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IS MONONYKUS A BIRD?

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ABSTRACT.—The avian status of *Mononykus* is refuted in this paper through a detailed analysis of its supposed avian characters. An extensive comparison between it and fossorial mammals (especially moles), as well as various bipedal archosaurs, indicates that some of its resemblances to extant birds are digging adaptations. Most of the others can be explained either by its digging adaptation or by its obligatory bipedalism. In addition, many of its features, as compared with birds (including *Archaeopteryx*), seem to be too primitive for avian flight, and there is no evidence indicating that the absence of flight in *Mononykus* was secondarily lost. Received 23 December 1994; accepted 16 February 1995.

MONONYKUS OLECRANUS is a very controversial Late Cretaceous animal from Mongolia. Perle et al. (1993) published information about it as a bird in *Nature*, and a more detailed description of this fossil was published recently (Perle et al. 1994). However, almost from the beginning, its avian status was doubted by many paleornithologists (Olson pers. comm., Martin and Rinaldi 1994, Ostrom 1994, Wellnhofer 1994). This animal was originally named *Mononychus olecranus*, and shortly thereafter renamed *Mononykus olecranus* because the former generic name was preoccupied by the coleopteran *Mononychus*. The materials of *Mononykus* include a partial skull, limbs, thoracic girdle, portions of ilium and pubis, and most vertebrae. According to M. Norell and L. Chiappe (pers. comm.), new material of this animal has been found from Mongolia, including the previously unknown digits II and III.

This fossil was believed to be a bird because it was asserted that several unambiguous characters indicated a closer relationship to modern birds than to *Archaeopteryx*. The purpose of my paper is to discuss whether or not these characters support the proposed avian status of *Mononykus*.

ANALYSIS OF CHARACTERS SUPPORTING AVIAN STATUS OF *MONONYKUS*

In the papers by Perle et al. (1993, 1994), five characters were proposed to be “unambiguous

diagnosing characters” of a new taxon called *Metornithes*, which was defined as a group within Avialae (see Gauthier, 1986; equivalent to class Aves) that excludes *Archaeopteryx*. In other words, they judged that *Mononykus* was the most primitive bird except for *Archaeopteryx*. The five characters are: (1) an ossified large and longitudinally oriented rectangular sternum; (2) an ossified sternal carina; (3) a prominent antitrochanter on ilium; (4) an undivided femoral trochanteric crest; and (5) a fibula that does not reach the tarsus. They did not specify other characters used to place *Mononykus* in the group Avialae; therefore, as I understand their approach, these five characters form their main evidence for the avian status of *Mononykus*. In addition to these, several other characters were either considered to be ambiguous characters of *Metornithes* or were simply compared with extant birds.

Before analysis of these characters, it is necessary to examine the digging habit of *Mononykus*. As clearly stated by Perle et al. (1993: 625), “the highly modified forelimb of *Mononykus* is similar to that of digging animals. The large process of the humerus, large olecranon process of the ulna, short massive forelimb elements and carpometacarpus, and sturdy claw suggest extremely powerful functional capabilities during adduction.” These features also are present in various digging animals, including moles, fossorial multituberculates, rodents, etc. In fact, digging habits are found in many mammalian orders like Monotremata, Marsupialia, Insectivora, Rodentia, Edentata, Pholidota, Tubulidentata, Carnivora, and Palaeonodonta (Kielan-Janorwska 1989). It is not difficult to find in *Mononykus* even more evidence for its

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digging habit, including an ossified large and longitudinally oriented sternum, and an ossified sternal carina. Recently, Ostrom (1994) pointed out: "Difficult as it may be to visualize this creature (*Mononykus*), there can be no mistake about its fossorial specializations."

With this sketch introduction to the fossorial habit of *Mononykus*, the evidence by which this digging animal was deemed a bird can be investigated. Characters 1 and 2 are in fact a character complex: (a) sternum ossified; (b) sternum large; (c) sternum longitudinally oriented; and (d) presence of sternal carina.

The sternum is ossified in various groups of tetrapods. In archosaurs, it is known to be ossified in birds and in pterosaurs (Eaton 1910), as well as in various dinosaurs (Romer 1956). As the seventh skeletal specimen of *Archaeopteryx* has an ossified sternum (Wellnhofer 1993), it is reasonable to believe that a sternum might be present in the ancestry of birds too. That the sternum is large is a relative concept. It is difficult to determine from this statement when a sternum can be called large. Furthermore, as *Mononykus* clearly is a digging animal, and a large manubrium is usually present in fossorial mammals, it is easy to understand that its relatively large size is probably related to the fossorial adaptation of the forelimb.

The sternum usually is longitudinally oriented in birds except in ratites. In *Archaeopteryx*, the sternum is wider than long, probably representing the most primitive condition of this structure in birds. The sternum is not markedly longer than wide in *Cathayornis* (Zhou in press) and *Concornis* (Sanz and Buscalioni 1992). In those dinosaurs that are known to have a pair of sterna, it is usually wider than long (Barsbold 1983). Among pterosaurs, the sternum is longer than wide (Eaton, 1910). Therefore, the ratio of the length to width may be an indicator of the flight capacity. The increase of this ratio also can be the result of another totally different adaptation—digging. The sternum is found to be greatly elongated in moles in comparison with the usual mammalian types (Slonaker 1920). Also, according to Campbell (1939), not only is the sternum usually longer than wide, but there is a tendency from the simple to complex (primitive to specialized) for the width of the manubrium to decrease in proportion to the length. In other words, the increase of the length-to-width ratio is closely related to the improvement of the digging power. Based on

this analysis, and considering the presence of digging habits in *Mononykus*, I conclude that its longitudinally oriented sternum can be most reasonably explained as further evidence of fossorial capacity.

With regard to the presence of a sternal carina, note that an ossified sternal carina is present in all known digging animals, including those in Insectivora (Slonaker 1920, Campbell 1939), Multitubercata (Kielan-Jaworowska 1989), and Rodentia (Barnosky 1981). Furthermore, the change of the carina in birds and moles is to a great degree similar to that of the length-to-width ratio. The carina is absent in *Archaeopteryx* and secondarily lost in ratite birds; it is initially developed in Early Cretaceous birds like *Cathayornis* (Zhou 1992) and *Concornis* (Sanz and Buscalioni 1992). A sternal carina has never been found in any dinosaurs, but it is reported in pterosaurs and bats. According to Campbell (1939), in digging moles, the ventral ridge (keel) becomes deeper from the simple to complex, and primitive to specialized genera. Undoubtedly, the sternal carina, just like flight, had arisen many times independently in tetrapods, and the two best known adaptations accounting for its appearance are flight and digging. With respect to the sternal carina in *Mononykus*, it is most reasonably explained as evidence for the digging power of this animal.

Before analyzing character 3, it is necessary to evaluate the differences between two types of antitrochanters in archosaurs. The avian type is positioned on the postero-dorsal rim of the acetabulum; the hadrosaur type is totally different. According to Romer (1927), the latter type of antitrochanter is a strong ridge running out at a right angle to the plane of the iliac blade approximately over the ischiadic articulation. Unfortunately, in Perle et al. (1993), the type was not clearly indicated, but according to the comparison and figures of this structure, I assume that it is of the avian type.

Character 3 is present in advanced birds, but absent in *Archaeopteryx* and *Cathayornis*. A similar structure called the supraacetabular flange is found on the antero-dorsal rim of the acetabulum in the ornithischian *Fabrosaurus australis*, which is small in length and probably an obligate biped (Santa Luca 1984). In the ornithopod dinosaur *Tenontosaurus tilleti* (Forster 1990), the supraacetabular rim is laterally thickened, dorsally canted, and forms a deep, parabolic embayment in the ventral iliac body. According

to Kurzanov (1983) and Molnar (1985), an ilium with antitrochanter of the avian rather than the hadrosaurian form is present in *Avimimus*. Although a marked projecting rim has not been reported among other theropods, it is found dorsally bounding the acetabulum in *Allosaurus* and *Dilophosaurus*.

The supraacetabular flange must have affected femoral orientation; the femoral head may have articulated underneath the flange, which would have transmitted mass between body and limb (Santa Luca 1984). A lateral expansion from the dorsal rim of the acetabulum can be explained by bipedalism, because such a structure not only extends the acetabular articular surface laterally, allowing a direct transmission between the femur and the ilium (Santa Luca 1984), but also makes it possible to not narrow the pelvis at the expense of the compact contact between the femur and the pelvis. (The pelvis has been found by Slonaker [1920] to be greatly narrowed in moles [G. Peng pers. comm.].) All of these factors are important for a bipedal life. Although the significance of the difference in the exact shape or position of the supraacetabular rim is not clear, it is almost certain that the avian type of antitrochanter (or similar structures) appeared many times in archosaurs. This character in *Mononykus*, therefore, is not definitive and not particularly informative.

Character 4 is the undivided femoral trochanteric crest. First, how was the conclusion on its homology reached? It might be that the lesser trochanter has degenerated, while the great trochanter has enlarged. According to X. Zhao (pers. comm.), in some dinosaurs the lesser trochanter is only slightly developed and may totally disappear in some animals. Besides, well-developed femoral trochanters are present in the more fossorial moles (Freeman 1979). Reed (1951) also noted that few major changes occur in the femora of soricoids except that the more fossorial moles have better developed processes on the proximal end of the bone. Romer (1956) noted that with the archosaur trend toward bipedalism and a resultant forward turning and semierect pose of the hindlimb, the femur has become greatly modified. Since digging and bipedalism are both characteristic of *Mononykus*, I suggest that the developed trochanteric crest also may be related to the animal's fossorial habit either directly or indirectly.

Character 5 is that the fibula does not reach

the tarsus. The fibula generally is only about two-thirds the length of the tibiotarsus in extant birds (Bellairs and Jenkin 1960). Romer and Parsons (1977), as well as Hinchliffe and Johnson (1980), pointed out that the tetrapod fibula often is reduced or fused with the shaft of the tibia, and in some taxa it has disappeared entirely. Hinchliffe and Johnson (1980) noted that archosaurs have a series of functional adaptations of the hindlimb and the hindlimb girdle, which are seen in many other bipedal types. In dinosaurs, those with bipedal habits usually have a relatively weaker fibula in comparison with those of quadrupedal types (G. Peng pers. comm.). For example, in *Deinonychus antirrhopus*, an obligatory biped beyond any doubt, the fibula is extremely slender and is much less robust than the tibia (Ostrom 1969). Therefore, the reduced fibula in *Mononykus* can be interpreted as related to bipedalism. Because the hindlimb is very slender and the forelimb short, it is likely that *Mononykus* was not only bipedal, but also an obligatory biped. A similar conclusion was reached by Ostrom (1994).

In summary, 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. In addition, none of them is unique to birds, and all are restricted to the hindlimb and pelvic girdle, which are most vulnerable to modification in the adaptation toward a bipedal life.

Before elaborating on the parallelism commonly observed between dinosaurs and birds, I will discuss other resemblances between *Mononykus* and extant birds. The humerus is said to have a single distal condyle and is on the cranial surface, as are both humeral condyles of extant birds (Perle et al. 1993). A single condyle is itself a very specialized feature for an archosaur. Talpids (moles), which dig with the forelimb, mainly use the lateral thrust technique in the digging stroke, and retraction is not important in the power stroke (Barnosky 1982). As there is no evidence that the head in *Mononykus* was used when digging, its digging stroke was probably made by the forelimbs in a way similar to that of moles. The lateral thrust was mainly used in the power stroke and when digging where the earth is pushed aside, the fore paws were thrust forward and the elbow must be

usually acutely angled posteriorly (similar to folding state of humerus and forearm in birds). It is clear why the single condyle is located on the cranial surface of the humerus, as are both humeral condyles of extant birds.

Another striking resemblance between *Mononykus* and extant birds is a retroverted pubis. The pubis not only is retroverted in ornithischian dinosaurs, but also in some saurischians. Barsbold (1983) concluded that the orientation of the pubic bone in the pelvis originated repeatedly in the process of the evolution of the different saurischian groups. Unfortunately, the reason for this caudal orientation is not well known (Romer and Parsons 1977). *Mononykus* also resembles extant birds in lacking an expanded pubic foot, which is present in many dinosaurs, but absent in many others. Even assuming that birds evolved from dinosaurian ancestors with an expanded foot, it is still an unsolved problem as to whether the immediate ancestor of *Mononykus* had such a foot.

The pubis and ischium lack a symphysis in *Mononykus*, which is another character similar to birds. Romer (1956) pointed out that

Pelvic modification associated, it seems certain, with a trend toward bipedal habits are seen in all branches of the group [archosaurs] and are most especially developed in pubis and ischium. In ornithischian (paralleling the birds) the ventral symphysis is much reduced. The two ischia are apposed, frequently for much of their length, but there is no strong fusion. The pubes are in contact distally in a few primitive ornithopods only.

According to Slonaker (1920), the greatest variation found in the pelvis of the different genera of the *Talpidae* is in the region of the pubic symphysis, which varies from a well formed symphysis to a relatively wide gap between the pubic bones. In conclusion, the character of lack of symphysis between the pubis and ischium must have arisen at many different times in archosaurs for various unknown reasons. In phylogenetic studies, this feature is not helpful in resolving relationships.

Mononykus also resembles extant birds in having an ulna longer than the humerus, but this almost certainly is due to the great elongation of the olecranon. A well developed olecranal process is characteristic of all fossorial mammals (Slonaker 1920, Lehmann 1963, Freeman 1979, Barnosky 1981).

PRIMITIVE CHARACTERS PRESENT IN *MONONYKUS* AND A COMPARISON WITH BIRDS

Primitive features or synplesiomorphy should not be employed as direct evidence for establishing phylogenetic relationships. However, this does not imply that primitive characters, therefore, can be completely ignored. While not acting as direct evidence for phylogenetic relationships, they can indicate the evolutionary level of the organism and, for practical purposes, provide indirect or auxiliary evidence for relationships, especially when useful synapomorphies are lacking or difficult to interpret.

In *Mononykus*: the anterior blade of the ilium is much shorter than the posterior one; the ulna is not markedly wider than the radius; the scapula and coracoid are similar to those in non-maniraptoran theropods (Perle et al. 1993, 1994); and the metatarsals are unfused (Perle et al. 1993, 1994). All of these characters are more primitive than in all known birds, including *Archaeopteryx*. In brief, the anterior blade of the ilium is longer and more robust than the posterior blade in *Archaeopteryx*. This feature also is found in the Early Cretaceous birds, such as *Cathayornis* (Zhou et al. 1992), *Sinornis* (Sereno and Rao 1992), and extant birds. The ulna in *Archaeopteryx* (Wellnhofer 1993) is wider than the radius. In *Sinornis* and *Cathayornis*, the ratio of the ulna to the radius is even greater. In extant birds, the ulna is almost twice as wide as the radius. Because the ulna supports the secondary flight feathers, its robustness can be viewed as a direct indication of flight capacity. Metatarsals are at least partially fused in *Archaeopteryx* (Ostrom 1976, Wellnhofer 1988), *Sinornis*, and *Cathayornis*. Perle et al. (1993) compared the unfused metatarsals of *Mononykus* with those of *Iberomesornis* (Sanz and Bonaparte 1992), but according to E. Kurochkin (pers. comm.) and Zhou (1995), the latter probably is a juvenile individual. In addition to the above features, *Mononykus* shows the presence of a long tail and unfused cervical ribs, which are more primitive features than those found in all birds except *Archaeopteryx*.

In summary, *Mononykus* shows many structural resemblances to dinosaurs, but few to birds. Although this fact alone will not provide definitive information concerning the relationship of *Mononykus* to birds, it is important that some of these structures are crucial to the flight

of birds. The lack of an avian appearance in these structures casts doubt on the "avian" status of this specialized animal.

DISCUSSION AND CONCLUSION

Mononykus is beyond doubt a fossorial animal. However, is it also a bird? To solve this problem, I first address two related questions. First, is there any unique avian character in *Mononykus*? Second, why was *Mononykus* previously held to be a bird?

The first question is easy to answer. No single character described for *Mononykus* is found only in birds. *Archaeopteryx* is accepted by most researchers as a bird because it possessed feathers. Indeed, as is commonly stated, without feathers in specimens of *Archaeopteryx*, it probably would not be recognized as a bird.

The second question, although never clearly stated, was implied in the papers of Perle et al. (1993, 1994). *Mononykus* was considered to be more closely related to extant birds than *Archaeopteryx* because it has several derived features including a carinate sternum and reduced fibula. However, they did not explain why these features were chosen. They provide at best a superficial resemblance between *Mononykus* and extant birds. Fortunately, the forelimbs were preserved in the specimen and clearly indicate that *Mononykus* is an animal specialized for digging (see above).

Among the five ambiguous characters linking *Mononykus* to extant birds and other resemblances between them, most can be explained by the acquisition of digging; others probably are related to obligatory bipedalism. There is no definite evidence supporting the avian status of *Mononykus*; it likely is a specialized dinosaur (whether it is a theropod is beyond the scope of this paper), with several avian similarities due to fossorial habits and obligatory bipedal locomotion. That birdlike dinosaurs are not birds does not mean that they have no resemblance to birds, but rather that the resemblances between them are either synplesiomorphies or independently acquired adaptations.

The analysis of the adaptive significance of avianlike characters in *Mononykus* is facilitated not only by the complete preservation of the specialized forelimbs, but also by the existence of various extant fossorial forms (e.g. moles) that have been subjected to detailed study. Also, the great accumulation of early birds and other

archosaurs, including dinosaurs, in recent years has improved our understanding of parallelisms that occur in archosaurs.

For example, Molnar (1985) gave a detailed analysis of the 18 avian characters listed by Kurzanov (1983) in *Avimimus*. Fourteen of them were confirmed by him as valid. Molnar (1985) also found that *Archaeopteryx* has eight of these characters—significantly fewer than *Avimimus* itself, and also fewer than are found piecemeal among theropods. Contrary to Molnar's conclusion, which recommended a reassessment of the position of *Archaeopteryx*, these resemblances are, in my view, either synapomorphies for *Avimimus* and birds, or independently developed in them. If these resemblances are not carefully analyzed, a dinosaur might easily be recognized as a more derived bird than a true early bird. This unfortunately has already happened with *Mononykus*.

Most birdlike dinosaurs occur late in the Cretaceous, at the end of dinosaurian history, whereas as ones go back through time to *Archaeopteryx* or beyond, they are less birdlike. Possibly, most of the avian characters of theropods are only convergently similar to birds, and *Mononykus* shows us how willing some people are to be deceived by such convergence.

Finally, *Mononykus* has some features that seem too primitive for the presence of flight. One could argue that flight has been secondarily lost in *Mononykus*, but how would this be known? There is no evidence that can account for the modification of these flight features. Fossorial life could force the shortening of the forelimb elements, but how can we explain the presence of short coracoid, the closeness of the width of the ulna and the radius, and the lack of fusion of the metatarsals. The most-parsimonious explanation is that *Mononykus* is not a bird and that its ancestors never possessed the capacity for flight.

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