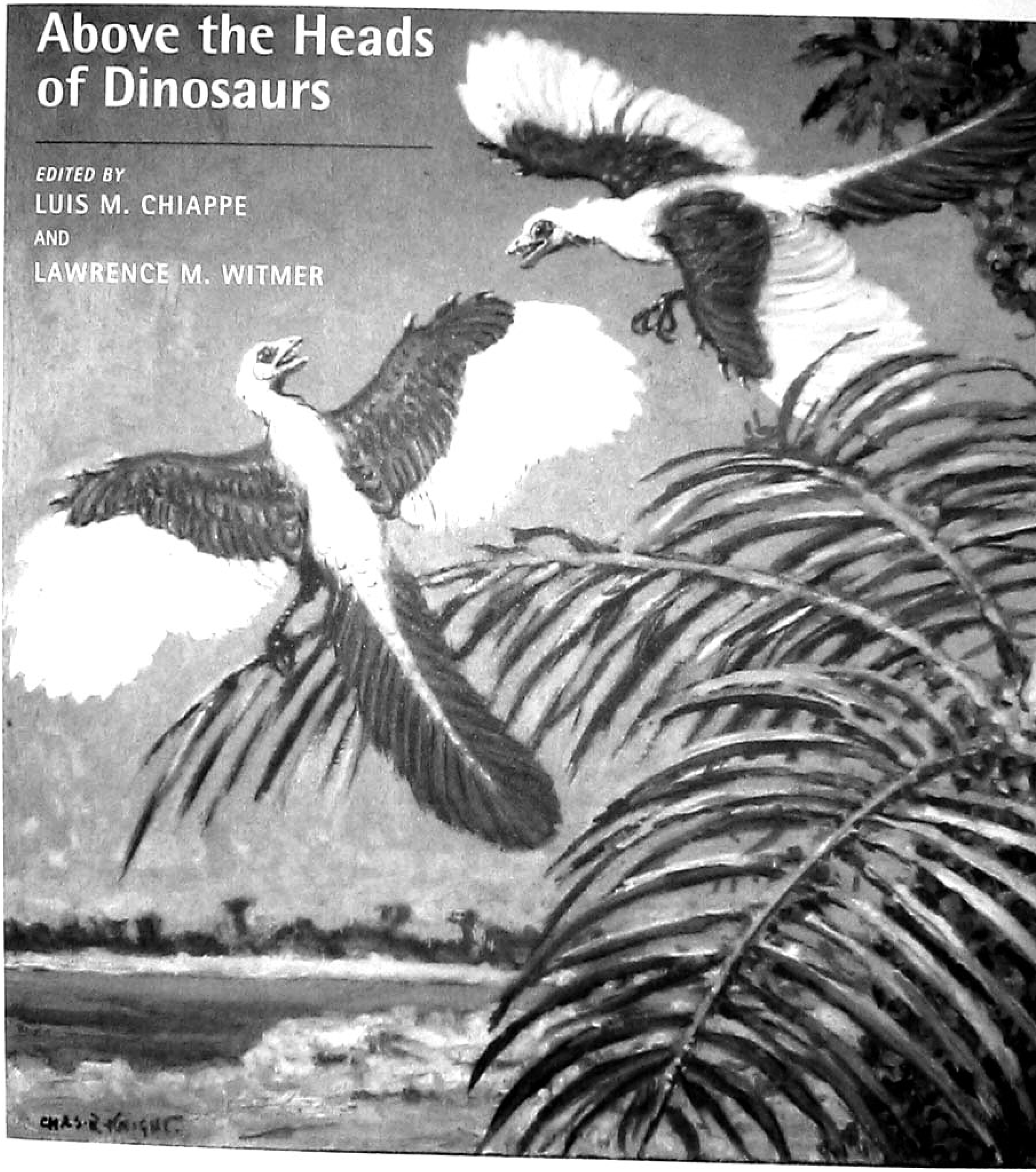
Mesozoic Birds



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Alvarezsaurid Relationships Reconsidered

FERNANDO E. NOVAS AND DIEGO POL

Mononykus, Shuvuuia, Patagonykus, Alvarezsaurus, and a few other more poorly known forms constitute Alvarezsauridae, a highly distinct group of theropods. Alvarezsaurids are easily distinguishable from other dinosaurs on the basis of an extensive list of apomorphic characters, which mainly correspond to their stout forelimbs and vertebral column. Alvarezsaurids have shaken our knowledge of early avian evolution because such very unusual morphological traits are found in association with clearly avian characters in the skull, vertebrae, pelvic girdle, and hindlimbs (Chiappe et al., 1996, 1998; Chiappe, Norell, and Clark, Chapter 4 in this volume). Such bizarre combinations of characters have generated disagreement among scientists as to their significance for the phylogenetic relationships of these taxa.

Variation in Hypotheses

Studies on alvarezsaurid morphology and systematics are divided between those supporting the avian relationships of alvarezsaurids and those regarding them as a different lineage of theropods, not related to birds. Proponents of the avian hypothesis (Perle et al., 1993, 1994; Chiappe et al., 1996, 1998; Novas, 1996, 1997; Forster et al., 1998; Chiappe, Norell, and Clark, Chapter 4 in this volume; Clark, Norell, and Makovicky, Chapter 2 in this volume) arrived at this conclusion through a cladistic approach, whereas most authors interpreting alvarezsaurids as nonavian theropods used a wide variety of arguments (Feduccia, 1994; Martin and Rinaldi, 1994; Ostrom, 1994; Wellnhofer, 1994; Zhou, 1995; Karkhu and Rautian, 1996; Martin, 1997; but see Sereno, 1997, 1999, who used strictly phylogenetic arguments). Divergence in opinion about the phylogenetic placement of alvarezsaurids is, however, wider than thought among supporters of nonavian hypotheses. For example, Karkhu and Rautian (1996) considered *Mononykus* and its kin as nonavian maniraptorans, without specifying particular relationships among maniraptorans. Martin and Rinaldi (1994) and Martin (1997) interpreted alvarezsaurids as related to Ornithomimidae. Others simply concluded that they were nonavian theropods, not offering any particular hypothesis of relationships (e.g., Feduccia, 1994, 1996; Zhou, 1995).

Untestable Assumptions

Perhaps the main argument against the avian hypothesis is that of the "morphological difference," which is based on the presumed improbability that certain evolutionary transformations may occur (Chiappe et al., 1996, 1997). This approach is evident in the criticisms of Wellnhofer (1994) and Zhou (1995), who claimed that wings cannot be transformed into the specialized forelimbs of alvarezsaurids, which are obviously adapted for purposes other than flight, and in the work of Karkhu and Rautian (1996), who claimed that the arctometatarsalian metatarsus of *Mononykus* is unsuitable for giving rise to the metatarsal structure characteristic of the Ornithurae. The argument of the "morphological difference" of the forelimbs, however, may be used (with the same negative result) against hypotheses supporting ornithomimid, nonavian maniraptoran, coelurosaurian, theropodan, or even dinosaurian affinities of *Mononykus.*

Zhou (1995) constructed an intricate objection against the avian hypothesis on the assumption that similar characters (for example, those shared by *Mononykus* and ornithothoracine birds in the sternum) cannot be considered homologous simply because they pertain to different functions. In so doing, the phylogenetic informativeness of such morphological characters is dismissed a priori. This approach, however, neglects the possibility that the differentiation of a function may occur within a structurally homologous framework (Lauder, 1994; Chiappe et al., 1997).

From a cladistic point of view, phylogenetic relationships are justified on the basis of synapomorphies, and evolutionary processes must be tested and explained only after the pattern of character distribution has been analyzed. A priori assumptions about evolutionary processes cannot be used to overturn a particular phylogenetic hypothesis (see also Chiappe, Norell, and Clark, Chapter 4 in this volume). Thus, the criticisms enumerated earlier are irrelevant for phylogenetic inference.

Mononykus and Its Kin in the Context of Coelurosaurian Phylogeny

It has been shown that certain characters originally hypothesized to be synapomorphic of Metornithes (Perle et al., 1993, 1994) evolved independently in *Mononykus* and ornithurine birds (e.g., loss of pubic symphysis, greater and anterior trochanters fused, fibula not in contact with the proximal tarsals, presence of femoral popliteal fossa, and presence of an accessory cnemial crest on the tibiotarsus). This explanation emerged after the inclusion of two additional taxa, interpreted by Novas (1996, 1997) as basal alvarezsaurids. Even though the inclusion of the Patagonian *Alvarezsaurus* and *Patagonykus* in the character analysis somewhat reduced the support for the placement of *Mononykus* within birds, the avian hypothesis remained unchallenged.

In an unpublished cladistic analysis adding new characters to those used by previous cladistic studies (mainly Chiappe et al., 1996, 1998; Novas, 1996, 1997; but not yet including those characters recently advanced by Sereno, 1999) and including additional nonavian coelurosaurian taxa (e.g., Troodontidae, Oviraptorosauria, Therizinosauridae, *Ornitholestes*, *Allosaurus*, and *Unenlagia*), alvarezsaurids are placed outside birds, as a distinct group of nonavian coelurosaurians (Fig. 5.1). This new phylogeny (obtained using Hennig86; Farris, 1988) also proposes a new hierarchical arrangement of the other coelurosaur taxa. For example, the monophyly of Arctometatarsalia and Bullatosauria (Holtz, 1994) is not supported by this analysis; instead, troodontids are hypothesized as the sister taxon of Dromaeosauridae plus Avialae (*sensu* Padian, 1997) in one tree, and the monophyly of Deinonychosauria (i.e., Troodontidae plus Dromaeosauridae; Gauthier, 1986) is supported in the other. The results obtained here contrast with those of previous authors (e.g., Gauthier, 1986; Russell and Dong, 1993; Holtz, 1994). Bremmer support of the tree nodes is not high (Fig. 5.1), indicating that additional information (new characters or taxa) may easily change the proposed topology.

In this new hypothesis, Alvarezsauridae is the sister taxon of a group formed by Therizinosauridae, Oviraptorosauria, Troodontidae, Dromaeosauridae, and Aves (this group is labeled "Node X" in Figure 5.1, in which the strict consensus tree of the two most parsimonious trees is depicted). Alvarezsaurids lack characters synapomorphic of such a group (e.g., cervical centra with kidney-shaped cranial articular surface; pronounced proximodorsal lip on manual unguals; absence of supracetabular crest; iliac postacetabular blade subvertically oriented, and medial flange of ilium strongly reduced; pedal unguals of digits III and IV dorsoventrally deep and with enlarged flexor tubercles). Thus, in the context of this new hypothesis, all the characters previously considered synapomorphic of Metornithes (Chiappe et al., 1996, 1998; Novas, 1996, 1997) are reinterpreted as independently acquired in Alvarezsauridae and Ornithothoraces.

The clash between the new hypothesis and that supporting the monophyly of Metornithes relies not merely on the addition of new characters but, most important, on the inclusion of new coelurosaurian taxa. This is demonstrated by the fact that the results are congruent with the avian hypothesis if the new pool of characters is scored in the same set of theropods used in previous papers (e.g., Chiappe et al., 1996, 1998; Novas, 1996, 1997). Instead, the simple inclusion of Troodontidae, or both Therizinosauridae and Oviraptorosauria, is sufficient to challenge the avian hypothesis. Clearly, the phylogenetic position of Alvarezsauridae is contingent on the interrelationships among other coelurosaurian taxa.

Although these results place alvarezsaurids within nonavian theropods, the suggestion of Martin and Rinaldi (1994) and Martin (1997) concerning the ornithomimid relationships of *Mononykus* is difficult to sustain. First, ornithomimids lack the synapomorphies uniting Alvarezsauridae with Node X (neural spines confined to caudals 1–12, semilunate carpal, ilium with caudodorsal margin ventrally curved in lateral view, pubis caudoventrally oriented with respect to the pubic pedicle of ilium, proximal fibula with medial fossa reduced or absent, proximal ulna with a cranially oriented notch for reception of radius and reduced ulnar proximal articular processes, pubic pedicle of ilium craniocaudally narrow, midcaudal vertebrae with short prezygapophyses, absence of a dorsal fossa on caudal process of coracoid, prominent ventral processes on cervicodorsal vertebrae). Second, if alvarezsaurids and ornithomimids are constricted to form a monophyletic group, the most parsimonious hypothesis requires five additional steps. Incorporating the new data of Sereno (1999) might change this assessment somewhat, but it is likely that many of these impediments to ornithomimid relationships will remain (see also Suzuki et al., 2002; Clark, Norell, and Makovicky, Chapter 2 in this volume).

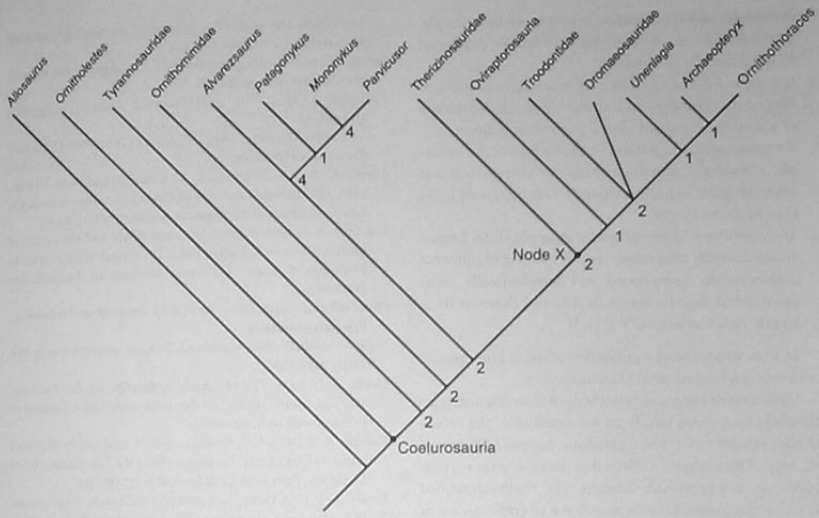

Figure 5.1. Strict consensus tree resulting from two most parsimonious trees (L = 309; CI = 0,48; RI = 0,54) yielded by Hennig86 (implicit enumeration command) (Farris, 1988). The information to construct the data matrix (Novas, unpublished data) was gathered from different sources: Gauthier, 1986; Russell and Dong, 1993; Holtz, 1994; Makovicky, 1995; Chiappe et. al., 1996, 1988; Martin, 1997; Novas, 1997; Novas and Puerta, 1997; the study of Sereno, 1999, was too recent to adequately incorporate into this analysis. The Bremmer support (Bremmer, 1994) is indicated in each node. This measure was calculated using the bs command in Nona (Goloboff, 1993a).

Although most authors devoted to theropod phylogeny currently use equally weighted parsimony as implemented in Hennig86 or PAUP (e.g., Gauthier, 1986; Russell and Dong, 1993; Holtz, 1994; Chiappe et al., 1996, 1998; Novas, 1996, 1997; Forster et al., 1998), a differential character weighting approach can also be used. For example, PeeWee (Goloboff, 1993b) is a program that sets differential weights for characters according to the amount of homoplasy they present on the tree. Under the PeeWee optimality criteria, the most parsimonious hypothesis is that in which the sum of all character weights (i.e., tree fit) is maximized. Our coelurosaurian data set was subjected to this kind of cladistic approach. Interestingly, under the exact solution commands ("wh" and "ms+"), the single most parsimonious tree supports the monophyly of Metornithes, placing alvarezsaurids within Aves. A possible explanation for this result is that most of the characters shared by alvarezsaurids and ornithothoracines are not present in other coelurosaurs, implying that such characters get the highest weights in trees supporting the monophyly of Metornithes. This is not the case for some of the characters supporting monophyly of Node X. For example, cervical centra with kidney-shaped cranial articular surface are present in *Ornitholestes*, while a subvertically oriented postacetabular blade of ilium with a medial flange strongly reduced is absent in Troodontidae. In sum, PeeWee resolves the conflict in favor of the hypothesis supported by characters lacking homoplastic steps.

It is beyond the scope of this chapter to judge the validity of the different parsimony approaches mentioned previously. Our aim, instead, is to emphasize the highly conflictive pattern of character distribution among coelurosaurian taxa, which causes such disparity in the analyses using differentially or equally weighted characters.

Conclusions

This discussion emphasizes once again that alvarezsaurids are a problematic group of theropods, because, although they present obvious similarities with Ornithothoraces, they lack the following derived characters that in the present cladistic analysis are synapomorphies of different hierarchical groups within Coelurosauria:

1. *Archaeopteryx* + Ornithothoraces (= Aves): for example, forelimb exceeding 86% of hindlimb length; developed bicipital tubercle of coracoid
2. *Unenlagia* + Aves (= Avialae): for example, caudal end of ilium dorsoventrally low and sharply pointed; presence of a prominent proximodorsal process on ischium
3. Dromaeosauridae + Avialae (= Maniraptora): for example, mandibular fenestra reduced or absent; coracoid subrectangular in profile; elongate radius, 76% or more than humerus length
4. Troodontidae + Maniraptora: for example, distal haemal arches cranially bifurcated; ventral tubercle of humerus craniocaudally compressed and longitudinally elongated; pedal digit IV longer than II and closer to III in length; raptorial ungual in digit II

In sum, we are facing a group that presents homoplasies wherever it is located within Coelurosauria.

Criticisms of the avian hypothesis of alvarezsaurid relationships have relied largely on assumptions of the evolutionary process more than on cladistic analysis (Chiappe et al., 1997). This discussion shows that the issue is more complex than was previously thought. The results presented here, however, should not be considered an endorsement of the previous criticisms of the avian hypothesis (e.g., Feduccia, 1994; Martin and Rinaldi, 1994; Wellnhofer, 1994; Zhou, 1995; Karkhu and Rautian, 1996), since these were based on spurious assumptions.

The phylogenetic position of alvarezsaurids highlights a major problem in dinosaur systematics: coelurosaurian phylogeny. The resolution of this problem will certainly affect any hypothesis of alvarezsaurid relationships. Whatever the phylogenetic position of alvarezsaurids may be, alvarezsaurids are crucial to the knowledge of coelurosaurian evolution because they offer a mosaic of characters that illustrates the great amount of homoplasy existent within these theropod dinosaurs (including birds).

Acknowledgments

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