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THE VERTEBRATE FAUNA OF THE UPPER PERMIAN OF NIGER—III, MORPHOLOGY AND ONTOGENY OF THE HINDLIMB OF *MORADISAURUS GRANDIS* (REPTILIA, CAPTORHINIDAE)

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ABSTRACT—We describe hindlimb elements of the large captorhinid *Moradisaurus grandis* (Reptilia: Captorhinidae) recently collected from the Upper Permian Moradi Formation of north-central Niger. This description is based primarily on an associated partial skeleton comprising a hemimandible, vertebral column, and partial left and nearly complete right hindlimb. Additionally, we report on a well-preserved, articulated, and essentially complete juvenile pes that provides important information on the ontogeny of the captorhinid tarsus. The hindlimb of *Moradisaurus* is stout and more massively built than in any other known captorhinid. The femur displays several features interpreted as adaptations to the demands of large body size, and the tibia and fibula have short, wide shafts and hypertrophied condyles and epicondyles. The astragalus is very derived, possessing two accessory ossifications and a relatively horizontal tibial articulation, indicating that the tibia was held more vertically than in other captorhinids. The calcaneum is co-ossified with distal tarsal five. The juvenile pes indicates that the captorhinid centrale arose from the fusion of two ossification centers, and that the captorhinid astragalus arose from the fusion of at least three ossification centers.

INTRODUCTION

The large, morphologically derived captorhinid *Moradisaurus grandis* was named by Taquet (1969) on the basis of a mandible collected from the Upper Permian Moradi Formation of north-central Niger. The remainder of the skull of this specimen was later described by de Ricqlès and Taquet (1982), who remarked on the great size of the animal compared to other captorhinids (skull length approximately 45 cm), as well as the large number of mandibular and maxillary tooth rows (10–12) present. Although the skull of *Moradisaurus* is well known, no postcranial elements have been described. In this paper we therefore describe the hindlimb of this taxon, based on new material collected in the spring of 2003 (Fig. 1; Sidor et al., 2005). Description of the new material adds to our knowledge of this derived captorhinid taxon, and demonstrates the influence of increased body size on captorhinid limb morphology. We also describe juvenile material that sheds light on the ossification pattern of the captorhinid tarsus.

Background

Moradisaurus grandis is a derived captorhinid, a member of the subfamily Moradisaurinae of de Ricqlès and Taquet (1982; a similar clade was termed 'group 6' by Gaffney and McKenna [1979]; see also de Ricqlès [1984] for a discussion of captorhinid systematics). The large body size and high tooth row counts in *Moradisaurus* are the culmination of trends apparent in geologically older captorhinids. The dental morphology of *Moradisaurus* and other large captorhinids has been interpreted as an adaptation to increasingly efficient herbivory (Dodick and Modesto, 1995; Hotton et al., 1997; Reisz and Sues, 2000).

Captorhinids are known from the Permo–Carboniferous boundary to the uppermost Permian, corresponding to a temporal range of about 50 million years. Species in the genus *Captorhinus*, from the Lower Permian of North America, have skull lengths less than 10 cm, and several have single tooth rows on the maxilla and mandible (*C. laticeps*, Heaton, 1979; *C. magnus*, Kissel et al., 2002; see also Berman and Reisz, 1986, for the small, single-rowed *Rhiodenticulatus* from New Mexico). However, *Captorhinus aguti* possesses two or three tooth rows (Bolt and DeMar, 1975; de Ricqlès and Bolt, 1983), and the genus *Labidosaurus* is comparatively large, although still possessing single tooth rows (Williston, 1910). The Lower Permian forms *Captorhinikos* (Olson, 1962a) and *Labidosaurikos* (Dodick and Modesto, 1995) are relatively derived, possessing skull lengths much longer than 10 cm and five or six tooth rows on both maxilla and mandible.

Also from North America are the poorly known Guadalupian (middle Permian) forms *Kahneria* and *Rothianiscus* (Olson, 1962b). Both taxa have about five tooth rows in the upper and lower jaws, and their skull lengths are comparable to that of *Captorhinikos*. The Russian form *Hecatogomphius* is likewise comparable in size and tooth row number, and is also middle Permian in age (Olson, 1962b). No captorhinids are known from the Upper Permian of North America, but sedimentary rocks of this age are lacking on that continent.

The Upper Permian of Africa has so far yielded four captorhinid taxa, divisible into two groups. The first group of two genera is morphologically conservative, consisting of small animals with single tooth rows: '*Protocaptorhinus*' from the middle Madumabisa mudstones (Upper Permian) of Zimbabwe (Gaffney and McKenna, 1979; regarded as Captorhinidae incertae sedis by Modesto, 1996) and *Saurorictus* from the *Tropidostoma* Assemblage Zone of South Africa (Modesto and Smith, 2001). Both taxa are morphologically primitive and their presence in the Upper Permian is surprising; for a discussion of the phylogenetic and biogeographic implications of these taxa, see Modesto and Smith (2001).

The second group of Upper Permian captorhinids comprises *Moradisaurus*, as well as an unnamed moradisaurine from the Argana Formation of Morocco, which is based on isolated tooth plates and postcranial fragments described by Jalil and Dutuit (1996). These authors also described an enigmatic maxilla possessing three rows of pointed, acrodont teeth; this element was designated the holotype of *Acrodenta irerhi* by Dutuit (1976), although Jalil and Dutuit (1996) refer to this taxon as *Acrodonta* (sic). The status of the Moroccan material is unclear due to the fragmentary nature of the material, but there is at least one, and possibly two, moradisaurines present in this fauna. It should also be noted that pareiasaur vertebrae were mistakenly included by Jalil and Dutuit (1996) in their discussion of moradisaurine remains from Morocco (Sidor et al., 2003).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; **FMNH**, Field Museum, Chicago; **MNHN**, Muséum national d'Histoire naturelle, Paris; **MNN**, Musée National du Niger, Niamey.

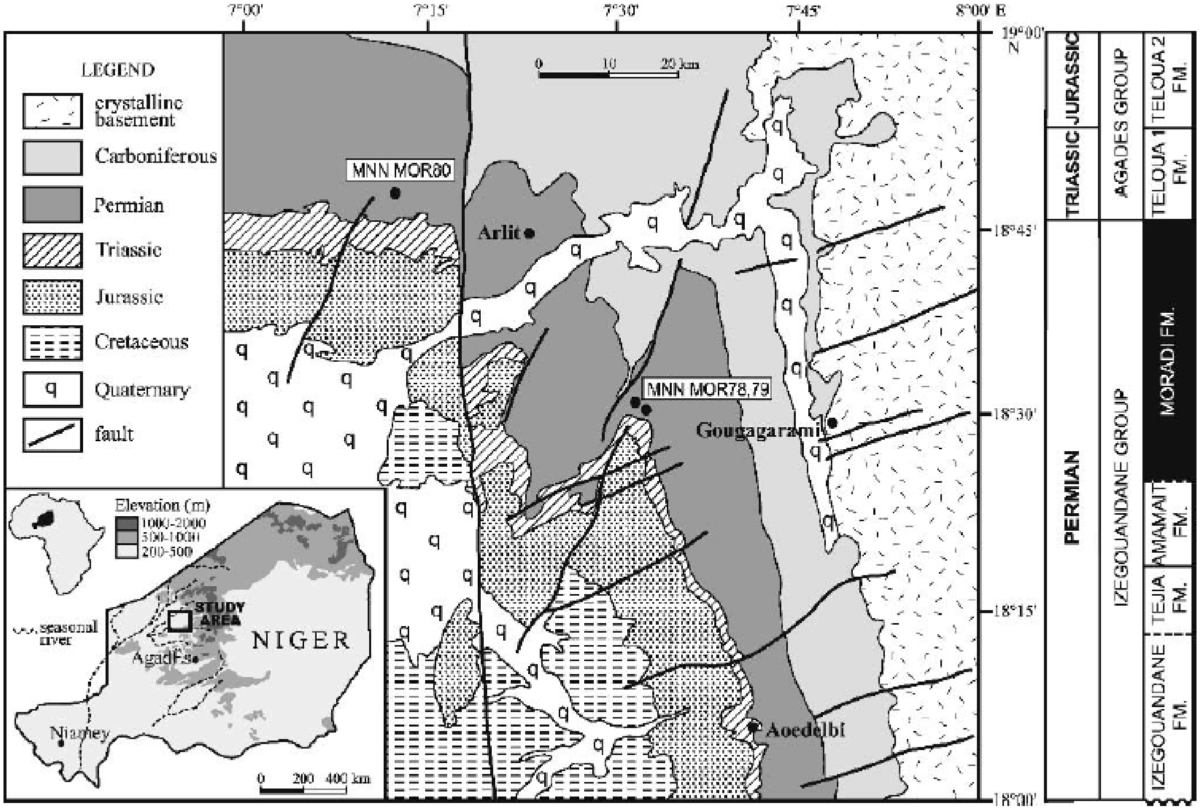

FIGURE 1. Stratigraphic column and geological setting of the Moradi Formation in the vicinity of Arlit, Niger. Specimens discussed in this paper are labeled near the approximate location of their discovery during the spring of 2003.

MATERIAL

We describe material from three individuals in this paper. The first (MNN MOR78) is a sub-adult with essentially complete right and fragmentary left hindlimb. The second (MNN MOR79) is a complete, articulated juvenile pes with associated fragments, and the third specimen (MNN MOR80) is an isolated right fibula.

The sub-adult specimen (specimen number MNN MOR78, Fig. 1) is an associated partial skeleton, comprising an articulated but badly weathered series of vertebrae, several disarticulated vertebrae and neural arches, a complete right hemimandible, fragments of the pelvic girdle, and various hindlimb elements. The limb elements were not articulated but were closely associated, occurring in a disorganized mass just beneath the hemimandible. Recovered hindlimb elements include a wellpreserved right femur, the distal portion of the left tibia, a complete right tibia, most of the right fibula, and weathered pieces of the left fibula. Also recovered was an essentially complete right pes, comprising astragalus, calcaneum, centrale, three loose distal tarsals, five metatarsals, and 11 phalanges. This specimen is referred to *Moradisaurus grandis* based on the lower jaw, which is very similar to the holotype mandible described by de Ricqlès and Taquet (1982). The hemimandible of MNN MOR78 differs from the latter only in size, being approximately 33 cm long, or 75% of the length of the type specimen. Full description of this jaw is deferred to a future paper on *Moradisaurus* cranial morphology. The tarsus of MNN MOR78 is fully ossified (see below), but the neural arches are not fused to the vertebral centra; these facts plus the relatively small size of the hemimandible lead us to believe that this animal had not grown to full adult size when it died.

The juvenile specimen consists of an articulated, well-preserved juvenile left pes (specimen number MNN MOR79) found about one km east of the adult specimen at the same stratigraphic level. The juvenile pes was found in articulation with a small, extremely weathered skeleton consisting of skull, axial column, ribs, and limbs; this skeleton was probably complete and articulated at one point but is not preserved. Additional collected elements include badly eroded moradisaurine tooth plates, several vertebrae and neural arches, the proximal ends of both humeri, the distal ends of both ulnae, two complete radii, the proximal end of the left tibia, the proximal ends of both femora, the right calcaneum, and numerous unidentifiable fragments. We restrict our discussion here to the pes, and to some comparative comments concerning the long bones of the hindlimb; these latter elements are very poorly ossified and carry little condyle morphology. Referral of this specimen to *Moradisaurus* was made on the basis of the tooth plates and other fragmentary skull elements, as well as similarities between the recovered limb elements and the sub-adult hindlimb of MNN MOR78.

The isolated right fibula (MNN MOR80) was found at a separate locality, about 20 km west of Arlit (Fig. 1). This locality is very rich and has yielded abundant pareiasaur and amphibian material. *Moradisaurus* material is rare at this location, but the fibula was found there, along with the distal end of a right femur. We tentatively refer these elements to *Moradisaurus* on the basis of their morphological similarity to elements preserved in MNN MOR78. The right fibula is largely complete and large, probably from an adult animal.

SYSTEMATIC PALEONTOLOGY

CAPTORHINIDAE Case, 1911

MORADISAURINAE de Ricqlès and Taquet, 1982

MORADISAURUS GRANDIS Taquet, 1969

Holotype—MNHN MRD1, comprising a skull and mandible.

Referred Material—MNN MOR78, partial subadult skeleton comprising right hemimandible, right hindlimb, and other postcranial elements; MNN MOR79, complete articulated juvenile left pes with associated limb and skull fragments; MNN MOR80, complete right fibula.

Locality and Age—The *Moradisaurus* specimens described in this paper were found in the spring of 2003 in the vicinity of the type locality, in almost flat-lying outcrops of the Moradi Formation about 25 km south-southeast of the mining town of Arlit (Fig. 1). The Moradi Formation is characterized by thick, friable, dark reddish-brown mudrocks, interspersed with beds of an indurated, matrix-supported conglomerate. The specimens were found in poorly-bedded mudrock directly beneath the ledgeforming conglomerate. The Moradi Formation is the uppermost unit of the Izegouandane Group, and uncomformably underlies the Triassic Teloua Formation. The exact age of the Moradi Formation is currently unknown, but is currently considered to be latest Permian (Taquet, 1972, 1976)

Revised Diagnosis—Derived captorhinid characterized by large (length approximately 45 cm), triangular skull with heavy ornamentation; occipital region enlarged; jaw articulation posteriorly placed; pterygoids and parasphenoid edentulous; mandible wide medio-laterally, with strongly developed coronoid process; maxilla and mandible with autapomorphic tooth batteries comprised of 10–12 rows of conical teeth, these batteries partially carried on wide flanges of bone extending lingually from maxilla and mandible. Distinctive characteristics of hindlimb include: very robust femur with reduced internal trochanter; hypertrophied intertrochanteric fossa, fourth trochanter, and adductor ridge; horizontally oriented proximal condyle; tibial plateau making acute angle with shaft of tibia; astragalus foreshortened with hypertrophied articulations for tibia, fibula, and calcaneum; tibial articulation large, making relatively shallow angle with body of astragalus, and extended medially by accessory ossification; calcaneum co-ossified with distal tarsal five; both astragalus and calcaneum possessing irregular accessory ossifications on their ventral surfaces; notch for perforating artery confined to astragalus only; metatarsals and phalanges stout and foreshortened.

DESCRIPTION

Femur

The right femur of MNN MOR78 (Fig. 2) was recovered from underneath the hemi-mandible and was broken into several pieces when found. The shaft and proximal articulation are well preserved, whereas the distal condyles are somewhat fragmentary, although the condylar surfaces for the epipodial bones are preserved. The length of the femur (proximal face to end of posterior condyle) is 159 mm, the antero-posterior length of the proximal articulation is 79 mm, and the antero-posterior width of the shaft is 28 mm at its narrowest point.

The femur is a stout and heavily built element, much more robust than the femur of *Labidosaurus* (Sumida, 1989) or even *Captorhinikos* (Olson, 1962a), with a relatively short shaft and hypertrophied condyles and processes. The proximal face comprises a well-defined acetabular articulation rimmed by a low ridge of bone. The articular surface is widest near its anterior margin, narrows posteriorly, and is oriented horizontally, unlike the articular surfaces of smaller captorhinids, which are angled antero-dorsally to postero-ventrally. The articular surface is also oriented at a right angle to the femoral shaft and therefore faces medially, rather than postero-medially as is the case in *Labidosaurus* (Sumida, 1989) and most pelycosaur-grade synapsids (although the femur of *Edaphosaurus* is very similar in this regard; Romer and Price, 1940). The fragmentary proximal femur from the second specimen (MNN MOR79) indicates that the proximal articulation was comparatively short antero-posteriorly in the juvenile.

Distal to the proximal face of the femur, the bone narrows and deepens as the shaft becomes more cylindrical. The posterodorsal surface of the femoral head carries a low boss or tubercle; we interpret this feature as the attachment site of the ischiotrochantericus, following Holmes' work on *Captorhinus aguti* (2003). The ventral portion of the femoral head is dominated by the intertrochanteric fossa, which is surrounded by a raised rim of bone, and is much deeper than the fossae of *Labidosaurus* or other captorhinids. The *Moradisaurus* femur is remarkable in that the internal trochanter is not well developed, consisting only of a thickened area in the anterior part of the rim of bone surrounding the intertrochanteric fossa. The femur of *Labidosaurus* has a large, well-developed internal trochanter (Sumida, 1989), as does the femur of *Captorhinus* (*C. aguti* and *C. magnus*, Kissel et al., 2002; Holmes, 2003). In contrast, the *Moradisaurus* fourth trochanter is extremely robust, consisting of a heavy, anteroposteriorly expanded block of bone projecting ventrally from the underside of the femur. The fourth trochanter is also more proximally placed than in other captorhinids, occurring at the base of the intertrochanteric fossa rather than farther distally on the shaft as it is in *Labidosaurus* (Sumida, 1989) or *Captorhinus* (Holmes, 2003). The femur of *Moradisaurus* possesses a sharp,

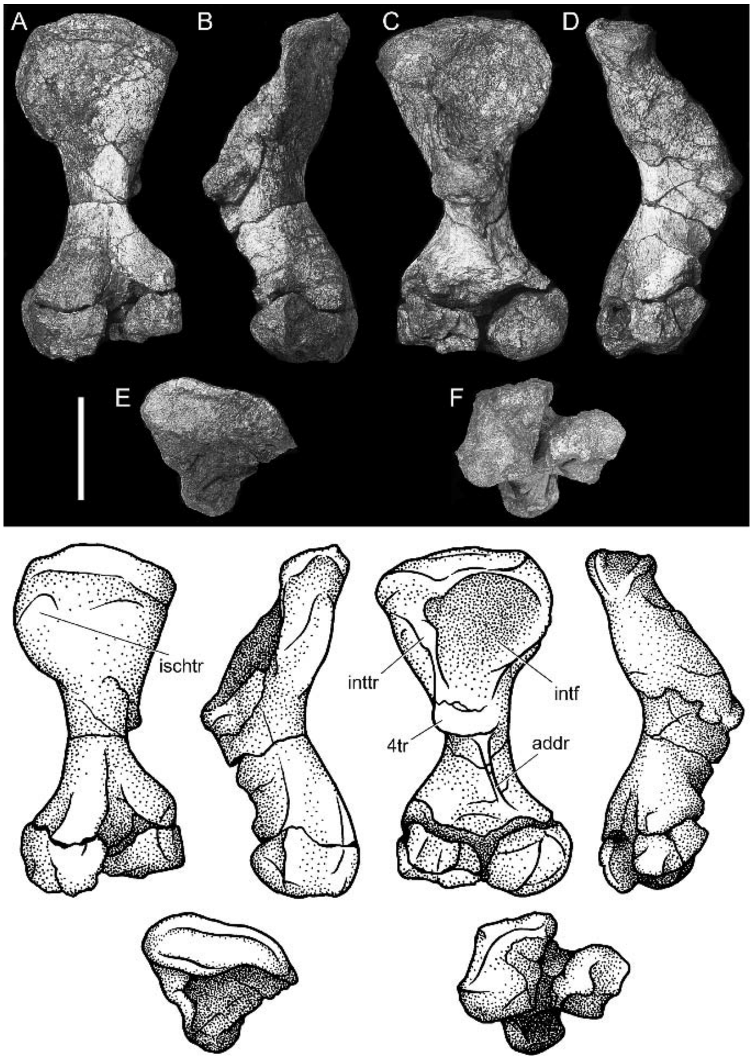

FIGURE 2. Right femur of *Moradisaurus grandis* (MNN MOR78); top, photographs, bottom, interpretive drawings. Views are: **A**, dorsal; **B**, posterior; **C**, ventral; **D**, anterior; **E**, proximal; **F**, distal. Scale bar equals 5 cm. **Abbreviations**: **4tr**, fourth trochanter; **addr**, adductor ridge; **intf**, intertrochanteric fossa; **inttr**, internal trochanter; **ischtr**, attachment for ischiotrochantericus m.

well-developed adductor ridge that trends distally and posteriorly from the distal face of the fourth trochanter onto the posterior condyle. This ridge is similar to those observed in other captorhinids, but is larger and more robust than in any other captorhinid taxon.

The popliteal fossa is short proximo-distally and rather shallow, whereas the intercomdylar groove on the dorsal side of the femur is wide and deep, producing a wide separation of the distal condyles. The distal condyles are damaged, although both preserve well-defined articular surfaces for the tibia. In addition, the posterior femoral condyle possesses a shallow groove on its posterior face for articulation with the fibula. The anterior condyle projects antero-laterally and is the shorter of the two condyles; the posterior condyle projects postero-laterally as in other captorhinids.

Tibia

The tibia of *Moradisaurus* (Fig. 3) measures 114 mm from the top of the intercondylar tubercles to the tip of the distal articulation with the astragalus. The tibial plateau measures 60 mm long antero-posteriorly, and 54 mm medio-laterally. The length of the astragalus articulation is 59 mm. The tibia is a massive bone with heavily reinforced articulations and a relatively short shaft, and its most distinctive characteristic is the angle that the proximal articulation makes with the shaft. In other captorhinids and in tetrapods generally, the plane of the tibial plateau makes a right angle with the axis of the shaft (Romer, 1956). In *Moradisaurus*, however, the plateau makes an acute angle with the shaft proximally, so that in a standing position the tibial shaft is directed toward the body as well as toward the ground. This shaft/condyle angle is repeated at the distal (astragalus) articulation.

The articulation for the posterior femoral condyle is similar to that in *Captorhinus* (Holmes, 2003), being a flat, lunate surface that is tilted somewhat posteriorly. The anterior tibial condyle is large, extending from the medial edge of the tibial plateau laterally out onto the top of the cnemial crest on the extensor surface. The cnemial crest is very well developed and possesses a ridged knob; this knob was probably the insertion of the triceps femoris following Holmes (2003). Holmes also noted a ‘swelling’ on the flexor surface of the tibia just distal to the tibial plateau in *Captorhinus*; he interpreted this as the common insertion of the flexor tibialis, puboischiotibialis, and pubotibialis. In *Moradisaurus* this feature is hypertrophied into a heavy boss that extends above the level of the tibial plateau, and then extends laterally between the femoral articulations to a confluence with the intercondylar eminences. Both condylar eminences are present as raised rims of bone surrounding a deep fossa at the center of the tibial plateau. The lateral edge of this fossa carries a clear insertion for the anterior cruciate ligament. The shaft of the tibia carries a faint, low ridge for the origination of the tibialis anterior on its medial face, and a prominent ridge on the lateral face for the insertion of the interosseous membrane. The origination of the tibialis anterior is poorly developed in *Moradisaurus* compared to that of *Captorhinus* (Holmes, 2003). The distal end of the tibia is expanded and globate, and carries a prominent articular surface that contacted the body of the astragalus. This articular surface proper is slightly smaller than the end of the tibial shaft and is rimmed by a low ridge.

FIGURE 3. Right epipodium of *Moradisaurus grandis*. Top, right tibia, MNN MOR78. Views are: **A**, posterior; **B**, lateral; **C**, anterior; **D**, medial; **E**, proximal; **F**, distal. Scale bar for tibia equals 5 cm. Bottom, right fibulae, MNN MOR78 (**G**, **I**) and MNN MOR80 (**H**, **J**), in posterior (**G**, **H**) and anterior (**I**, **J**) views. Scale bar for fibulae equals 3 cm

Fibula

The right fibula of MNN MOR78 is significantly weathered, but does preserve the proximal condyle and the shaft. The head of the left fibula is well preserved, allowing reconstruction of the complete fibula down to the distal articulation with the tarsus. This region is not preserved on the right fibula, and is present but heavily weathered on the distal fragment of the left fibula. The proximal condyle of the fibula is a well-demarcated, crescentshaped surface that opens anteriorly and dorsally to accept the femur. Just posterior to the femoral articulation, on the extensor surface of the fibula, is a large tuberosity for the insertion of the iliofibularis. This tuberosity is larger in *Moradisaurus* than in either *Labidosaurus* (Sumida, 1989) or *Captorhinus* (Holmes, 2003). The shaft of the fibula of *Moradisaurus* is also more strongly curved than in either of the aforementioned taxa, although some larger members of the diadectomorph genus *Limnoscelis* display a similar degree of curvature (Berman and Sumida, 1990; Sumida, 1997), as does the diadectid *Orobates* (Berman et al., 2004).

The distal end of the fibula is preserved on the isolated right fibula (MNN MOR80; Fig. 3). This element is larger (length 156 mm) and much more robust than the fibula of MNN MOR80, but in all other details is identical to it. The shaft of the fibula is remarkable in the degree of antero-lateral curvature; the fibulae of all captorhinids are curved in this way, but the curve in *Moradi-saurus* is more pronounced than in any other taxon. The distal end of the fibula is expanded and ends in a long articulation for the tarsus; this articulation faces almost directly anteriorly, rather than antero-ventrally as is the case in other captorhinids (Sumida, 1989; Holmes, 2003) or pelycosaur-grade synapsids (Romer and Price, 1940). The distal articular surface is divided into two clear surfaces, the antero-proximal of which was for the astragalus. The shape of this articu-lar surface is a close match for the fibular articulation on the astragalus of MNN MOR78. The second, postero-distal articulation was presumably for the calcaneum. This articulation extends onto the posterolateral face of the posterior epicondyle, and may indicate that the calcaneum rode up over the end of the fibula at some point in the step cycle.

Adult Pes

The essentially complete right pes of MNN MOR78 is illustrated in Figure 4. The pes was disarticulated but closely associated when found, and we are reasonably certain that all of the elements belong to the right pes. However, the assignment of positions to some of the bones is questionable. Our assignments of the astragalus, the calcaneum, the centrale, and metatarsals 1–5 seem secure, although the identities and positions of the remaining elements—the distal tarsals and individual phalanges—is more subjective. One distal tarsal is certainly missing, and the positions of the others were determined via comparison with the distal tarsals of *Captorhinus* illustrated by Holmes (2003); hence their identities should be taken as provisional. The proximal phalanges are slightly longer than the other phalanges and possess a diagnostic proximal articulation for the metatarsals. However, their position in digits 1–5 is subjective, as is the position of the remaining phalanges. The phalangeal formula is reconstructed as 2-3-4-5-4, and was determined with certainty from the juvenile pes. All elements of the *Moradisaurus* pes are foreshortened and extremely robust relative to those of other captorhinids. These traits are the culmination of trends observable in smaller and less derived members of the clade (Peabody, 1951:343); Sumida (1989) notes that the distal pedal phalanges of *Labidosaurus* and *Captorhinikos* are short

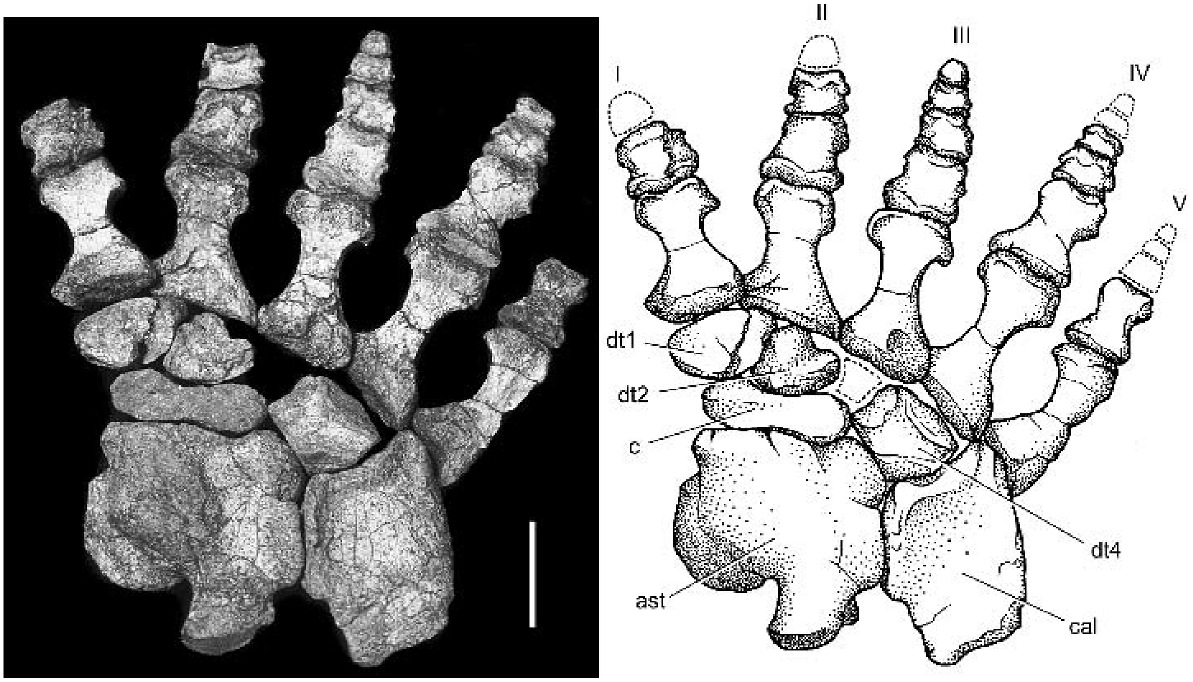

FIGURE 4. Reconstructed adult right pes of *Moradisaurus grandis* (MNN MOR78) in dorsal view. **Abbreviations**: **ast**, astragalus; **c**, centrale; **cal**, calcaneum; **dt**, distal tarsal. Scale bar equals 3 cm.

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and stubby relative to those of *Captorhinus*, resulting in a pes that is relatively short and wide. However the astragalus, the calcaneum, the metatarsals, and the proximal phalanges of the former taxa are proportioned similarly to corresponding elements of *Captorhinus*. In *Moradisaurus*, however, all phalanges and metatarsals are extremely foreshortened and stubby, and possess heavily reinforced condyles and epicondyles. This foreshortened and robust build also characterizes the proximal tarsals, yielding an astragalus that is derived relative to that of other reptiles.

As in other amniotes, the proximal tarsal row of *Moradisaurus* comprises two elements, the astragalus and the calcaneum (Fig. 5). The astragalus of *Moradisaurus* is a massive bone, foreshortened proximo-distally, with a stout and short fibular process. This process carries a deep, rimmed cup on its proximal surface for articulation with the fibula. Distal to the fibular process is the body of the astragalus, which carries a prominent area for articulation with the tibia on its dorsal surface. The tibial surface of the astragalus in *Moradisaurus* is relatively larger than that in other captorhinids, and makes a shallow angle (about 30 degrees) with the body of the astragalus. In other captorhinids the tibial surface makes a steep angle (greater than 45 degrees) with the body of the astragalus. In addition, the tibial surface of *Moradisaurus* is extended by a novel ossification (Fig. 5:ao). Extending medially from the edge of the astragalus, this feature is an irregular, discoid process of poorly finished bone. Together with the tibial surface, this excrescence produces a platform for articulation with the tibia that is circular in dorsal view and makes a shallow angle with the body of the astragalus. This circular surface differs radically from the steeply angled, trapezoidal tibial articulation found in *Captorhinus* (Holmes, 2003) and *Labidosaurus* (Sumida, 1989).

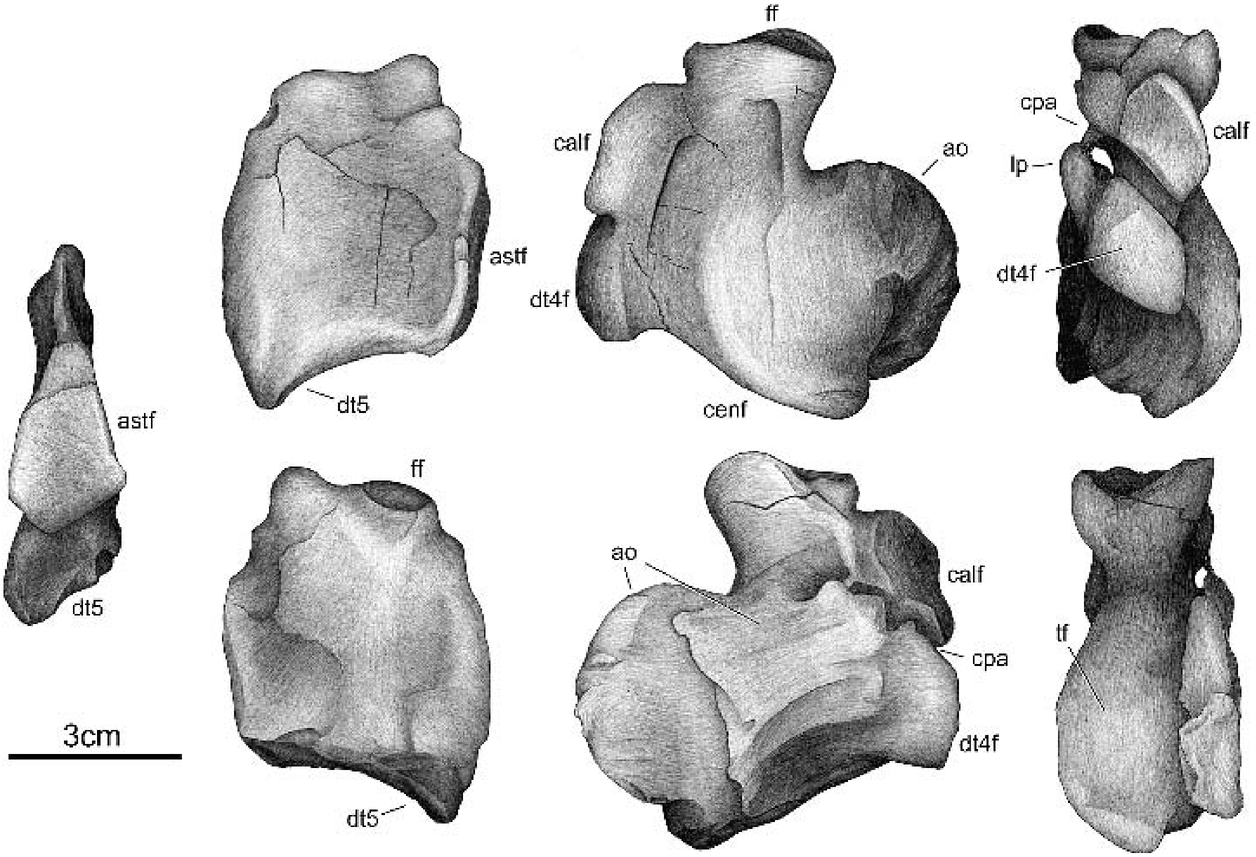

FIGURE 5. Detail drawings of the right astragalus and calcaneum of *Moradisaurus grandis* (MNN MOR78). Left element is the calcaneum, in medial (left), dorsal (top), and ventral (bottom) views. Right element is the astragalus, in dorsal (top), ventral (bottom), lateral (top right), and medial (bottom right) views. **Abbreviations**: **ao**, accessory ossification; **asft**, facet for astragalus; **calf**, facet for calcaneum; **cenf**, facet for centrale; **cpa**, canal for perforating artery; **dt4f**, facet for distal tarsal 4; **dt5**, distal tarsal five; **ff**, facet for fibula; **lp**, ligament process; **tf**, facet for tibia.

The lateral edge of the astragalus is complex, carrying two distinct processes for articulation with other tarsal elements. The proximal of these processes is surmounted by an articular surface for the calcaneum; the curvature of this surface closely matches the corresponding, medial, face of the calcaneum. The calcaneal articulation of the astragalus is separated from the fibular process by a deep furrow. In other captorhinids the calcaneal and fibular articular surfaces are confluent, and this is also the case in pelycosaur-grade synapsids (Romer and Price, 1940). The second, distal process carries an articular surface for distal tarsal four. This articular surface is domed and appears to have been very mobile. Between the proximal and distal processes on the lateral edge of the astragalus is a deep groove trending from distal dorsal to proximal ventral, interpreted by us as a canal for the perforating artery. This canal is deep and carried entirely on the astragalus; there is no corresponding notch on the anteromedial corner of the calcaneum, as is the case in other captorhinids. The distal margin of the astragalus carries a broad, sigmoid articulation for the centrale.

The ventral surface of the astragalus is dominated by a second accessory ossification, comprising a rugose and poorly finished mass of bone applied to the ventral face of the element. This ossification blends laterally into a robust boss just proximal to the process for distal tarsal four; we interpret this feature as a ligament attachment similar to the one noted by Berman and Henrici (2003) on the ventral face of the diadectid astragalus. This boss overhangs the continuation of the canal for the perforating artery, which crosses the ventral face of the astragalus from lateral to medial, and is incompletely roofed by the irregular edge of the accessory ossification.

The calcaneum of *Moradisaurus* is also derived compared to that of other captorhinids, mostly obviously at its distal margin. Here the calcaneum bears a large, pointed process laterally that we interpret as the fifth distal tarsal, which has co-ossified with the body of the calcaneum. We believe that this condition is unknown in any other amniote (see Sumida, 1997, for partial review). There is no obvious line or demarcation to indicate the seam of co-ossification with distal tarsal five. As in other amniotes, the medial face of the calcaneum bears an articular surface for the astragalus; this surface is shorter proximo-distally and deeper dorso-ventrally than in other captorhinids, and is gently saddle-shaped. This face is a close match with the corresponding articular process on the astragalus. The calcaneum has no articular facet for distal tarsal four, and does not carry a groove for the perforating artery. The proximal edge of the calcaneum is very thin, and bears ventrally a small, ovoid depression that is probably the articular facet for the fibula. This feature is also unknown in other amniotes. Lastly, the ventral surface of the calcaneum bears a low keel of poorly finished bone, analogous to the accessory ossification on the ventral face of the astragalus, but more poorly developed.

The distal tarsals of *Moradisaurus* (Fig. 4) are much more similar to those of other captorhinids than are the astragalus and the calcaneum. The centrale is a bilobate, peanut-shaped element whose proximal face articulates with the distal face of the astragalus. If the hypothesis that distal tarsal five is fused with the calcaneum is correct, then four of the (presumably) five distal tarsals are present in MNN MOR78; two of the three loose elements are poorly preserved and bear little informative morphology. The last, largest distal tarsal (here interpreted as distal tarsal four, but possibly distal tarsal three) bears three distinct articular facets, one for a metatarsal, one for the neighboring distal tarsal, and one for the astragalus and the calcaneum. The metatarsals and the phalanges are also similar to those of other captorhinids except for their extreme heaviness of build and proximo-distal compression.

Juvenile Pes

The juvenile pes of *Moradisaurus grandis* is represented here by the essentially complete, articulated foot (MNN MOR79; Fig. 6). This specimen is the most complete and best-preserved moradisaurine pes known, and also represents a very early ontogenetic stage in the growth of the animal. If one accepts that MNN MOR78 is a subadult based on the length of the jaw (i.e., 75% of the holotype jaw) and well-ossified tarsus, then MNN MOR79 must be much younger based on the poor ossification of the tarsus and its small size. A rough idea of the size difference between the subadult and juvenile pedes was calculated as the geometric mean of the lengths of the four measurable metatarsals in each foot (the proximal end of metatarsal 3 is crushed in the juvenile, prohibiting accurate measurement). This mean for the subadult is (31*31*40*38).25 _ 47.8 mm, whereas the mean for the juvenile is (42*45*54*51).25 _ 34.8

mm, or about 73% of the size of the subadult. This figure is similar to those obtained when limb bone measurements are compared between the two specimens. We estimate that the juvenile would have been about half the size of the holotype animal.

The metatarsals and the phalanges of the juvenile pes are more lightly built than those of the subadult, and their condyles are poorly ossified; however, these elements are still very squat and robust compared to those of other captorhinids. All phalanges are present save the terminal of digit five, and so the phalangeal formula was most probably 2-3-4-5-4. The terminal phalanges of digits one and two are large and expanded at their tips, indicating that claws on these two digits were broad and flat. In contrast, the ungual phalanges of digits three, four, and five are tiny, and their claws would have been inconsequential. The pes also preserves at least three sesamoid bones. These poorly ossified elements were found at the base of the more proximal phalanges of digits two and three and were probably embedded within the flexor tendons of the animal in life.

The calcaneum is a very poorly ossified disc with areas of finished bone on its dorsal and ventral surfaces, separated by a wide zone of unfinished bone. The medial face of the calcaneum is fragmented and carries no indication of the astragalar articulation; the calcaneum also lacks the co-ossified distal tarsal five observed in the subadult specimen, and distal tarsal five could not be identified with certainty. Distal tarsal four is in life position but poorly ossified, as are the two other distal tarsals, whose numbers are indeterminate. Two additional ossifications are identified here as components of the centrale (Figs. 6, 7) and are near life position. These elements are not co-ossified, and we hypothesize that they represent centralia one and two of Peabody (1951). Peabody, and authors after him (e.g., Kissel et al., 2002), have considered the centrale proper of amniotes to be homologous to co-ossified centralia one and two in the amphibian condition. Our data directly support this hypothesis, as the two ossifications in the juvenile of *Moradisaurus* give rise to a single, peanut-shaped centrale in the adult (see Fig. 4).

The juvenile astragalus of *Moradisaurus* is represented in dorsal view in Figure 7. The astragalus is incompletely prepared, because the ossification of the elements is so poor that there is little differentiation between the bone and the matrix. The two ossifications representing the centrale are still attached to the distal end of the astragalus by matrix. As preserved, the astragalus is in two pieces, the more proximal of which is an unremarkable mass of unfinished bone that we interpret as the proximal fragment of the intermedium. The more distal of the two pieces is complex, consisting of three masses separated by deep grooves. This element has small areas of finished bone on its dorsal and ventral surface, as well as a deep notch on its ventral surface indicating the position of the perforating artery. We therefore hypothesize that this mass is the distal fragment of the intermedium. The larger of the two distal masses is clearly the tibiale, as it is the most medial of the elements, and possesses a surface for articulation with the tibia. The last mass is identified as the proximal centrale based on its position. Overall this astragalus is very similar to the immature astragalus of *C. magnus* figured by Kissel et al. (2002:fig. 7), being clearly comprised of at least three elements, the only difference being a comparative lack of ossification. The significance of the division of the intermedium into two pieces is a topic of current research.

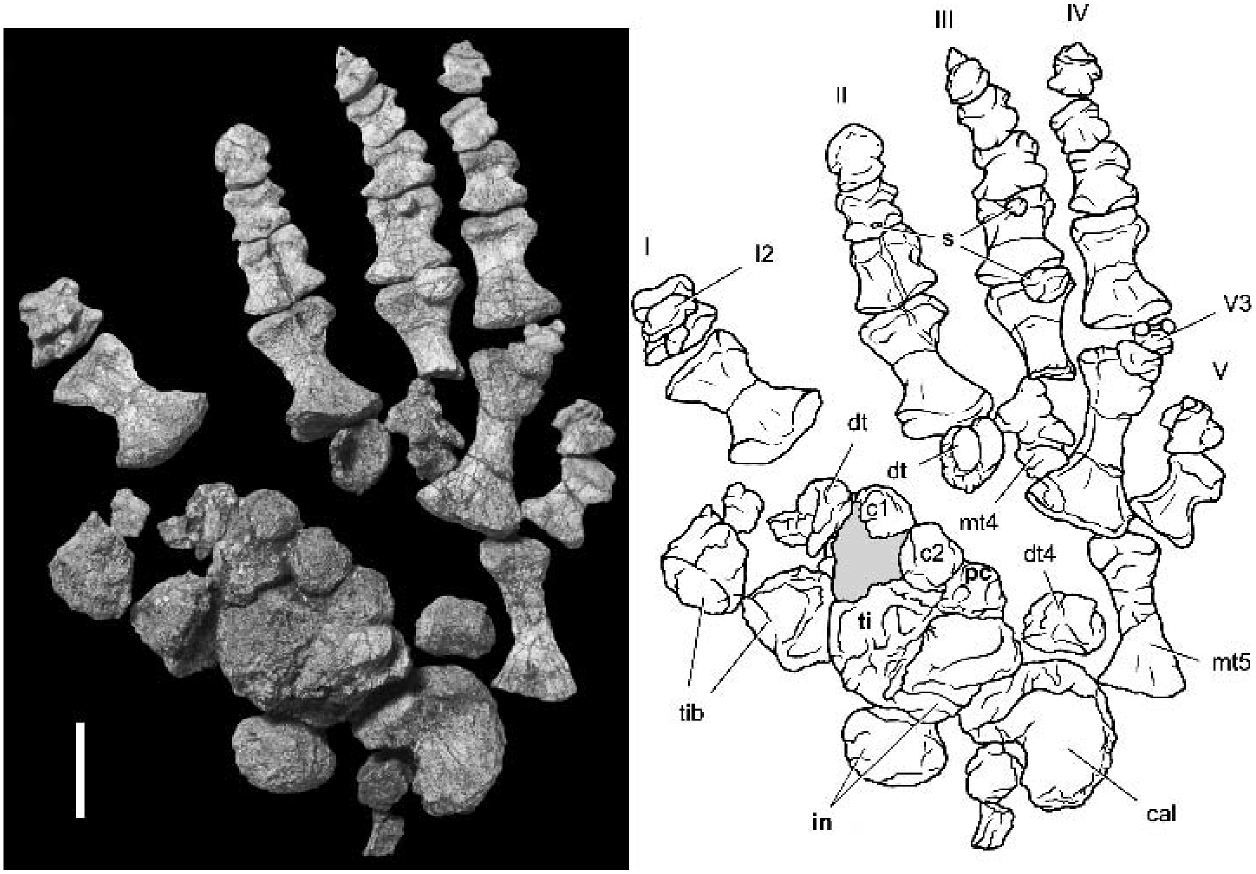

FIGURE 6. Juvenile left pes of *Moradisaurus grandis* (MNN MOR79) in ventral view. **Abbreviations**: **ast**, astragalus; **c1**, first centrale; **c2**, second centrale; **cal**, calcaneum; **dt**, distal tarsal, **mt**, metatarsal; **pc**, proximal centrale; **s**, sesamoid; **ti**, tibale; **tib f**, fragments of tibia. Labels in bold in the figure refer to separate juvenile portions of the adult astragalus. Nomenclature of the astragalus ossifications follows Peabody (1951). Scale bar equals 2 cm.

DISCUSSION

Effects of Body Size

The limb morphology of *Moradisaurus* is elephantine, stubby, and massive, comparable to that of a pareiasaur rather than the more gracile *Captorhinus*. This morphology is the culmination of trends expressed throughout the history of the Captorhinidae. The simplest of these trends is an increase in body size; *Moradisaurus* is not only one of the latest captorhinids but is also the largest known captorhinid. Concomitant with this body size increase is a trend toward dental specialization, as small animals with single tooth rows give way to larger taxa with dental batteries comprised of many tooth rows. This derived dentition has been interpreted as an adaptation to a herbivorous diet, and the Captorhinidae are one of the first tetrapod groups to evolve herbivorous members (Hotton et al., 1997). In these animals the head is strikingly large compared to the size of the rest of the body (Olson, 1962a; in *Moradisaurus* the length the jaw greatly exceeds the lengths of the femur and tibia combined). In discussing the morphology of the *Moradisaurus* hindlimb we must, therefore, consider at least two factors that might influence the structure of the locomotor system: scaling responses to body size increase, and responses to the demands of an increasingly herbivorous lifestyle.

It is tempting to assume that the robust build of *Moradisaurus* is simply a response to large body size. However, there are several lines of evidence that suggest this may not be the only factor involved. In his review of limb scaling in terrestrial animals, Biewener (2000) points out that the skeletal system tends to scale isometrically up to a body mass of about 300 kg. He explains this somewhat counterintuitive finding with the observation that larger animals progressively limit limb posture to maintain adequate safety factors on long bones. Increases in body mass are, therefore, accommodated by changes in posture and associated kinematics rather than positive allometries in skeletal elements. We do not currently have sufficient data to constrain a body mass estimate for *Moradisaurus*, but believe that adult body mass was probably less than 300 kg. *Moradisaurus* is huge for a captorhinid, but is really not an extremely large animal; the femur is only 16 cm long in an animal with a jaw length of 33 cm. Given this modest body size there does not seem to be an a priori reason to expect a great increase in *Moradisaurus* limb robusticity based on scaling effects alone.

This impression is reinforced by the femora of pelycosaurgrade synapsids. Animals such as *Ophiacodon*, *Sphenacodon*, and *Dimetrodon* (Romer and Price, 1940) have femora as long as or longer than *Moradisaurus*, but their construction is much more gracile, thereby demonstrating that primitive amniotes of comparable size do not require the degree of robusticity seen in *Moradisaurus*. Body-mass estimates for the genus *Dimetrodon* reach about 250 kg in an animal with a femur 25 cm long, whereas those for *Edaphosaurus* reach about 190 kg in an animal with a femur 21.5 cm long (Romer and Price, 1940:470–471).

Biewener's work does suggest, however, that it might be fruitful to look for evidence of postural changes between *Moradisaurus* and a much smaller animal such as *Captorhinus*, and we do see some evidence of this. The articular surface on the head of the femur is oriented horizontally in *Moradisaurus*, whereas in *Captorhinus* this surface is oriented at an angle of about 45 degrees to a (horizontal) plane described by the shaft and distal condyles, trending from antero-dorsal to postero-ventral (Holmes, 2003). *Labidosaurus* is intermediate in this regard, its articular surface making a plane of about 30 degrees to the horizontal (Sumida, 1989). The significance of this change in angle is unknown, although it may indicate that the femur of *Moradisaurus* was restricted to antero-posterior movement and underwent less rotation during the step cycle than proposed for *Captorhinus* by Holmes (2003). Such a limiting of the movement of the femur would result in a slower, plodding gait.

The intertrochanteric fossa and adductor ridge are very well developed in *Moradisaurus*, as indeed they are in *Labidosaurus* and in other basal amniotes. Sumida (1989, 1997) describes these features as the points of attachment for the main limb adductors (puboischiofemoralis externus and adductor femoris, respectively). In an animal with a sprawling gait these muscles would be important for keeping the trunk clear of the ground when walking, and their very robust development in *Moradisaurus* is, therefore, not surprising. The most obvious difference in this region between *Moradisaurus* and other captorhinids is the very reduced internal trochanter. The small size of this feature may imply a lack of development of the more anterior fibers of the puboishiofemoralis externus and a limiting of anterior limb excursion. It is also possible that a decrease in femur rotation at the end of the step cycle, hypothesized above, obviated the need for strong limb protraction. Another marked difference between *Moradisaurus* and other captorhinids is the great size of the fourth trochanter. This feature is believed to be the insertion of the caudifemoralis (Sumida, 1989; coccygeofemoralis of Holmes, 2003), the principal retractor of the hindlimb. The large size of this feature may indicate corresponding development of the caudifemoralis for more powerful retraction, and this would be a logical response to body-size increase.

Features of the epipodium also seem to indicate a change in posture relative to other captorhinids. These features include the tilting of the tibial articulations—both proximal and distal—away from a 90 degree angle to the shaft, and a corresponding re-orientation of the distal end of the fibula so that its articulations for the proximal tarsals point anteriorly rather than anteroventrally. If one considers the limb standing with the femur held directly away from the body axis, the tilting of the tibial articulations implies that the epipodium would slant back toward the body as well as downward. The changes to the orientation of the distal head of the fibula are more difficult to interpret, but may indicate a difference in the relative positions of the astragalus and calcaneum.

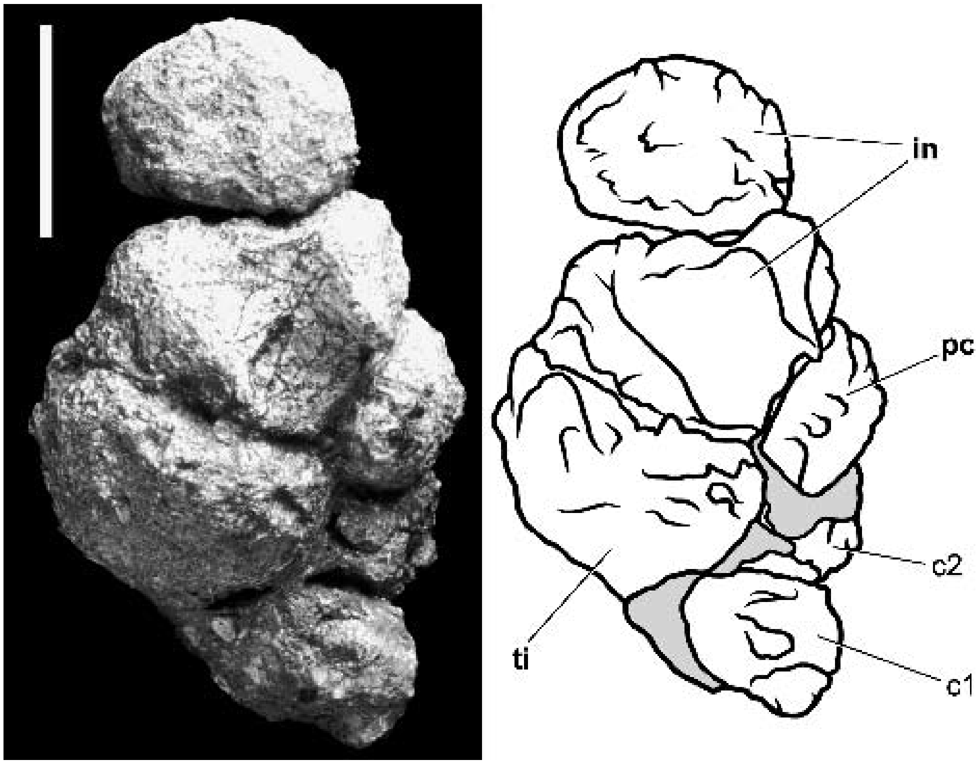

FIGURE 7. Detail of the juvenile astragalus of *Moradisaurus grandis* (MNN MOR79) in dorsal view. **Abbreviations**: **c1**, first centrale; **c2**, second centrale; **in**, intermedium fragments; **pc**, proximal centrale; **tib**, tibiale. Labels in bold in the figure refer to separate juvenile portions of the adult astragalus. Nomenclature of the astragalus ossifications follows Peabody (1951). Scale bar equals 2 cm.

The most obvious indicator of postural change between *Moradisaurus* and other captorhinids is found in the tarsus. In the astragalus we find a clear indication that the tibia was held more vertically than in other captorhinids, based on the relatively shallow angle between the tibial articulation and the body of the astragalus. The development of the accessory ossification that extends this surface medially also implies that forces from the tibia were exerted much more vertically than in smaller animals. This suggests that the *Moradisaurus* pes may have been held in a more horizontal posture (plantigrade) than the more digitigrade posture proposed for *Captorhinus* (2002). Such a posture may have resulted in the proximal tarsals contacting the ground, either directly or via a cartilaginous pad, and may help to explain the accessory ossifycations on the ventral surfaces of the astragalus and calcaneum. A change in limb posture of this type is a logical response to body size increase.

We examined the astragali of other captorhinids in an attempt to find indications of some of the distinctive features displayed by *Moradisaurus*. Examination of the astragali of *Captorhinus* (Fort Sill material at the AMNH and FMNH), *Labidosaurus* (FMNH UC634), and *Rothianiscus* (FMNH UR967) revealed that all were very similar; they were not foreshortened, the fibular process was long, the tibial articulation made a steep angle with the body, and no accessory ossifications were found. This is especially remarkable for the astragalus of *Rothianiscus*, whose length of about 5 cm approaches that of *Moradisaurus* (about 7 cm). Therefore, no indications of a response to increasing body size were found in the *Labidosaurus* or *Rothianiscus* astragali, and these features are truly autapomorphic for *Moradisaurus*.

The evolution of an herbivorous lifestyle may also account for the great robusticity of the *Moradisaurus* hindlimb. Testing this hypothesis is difficult, however, because work on this topic in early amniotes has been qualitative (e.g., Hotton et al., 1997). It is worth noting that other primitive amniote taxa with tooth batteries similar to those of *Moradisaurus* also have squat and massively built bodies with heavy limbs (i.e., rhynchosaurs, Carroll, 1988; edaphosaurids, Romer and Price, 1940), and this body type is also shared by the herbivorous pareiasaurs and dicynodonts. The convergent evolution of this body type in different clades may imply a common constraint or set of causal mechanisms of the kind advanced by Hotton et al. (1997), although the cautions of Gould and Lewontin (1979) concerning the attribution of adaptive significance to morphology must be born in mind. These animals may have been slow simply because they had no reason to be fast. Yet the convergent evolution of the robust body type in concert with herbivory is suggestive, and might be open to further investigation given a robust phylogeny and morphometric data.

Astragalar Ossification

The poorly ossified juvenile astragalus described above offers data bearing on the origin of the amniote astragalus. The homologies of this element have been debated, but the prevailing wisdom during the later half of the twentieth century was based on that of Peabody (1951), who hypothesized that the amniote astragalus arose through the co-ossification of three originally separate elements found in amphibian-grade tetrapods. Rieppel (1993) questioned this view based on his re-examination of Peabody's material of *Captorhinus aguti,* and posited that the amniote astragalus was a neomorph arising from a single ossification center. However, recent work by Kissel et al. (2002) on the captorhinids *C. magnus* and *Labidosaurus* has documented convincing new evidence in support of Peabody's original hypothesis of a tripartite astragalus. Berman and Henrici (2003) report a similar condition in a diadectid (later christened *Orobates pabsti* by Berman et al., 2004), thus extending this ossification pattern to the common ancestor of Diadectomorpha and Amniota.

The poorly ossified juvenile astragalus of *Moradisaurus* presented here is further evidence in support of Peabody (1951). This astragalus is composed of at least three ossified masses that are poorly co-ossified, a condition very similar to that reported by Kissel et al. (2002). We identify these three masses as homologues of the intermedium, the tibiale, and the proximal central following Peabody (1951) and Kissel et al. (2002). Direct evidence in support of the hypothesis of a tripartite origin of the amniote astragalus has thus been found in three captorhinid genera as well as in the Diadectidae; this implies that tripartite ossification was the plesiomorphic condition in basal amniotes (i.e., from outside Amniota to Eureptilia; taxonomy follows Laurin and Reisz, 1995). The novel ossification pattern observed in the astragali of extant diapsids and turtles is, therefore, phylogenetically more recent than supposed by Rieppel (1993).

Summary

In summary, the hindlimb of *Moradisaurus* gives the overall impression of a slow and heavy animal whose step kinematics may have differed significantly from those inferred for other captorhinids. Inferred changes in posture and kinematics are logically interpreted as a response to large body size. However, body size increase alone is probably not a sufficient explanation for the overall limb robusticity of *Moradisaurus*. Adaptation to an herbivorous lifestyle may have made a contribution, but this has not been demonstrated, and possible causal links are tenuous. Lastly, the juvenile astragalus of *Moradisaurus* adds convincing evidence to an emerging consensus on the homologies of the amniote astragalus; this consensus is essentially that first articulated by Peabody (1951), and supported recently by Kissel et al. (2002).

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