

Mononykus and Birds: Methods and Evidence

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In a recent article Zhou (1995) criticized our hypothesis (Perle et al. 1993, 1994; Chiappe 1995a,b) that the Late Cretaceous *Mononykus* is the sister taxon to all other birds except *Archaeopteryx*. He concluded that "The most-parsimonious explanation is that *Mononykus* is not a bird and that its ancestors never possessed the capacity for flight," although he does not provide a new hypothesis for the relationships of this taxon. Here, we reply. Our response is less concerned with the specifics of Zhou's character analysis, and instead focuses on fundamental differences in approach between Zhou and ourselves. These differences are rooted in our conviction that estimation of genealogy is contingent only on empirical evidence (i.e. character distribution among taxa), and that phylogenetic hypotheses need to be tested and refined by the addition of characters and taxa.

This method is in sharp contrast to Zhou's approach, which focuses on attempts to correlate the peculiar morphology of *Mononykus* with digging habits. From this proposal he offers the phylogenetic conclusion that this creature cannot be a bird. Here, we point out several methodological problems and inconsistencies in Zhou's approach. Several mischaracterizations of the evidence in Zhou's paper also require clarification. For simplicity, the following discussion is divided between these issues.

Methodology.—Zhou presents two major conclusions: (1) apomorphic similarities shared by *Mononykus* and birds are *Mononykus*' adaptations for digging, and (2) these similarities evolved convergently in *Mononykus* and birds. Tying morphology of extinct organisms to a particular function is a difficult task (Lauder 1995). Several of the features correlated with digging activities by Zhou apparently are based only on his own intuition. This is best exemplified by his statement (p. 960) that "Since digging and bipedalism are both characteristic of *Mononykus*. . . the developed trochanteric crest also may be related to the animal's fossorial habit . . ." All birds more advanced than *Archaeopteryx* and basal Alvarezsauridae (a taxon including *Mononykus* and its South American allies; see Novas 1996), along with oviraptorid theropods, have a trochanteric crest (the result of the fusion of the primitive theropod lesser and greater trochanters; see

Gauthier 1986). Yet, all of these organisms are bipedal, and none has ever been regarded (or observed) to be fossorial.

Zhou's second point is that the similarities among *Mononykus* and other birds are due to homoplasy. For example, Zhou accepts that *Mononykus* shares a longitudinally oriented and carinate sternum with birds more advanced than *Archaeopteryx* (p. 959). Nevertheless, despite the absence of such a sternum in *Archaeopteryx* (Wellnhofer 1993) or in any non-avian dinosaur (Barsbold 1983)—a fact acknowledged by Zhou—he regards these similarities as "most reasonably explained" by convergent evolution. Zhou's argument hinges on functional considerations. He seems to believe that if similar structures have different functions they cannot be homologous. He emphatically points out (p. 960) that ". . . among the five purported avian characters, the first two almost certainly are digging adaptations. The other three probably are related to digging directly or indirectly. Hence, the five characters are *not phylogenetically informative*" (italics added). In Zhou's argument, the explanation of a particular structure as an adaptation for burrowing takes precedence over the explanation of this structure as evidence for a close relationship. The fallacy of such an argument, whereby untestable adaptationist scenarios overturn the powerful test of phylogeny provided by shared derived characters, has been frequently pointed out (e.g. Gould and Vrba 1982, Lauder 1994, 1995). Furthermore, the fact that *Mononykus* shares structures with extant burrowing mammals (e.g. moles) is irrelevant in establishing its phylogenetic relationship to other vertebrates unless a close relationship between this archosaur and this group of placental mammals is seriously being entertained.

In phylogenetic inference, hypotheses are tested by the distribution of characters among taxa. Phylogenetic hypotheses are rejected only by their replacement with other more-parsimonious hypotheses. A life style (e.g. fossorial) can be regarded as a behavioral character, but by itself is incapable of replacing a well-supported phylogenetic hypothesis. That is not to say that such a character is invalid in phylogenetic study (Wenzel 1992, Lauder 1994). However, it must be evaluated en masse with the ensemble of other characters. Together, it is the congruence of all the evidence that determines which characters have a single origin

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and which originated via convergence (Patterson 1982, de Pinna 1991, Wenzel 1992, Rieppel 1994).

Zhou is also careless regarding the phylogenetic utility of primitive versus derived characters. Rightfully, he emphasizes the deficiency of primitive characteristics for discovering phylogenetic relationships (p. 961). However, he has not given up on the phylogenetic importance of primitive characters, stating that (p. 962) "the lack of an avian appearance in these [primitive] structures casts doubt on the 'avian' status of this specialized animal" (i.e. *Mononykus*).

Zhou's approach epitomizes a widespread but flawed view of the early evolution of birds, in which taxa *a priori* are expected to fit an intuitive notion of "bird" and accordingly, to have a particular "avian" life style (Chiappe 1995b). Thus, the assumption of digging habits in *Mononykus* supposedly invalidates its phylogenetic placement within Aves (= Avialae sensu Gauthier 1986). Under this view, however, whales and bats would be placed outside Mammalia simply because they are completely aquatic and capable of flight, respectively, characters that are far unlike those of the "ideal" mammal.

Anatomy.—Zhou's anatomical comparisons also fail to support his claim. For example, he treats the antitrochanter and the supracetabular crest as synonyms. Yet, these structures clearly are non-homologous as is demonstrated by the presence of *both* features together in several taxa (e.g. *Mononykus* and *Patagopteryx*; see Perle et al. 1994, Chiappe 1996). Incidentally, and in contrast to Zhou's claim (p. 959), the antitrochanter of *Mononykus* is illustrated by a stereo-pair photograph in Perle et al. (1994), a paper cited by Zhou.

The phylogenetic placement of *Mononykus* within birds is supported by an extensive list of synapomorphies (Perle et al. 1993, Chiappe 1995b, Chiappe et al. 1996). These include synapomorphies diagnosing Aves (= Avialae sensu Gauthier 1986) and those shared between *Mononykus* and more advanced birds (Metornithes of Perle et al. 1993). Avian synapomorphies present in *Mononykus* include a caudal vertebral count smaller than 25–26 elements, teeth with unserrated crowns, a caudal tympanic recess that opens inside the columellar recess and not in the paraoccipital process, and short or reduced prezygapophyses in distal caudal vertebrae. Among the synapomorphies of Metornithes are the prominent ventral processes of cervico-dorsal vertebrae, sternum of longitudinal rectangular shape, ossified sternal keel, distal carpals fused to metacarpals, pelvis with prominent antitrochanter, and an ischium more than two-thirds the length of the pubis. Furthermore, *Mononykus* possesses several features that are ambiguous synapomorphies exclusive to both Aves and Metornithes. These characters have an ambiguous optimization because they are unknown in *Archaeopteryx*; consequently, they may be synapomorphies of either Aves (Avialae sensu Gauthier 1986) or Metornithes. The fact that these characters are both absent in the outgroups

(e.g. dromaeosaurid theropods) and present in birds more derived than Metornithes provides further support for the avian relationship of *Mononykus* (Chiappe et al. 1996). Among these characters are a wide vertebral foramen in the dorsal vertebrae, a laterally projecting fibular tubercle for m. iliofibularis, a quadratojugal not contacting the squamosal, absence of a medial fossa on the proximal end of the fibula, and the absence of a postorbital-jugal contact.

A phylogenetic hypothesis is open to test by the addition of new characters, the addition of new taxa and the reevaluation of other characters. In this way phylogenies can be corroborated or rejected and replaced with others. Rejection of our phylogenetic hypothesis requires only that our critics propose an alternative hypothesis that better summarizes the evidence. Then we would be able to argue specific points of this debate. Paradoxically, our critics do not want to restrict themselves to this arena of data and evidential support (see Chiappe et al. 1995, 1996). Instead, Zhou and others (e.g. Martin and Rinaldi 1994; Feduccia 1994, 1996) prefer to keep this argument in the realm of untestable scenarios where special knowledge of the mechanisms of the evolutionary process are tantamount to evidential criteria (see Chiappe et al. 1995, 1996; Norell and Chiappe 1996). Thus, Zhou's conclusion that "The most-parsimonious explanation is that *Mononykus* is not a bird . . ." does not rely on the modern use of parsimony as an optimality criterion for choosing among alternative phylogenetic hypotheses (Farris 1983), but on the subjective criterion of what appears to be more reasonable for him.

In sum, Zhou seems to have no doubts about the fossorial specializations of *Mononykus*; we are skeptical (see Norell et al. 1993, Chiappe 1995b). More to the point, even if *Mononykus* were fossorial, this has no bearing on phylogenetic inference. Furthermore, Zhou dismisses the phylogenetic significance of characters that are unique to *Mononykus* and birds among archosaurs. We have pointed out several of these important characters, and various others, although not exclusive to birds, provide further support of our hypothesis within the framework of cladistic analysis. Lastly, Zhou believes that the placement of *Mononykus* within birds (and therefore in the context of dinosaurs) shows "how willing some people are to be deceived by . . . convergence." Without claiming to be the ultimate truth, our methods reject *a priori* assumptions about how evolution works in specific cases and peremptory assertions about the relationships and origin of birds.

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