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THE CLOSEST RELATIVES OF BIRDS

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Resúmen. – Los ancestros más cercanos de las aves. – El origen de las aves, el clado originado a partir del ancestro común de *Archaeopteryx* del Jurásico tardío y las aves vivientes, ha estado inmerso dentro de un gran debate científico durante toda la historia de la biología evolutiva. Si bien muchas hipótesis diferentes sobre el origen de las aves han sido propuestas en los últimos dos siglos, hoy en día existe un enorme consenso en favor de la idea de que las aves evolucionaron a partir de dinosaurios terópodos clasificados dentro de los Maniraptora. El sustento osteológico de esta hipótesis es enorme. Los esqueletos de dinosaurios maniraptores como los dromaeosáuridos, troodóntidos y oviraptóridos, comparten muchas similitudes con aquellos de las aves. Además, una serie de espectaculares descubrimientos realizados durante la última década ha brindado diversas líneas de evidencia que complementan el ya inmenso cúmulo de características osteológicas que sustenta la hipótesis Maniraptora. Esta reciente evidencia deriva fundamentalmente del estudio de la morfología de los huevos y de la anatomía tegumentaria, pero también incluye inferencias de comportamiento basadas en un pequeño, pero extraordinario, número de fósiles. Todos estos descubrimientos han documentado la presencia de atributos tales como plumas, empollamiento, ovodeposición secuencial (autocrónica), y otras características avianas en dinosaurios maniraptores basales. La evidencia disponible sugiere fuertemente que las aves deben ser clasificadas dentro de los terópodos y que muchos atributos previamente considerados como únicos de las aves (desde el comportamiento de empollamiento a la capacidad de volar) evolucionaron por primera vez en dinosaurios maniraptores. Si bien los críticos de la hipótesis Maniraptora han resaltado problemas temporales y ontogenéticos, dichas objeciones son claramente irrelevantes. Los dos argumentos más frecuentemente utilizados, la llamada "paradoja temporal" y la homología de los dedos de la mano aviana, se encuentran embebidos en inconsistencias lógicas. Quizás más importante es el hecho de que los críticos de la hipótesis Maniraptora han sido incapaces de formular una hipótesis filogenética alternativa que pueda explicar la enorme similitud entre terópodos no-avianos y aves, dentro del marco de la parsimonia cladista.

Abstract. – The origin of birds, the clade originating from the common ancestor of the Late Jurassic *Archaeopteryx* and extant birds, has been at the center of a heated debate throughout the history of evolutionary biology. Although many disparate hypotheses of bird origins have been proposed in the last two centuries, an overwhelming consensus exists in support of the idea that birds evolved from maniraptoran theropod dinosaurs. Osteological support for this hypothesis is plentiful. The skeletons of such maniraptoran dinosaurs as dromaeosaurids, troodontids, and oviraptorids, share a great deal of similarity with those of birds. In addition, a series of spectacular discoveries in the last decade has provided new lines of evidence that supplement the already overwhelming osteological data. This recent evidence is derived primarily from the study of egg morphology and integumentary anatomy but also includes behavioral inferences based on a handful of rare fossils. These discoveries have documented the presence of feathers, brooding behavior, autochronous ovideposition, and other avian attributes among basal maniraptoran dinosaurs. The available evidence strongly supports the classification of birds within theropods and indicates that many avian attributes previously thought to be unique to birds (from brooding behavior to flight) first evolved among maniraptoran dinosaurs. Although dissenters of the Maniraptoran hypothesis of bird origins have countered by highlighting temporal and developmental limitations, these criticisms are clearly spurious. The most frequently voiced arguments, the so called "temporal paradox" and the homology of the digits of the avian hand, are tainted by logical inconsistencies. Perhaps the most important is the fact that these dissenters have been unable to produce alternative phylogenetic hypotheses that could explain, within the methodological framework of cladistic parsimony, the vast amount of similarity between non-avian theropods and birds. *Accepted 11 December 2003.*

Key words: Bird origin, evolution, Theropoda, Maniraptora.

INTRODUCTION

Birds diversified more than 150 million years ago. Their oldest known records are still from the Late Jurassic of southern Germany, where *Archaeopteryx* was first discovered in the mid-19th century. Identifying the closest relatives to the group's ancestor (the most recent common ancestor of *Archaeopteryx* and modern birds) has been a matter of scientific debate and scrutiny throughout the history of evolutionary biology. As early as the 18th century, birds were placed immediately ahead of flying fishes in the 'chain of being' postulated by the naturalists of that time. With the advent of evolutionary thinking, especially after Darwin's theory of evolution by natural selection, more explicit hypotheses of relationships were formulated. Indeed, in post-Darwinian times, birds were considered to be most closely related to a variety of extinct and extant lineages of reptiles, including turtles, lizards, crocodylomorphs (modern crocodiles and its Triassic relatives), a diversity of basal archosaurs and archosauromorphs (e.g., the Triassic *Euparkeria*, *Longisquama*, and *Megalancosaurus*), pterosaurs (pterodactyls and their kin) as well as theropod and ornithischian dinosaurs (Fig. 1). Today, however, although most of these hypothetical relationships have been abandoned, the theropod hypothesis is receiving nearly universal acceptance. Hypotheses identifying crocodylomorphs, basal archosaurs, or basal archosauromorphs as the closest relatives of birds have occasionally resurfaced in the recent literature but these have been used more as default hypotheses than as real alternatives to the theropod origin of birds. Indeed, a close examination of these "alternative" hypotheses reveals a lack of empirical support because character evidence in support of these hypotheses has also been discovered among theropod dinosaurs. Furthermore, these "alternative" hypotheses have continued to be framed outside modern systematic methods (i.e., cladistics), and thus also lack the rigor of current phylogenetic hypotheses.

Today, the debate on bird ancestry has been resolved. The uncertainties that led to this long controversy, both empirical and methodological, have been clarified. The closest relatives of birds can be found among theropod dinosaurs, the carnivorous predators that ruled the Mesozoic ecosystems. The history of this fascinating scientific debate has been summarized in a number of recent reviews, among them those of Witmer (1991, 2002), Padian & Chiappe (1998), Chiappe (2001), and Prum (2002). A discussion in Spanish can also be found in Chiappe & Vargas (2003). In this paper, addressed to the ornithological community, I hope to convey the message that the scientific hypothesis of their diverse disciplines, from ecology to behavior to systematics, will greatly benefit from incorporating the notion that modern birds are highly specialized, short-tailed, and flighted theropod dinosaurs.

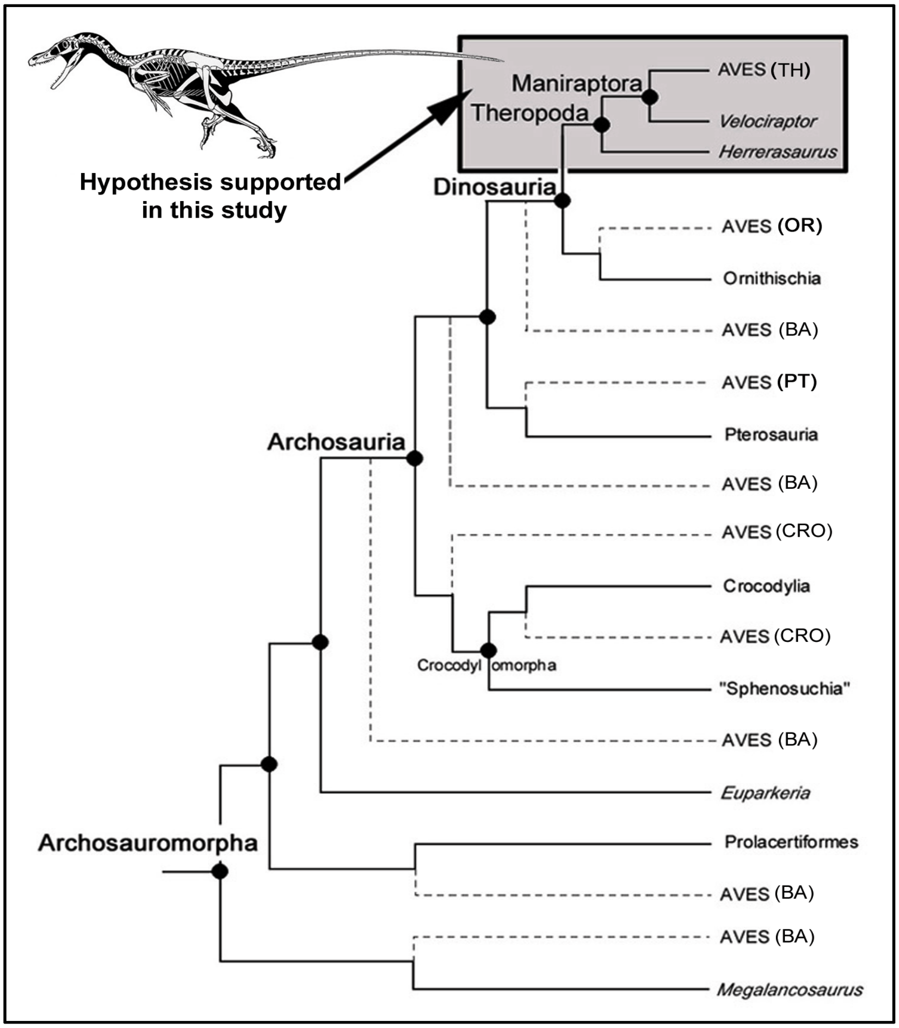

FIG. 1. Cladogram illustrating the diversity of hypotheses of the origin of birds (within Archosauromorpha). BA, hypotheses that relate birds to some basal archosaurs or basal archosauromorphs; CRO, hypotheses in support of a crocodylomorph origin of birds; OR, a hypothesis in favor of a common origin between birds and ornithischian dinosaurs; PT, a hypothesis supporting the ancestry of birds from pterosaurs (flying reptiles); TH, hypotheses in favor of the origin of birds from theropod dinosaurs; this hypothesis is the one endorsed in the present study. Modified from Chiappe & Vargas (2003).

HISTORY OF THE THEROPOD HYPOTHESIS OF BIRD ORIGINS

The first suggestion that birds could have been related to dinosaurs came soon after the publication of Darwin's "Origin of Species". Similarities in the structure of the tarsus led Gegenbaur (1864) to place the small, Late Jurassic theropod *Compsognathus* in an intermediate position between birds and other rep-

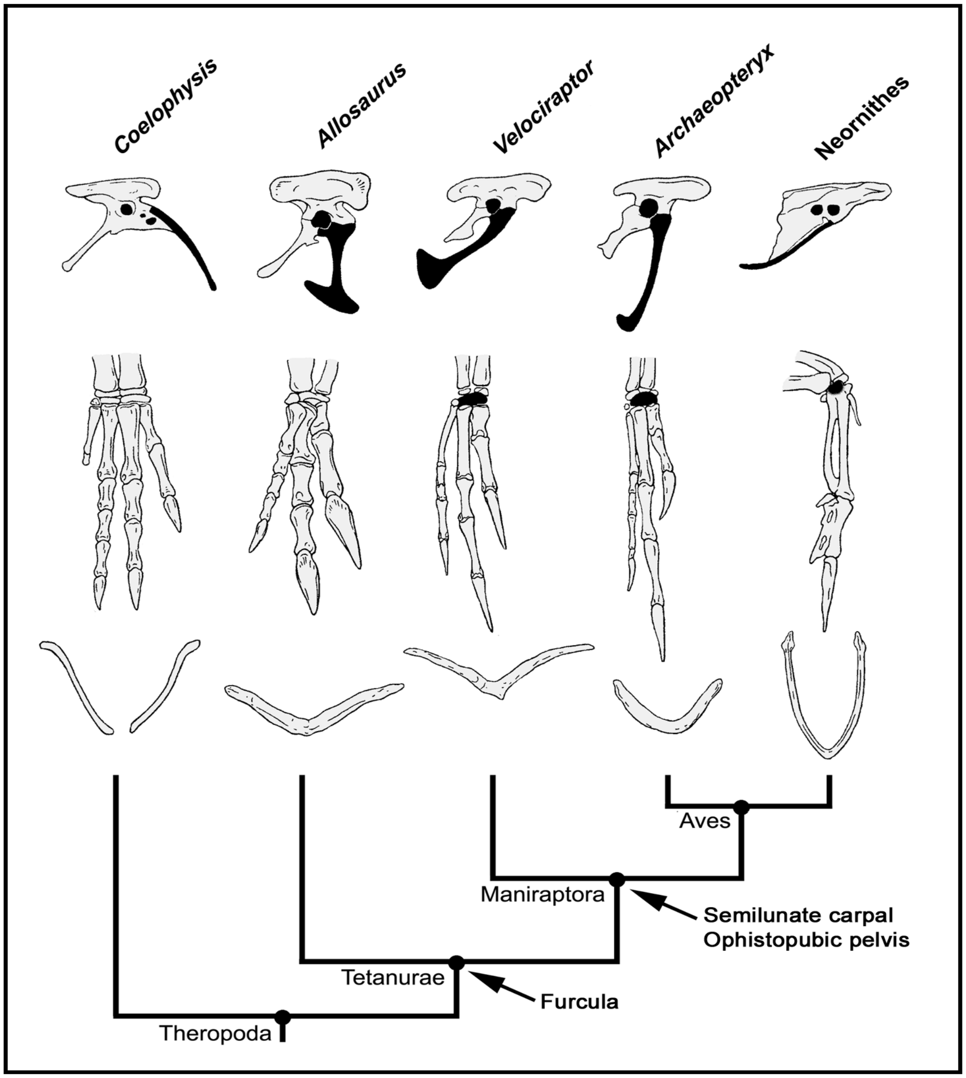

FIG. 2. Some osteological synapomorphies in support of the maniraptoran origin of birds. Modified from Chiappe & Vargas (2003).

tiles. At about the same time, Cope (1867) compared the tarsus of the Jurassic theropod *Megalosaurus* to that of an ostrich and, on the basis of this and on similarities in the elongation of the neck vertebrae and the lightness of the skull, he argued for a close relationship between theropods and birds. Despite these initial considerations, it was Huxley (1868, 1869) who championed the 19th century discussions of the origin of birds from theropod dinosaurs. In 1869, Huxley argued that "if the whole hind quarters, from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us referring them to the Dinosauria." (Huxley 1869). During the second half of the 19th century, the theropod hypothesis of bird origins was one of a pool of other hypotheses. Just as today, detractors argued that the similarities between birds and theropod dinosaurs could well be explained by convergence [see Seeley's discussion in Huxley (1869)]. In the early 20th century, with the discovery of more generalized, Triassic archosaurs, in particular the South African *Euparkeria* (Broom 1913), the theropod hypothesis lost ground. Theropods were deemed as too specialized to be the ancestors of birds (Heillman 1926). Such a notion dominated the field for several decades (see Romer 1966) until the early 1970s, when renewed interest on the origin of birds took place (see Witmer 1991). Among this new wave of interest was Ostrom's work on *Archaeopteryx* (Ostrom 1973, 1976), who revitalized Huxley's hypothesis of the theropod origin of birds. During the thirty years that has passed since Ostrom's initial work on bird origins, a large quantity of fossil documentation supporting the dinosaurian ancestry of the group has been accumulated. Today, despite disagreement regarding the specific theropod clade phylogenetically closest to birds (e.g., dromaeosaurids, troodontids, oviraptorids), an overwhelming consensus exists in support to the notion that birds evolved from maniraptoran theropods (Chiappe & Dyke 2002).

EVIDENCE FOR THE MANIRAPTORAN ORIGIN OF BIRDS

Several lines of evidence converge in support of the hypothesis that the closest relatives of birds are to be found among maniraptoran theropod dinosaurs (Chiappe 2001). The most visible evidence of this hypothesis is based on comparisons of the osteology, behavior, oology, and integument of birds with that of a variety of nonavian theropods. These lines of evidence are summarized below.

Osteology. A multitude of derived osteological characters are shared by all, or some, nonavian maniraptoran theropods and birds (Fig. 2). Comparisons between these taxa are greatly assisted by the many newly discovered basal birds (Padian & Chiappe 1998, Chiappe & Dyke 2002), which possess a skeletal morphology only slightly modified from the ancestral maniraptoran condition. Some of these derived characters are the presence of rostral, dorsal, and caudal tympanic recesses (air spaces connected to the ear region), ventral processes on cervicothoracic vertebrae, ossified ventral segments of thoracic ribs, forelimbs that are more than half the length of hindlimbs, a semilunate carpal bone allowing swivel-like movements of the wrist, clavicles fused into a wishbone (probably a synapomorphy of a more inclusive theropod group), a pubic peduncle of the ilium longer than the ischiadic peduncle (these peduncles form the front and rear borders of the hip-socket), a vertically to caudoventrally oriented pubis ending in a boot-like expansion that projects only caudally, an ischium two-thirds or less the length of the pubis, a femur with a feeble fourth trochanter (the attachment of the caudofemoralis longus muscle), and many other characters distributed over the entire skeleton (Novas & Puerta 1997, Holtz 1998, Sereno 1999, Clark *et al.* 2002). Birds also share a number of derived characters with more inclusive theropod clades such as the Coelurosauria, Tetanurae, and Neotheropoda, and evolutionary trends towards the modern avian condition can be seen when these are examined across cladograms of theropods

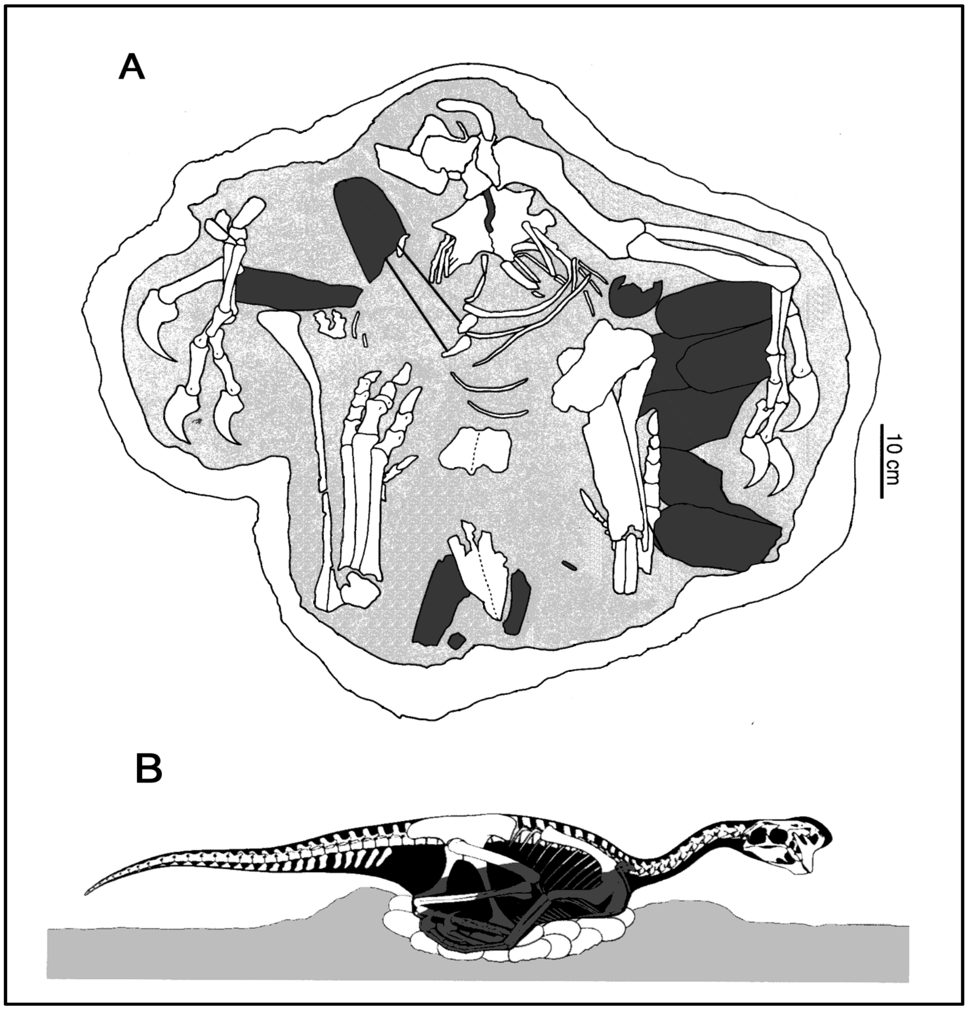

FIG. 3. A partial skeleton of the oviraptorid *Citipati* from the Late Cretaceous of the Gobi Desert brooding a clutch of its own eggs (A) and an interpretation of the posture of this animal when in life (B). Modified from Clark *et al.* (1999).

(e.g., forelimb elongation, pubic rotation, braincase amplification, stiffening of the tail). Indeed, many osteological features previously thought to be exclusively avian, such as a furcula, laterally facing glenoids, large bony sterna, uncinate processes on ribs, have now been discovered among nonavian maniraptorans (Padian & Chiappe 1998).

Behavior. Evidence of the behavior of extinct organisms is rarely preserved in the fossil record. A handful of extraordinary discoveries, however, have shed light on the nesting conduct of certain nonavian maniraptorans. Several skeletons of Late Cretaceous oviraptorids from the Gobi Desert, belonging to both *Oviraptor* (Osborn 1924) and *Citipati*

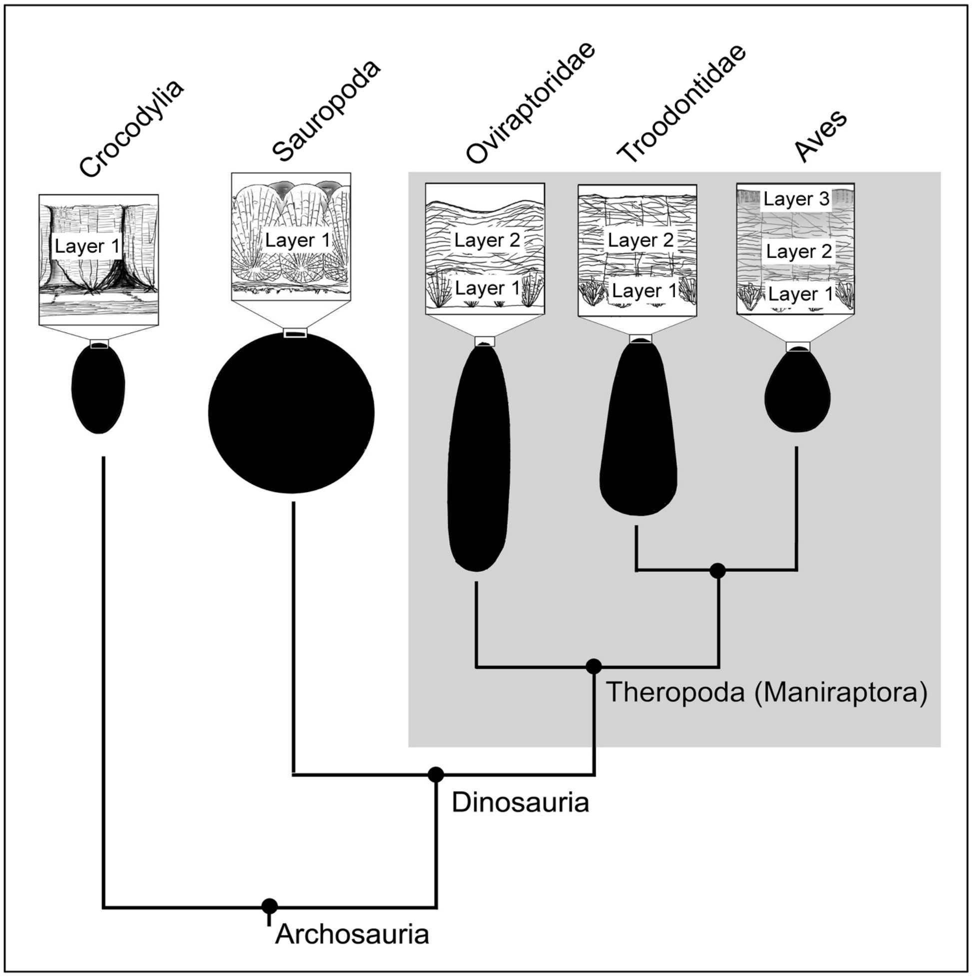

FIG. 4. Some oological synapomorphies in support of the maniraptoran origin of birds. Note the presence of two or more layers in the eggshell of oviraptorids, troodontids, and birds, and the asymmetric shape of the egg in the last two lineages. Modified from Chiappe & Vargas (2003).

(Clark *et al.* 2001), have been discovered on top of their clutches of eggs (Fig. 3). The specimens of *Citipati* show that the animals adopted a posture similar to those of brooding birds, with their legs tucked inside an open space at the center of the clutch and their forelimbs surrounding the periphery of the clutch (Clark *et al.* 1999). An oviraptorid embryo inside an egg of comparable morphology to those in these clutches strongly supports the idea that these specimens were brooding their own nest (Clark *et al.* 1999). These discoveries have forced the reinterpretation of inferences made decades ago on the basis of the holotype of *Oviraptor philoceratops* (Osborn 1924) which, because it had also been found on top of a clutch of eggs, had been interpreted (and consequently named) as an egg-predator (Norell *et al.* 1995). A similar discovery of a Late Cretaceous troodontid skeleton from Montana in an identical brooding position suggests that, regardless of its specific function (e.g., protection, incubation), the typical avian nesting behavior (i.e., adults sitting on top of their nests) was widespread among nonavian maniraptorans.

Oology. The general morphology and microstructure of calcified eggs is specific to certain groups of extant and extinct reptiles (Mikhailov 1997, Grellet-Tinner 2000). Until recently, the precise characteristics of the eggshell microstructure of nonavian theropods remained elusive due to the absence of diagnostic embryonic material. The discovery of the Gobi oviraptorid embryo provided the first definitive evidence of a nonavian theropod egg (Clark *et al.* 1999). Since then, other nonavian maniraptorans embryos have been found. These include other species of oviraptorids (Weishampel *et al.* 2000), therizinosaurids (Manning *et al.* 2000), and troodontids (Varricchio *et al.* 2002). Comparative studies between the eggshell microstructure of these eggs and those of extant birds have revealed features exclusively common to them (Fig. 4) (Mikhailov 1992, Varricchio *et al.* 1997, Zelenitzky *et al.* 2002, Grellet-Tinner & Chiappe 2004). One of these features involves the presence of more than one distinct microstructural layer, most commonly distinguished by the differential disposition of the calcitic crystals (Grellet-Tinner & Chiappe 2004). The dinosaurian eggshell is characterized by the presence of shell units, of which the inner portion is formed by a crystalline structure that radiates from a core, often termed the organic core. In nonavian theropods, these units also possess an external zone with a more spongeus microstructural appearance, although in thin sections this layer exhibits a more laminar appearance (this layer is often referred as the squamatic zone). In birds, this external zone may grade into, or be completely separated from, a third, outermost zone and, in paleognaths, even a fourth zone can be recognized (Grellet-Tinner 2000). Even though up to now only two layers have been found in the eggshell of nonavian theropods, no other group of nonavian reptiles possesses a similar zonation. Additional character states shared by the eggs of nonavian maniraptorans and those of birds include a reduction in the porosity of the shell, a relative increase in the volume of the egg (with respect to the size of the adult), and the presence of a longer axis (eggs that are elongated) (Zelenitzky *et al.* 2002). Another oological feature easily recognizable is the presence of asymmetrical eggs, those in which one pole is narrower than the other. While turtles, crocodiles, and nearly all non-avian dinosaurs are characterized for having symmetrical eggs, the eggs of birds and those of troodontid maniraptoran theropods have one pole that is narrower than the other. Further similarities between nonavian maniraptorans and birds involve the mode of ovideposition. Unlike in the clutches of other dinosaurs where eggs have no spatial arrangement, in theropod clutches, the eggs are clearly arranged in pairs. Such a pairing is suggestive of autochronous ovideposition, a mode of deposition in which eggs are not laid *en masse* but sequentially, at discrete time intervals. The pairing of eggs found in fossil egg-clutches attributed to theropod dinosaurs thus suggests that it could have taken several days for a theropod female to lay its egg-clutch (Varricchio *et al.* 1997, Grellet-Tinner & Chiappe 2004), a condition shared with birds.

Integument. Feathers have always been the quintessential bird feature. In recent times, however, feathers have been found in a variety of maniraptoran theropods, whose skeletons are found in a series of Early Cretaceous lacustrine deposits in the northeastern corner

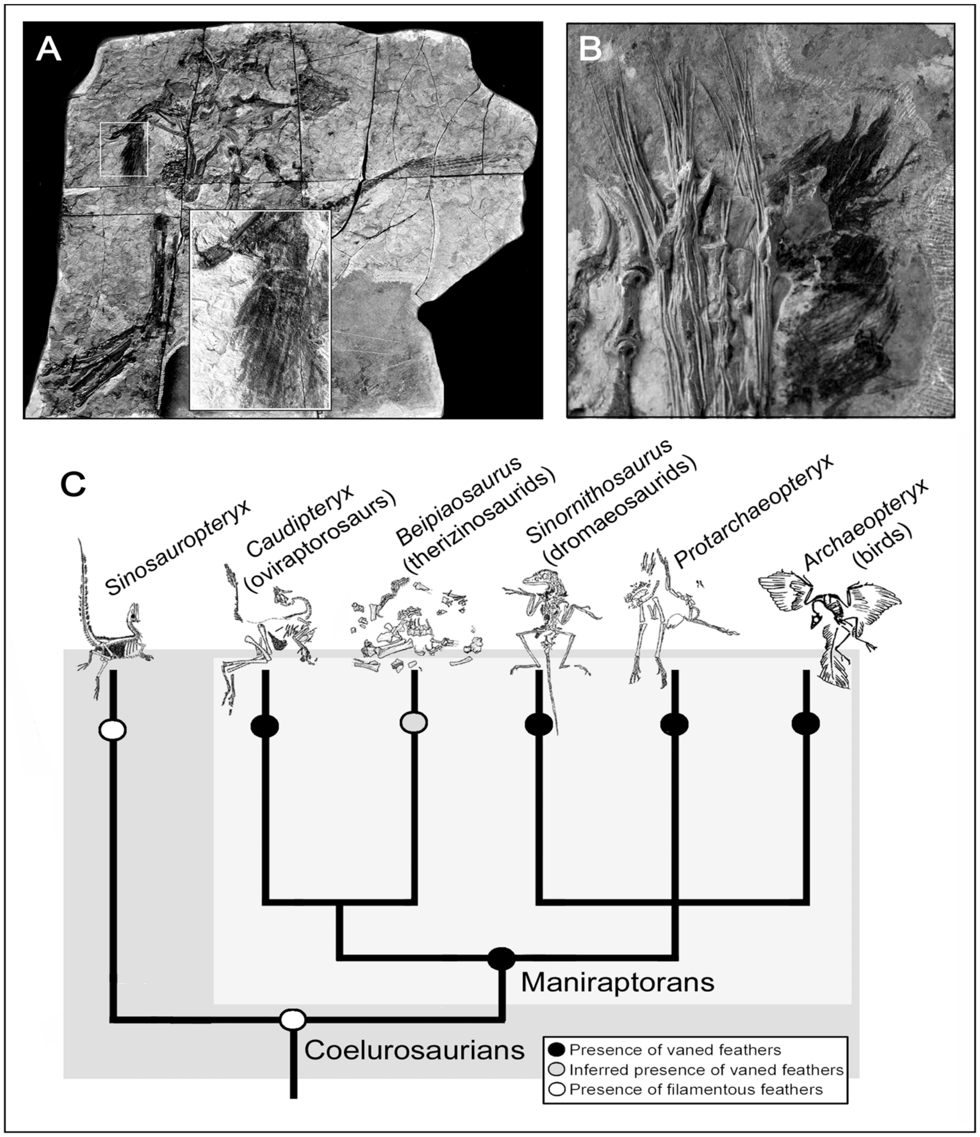

FIG. 5. The integument of nonavian maniraptorans (A, B) and a cladogram (C) illustrating the phylogenetic relationships of known feathered nonavian theropods. A represents the oviraptorosaur *Caudipteryx*. The inset highlights the vaned feathers attached to the distal end of the forelimb. Note also the tuft of feathers attached to the tail of this dinosaur. B represents filamentous feathers surrounding the tail of the dromaeosaurid *Sinornithosaurus*. Modified from Chiappe & Dyke (2002).

of China (Fig. 5). Carbonized remains of feathers are now known for the therizinosaurid *Beipiaosaurus* (Xu *et al.* 1999), the oviraptorosaur *Caudipteryx* (Ji *et al.* 1998, Zhou & Wang 2000), the dromaeosaurids *Sinornithosaurus* (Xu *et al.* 1999) and *Microraptor* (Xu *et al.* 2000

2003), and the long-armed *Protarchaeopteryx* (Ji *et al.* 1998), which phylogenetic placement among maniraptorans is less well-known. Integumentary structures interpreted as feathers have also been found in more primitive theropods such as the basal coelurosaurian *Sinosauropteryx* (Chen *et al.* 1998, Currie & Chen 2001), also from the same Early Cretaceous rocks of China. While the latter exhibits feathers that are filament-like, with a minimal degree of branching, *Caudipteryx*, *Protarchaeopteryx*, *Sinosauropteryx*, and *Microraptor* display pennaceous feathers with distinct shafts and vanes. Down-like feathers also cover portions of the skeletons of all these taxa. A fan-shaped cluster of pennaceous feathers is attached to the distal part of the tail of *Caudipteryx* (Fig. 5). Frond-like tails similar to those in *Archaeopteryx* are present in the dromaeosaurids *Sinosauropteryx* and *Microraptor*, although these pennaceous feathers are more restricted to the distal half of the tail. Long pennaceous feathers are also attached to the tip of the forelimbs of *Caudipteryx* (Ji *et al.* 1998) (Fig. 5) while in the tiny *Microraptor gui*, they form a wing of essentially modern design (Xu *et al.* 2003). There is also the remarkable presence in the latter taxon of pennaceous feathers attached to the distal half of the hindlimb. Such an attribute has been used to argue that *Microraptor gui* was able to glide using these hindlimb feathers as an additional airfoil (Xu *et al.* 2003). Despite functional considerations that make this idea untenable (Chiappe & Vargas 2003), there is little doubt that with such a small wing loading, *Microraptor gui* was able to fly [see Padian & Chiappe (1998) for a recent discussion on the origin of flight]. The presence of feathers in so many coelurosaurian taxa suggests that these integumentary appendages evolved in the common ancestor of the group if not earlier. Given the evidence at hand, the presence of simple, filament-like feathers is considered as a synapomorphy of Coelurosauria while the presence of more derived, pennaceous feathers is interpreted as synapomorphic of Maniraptora. These discoveries not only document the presence of feathers outside birds but also, suggest that some nonavian theropod dinosaurs (e.g., *Microraptor gui*) may have been able to fly.

CRITICISMS OF THE MANIRAPTORAN HYPOTHESIS OF BIRD ORIGINS

The evidence summarized above is so compelling that the idea that birds are the descendants of a maniraptoran ancestor has been accepted by a great number of evolutionary biologists. Nonetheless, the maniraptoran hypothesis of bird origins is not exempt of critics, even though it is fair to say that these represent only a tiny fraction of specialists. Concerns have been expressed primarily highlighting apparent inconsistencies within the known fossil record and with the inferred homology of certain structures. These apparent inconsistencies are briefly discussed below.

INCONSISTENCIES WITHIN THE KNOWN FOSSIL RECORD

This criticism highlights the chronological gap between the oldest known bird, the Late Jurassic *Archaeopteryx*, and the Cretaceous nonavian maniraptorans that are typically used in discussions of bird origins (e.g., *Deinonychus*, *Velociraptor*, *Oviraptor*). This argument has become known as the "temporal paradox" since it highlights the inconsistency of arguing that birds evolved from creatures that lived several million years after their own origin (Feduccia 1996, 1999). However, examination of the theoretical basis and supporting evidence of the "temporal paradox" indicates that this argument stems from philosophical misconceptions, disregards critical fossil evidence, and it constitutes an artifact caused by not considering all alternative hypotheses of bird origins at the same time (Brochu & Norell 2000).

In the first place, the "temporal paradox" stems from a philosophical misconception because none of these Cretaceous dinosaurs is regarded as the direct ancestor of birds (Padian Chiappe 1998, Witmer 2002). In modern times, the hypothesis of a maniraptoran ancestry of birds has been framed as a cladistic hypothesis that postulates the existence of a most recent common ancestor of these Cretaceous dinosaurs and *Archaeopteryx* that obviously existed before the divergence of the oldest of these taxa, *Archaeopteryx* (e.g., Gauthier 1986, Forster *et al.* 1998, Holtz 1998, Sereno 1999, Norell *et al.* 2001, Clark *et al.* 2002). Thus, in contrast to what has been claimed by the proponents of the "temporal paradox", the maniraptoran hypothesis does set the origin of birds in pre-Jurassic times.

In addition, the absence of the pre-Cretaceous maniraptorans the "temporal paradox" seems to highlight has long been proved to be mistaken. Late Jurassic maniraptorans have been known for decades, even if from fragmentary remains (Padian & Jensen 1980), and a lower jaw of a maniraptoran therizinosaurid, *Eshanosaurus deguchiianus*, has been discovered in the Early Jurassic of China (Xu *et al.* 2001). This and the fact that the stratigraphic ranges of theropod groups containing the clade Maniraptora have been recently extended back by many millions of years [e.g., basal tetanurans are now known from the Late Triassic; Arcucci & Coria (2003)], suggest that the divergence of maniraptorans occurred much earlier than in the Late Jurassic. The fact that maniraptoran fossils are exceedingly rare in pre-Cretaceous times may be related to a clear bias against small-sized dinosaurs of Jurassic age (most maniraptorans are of relatively small size) and the much smaller volume of Jurassic outcrops than those of Cretaceous age (Clark *et al.* 2002).

Finally, the "temporal paradox" appears to exist only if one considers the temporal gap between the 100-million-year old *Deinonychus*, to take an example of a well-known dromaeosaurid, and the 150-million-year old *Archaeopteryx*. Yet, as shown by the statistical test of Brochu & Norell (2000), when other records of well-known maniraptorans are included (e.g., the 125-million-year old dromaeosaurids *Sinornithosaurus* and *Microraptor*) and when hypotheses of bird origins are compared against each other, placing birds within groups indicated by hypotheses (e.g., crocodylomorphs or more basally within archosaurs; see Fig. 1) other than the theropod hypothesis may increase the temporal disparity by as much as 15%. Thus, when the "temporal paradox" is considered in the context of current alternative hypotheses of bird origins (Fig. 1), the maniraptoran hypothesis is temporally the most consistent (Brochu & Norell 2000).

INCONSISTENCIES WITH THE INFERRED HOMOLOGY OF SOME STRUCTURES

Embryology of the avian hand. Opponents to the maniraptoran origin of birds (e.g., Feduccia 1999, 2003) have highlighted the conflict between the correspondence of the three wing digits of birds with respect to the ancestral pentadactyl hand of tetrapods, as indicated by embryological studies, and that inferred from the palaeontological evidence. Embryological investigations of extant birds have identified five precartilaginous condensations of which only those in positions II, III, and IV develop into the three osseous digits of the adult hand (Feduccia & Nowicki 2002, Larsson & Wagner 2002). This observation has often been extrapolated to include all birds, even the Late Jurassic *Archaeopteryx*, and the three fingers of the avian hand have been identified as homologous to digits II–IV of

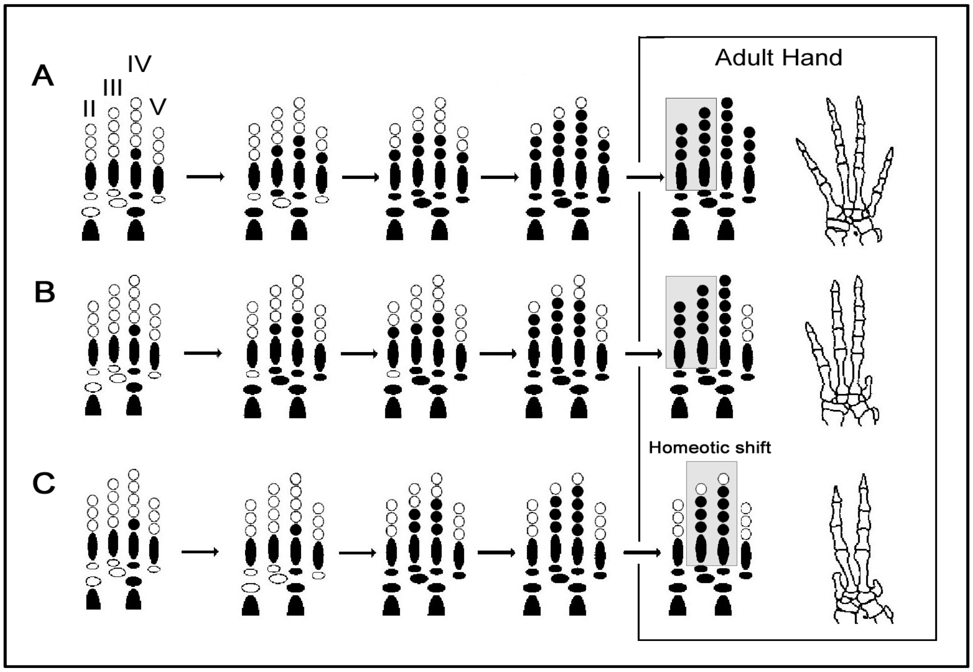

FIG. 6. Chondrification and ossification patterns of the right hand of the scincid lizards *Hemiergis perioni* and *H. quadrilineata* – an example of a homeotic frame shift in the development of the hand of a tetrapod. *H. perioni* includes morphs with three and four manual digits (A, B). In these morphs, digital condensations II and III develop into the two anteriormost digits of the adult hand, which have three and four phalanges, respectively. Adults of *H. quadrilineata* have only two manual digits, the anteriormost of them with three phalanges and the other one with four phalanges (C). While in *H. perioni* the two anteriormost manual digits, those with three and four phalanges, ossify from condensations II and III, in *H. quadrilineata*, these digits ossify from condensations III and IV. The morphological similarity between the mature digits of this species and digits II and III of other *Hemiergis* species is such that the positional identity of the two digits of *H. quadrilineata* can only be verified through ontogenetic studies. Modified from Shapiro (2002).

the ancestral pentadactyl hand (Burke & Feduccia 1997, Feduccia 1999, Feduccia & Nowicki 2002). In contrast, inferences based on the transformation of the hand as observed from fossils representing different stages of dinosaur evolution have identified the homology of the three fingers of *Archaeopteryx* as those corresponding to digits I, II, and III of the ancestral pentadactyl hand. This paleontological evidence shows a trend of reduction of the outermost two digits (VI and V) from the most basal theropods, where these digits are abbreviated but still present, to tetanuran theropods bearing a tridactyl hand (Padian & Chiappe 1998). The three digits of the latter theropods have the same phalangeal formula as digits I, II, and III of the primitive five-fingered theropods, thus indicating that the three fingers of tetanurans (a group that also includes Maniraptora) correspond to digits I–III of the ancestral pentadactyl hand. The remarkable similarity in morphology, proportions, and phalangeal formula of the manual digits of certain nonavian maniraptorans (e.g., *Velociraptor*, *Deinonychus*) to those of *Archaeopteryx* has extended this conclusion to this and to other basal birds.

Two different issues are involved in this controversy. On the one hand is the question of whether there is empirical basis for extrapolating the ontogenetic development of modern birds to *Archaeopteryx*. On the other hand is whether the maniraptoran ancestry of birds can be sustained even if nonavian theropods developed their manual digits through a developmental pathway different than that of modern avians. The extrapolation of the embryogenesis of the hand of extant birds to archaic avian lineages including *Archaeopteryx* appears unwarranted given that the hand of modern birds is highly transformed and that embryological evidence is unavailable for either *Archaeopteryx* or any other basal avian lineage. Indeed, the fact that the hand of *Archaeopteryx* is remarkably similar to that of nonavian maniraptorans such as dromaeosaurids (Ostrom 1976) suggests that if any developmental trajectory is to be extrapolated to this Late Jurassic bird, it should be the one inferred for dromaeosaurid theropods. The second issue, namely whether embryogenetic differences should take precedence over the enormous volume of evidence supporting the phylogenetic relationship between birds and certain lineages of nonavian maniraptorans, is also problematic. Certainly, such an approach would be in direct conflict with the parsimony methods endorsed by modern systematic techniques. If the maniraptoran origin of birds is to be rejected because the digits of the hand of living birds have ontogenetic trajectories different from those inferred for extinct maniraptorans, the unquestionable similarities in the osteology, plumage, oology, and behavior of all these organisms would have to be explained in the context of evolutionary convergence. Nonetheless, the apparent incongruence between the manual osteogenesis of modern birds and that of their nonavian theropod relatives can be explained without resorting to a different phylogenetic hypothesis. Wagner & Gauthier (1999) have argued that homeotic frame shifts could have led to a developmental pattern in which digits that previously ossified from condensations I–III became ossified from condensations II–IV. Homeotic frame shifts are relatively common among other vertebrate lineages. An illustrative example involves the development of the hand of the two-toed earless skink (*Hemiergis quadrilineata*), an Australian scincid lizard (Shapiro 2002) (Fig. 6). Many studies have documented the fact that ontogenetic trajectories do evolve and that these transformations could occur without affecting either the morphology or function of the developing structure (Wagner & Misof 1993, Mabee 2000, Hall 2003). These structures are homologous, even if their development pathways are different.

Lung structure and ventilation. Interpretations of soft structures supposed to indicate visceral compartmentalization in the early Cretaceous basal coelurosaurian theropod *Sinosauropteryx prima* (Chen *et al.* 1998) played a paramount role in Ruben *et al.*'s (1997) claim that nonavian theropods had a crocodile-like, hepatic-piston mechanism for lung ventilation. Ruben *et al.* (1997) questioned the close relationship between birds and nonavian theropods on the basis of this interpretation, because according to these authors, the transition from the crocodile-like pulmonary system to the flow-through lung system of birds would have required the evolution of a diaphragmatic hernia in the alleged partition that would have compromised the efficiency of the pulmonary system of the transitional forms.

As in the case of other critics to the theropod hypothesis of bird origins, this argument is based on problematic interpretations. Detailed studies of the skeleton of the specimen of *Sinosauropteryx prima* used by Ruben *et al.* (1997) have demonstrated that the structure interpreted as a septum separating the abdominal cavity from the thoracic cavity is a preservational artifact (Currie & Chen 2001). Furthermore, the osteological correlates of the avian flow-through lung are well-known among nonavian theropods, in particular the vertebral pneumatization for the entrance of pulmonary air sacs. The presence of intracostal articulations delimiting costal and ventral ribs and the relatively large ossified sternal plates of nonavian maniraptorans also suggest that the coordinated costal and sternal movements that ventilate the lungs of extant birds may have already been present in these dinosaurs (Clark *et al.* 1999). There is undeniable evidence for the presence of skeletal structures correlated to the avian system of lung structure and ventilation among nonavian theropods.

CONCLUSION

Recent fossil discoveries have drastically change the volume of available evidence for deciphering the historical relationships of birds. This new evidence has shown that many of the features previously considered to be avian trademarks first evolved within theropod dinosaurs. Criticisms leveled by the opponents of the theropod ancestry of birds are empirically and methodologically misleading; no alternative phylogenetic hypothesis has been framed within rigorous cladistic methods. The notion that the closest relatives of birds must be found among maniraptoran theropods is today indisputable.

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