservative; only features that characterize at least two related taxa can be inferred unequivocally in the fossil. Extrapolatory analyses are required for the resolution of equivocal phylogenetic inferences and the inference and interpretation of autapomorphies in fossils.

(*b*) *Inferences in a series of related fossil taxa*

The same extant taxa often provide the frame of reference for inferences in several fossil taxa. Figure 4 describes the relationships among three extant taxa, A, B and C, and four fossil taxa X_1, X_2, X_3 and X_4. This phylogenetic pattern is equivalent to that in figure 3*a* except that four fossil taxa instead of one are positioned between A and B. Although A is more closely related to X_1 than to any of the other fossil taxa, all four fossil taxa are more closely related to A than they are to any other extant taxon; if any one of the four fossil taxa is considered alone the phylogeny in figure 3*a* is obtained. Thus, the comparative context for inferences regarding unknown attributes in the four fossil taxa using the phylogeny is identical; there is no justification for the transfer of attributes from A to X_1 but not to the other fossil taxa. The phylogenetic pattern in figure 4 corresponds to that argued for Aves, Crocodylia, Lepidosauria and various extinct archosaurian clades (Gauthier 1986; Gauthier *et al.* 1988*a*). Based on the phylogeny alone there is no justification for the transfer of attributes of

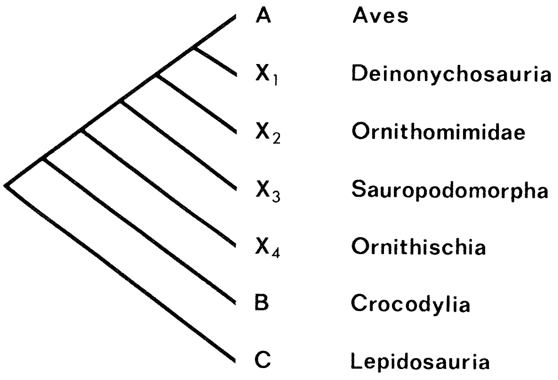

Figure 4. A pattern of phylogenetic relationship among four fossil taxa, X_1, X_2, X_3 and X_4, and three extant taxa, A, B and C, with an example based on the relationships among diapsids (simplified from Gauthier (1986) and Gauthier *et al.* (1988*a*)).

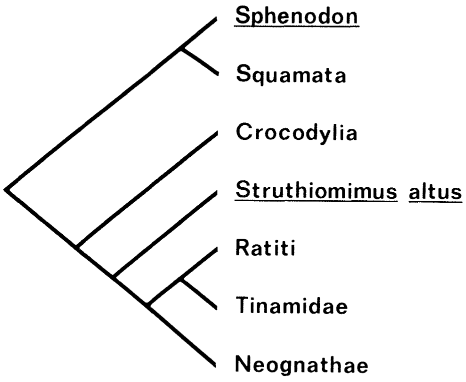

Figure 5. The comparative context for the phylogenetic inference of unknown features in *Struthiomimus altus*. Relationships are simplified from Cracraft (1974, 1986) and Gauthier *et al.* (1988*a*).

birds to closely related theropod taxa (X_1, X_2) but not to the Sauropodomorpha and Ornithischia. In each instance, unequivocal inference of the feature in the fossil taxon requires that the character state also be present in a more distantly related extant taxon such as the Crocodylia or Lepidosauria. Although the phylogeny predicts that Aves and various theropod taxa share features not present in Sauropodomorpha and Ornithischia, the relationships alone provide no justification for the transfer of particular attributes from Aves to other theropods but not to more distantly related dinosaurian taxa. Such a transfer would amount to an arbitrary decision regarding the position of a character transformation on the cladogram.

(*c*) *Computer algorithms for assigning character states to internal nodes*

Computer algorithms provide an objective method for making these phylogenetic inferences because they assign character states to the internal nodes of most-parsimonious cladograms and identify any ambiguity associated with those nodes (Farris 1970; Swofford & Maddison 1987). If particular features of terminal taxa are unknown, as in the case of unpreserved attributes, character state assignments to internal nodes, such as the fossil–extant nodes, may be equivocal. Algorithms included in computer software such as PAUP (Swofford 1991) will resolve this ambiguity based on the topology of the tree; thus, the DELTRAN option forces transformations away from the root toward the terminal taxa and the ACCTRAN option does the reverse. Such decisions are either arbitrary or based on a particular model of evolutionary process. The use of these algorithms to resolve ambiguity in the phylogenetic inference of unpreserved attributes should be avoided. Extrapolatory analysis of the known attributes of the fossil is the appropriate method for choosing among alternative resolutions because it can provide a non-arbitrary, biologically based inference regarding the unpreserved attribute.

4. COMPARISON OF PHYLOGENETIC AND EXTRAPOLATORY INFERENCES

Nicholls & Russell (1985) presented an ostensively functional analysis of the forelimb of the ornithomimid *Struthiomimus altus* which included the reconstruction of portions of the musculature of the shoulder. This extrapolatory analysis entailed form–function correlation and was based on comparisons with three extant analogues that were expected to provide different insights into the anatomy in the fossil: (i) crocodylians, in which similarities were expected to reflect phylogenetic history; (ii) ratite birds, *Struthio* in particular, in which similarities were expected to reflect homoplastic resemblance due to convergent body form; and (iii) chameleons, which were chosen because of similarities in the primary shoulder girdle and could be considered a 'control' for comparisons between the other two models. Although these models are representatives of the taxa appropriate for a phylogenetic analysis, Nicholls & Russell's (1985) approach was primarily functional. Comparisons utilized particular extant taxa as functional analogues rather than the inferred ancestral morphotypes of those groups. In addition, some muscle attachment sites were inferred directly from appropriately positioned scars or delimitable osteological features.

The comparative context for phylogenetic inferences in the ornithomimid *Struthiomimus* is depicted in figure 5. Relationships among the avian taxa (Cracraft 1974, 1986) are required to infer the ancestral avian morphology. The distribution of morphology among these six extant taxa was used to infer the morphology of the six shoulder muscles in *Struthiomimus* considered by Nicholls & Russell (1985). Information on the myology of the extant taxa was gleaned from the following sources: *Sphenodon* (Miner 1925; Holmes 1977; Russell 1988, unpublished results); squamates, *Iguana* in particular (Holmes 1977; Russell 1988, unpublished results), crocodylians (Holmes 1977; Nicholls & Russell 1985), ratites (McGowan 1982; Nicholls & Russell 1985), Tinamidae (Hudson *et al.* 1972), and neognaths (Berger 1954, 1960, 1966; McGowan 1986).

The phylogenetic and extrapolatory inferences are compared in table 1. Comparisons include: (i) instances in which the phylogenetic and extrapolatory inferences are essentially identical; (ii) instances in which the phylogenetic inference is equivocal and the extrapolatory arguments suggest one of the phylogenetic alternatives; and (iii) instances in which the phylogenetic and extrapolatory inferences differ (table 2). Evaluation of particular instances within these three categories provides a basis for elucidating the precise role that each approach plays in the reconstruction of the musculature in the fossil taxon.

(*a*) *Category 1*

Phylogenetic inference usually provides decisive results, at least in part, regarding the elements to which particular muscles attach; this reflects widespread conservatism in muscle attachments at this coarse level of resolution. Because this conservatism

Table 1. *Comparison of phylogenetic inferences with the results of the functional analysis of Nicholls & Russell (1985) for selected muscles in the shoulder of Struthiomimus*

	phylogenetic inference	functional inference
M. deltoides scapularis:		
origin	scapula (at least in part), extent, exact position and additional heads from other elements equivocal (on blade in reptiles, closer to glenoid and with additional heads from other elements in Aves)	scapula, on anterolateral surface of blade
insertion	humerus, on deltopectoral crest, distal extent equivocal (proximal in reptiles, extends distally in Aves)	humerus, proximally in shallow depression on dorsal surface, posterior to deltopectoral crest
M. deltoides clavicularis:		
origin	clavicle, medial portion	scapular prominence, muscle unreduced
insertion	equivocal (on deltopectoral crest of humerus in reptiles, on antebrachium, manus and associated muscles in Aves)	humerus, figure 11 indicates a relatively distal attachment
M. coracobrachialis brevis:		
origin	coracoid, lateral surface, close to glenoid, size equivocal (large in reptiles, smaller in Aves)	coracoid, in trough-like depression, ventral to glenoid on dorsal margin of posterior coracoid process
insertion	humerus, on ventral (flexor) or equivalent surface of proximal end	humerus, figure 11 indicates ventral surface of proximal end
M. coracobrachialis longus:		
origin	coracoid, posteroventral portion (posterior coracoid process) of lateral surface (equivocal regarding extension onto sternum – only in Aves)	coracoid, lateral surface of posterior coracoid process
insertion	humerus, position equivocal (entepicondylar crest in reptiles, proximally in Aves)	humerus, figure 11 indicates a distal site
M. supracoracoideus:		
origin	equivocal because of variation in extant taxa, probably at least in part from coracoid	bipartite, from anterior portion of lateral surface of coracoid, and from anteroventral portion of lateral surface of scapula
insertion	humerus, proximal portion of deltopectoral crest	humerus, more distally on deltopectoral crest
M. biceps brachii:		
origin	coracoid, lateral surface near glenoid (second origin from humerus (only in Aves) equivocal)	coracoid, biceps tubercle (anteroventral to glenoid on lateral surface)
insertion	radius and ulna, proximal ends	radius and ulna, proximal ends?
M. scapulotriceps:		
origin	scapula, dorsal to glenoid on lateral surface or posterior margin	scapula, scar on dorsal lip of supraglenoid buttress
insertion	ulna, olecranon process	ulna, olecranon process (implied)

usually also applies to the models chosen by Nicholls & Russell (1985), results of the functional analysis generally agree with these phylogenetic inferences. Some agreements between the two approaches regarding more precise attachment sites also reflect conservatism among the taxa studied rather than an agreement between phylogenetic inferences and detailed functional arguments (e.g. insertion of the M. coracobrachialis brevis on the proximal ventral surface of the humerus, insertion of the M. biceps brachii on the proximal end of the radius and ulna, and insertion of the M. scapulotriceps on the olecranon).

Agreement between separate phylogenetic and extrapolatory inferences does occur in other instances. Although the clavicle, the expected site of origin for the M. deltoides clavicularis, is lost in *Struthiomimus*, phylogeny suggests that the muscle is present; loss of the muscle in ratites is considered an autapomorphy. Nicholls & Russell (1985) argued for the presence of the muscle on functional grounds. The unreduced nature of the forelimbs, together with their carriage and probable involvement in prehension, suggested an unreduced M. deltoides clavicularis. Origin from the scapular prominence as in *Alligator* would have allowed for strong protraction and elevation of the humerus. Phylogeny suggests that the M. coracobrachialis longus took origin from the posterior coracoid process; Nicholls & Russell's basis for the same conclusion was the size of the process and the powerful humeral retraction and adduction that would result from an origin significantly posterior to the glenoid.

(*b*) *Category 2*

In many instances phylogenetic inference produces an equivocal assignment at the fossil–extant node. In

Table 2. *Categorization of the comparison between the phylogenetic inferences and the results of the functional analysis of Nicholls & Russell (1985) for selected muscles in the shoulder of Struthiomimus*

Category 1. Agreement between the phylogenetic and functional inferences	
M. deltoides clavicularis	– origin (in part)
M. coracobrachialis brevis	– origin (in part) – insertion
M. coracobrachialis longus	– origin (in part)
M. biceps brachii	– origin (in part) – insertion
M. scapulotriceps	– origin – insertion
Category 2. Agreement between one of the alternatives suggested by the phylogenetic inference and the functional inferences	
M. deltoides scapularis	– origin – insertion
M. deltoides clavicularis	– insertion
M. coracobrachialis longus	– origin (in part) – insertion
M. biceps brachii	– origin (in part)
Category 3. Disagreement between the phylogenetic and functional inferences	
M. deltoides clavicularis	– origin (in part)
M. coracobrachialis brevis	– origin (in part)
M. supracoracoideus	– origin – insertion

most cases this reflects differences in morphology between lepidosaurs and crocodylians on the one hand, and birds on the other. Although many of these differences reflect structural modifications in the avian forelimb that are associated with the flight apparatus, one should not assume that the morphology in *Struthiomimus* necessarily matches that in extant non-avian diapsids. Extrapolatory analysis provides a basis for making a decision among the alternatives suggested by the phylogeny.

The phylogenetic inference regarding the position of the origin and insertion of the M. deltoides scapularis on the scapula and humerus, respectively, is equivocal. In lepidosaurs and crocodylians the muscle takes origin from the scapular blade, whereas in birds the origin is closer to the glenoid; the muscle inserts on the deltopectoral crest region in all extant taxa but tends to extend further down the humeral shaft in birds. Nicholls & Russell's (1985) inferences conform to the morphology in the non-avian taxa in each instance. An origin from the scapular blade was inferred from the unreduced nature of this structure, which resembles that in *Alligator* and *Chamaeleo*; in this position the muscle would have been effective in humeral protraction and elevation. A relatively proximal insertion on the humerus was inferred from a shallow depression on the dorsal surface, posterior to the deltopectoral crest. In contrast, Nicholls & Russell's conclusion regarding the origin of the M. biceps brachii seems to be based on negative evidence, or an implicit assignment of *Struthiomimus* to the reptilian grade, rather than on a functional argument. Aves have a second humeral origin for this muscle that is absent in lepidosaurs and crocodylians; thus the phylogenetic inference is equivocal. Nicholls & Russell inferred only the coracoid origin, stating that there is no evidence for the humeral origin. No functional argument for this conclusion is presented.

(*c*) *Category 3*

In a few instances the functional inferences of Nicholls & Russell (1985) differ from the alternatives suggested by the phylogeny. In one instance (origin of M. deltoides clavicularis) the phylogenetic inference is impossible based on the known morphology of *Struthiomimus*; in other cases the functional analysis suggested a different choice among possible alternatives.

The phylogenetic inference that M. deltoides clavicularis takes origin from the clavicle is incompatible with the absence of this element in *Struthiomimus*. Nicholls & Russell reconstructed the muscle with its origin on the large scapular prominence as in *Alligator*, which also lacks clavicles. The inference was based on a particular functional analogue; its inferred position would have maintained the action of the muscle and its positional relation with the M. deltoides scapularis.

The phylogenetic inference regarding the origin of the M. supracoracoideus is extremely equivocal because of the variety of character states among the extant taxa. It is restricted to the external surface of the coracoid plate in lepidosaurs, extends dorsally onto the scapula in the Crocodylia, and extends onto the sternum, associated membranes and occasionally the furcula in Aves. The highly modified morphology of most birds, that can be associated with flight (Ostrom 1974*a*, 1976), does not occur in *Struthio*; thus this alternative was not considered by Nicholls & Russell. They reconstructed the M. supracoracoideus as a bipartite muscle with origins from both the coracoid and scapula as in *Alligator* and *Chamaeleo*. Phylogeny predicts a coracoid origin but interprets the crocodylian origin from the scapula as an autapomorphy. The structure of the glenoid suggested that the humeral protractors were well developed, and Nicholls & Russell proposed that the M. supracoracoideus extended dorsally onto the blade of the scapula, a condition most like that of *Chamaeleo*. This would have enhanced forereach and provided significant humeral elevation. However, a number of muscles could potentially provide the range of movements suggested by the glenoid; the solution chosen by Nicholls & Russell followed from the use of *Chamaeleo* as a functional analogue. It could be argued that it is more parsimonious to ascribe these functions to muscles normally present on the scapula, such as the deltoids that also elevate and protract the humerus, rather than to postulate the extension of other muscles onto the scapula. It could be counter-argued, however, that the observed morphology in *Chamaeleo* provides a known solution to this functional demand and that it is reasonable to assume that a similar solution occurred in *Struthiomimus*. The precise origin of the

M. coracobrachialis brevis and the insertion of the M. supracoracoideus inferred by Nicholls & Russell also differ from the phylogenetic inferences. In each instance the attachment was associated with a particular osteological landmark which differs somewhat in position from the location suggested by phylogeny.

(*d*) ***Summary and discussion***

Most comparisons between the phylogenetic inferences and the results of the extrapolatory analysis of Nicholls & Russell (1985) belong to the first two categories (table 2); thus, the results of the two approaches are compatible in most instances. None the less, in some of the instances in category 1, the functional inferences are implicitly phylogenetic. Much of the consistency in muscle position among Nicholls & Russell's three functional analogues probably reflects the common ancestry shared by those taxa as much or more than it reflects functional constraints. The separate phylogenetic analysis provides a basis for recognizing the influence of phylogenetic history on the functional arguments. Only those functional arguments that are free of phylogenetic reasoning lend independent support to the phylogenetic inferences. For instances in category 2, the functional and anatomical analyses provide a basis for choosing among equivocal phylogenetic inferences. Instances in category 3 can provide a basis for rejecting the phylogenetic inference. Such a decision must be based on a relative assessment of the evidence in support of the phylogenetic and anatomical or functional arguments. The decision will be unproblematic when the anatomy indicates that the phylogenetic inference is impossible. Often, however, the functional inference will depend on a nomological generalization of uncertain validity and, thus, the basis for rejection of the phylogenetic inference will be weak. Nicholls & Russell's reconstruction of the origin of the M. supracoracoideus was based largely on the anatomy of *Chamaeleo*; however, as discussed above, their argument is only one of a number that could be proposed and there is no rigorous rationale for choosing among them.

5. DISCUSSION

Phylogenetic inference is a powerful approach to the inference of attributes in fossils which has been ignored in many studies that emphasize the extrapolatory approach. Munthe (1989) took a laudably conservative approach to functional reconstruction of the musculature in the Borophaginae. Reconstruction was based on osteological information and comparisons with the musculature of *Canis*, *Felis* and *Crocuta*. In several cases the osteological information and functional analysis failed to provide the decisive inference regarding borophagine musculature that a phylogenetic analysis using the same taxa would have supplied. For example, Munthe was unable to determine whether or not the M. deltoides had a two-headed origin from the scapula; however, because two heads characterize recent carnivorans, the phylogenetic evidence for two heads in the Borophaginae is strong.

Phylogenetic inference of attributes in fossil taxa should not be based on single extant comparative models; instead, the fossil should be placed within a closed descent community wherein attributes in both the extant sister group and more distantly related clades are considered. This approach determines whether attributes can be unequivocally transferred to the fossil and avoids *a priori* gradistic assumptions regarding its features. Many reconstructions of dinosaurs utilize non-avian diapsids, and especially crocodylians, as primary models (see, for example, Russell 1972; Coombs 1978) whereas others utilize birds (Galton 1969; Cooper 1981). Whereas dinosaurs were traditionally restored as 'reptiles', some 'cladists' have made the opposite mistake of overemphasizing avian features in their reconstructions, especially of theropods. For example, part of Padian & Olsen's (1989) argument for preferring an avian, rather than a crocodylian, 'paradigm' for theropods is 'phylogenetic'; as extant theropods, Aves is the extant sister taxon of individual extinct theropod taxa. Such choices appear to reflect a decision on the part of the investigator to place primary emphasis on either a 'reptilian' assessment of the dinosaur taxon or the assumed closest cladogenic relationship to birds, and entail *a priori* assumptions regarding the position of particular transformations on the cladogram. Such decisions will greatly influence the outcome as the number of equivocal phylogenetic decisions in *Struthiomimus* illustrates. This reflects the large number of character transformations that occurred in the lineage leading to birds after cladogenic separation of that lineage from the lineage leading to the Crocodylia. The *Struthiomimus* example demonstrates the equivocal nature of phylogenetic inferences in any fossil taxon whose extant sister group is Aves regarding features that differ between Aves and extant non-avian diapsids. This situation characterizes phylogenetic inference in most extinct archosaurs, including pterosaurs and dinosaurs. Proper phylogenetic inference avoids *a priori* assumptions and considers the morphology of birds, crocodylians and other extant taxa. Reconstructions and analyses that utilize this more complete phylogenetic context include those of Ostrom (1974*b*) and Gatesy (1990).

The proposed method of phylogenetic inference provides the precise phylogenetic context that is lacking in many previous reconstructions of fossil taxa. Holmes (1977) described the osteology and reconstructed the musculature of the pectoral limb of small captorhinids. He viewed the captorhinids as closely related descendants of the ancestral amniote, and considered their osteology and musculature to be representative of the latter. Although some musculature was reconstructed from muscle scars, the positions of others were inferred solely from the musculature of extant turtles and diapsids. The consistency in much of the musculature of extant taxa was used to infer a similar pattern for primitive amniotes (i.e. captorhinids). However, Holmes's analysis lacked a precise phylogenetic framework that would have guided

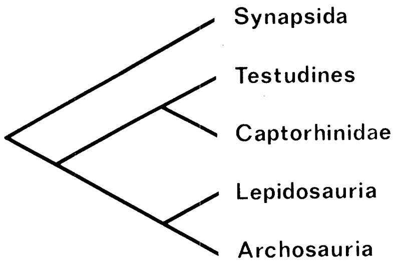

Figure 6. Phylogenetic relationships among the Captorhinidae and the major extant clades of amniotes (modified from figure 4.4 in Gauthier *et al.* (1988*b*)).

decisions on appropriate comparisons. Because he considered captorhinids representative of primitive amniotes, and because many attributes of the pectoral limb of turtles were considered apomorphic, the diapsids *Sphenodon*, *Iguana* and *Crocodylus* were considered the best extant models for the musculature of captorhinids. His choice of extant models involved *a priori* gradistic assumptions regarding captorhinids. However, recently proposed phylogenetic relationships suggest that captorhinids are more closely related to the Testudines than to other extant reptiles (Gaffney & Meylan 1988; Gauthier *et al.* 1988*b*). Consequently, inferences about captorhinids require comparisons among attributes of turtles and various other amniote clades (figure 6). Features shared by turtles, lepidosaurs and archosaurs can be transferred to their common ancestor and to captorhinids as well. In contrast, the phylogenetic evidence is equivocal for features that differ between turtles and diapsids. As their extant sister group, turtles most strongly constrain phylogenetic inferences for captorhinids.

Because phylogenetic inferences are based on a particular phylogenetic hypothesis, the fossil taxa to which particular features can be transferred may change with revision of the phylogeny. Jenkins (1990) presented a hypothesis of mammalian relationships that suggests that monotremes evolved from pre-tribosphenic therians during the late Jurassic or early Cretaceous (figure 7*a*). He argued correctly that features such as endothermy, fur, sweat glands, and 'modern' cardiovascular and respiratory systems, that are shared by monotremes, metatherians and eutherians, were probably present in their most recent common ancestor. Because Jenkins's phylogeny suggests that monotremes are extremely closely related to other extant mammals these attributes can be transferred to only one extinct clade (figure 7*a*). However, other phylogenetic hypotheses consider the Monotremata more distantly related to therians (figure 7*b*); using Rowe's (1988) phylogeny, attributes shared by all extant mammals can be inferred in a larger number of extinct clades (e.g. *Peramus*, multituberculates).

Unequivocal transfer of features from extant to fossil taxa by using phylogeny is limited to features that occur in at least two pertinent extant clades. Thus, for fossil taxa that are members of the stem lineage of a major group or are only distantly related to extant clades, unequivocal inferences will be limited to features that are retained in a broad series of extant lineages. Thus, the method is inherently conservative. Inferences regarding a number of fossil taxa with similar relationships to extant clades will necessarily be similar. The similarity between Sumida's (1989) reconstructions of the appendicular musculature of the Permian captorhinid *Labidosaurus* and those postulated for other primitive amniotes and Permo-Carboniferous labyrinthodonts (see, for example, Romer 1922; Miner 1925) reflects a reliance on the same extant reptilian and amphibian models. Sumida (1989) cautioned that the conclusions of his and previous studies regarding the 'conservative' nature of reptilian appendicular musculature may be due to the reliance on the known anatomy of extant taxa in the reconstruction of early tetrapods. None the less, when these comparisons and transfers are framed within the proper phylogenetic context they are valid. The phylogeny indicates the extant taxa that should form the basis for comparison, and the fossil taxa to which features can be transferred.

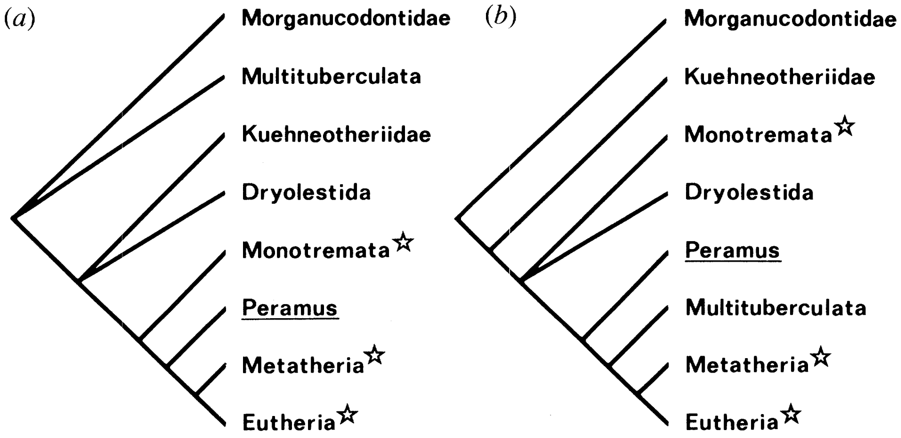

Figure 7. (*a*) The phylogenetic relationships among selected mammalian clades implied by Jenkins (1990, figure 1); (*b*) the phylogenetic relationships among the same mammalian clades as proposed by Rowe (1988). Extant clades are indicated using stars.

Phylogenetic relationships in themselves provide no basis for choosing among equivocal assignments at the fossil–extant node. Such decisions must be based on extrapolatory analyses rather than an *a priori* assumption regarding the fossil taxon. Many inferences in dinosaurs are based solely on the latter. In the absence of other direct or indirect evidence, Paul (1988) is correct in arguing that it is just as speculative to portray small theropods with naked skin as to show them insulated with feathers. However, Paul restored small theropods with feathers because of their overall similarity to *Archaeopteryx*, thus applying reasoning that is incompatible with the phylogenetic approach advocated herein. Decisions must be based on available extrapolatory evidence, however weak it may be. Given equivocal phylogenetic evidence and no available additional information regarding the occurrence of a feature, it is usually considered more conservative to assume its absence. Nicholls & Russell (1985) restored the M. biceps brachii with a single origin in *Struthiomimus* because of the lack of evidence for the second humeral head that occurs in birds. However, in the absence of extrapolatory arguments for its absence, it is equally parsimonious to assume that the second head was present.

The comparisons used in many extrapolatory analyses are necessarily formulated within a phylogenetic context (dashed arrow in figure 1). Gatesy (1990) analysed the role of the caudofemoral musculature in theropod locomotion. His comparisons were presented within a precise phylogenetic context and, as a result, a convincing argument was presented for a series of transitions in these features in the lineage leading to birds.

Extrapolatory analyses provide the only scientific basis for choosing between phylogenetic alternatives or for rejecting the inferences suggested by phylogeny. The strength of these extrapolatory arguments is directly related to the validity of the underlying biological generalization. For example, well-supported biomechanical arguments regarding anatomical constraints in large terrestrial vertebrates provide the justification for using large graviportal mammals as functional analogues in the interpretation of sauropod posture and locomotion. These comparisons may necessarily lack any precise phylogenetic context and involve non-homologous functional systems.

Phylogenetic inferences are often equivocal and many 'obvious' inferences in fossil taxa are necessarily based on extrapolation. Even the identification of a geological object as a fossil involves extrapolation (Kitts 1974). Flight in pterosaurs is an extrapolation; flight is unobservable in extinct taxa, and the closely related extant groups (Crocodylia, Aves) provide equivocal phylogenetic evidence. The consensus regarding at least some degree of aerial locomotion in this group reflects arguments based on form–function correlation and biomechanical analysis. Sound generalizations regarding skeletomuscular relationships in vertebrates may provide justification for Holmes's (1977) preference for using non-avian diapsids, rather than turtles, as extant models for some of the musculature in captorhinids. Although turtles may be the extant sister group of captorhinids (figure 6), the marked differences in the pectoral girdles of the two groups argue strongly for differences in the associated musculature.

Extrapolatory analyses may provide a sound basis for rejecting phylogenetic inferences and are the only means whereby autapomorphic features can be interpreted or inferred in extinct taxa. Although phylogenetic inference had suggested that the large Eocene bird *Diatryma* was primarily herbivorous (Andors 1988), Witmer & Rose (1991) presented a strong argument for carnivory in this taxon based on biomechanical design analysis. The elongated neural spines and associated anatomy of certain sphenacodont pelycosaurs suggest a large 'sail', a structure that is absent in closely related taxa and extant organisms. Hypotheses regarding the function of the sail as a thermoregulatory device can be assessed effectively only by biomechanical design analysis (Bramwell & Fellgett 1973; Haack 1986).

None the less, if the nomological statements underlying the particular extrapolatory analysis are poorly substantiated, the validity of the results will be suspect. The generalization may be inadequately tested (skeletomuscular relationships in vertebrates (Bryant & Seymour 1990)) or inappropriate to the fossil taxon in question. Nicholls & Russell (1985) used *Chamaeleo* as a functional analogue for the shoulder musculature in *Struthiomimus* because of the similarity in their scapulocoracoids. However, this similarity in osteology does not ensure that their shoulder musculatures are equivalent functional systems. The necessary nomological generalizations linking a particular scapulocoracoid morphology to a particular musculature may not be valid. Without the historical constraint of a closed descent community and established nomological generalizations, one must consider the possibility of different form–function relations. Detailed solutions to even narrowly constrained functional demands can differ considerably (e.g. the flight apparatus in Aves, Chiroptera, Pterosauria and Insecta).

6. CONCLUDING REMARKS

The proposed research programme attempts to improve upon previous protocols for inferences in fossils (see, for example, Rudwick 1964; Seilacher 1970; Raup 1972; Dodson *et al.* 1990) by including all valid approaches within the context of modern phylogenetic theory. The programme incorporates both phylogenetic and extrapolatory approaches within a stepwise procedure beginning with phylogenetic inference. This avoids the problems inherent in answering questions of 'how it works' before considering questions of relationships; the latter can lead to inappropriate comparisons and spurious conclusions. The phylogenetic perspective inherent in this research programme is an additional demonstration of the central role of phylogenetic systematics in comparative biology.

Dodson *et al.* (1990) noted palaeobiology's twin hazards of forcing extinct taxa into the molds of extant organisms and engaging in unreasonable speculation. Three approaches to inferences in dinosaurs, specifically regarding their behaviour, were listed: uniformitarianism, pattern matching, and speculation. The first two represent the phylogenetic and extrapolatory approaches within a different guise. Speculation was characterized as the 'most untrustworthy, most maligned, but sometimes most fruitful approach' (Dodson *et al.* 1990, p. 32). Such assessments are problematic because it is often difficult to separate unbridled speculation from well-reasoned speculative hypotheses that are potentially testable. Only the latter are scientifically defensible. The proposed research programme provides a framework for discriminating between the two and thus confining the inferences of unpreserved attributes of fossils to the scientific arena.

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