

# Evolution and Homology of the Astragalus in Early Amniotes: New Fossils, New Perspectives

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**ABSTRACT** The reorganization of the ankle in basal amniotes has long been considered a key innovation allowing the evolution of more terrestrial and cursorial behavior. Understanding how this key innovation arose is a complex problem that largely concerns the homologizing of the amniote astragalus with the various ossifications in the anamniote tarsus. Over the last century, several hypotheses have been advanced homologizing the amniote astragalus with the many ossifications in the ankle of amphibian-grade tetrapods. There is an emerging consensus that the amniote astragalus is a complex structure emerging via the co-ossification of several originally separate elements, but the identities of these elements remain unclear. Here we present new fossil evidence bearing on this contentious question. A poorly ossified, juvenile astragalus of the large captorhinid *Moradisaurus grandis* shows clear evidence of four ossification centers, rather than of three centers or one center as posited in previous models of astragalus homology. Comparative material of the captorhinid *Captorhinikos chozaensis* is also interpretable as demonstrating four ossification centers. A new, four-center model for the homology of the amniote astragalus is advanced, and is discussed in the context of the phylogeny of the Captorhinidae in an attempt to identify the developmental transitions responsible for the observed pattern of ossification within this clade. Lastly, the broader implications for amniote phylogeny are discussed, concluding that the neomorphic pattern of astragalus ossification seen in all extant reptiles (including turtles) arose within the clade Diapsida. *J. Morphol.* 267:415–425, 2006. © 2006 Wiley-Liss, Inc.

**KEY WORDS:** amniote; ankle; astragalus; captorhinid; homology

The tarsus in amniotes differs radically from that of anamniote tetrapods. Relative to amphibian-grade taxa, amniotes have fewer bony elements in the ankle, and the elements play an increased, more active role in locomotion by stiffening and stabilizing the pes (Sumida, 1997). This repatterning of the tarsus has long been considered a key innovation in the transition between amphibian-grade and reptilian-grade tetrapods (Romer, 1956; Gauthier et al., 1988), allowing increased terrestriality and locomotor efficiency. Unfortunately, this transition is not well understood; the homologies of the various

tarsal elements are unclear, rendering the study of specific joint articulations difficult (Sumida, 1997, p. 387). New data and new insights on the developmental and evolutionary repatterning of the amniote ankle are therefore of prime importance, for they bear on one of the key transitions in tetrapod history: the attainment of full terrestriality after the long transition from fin to limb (Clack, 2002).

Perhaps the most important novelty within the amniote tarsus is the astragalus, a large, complex bone comprising the primary area of articulation for the distal tibia. The definitive astragalus first appears at the origin of the clade Amniota (Fig. 1A); amphibian-grade tetrapod taxa below this node, such as seymouriamorphs and anthracosaurs (regardless of the current debate over their relationships to each other and to Amniota; Clack, 2002), generally maintain the pattern of tarsal bones characteristic of most anamniote tetrapods, while synapsids and reptiles possess a true astragalus (relationships from Coates, 1996; Sumida, 1997). This obvious correlation between amniote origins and the appearance of the astragalus has led to a long discussion of the homologies of this bone (Gegenbauer, 1864; Zittel, 1932; Romer, 1956; Rieppel, 1993; Kissel et al., 2002; Berman and Henrici, 2003). However, a lack of definitive evidence has precluded a satisfactory resolution. Here we present new fossil evidence that may help to resolve this debate.

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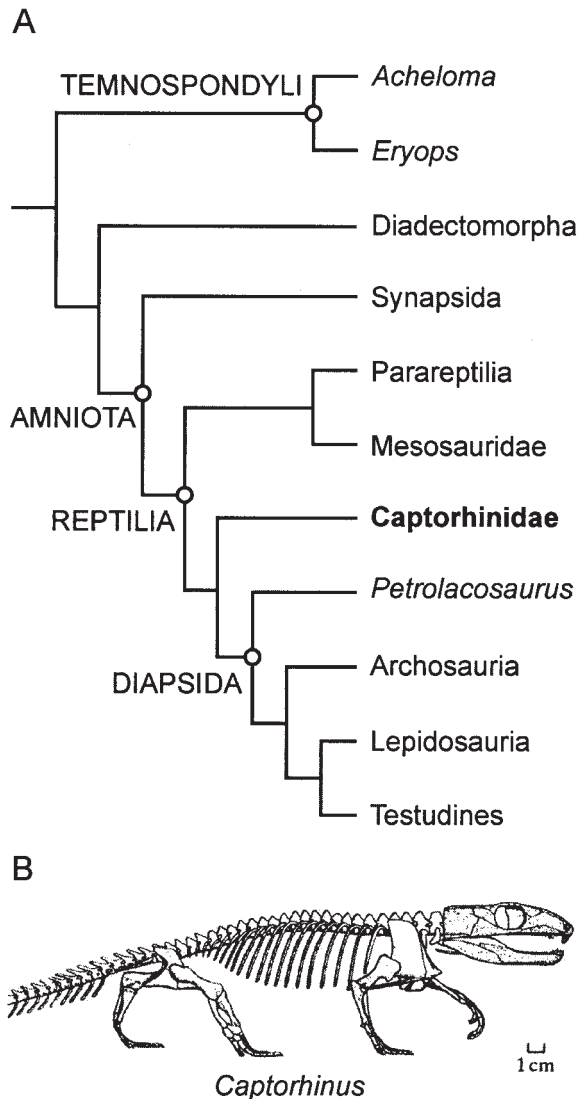


Fig. 1. **A:** Tetrapod phylogeny showing relationships of taxa discussed in this article. Topology follows Modesto and Anderson (2004), Hill (2005). **B:** Skeleton of the representative captorhinid reptile *Captorhinus laticeps*, after Heaton and Reisz (1980).

### Captorhinid Reptiles and Comparative Taxa

Reptiles of the clade Captorhinidae (Fig. 1B) offer a unique opportunity to study the ossification of the tarsus in early amniotes. Captorhinids are a group of basal, generalized early reptiles with an excellent fossil record beginning in the Pennsylvanian (Wideman and Sumida, 2004) and spanning the Permian (~300 million to 250 million years ago; Modesto and Smith, 2001). Because of their great age, excellent fossil record, and generalized anatomy, captorhinids have long been used as exemplars in discussions of reptile evolution (Romer, 1956). From a modern phylogenetic perspective, captorhinids are appealing because they are the most primitive eureptiles (Modesto and Anderson, 2004; Fig. 1), and as such

are archaic members of the clade that includes all modern reptiles. The ankles of extant diapsids are quite derived in terms of both morphology and development relative to more basal amniotes (Rieppel and Reisz, 1999), whereas the ankle morphology and development of captorhinids is quite primitive (Kissel et al., 2002; Holmes, 2003). Recent functional work on the ankle of *Captorhinus* has demonstrated that it had a mesotarsal joint, an important innovation allowing more efficient terrestrial locomotion (Holmes, 2003). Captorhinids are therefore a logical group in which to study ankle evolution, because they form an anatomical and functional link between modern, derived diapsids on the one hand and more basal amniotes and anamniote tetrapods on the other. Lastly, the excellent fossil record of the group, consisting of literally thousands of specimens, affords ample opportunity for the study of both juvenile and adult animals within a phylogenetic framework.

Phylogenetic uncertainty has hindered a clear understanding of the morphological configuration present in the ankles of amniote precursors (Clack, 2002, pp. 267–277). The one clade that all agree is very close to the origin of amniotes—Diadectomorpha—has autapomorphic ankle morphology (Sumida, 1997; Berman and Henrici, 2003). Fortunately, the morphology of the tarsus in most basal tetrapods is generalized and fairly conservative. Permo-Carboniferous taxa as varied as the colosteid *Greererpeton*, the temnospondyl *Acheloma*, and the highly terrestrial embolomere *Proterogyrinus* share a canonical pattern of seven tarsal ossifications comprising intermedium, tibiale, fibulare, and four centralia (Holmes, 1984; Godfrey, 1989). In this article we use the temnospondyl *Acheloma* (previously known as “*Trematops*”; this taxon was declared a junior synonym of *Acheloma* by Dilkes and Reisz, 1988) as an exemplar taxon for the primitive condition outside of Amniota. There are several justifications for doing this, the two most germane being the highly conservative nature of the tarsus in basal tetrapods and the fact that *Acheloma* is a large animal with a well-ossified tarsus. Many basal tetrapods, especially of small body size, have poorly ossified tarsi and therefore lack detailed information on the articulations of some elements and on the location of soft tissue structures such as the perforating artery. A last justification for using *Acheloma* as an exemplar taxon is simply historical: authors from Peabody (1951) to Romer (1956) to Shubin (2002) all accept *Acheloma* as an accurate representation of the generalized condition from which both amniotes and lissamphibians evolved.

### Previous Models of Astragalus Homology

Before the work of Peabody (1951), Romer and earlier workers had entertained various hypotheses

for the homology of the amniote astragalus (reviewed in Romer, 1956, pp. 392–393); however, in *Osteology of the Reptiles* Romer accepted Peabody's contention that the amniote astragalus is formed from the fusion of three elements present in amphibian-grade tetrapods: the tibiale, the intermedium, and the "proximal centrale" (Fig. 2). This "three-center model" was the conventional wisdom until challenged by Rieppel (1993), who advanced a new model based on his study of tarsal ossification in extant reptiles. Rieppel disputed Peabody's interpretation of juvenile *Captorhinus aguti* fossils, and concluded that the ossification pattern seen in all modern reptiles (i.e., ossification from a single center, or the "one-center model"; Fig. 2) was phylogenetically ancient, because it was also present in mesosaurs, a group of aquatic reptiles from the Early Permian. Therefore, the developmental reorganization necessary to replace the various stem tetrapod tarsal ossifications with the novel amniote astragalus would be a neomorph of all Amniota. In this view the amniote astragalus lacks a direct homologous precursor among amphibian-grade tetrapods, and furthermore does not bear on the ongoing debate concerning parareptile versus diapsid affinities of turtles (Rieppel and Reisz, 1999; Hill, 2005, and references therein).

Recent work has seemingly overturned Rieppel's one-center model. Kissel et al. (2002) presented juvenile, partially ossified astragali from the captorhinid taxa *Labidosaurus hamatus* and *Captorhinus major* that clearly show three ossification centers. Additionally, Berman and Henrici (2003) documented several well-preserved, partially ossified diadectid astragali that similarly show at least three ossification centers. All of these authors have adopted Peabody's original three-center model, i.e., that the astragalus in basal amniotes is formed from the fusion of three ossification centers directly homologous to the amphibian intermedium, tibiale, and "proximal centrale." Phylogenetically, this finding implies that the ossification pattern seen in all extant reptiles, in which the astragalus ossifies from a single center (reviewed in Rieppel, 1993), must characterize a clade crownward of Captorhinidae (Fig. 1). In this view the one-center model is not phylogenetically ancient, and diagnoses a clade of derived diapsids only.

One uncertainty persists concerning the three-center model—the identity of the "proximal centrale." Peabody (1951) is clear at the beginning of his article that the amphibian tarsus (exemplified by *Acheloma*) includes four centralia (c1–c4); the same condition occurs in *Eryops* (pers. examin., see below) and is the generally accepted ancestral condition from which recent anamniote and amniote tetrapods presumably evolved (Romer, 1956; Shubin, 2002). Distal centralia c1 and c2 (Fig. 2) are thought to form the centrale proper of amniotes (Peabody, 1951; Romer, 1956), and are in fact separate in some

basal synapsids (Romer and Price, 1940). However, Peabody is vague about the fate of c3, one of the two more proximal centralia. He maintains that the second, larger proximal centrale (c4) contributes to the amniote astragalus, and terms c4 the "proximal centrale." Yet c3 and c4 are both proximal relative to the positions of c1 and c2. Peabody is clearly referring to c4 as the "proximal centrale"; he makes only one brief comment on the fate of c3 (Peabody, 1951, p. 343), hypothesizing that it becomes incorporated in distal tarsal 4 (dt4). Peabody presents no evidence for this assertion. In the rest of the text he refers to c4 as the "proximal centrale," and in all later literature workers have adopted this terminology. There is no further discussion, however, of the fate of c3, although new fossil evidence indicates that this element may in fact play a role in the formation of the amniote astragalus.

## MATERIALS AND DESCRIPTION

### New Fossil Evidence

Recent field work in Niger (Sidor et al., 2005) has resulted in the collection of significant new material of *Moradisaurus grandis* Taquet 1969, the largest, most derived, and youngest occurring captorhinid. The discovery of a complete, articulated, and very poorly ossified pes (MNN MOR79, Fig. 3), in conjunction with well-ossified subadult pedal material (MNN MOR78), affords an unprecedented opportunity to study the ossification history of the captorhinid tarsus in a large-bodied form. In the juvenile specimen, none of the individual ossification centers contributing to the astragalus or centrale are co-ossified (Fig. 4A).

The fossil shown in Figure 4A comprises six ossified masses, and comprises the proximo-medial elements of the complete juvenile pes (O'Keefe et al., 2005; Fig. 3). All elements are poorly ossified, and all lack cortical bone surface indicative of perichondral ossification except for the central element (c4, terminology from Fig. 2), which possesses small islands of cortical ossification on both its ventral and dorsal surfaces. The gross homologies of this complex are easily established; the fossil was discovered in articulation (fig. 6 in O'Keefe et al., 2005), just medial to a poorly ossified but identifiable calcaneum, and proximal to a complete distal tarsal row. The central element also possesses a shallow groove for the perforating artery on its ventral surface, establishing beyond doubt that this complex contains the astragalus. Just proximal to the central element, one large element is identifiable as the tibiale based on its location and its possession of a broad surface for articulation with the tibia. Distal to this element are two masses that, based on position, are probably homologous to the distal centralia c1 and c2 of Peabody (1951); the lack of fusion between these elements demonstrates that the captorhinid centrale arises via the fusion of these two centralia, a condi-

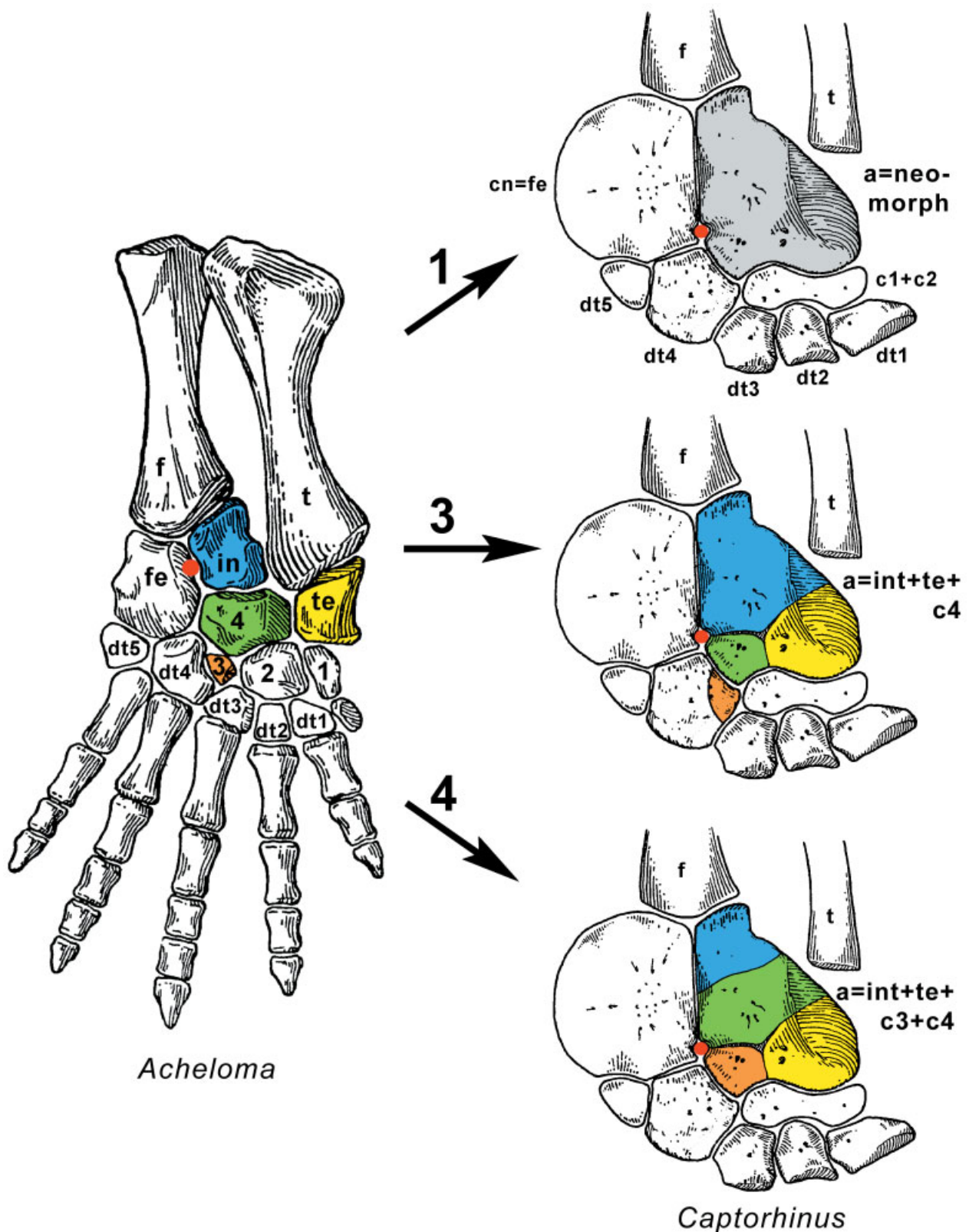


Fig. 2. Morphology and models of homology between the tarsi of anamniote and amniote tetrapods, based in part on Peabody (1951). *Acheloma* is a temnospondyl, an amphibian-grade tetrapod, and its tarsus is thought to represent the primitive condition from which the amniote tarsus evolved. *Captorhinus* is a captorhinid eureptile. The arrows with large numbers represent models of astragalus formation; the one-center model of Rieppel (1993), the three-center model of Peabody (1951) and later authors, and the four-center model (this study). Four ossifications in *Acheloma* are color-coded to the parts of the reptilian astragalus each is thought to represent under each model: intermedium, blue; tibiale, yellow; c4, green; c3, orange. A, astragalus; c1–c4, centralia 1–4; cn, fe, calcaneum, fibulare; dt1–5, distal tarsal 1–5; f, fibula; fe, fibulare; in, intermedium; t, tibia; te, tibiale.



Fig. 3. Juvenile left pes of the captorhinid reptile *Moradisaurus grandis*, MNN MOR 79, from the Upper Permian Moradi Formation of northern Niger. Fossil is in ventral view; length ~15 cm. Note lack of fusion among ossification centers contributing to the astragalus, bottom.

tion previously supposed but never demonstrated. In general, the morphology of this complex is very similar to other juvenile captorhinid astragali illustrated by Kissel et al. (2002), except that the present specimen is relatively poorly ossified.

We also studied comparative material of another derived captorhinid, *Captorhinikos chozaensis* Olson 1954, previously figured and discussed briefly by Olson (1962). This juvenile astragalus (USNM 21275; Fig. 4B) shows three ossification centers, which Olson homologized to the amphibian intermedium, tibiale, and “proximal centrale” following Peabody’s three-center model. However, our reexamination of this specimen reveals that the astragalus is incomplete; the tibiale ossification had not fused with the rest of the astragalus at the time of death, and is absent in the fossil. This interpretation is confirmed by the fact that the mass identified as the tibiale by Olson possesses a notch for the perforating artery, a feature always carried by the “intermedium,” never by the tibiale (Romer, 1956). The juvenile *C. chozaensis* astragalus therefore replicates the condition seen in the juvenile *Moradisaurus grandis* astragalus, and apparently ossified from four centers. The *C. chozaensis* astragalus is more completely ossified,

however, and the line of fusion between the two masses comprising the “intermedium” is a distinct line running completely around the element. The location of this line of fusion is in an identical location to the hiatus between the two masses comprising the “intermedium” in the *M. grandis* astragalus. The two fossil astragali figured here therefore present strong evidence that the astragalus of large captorhinids arises through the co-ossification of four elements, not three as hypothesized by Peabody (1951).

## RESULTS

### Homologies of Observed Elements

According to the Peabody’s three-center model, the astragalus comprises ossifications homologous to the amphibian tibiale, intermedium, and “proximal centrale” (=c4). However, the juvenile astragalus of *Moradisaurus grandis* clearly contains four masses, not three. As stated above, the identification of the tibiale seems certain. However, the identities of the other three elements of the complex are more difficult to establish.

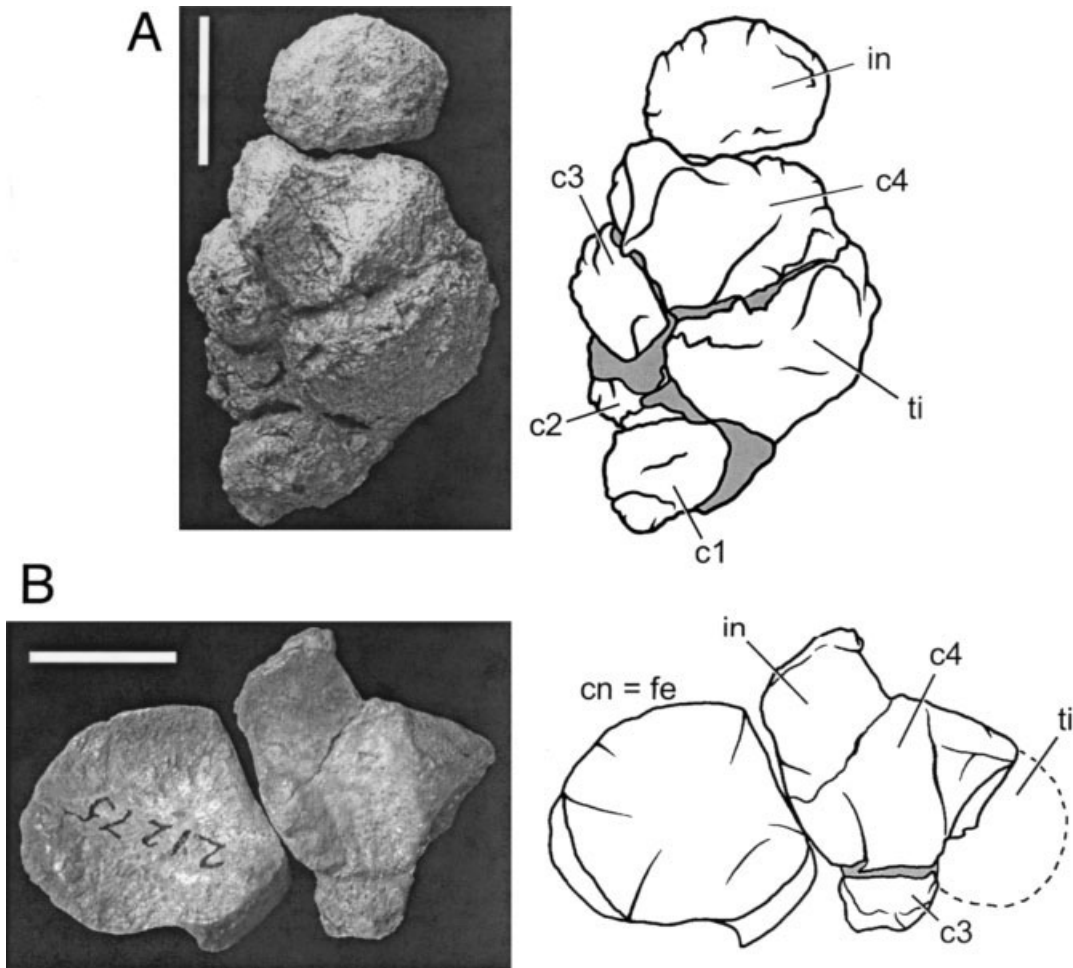


Fig. 4. Fossilized juvenile astragali described in this article. **A:** MNN MOR79, *Moradisaurus grandis* Taquet 1969, left astragalus in dorsal view, reversed. **B:** USNM 21275, *Captorhinikos chozaensis* Olson 1954, right astragalus in dorsal view; dotted line represents location of the tibiale. Abbreviations as in Figure 1. Scale bars = 2 cm in **A**; 1 cm in **B**.

As currently prepared, the *Moradisaurus grandis* fossil is in two pieces, with the most proximal mass separated from the rest of the astragalus. This element is very poorly ossified and lacks any morphological clues that might help establish its identity. Based on its proximal position, however, the mass is probably the intermedium or a part of it. More distal to this mass is a second, better-ossified mass. This mass is also securely identifiable as part of the “intermedium”—as defined by the three-center model—based on its location, and by the presence of a groove for the perforating artery on its ventral surface. Therefore, two masses seem assignable to the “intermedium.” There are at least two possible explanations for this: the intermedium portion of the astragalus is simply broken, or the “intermedium” portion ossified from two centers. There is not sufficient evidence in the fossil alone to differentiate between these two possibilities. Suggestive, however, is the globular state of the proximal fragment, and the lack of a clear fit or plane of fracture be-

tween the two pieces. We can therefore construct two hypotheses for this fossil.

**Three-center hypothesis.** The juvenile *Moradisaurus grandis* astragalus is comprised of the amphibian c4, intermedium, and tibiale. The amphibian c3 is absent, either lost or incorporated into another element. The intermedium is simply broken in half, and the lack of a clear fracture between the pieces of the intermedium is due to the poor ossification of the element. The element c3 is either lost entirely or incorporated in dt4, although no evidence exists for either possibility.

**Four-center hypothesis.** The amniote astragalus is comprised of both the amphibian c3 and c4, as well as the intermedium and tibiale. Because *Moradisaurus grandis* is very large relative to other captorhinids, ossification is delayed, and the specimen is quite young. It therefore records an early developmental stage before the fusion of the c4 ossification center with the intermedium ossification center. The fusion of these two centers would occur before

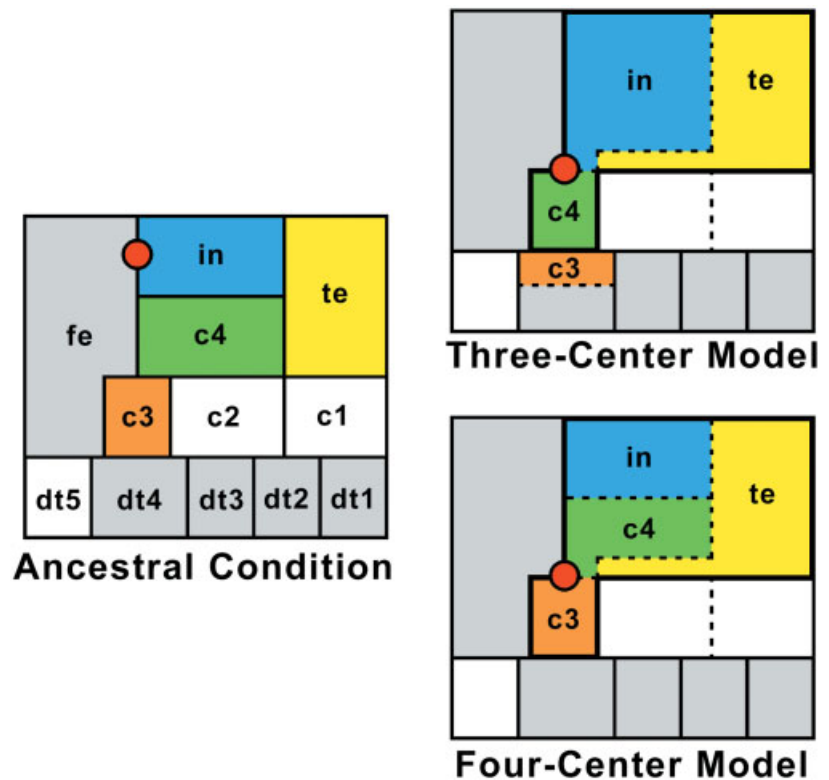


Fig. 5. Block models of tarsus ossification homologies, following the convention of Shubin and Wake (1996). Color coding matches that in Figure 1; additionally, the elements of the metapterygial axis are colored gray. The elements contributing to the amniote astragalus are outlined in bold and fused elements are indicated by dotted lines. The red circle indicates the location of the passage of the perforating artery. The three-center model is advocated by Peabody and more recent authors; the four-center model is proposed in this article.

the fusion of the composite “intermedium,” tibiale, and c3 observed in smaller, more primitive captorhinid genera.

## DISCUSSION

The realization that the astragalus of large captorhinids seemingly ossified from four centers suggests the question of the homology of these ossification centers. The tarsus of anamniote tetrapods, exemplified by *Acheloma*, contains four separate ossifications in this region: the intermedium, the tibiale, and two proximal centralia (c3 and c4; Figs. 2, 5). The identity of the most medial of these elements, the tibiale, seems secure. This element is the primary location for the articulation of the tibia, and its chondrogenetic precursor segments from that of the tibia proper early in development (Shubin and Alberch, 1986). The tibiale also articulates distally with the distal centralia and laterally with the central series of ossifications (Figs. 2, 5). These relationships of the tibiale are unchanged within amniotes (Romer, 1956), and identification of the tibiale in the *Moradisaurus grandis* tarsus is based on these positional relationships, as well as the presence of a broad surface for articulation with the tibia. This surface is well-developed even though the bone is poorly ossified, and is quite similar to the tibial surface found in captorhinids generally (Kissel et al., 2002).

The homologies that are most difficult to determine are those of the central series, namely, the intermedium and the two centralia that lie between the tibiale medially and the fibulare laterally. One great conceptual aid in establishing the homologies of these elements is the “metapterygial axis” of Shubin and Alberch (1986; gray elements, Fig. 5). This pattern of limb topology is highly conserved throughout tetrapods, and in fact is one of the fundamental components of the pentadactyl tetrapod bauplan as defined by Hinchliffe (2002, p. 843). The elements of this metapterygial axis (the fibulare and distal tarsals 4 through 1) form a stable frame of reference within the tetrapod tarsus, a frame that does not change throughout early amniote phylogeny. This frame can be used to establish the homologies of other structures surrounding it. We therefore take the calcaneum—the adult derivative of the fibulare—as our landmark when interpreting the homologies of the more medial tarsal ossifications.

Given that there are apparently four ossifications contributing to the astragalus in the fossils described above, and four bones in this area in amphibian-grade tetrapods, it is tempting to simply assign the identities of the amphibian bones to the reptilian ossification centers. However, there are two reasons to be cautious in doing this. The first is that the tarsus in reptiles is reorganized, with co-ossifications and novel contacts between bones that make the establishment of homology difficult based

on positional information alone. The second, and perhaps more compelling, reason to be cautious is the position of a soft-tissue structure, the perforating artery. This vessel passes from the ventral to the dorsal surface of the autopod in both amphibian-grade and reptilian-grade tetrapods, traveling between the tarsal ossifications, and leaving evidence of its passage in the form of prominent grooves in larger taxa (Romer, 1956). In temnospondyls, the perforating artery passes between the intermedium and calcaneum (Fig. 5); we verified this condition by examining material of the large temnospondyl *Eryops* (MCZ 7551, 7552). In captorhinids, the perforating artery also passes between the calcaneum and the central series of ossifications, and the presence of a canal for this artery formed the basis for Peabody's (1951) assertion that the large proximal mass of the astragalus was homologous to the amphibian intermedium only.

However, in *Eryops* and in temnospondyls generally, the perforating artery passes between calcaneum and intermedium in a very proximal location, at the level of the proximal third of the calcaneum. In captorhinids and other amniotes, the perforating artery skirts the calcaneum near its distal end. Therefore, relative to the calcaneum, the location of the perforating artery has moved distally in amniotes, and the homology statement "presence of perforating artery canal = intermedium" must be called into question. In fact, the location of the perforating artery in captorhinids is topologically identical to the position of the junction of the fibulare, c4, and dt4 in amphibians. If the hypothesis that the perforating artery has moved distally is correct, it implies strongly that the "intermedium" of the three-center model contains the ossification centers of both the amphibian intermedium and c4.

The condition of the astragalus in pelycosaur-grade synapsids would be of great interest given that this clade is the sister taxon to the rest of Amniota; however, we have been unable to find any described juvenile synapsid material that might shed light on the ossification history in this clade. It is worth noting, however, that in some synapsids the perforating artery is more proximal than in other basal amniotes, although it is still quite distal relative to amphibian-grade tetrapods (Romer and Price, 1940). The significance of this observation is unknown, and further research in this clade is needed.

There is precedent for independent movement of the location of the perforating artery: in extant lepidosaurs and turtles the artery has moved to a very proximal location between the distal ends of the tibia and fibula (Rieppel, 1993). Rieppel linked this movement to the novel formation of an active joint between the astragalus and calcaneum in lepidosaurs. Captorhinids are also interpreted as possessing an active joint between calcaneum and astragalus (Holmes, 2003; O'Keefe et al., 2005), and thus

might also have required a relocation of the artery. The fact that the artery moves distally in captorhinids, but proximally in lepidosaurs, lends credence to Holmes' belief that the mesotarsal joint in captorhinids and other basal amniotes is not homologous to that seen in lepidosaurs.

The hypothesis that the "intermedium" of the three-center model incorporates the amphibian c4 is also supported by positional information (Fig. 5). The three-center "proximal centrale" is much closer in size and positional relations to the amphibian c3 rather than c4. The amniote "proximal centrale" does not come anywhere near the tibia, while there is a contact between the tibia and the amphibian c4. Also, the amphibian c4 has a large contact with the fibulare, whereas c3 does not. In order to create the condition of the three-center model, the intermedium must be greatly expanded to fill the position of c4, c4 must shrink and move distally to displace c3, and c3 must either disappear or move distally for incorporation in dt4. In the four-center model none of these changes are necessary, and c3 and c4 retain their original sizes and positional relationships. Based on positional information, therefore, the "proximal centrale" is mostly likely identifiable with the amphibian c3, not c4.

### Developmental Transitions in Captorhinids

In the four-center model proposed here the ossification centers of the amphibian intermedium and c4 retain their original sizes and locations, and both contribute to the captorhinid astragalus. The fact that these two centers have not been recognized as separate ossifications in smaller captorhinids has several possible explanations. We may simply not have fossils from young enough animals to preserve this stage of development; early proximal ossification is a common feature of tetrapod limb ossification (Hinchliffe, 2002), and the intermedium and c4 might therefore be expected to co-ossify before the other elements contributing to the astragalus. However, thousands of specimens of the small captorhinid *Captorhinus aguti* are known from the Fort Sill fissure fill deposits. Peabody (1951) believed that he saw evidence of a tripartite astragalus in some of this material, but his evidence was questioned by Rieppel (1993) and is not definitive. Only in larger captorhinids (e.g., Kissel et al., 2002) is there strong evidence for a tripartite or tetrapartite astragalus, and the recognition of this pattern is remarkable given the relative paucity of specimens known from these animals. The observed pattern of progressively delayed fusion of ossification centers seen within the Captorhinidae (Fig. 6) may therefore be real. It is possible that a change in developmental timing occurred with increased body size, so that the fusion of originally separate elements happened later relative to their ossification history in



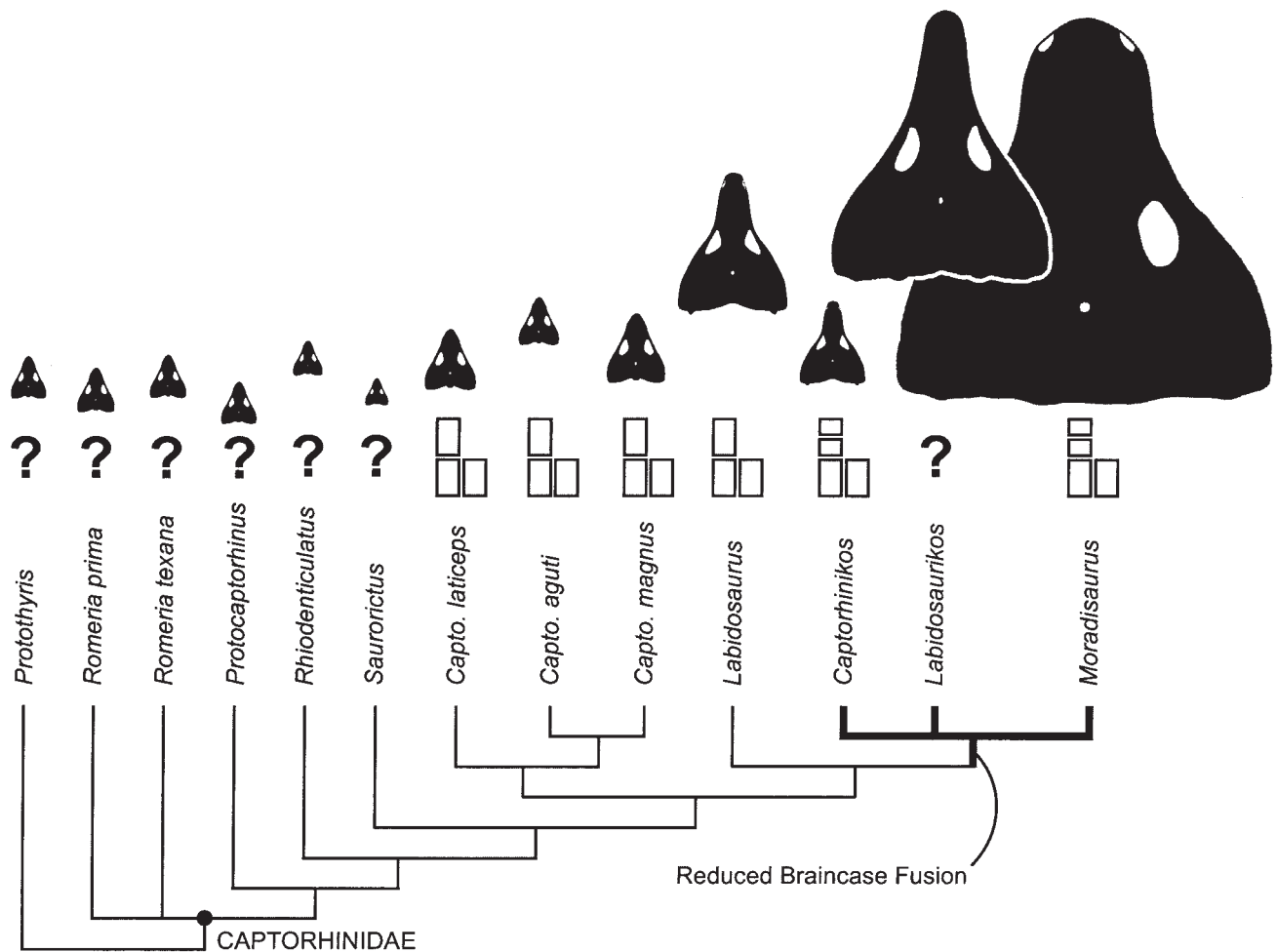


Fig. 6. Captorhinid phylogeny, body size evolution, and degree of ossification. Cladogram topology based on that of Modesto and Smith (2001) and de Ricqlès (1984). Pattern of astragalus ossification is schematic, with either one, three, or four ossifications shown (see text for discussion). Thickened lines denote decreased consolidation of the braincase. Skull outlines depict relative size, based on skull measurements given in the following sources: *Protothyris* (Müller, pers. commun.); *Romeria prima* (Müller, pers. commun.); *Romeria texana* (Müller, pers. commun.); *Protocaptorhinus* (Müller, pers. commun.); *Rhiodenticulatus* (Berman and Reisz, 1986); *Saurorictus* (Modesto and Smith, 2001); *Captorhinus laticeps* (Heaton and Reisz, 1980); *Captorhinus aguti* and *Captorhinus magnus* (Kissel et al., 2002); *Labidosaurus* (Modesto, pers. commun.); *Captorhinikos* (Olson, 1962); *Labidosaurikos* (Dodick and Modesto, 1995); *Moradisaurus* (de Ricqlès and Taquet, 1982).

larger animals. This hypothesized change in timing would afford progressively earlier views of astragalus ossification history in animals of progressively large body size. The possible mechanics of this transition are a topic of current research.

### Conclusion and Phylogenetic Implications

A four-center model for the homology of the amniote astragalus is supported by several lines of evidence. The first is new fossil data from *Moradisaurus grandis* and *Captorhinikos chozaensis*. Well-preserved juvenile astragali from both taxa clearly display four ossification centers, not one or three centers as proposed in previous models of astragalus homology. We propose that these four centers are homologs of the intermedium, tibiale, c3, and c4 of

anamniote tetrapods. The astragali of larger, derived captorhinids may show all four contributing masses due to a delay in the onset of fusion among tarsal elements relative to smaller, more primitive animals; captorhinid taxa of decreasing body size show a corresponding decrease in the number of identifiable ossifications contributing to the astragalus. The early state of ossification of the *M. grandis* juvenile astragalus may therefore arise from a heterochronic delay in ossification related to the attainment of large body size, as hypothesized for other relatively large captorhinids by Kissel et al. (2002). However, pelycosaur-grade synapsids reach comparable body sizes, apparently without this type of heterochrony. This effect may therefore be a feature of captorhinids only rather than a generalized property of basal amniotes.

The location of the perforating artery has moved distally relative to the calcaneum in captorhinids and other basal amniotes, and so is a poor landmark for use in establishing the homology of the intermedium. Additionally, the positional relationships of c3 and c4 are much more conservative under the four-center model, requiring less reorganization of the tarsus than does the three-center model. We therefore conclude that the captorhinid astragalus arose from the co-ossification of four elements present in anamniote tetrapods: intermedium, tibiale, c3, and c4. More comparative research is clearly needed on the detailed evolution of the astragalus across the anamniote–amniote boundary, particularly in diadectids, where partially ossified material is known. The condition in pelycosaur-grade synapsids is also critical and in need of further examination.

The recognition that the astragalus of early amniotes ossified from multiple centers is important from a phylogenetic perspective because it implies that the ossification pattern seen in all Recent reptiles—ossification from a single center—is a phylogenetically recent innovation, having occurred near the origin of Diapsida. The primitive diapsid *Hovasaurus*, for which good growth series are known, demonstrates ossification of the astragalus from a single center (Carroll, 1997, p. 248). The phylogenetic position of *Hovasaurus* is currently unresolved, however, and the taxon is also aquatic, a trait known to influence timing of ossification. The early araeoscelid diapsid *Petrolacosaurus*, on the other hand, shows evidence of ossification from multiple centers (Peabody, 1951; Carroll, 1964). The change in development to a single ossification center therefore seems localizable to somewhere within the base of Diapsida. Furthermore, it seems clear that the marked similarities in the ossification and structure of the tarsus between lepidosaurs and turtles noted by Rieppel and Reisz (1999) are shared derived characteristics uniting these taxa within Diapsida. Importantly, the presence of a primitive, four-center ossification pattern in captorhinids implies that all nondiapsid reptiles save Parareptilia have this primitive ossification pattern, and that this is strong evidence precluding an anapsid ancestry for turtles. The sole exception is Parareptilia, where the presence of the aquatic Mesosauridae as an outgroup renders the character reconstruction equivocal. Establishing the ossification history of the astragalus in parareptilian taxa is therefore a prime subject for future research.

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