

Chapter 2

The Ankle Structure of Two Pterodactyloid Pterosaurs from the Santana Formation (Lower Cretaceous), Brazil

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ABSTRACT

The extremely well-preserved tarsus of the tapejarid *Tapejara* sp. and the anhanguerid *Anhanguera piscator* (Pterosauria, Pterodactyloidea) are described and regarded as representative of the ankle structure of Pterosauria. The pterosaur ankle joint (PAJ) shows the following features: astragalus mediolaterally elongated forming a hemicylinder; proximal part of the astragalocalcaneal contact characterized by a ridge bordered on each side by a depression on the astragalus that has a perfect counterpart in the calcaneum, and distal part that is concavo-convex, with the concavity present in the astragalus; calcaneum extremely reduced not reaching the posterior portion of the tarsus; absence of an astragalar posterior groove, perforating foramen, calcaneal tuber, and astragalar ascending process; proximal tarsals fusing very early in ontogeny, forming a tibiotarsus.

The main movement between the crus and foot in the PAJ occurs between the proximal and distal tarsals as in the advanced mesotarsal-reversed joint (AM-R). The main differences from the latter are the lack of an ascending process and the extreme reduction of the calcaneum that make the PAJ unique. The absence of an astragalar groove and the reduction of the calcaneum reinforce the hypothesis that pterosaurs are basal ornithomirans and closely related to the Dinosauromorpha. As has been demonstrated by this and other studies, the ankle structure (a complex of characters) is phylogenetically informative and, in the light of characters from other parts of the animal's body, can contribute to a better understanding of archosaur relationships.

INTRODUCTION

The study of the ankle structure in archosaurs (sensu lato) has received much attention over the years, particularly after Krebs (1963) described an unusual ankle joint of a "pseudosuchian" reptile from the Triassic of Monte San Giorgio (Switzerland). This animal exhibits an ankle structure similar to that found in crocodilians, with the astragalus and calcaneum articulating in a concavo-convex facet, with the concavity situated on the latter. The astragalus of this specimen forms a unit with the crus while the calcaneum is more closely connected with the distal tarsals and metatarsals, functionally differing from the mesotarsal joint of most other reptiles (Krebs, 1963). Walker (1964) and Bonaparte (1972) recognized another ankle joint morphology in ornithomirans that also shows a

concavo-convex articulation surface between astragalus and calcaneum, but with the concavity situated in the former. Those two basic types of archosaurian ankle structures were designated respectively as crocodile-normal (CN) and crocodile-reversed (CR) joints by Chatterjee (1978) and differ from the primitive mesotarsal joint (PM, see Chatterjee, 1982) found in more basal archosauriforms (sensu Sereno, 1991) like *Proterosuchus*. Cruickshank (1979) used these ankle joints as the basis for dividing Archosauria into two lineages. Since then, more morphological variations of the ankle structure have been recognized (see Sereno and Arcucci, 1990, for a review), resulting in distinct classifications and evolutionary scenarios for the Archosauria (e.g., Chatterjee, 1982; Cruickshank and Benton, 1985; Parrish, 1993),

which have produced extensive debates in the literature (e.g., Cruickshank, 1981; Cooper, 1981; Parrish, 1988; Gauthier, 1988; Cruickshank and Benton, 1988; Dyke, 1998).

Pterosaurs, however, never played a major role in the “ankle-phylogeny” discussions because the ankle structure of this extinct volant clade of archosaurs remained essentially unknown. Besides being regarded as a mesotarsal joint (Wellnhofer, 1978; Padian 1983a, 1983b), the particular relation between the proximal tarsals (astragalus and calcaneum) was never observed in detail. There are two main reasons that account for this. The first one is related to the preservation of pterosaur specimens in general: besides being incomplete (e.g., lacking hindlimbs), most show broken and flattened bones, hindering the observation of anatomical details, particularly of the small elements that form the tarsus. The second explanation is that in the vast majority of the specimens where the hindlimb and foot are preserved, the proximal tarsals tend to be fused with the tibia forming a tibiotarsus (e.g., Wellnhofer, 1978; Padian, 1983a; Clark et al., 1998; Bennett, 2001). This led to the general assumption that the astragalus and calcaneum fused with the tibia early in ontogeny, which is particularly true for pterodactyloids (e.g., Kellner and Tomida, 2000).

In this paper, I describe in detail the unfused tarsus of two pterosaurs preserved in three dimensions that were recovered from the Romualdo Member, Santana Formation, Araripe Basin, Brazil. This deposit has furnished extremely well-preserved fossils (see Maisey, 1991, for a general review), including some of the finest pterosaur material known (Kellner, 1994). Based on palynomorphs, a late Aptian to early Albian age is suggested for the Romualdo Member (Pons et al., 1990).

The specimens belong to the tapejarid *Tapejara* sp. and the anhanguerid *Anhanguera piscator*, two distantly related pterodactyloid pterosaurs (fig. 2.1). The pterosaur ankle joint (PAJ) described herein is regarded as expressing the general condition for Pterosauria; its similarities with and differences from other archosaurian ankle joints are discussed.

MATERIAL AND METHODS

The tapejarid specimen is part of an almost complete skeleton (lacking the skull) in the Desiree Collection (former number CD-R-019), permanently housed in the Paleovertebrate Sector of the Department of Geology and Paleontology, Museu Nacional/UFRJ, Rio de Janeiro, under the number MN 6532-V. It represents a comparatively small pterosaur with an estimated wing span of 1.2 m (based on Sayão and Kellner, 1998). This individual is considered a juvenile because all bones normally fused in ontogenetically mature specimens are unfused (Kellner, 1995b). It is referred to *Tapejara* sp., based on the size and shape of several elements that could be compared with another specimen that includes cranial and postcranial bones (Wellnhofer and Kellner, 1991). Both feet are preserved with a well-preserved tarsus. The left tarsus (figs. 2.2–2.5) was fully prepared and all the elements were isolated, while the right tarsal elements were left articulated for comparisons. The preparation was done using formic acid, following the procedures developed for fossils preserved in calcareous limestone from the Santana Formation (Rutzky et al., 1994; Kellner, 1995a).

The anhanguerid tarsus (figs. 2.6, 2.7) described here is part of the holotype of *Anhanguera piscator* housed in the National Science Museum (Tokyo) under the number NSM-PV 19892. A cast is deposited in the Paleovertebrate Sector of the Department of Geology and Paleontology, Museu Nacional/UFRJ, Rio de Janeiro (MN 5023-V). It represents a very young animal, not fully grown at time of death, despite its large size (wing span: approx. 5 m; Kellner and Tomida, 2000). The material consists of the tarsal elements and metatarsals from the right foot, which were briefly reported by Kellner and Tomida (1993). The proximal tarsals are well preserved, but the distal tarsals, including the metatarsals, are incomplete. The preparation of the specimen was done mechanically.

DESCRIPTION

The tarsus of both specimens is composed of four bones: astragalus and calcaneum positioned proximally and tarsals 3 and 4 positioned distally. The astragalus, consisting

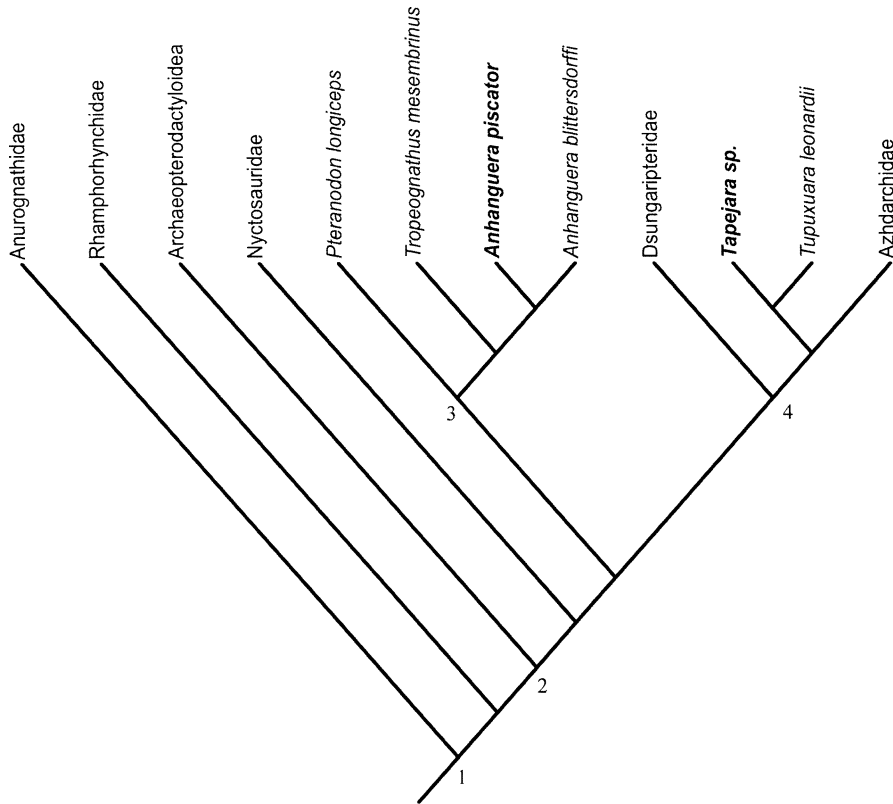


Fig. 2.1. Simplified cladogram showing the phylogenetical position of *Tapejara* sp. (Tapejaridae) and *Anhanguera piscator* (Anhangueridae). **1**, Pterosauria; **2**, Pterodactyloidea; **3**, Pteranodontoidea; **4**, Tapejaroidea. For data matrix and character descriptions see Kellner (1996, 2003).

of a mediolaterally elongate hemicylinder (figs. 2.2, 2.3), is the largest element of the tarsus. The astragalar-tibial articulation facet is slightly concave. In *Tapejara* sp. this bone has a trapezoidal outline in proximal view, except for the anterolateral surface where it shows an indentation to receive the proximal portion of the calcaneum. The astragalocalcaneal articulation surface, observed in lateral view (fig. 2.3A), shows some complexity and can be divided into two main portions. The proximal portion shows a small proximodistally oriented ridge that fits into a small recess on the proximal surface of the calcaneum. On each side of this ridge there is a depression of different shape: the anterior is oval and becomes shallower anteriorly; the posterior depression is cuneiform, with the main axis directed proximodistally. The distal portion of the astragalocalcaneal articulation surface is marked by a well-developed

concavity that is large compared to the proximal portion. In the middle part of this articulation surface there is a deep concavity that does not end in a foramen.

Distally the astragalus forms the entire medial condyle and the posterolateral portion of the lateral condyle of the tibiotarsus. This region is broad and convex, showing a smooth surface. In *Tapejara* sp., the lateral condyle (consisting mostly of the calcaneum) is larger than the medial condyle and the intercondylar sulcus is shallow (fig. 2.2B). Anteriorly, the astragalus receives distal tarsal 3 (dt3) and part of distal tarsal 4 (dt4). The medial surface is flat and pierced by nutrient foramina; a larger foramen is situated on the posterior corner (fig. 2.2A). No metatarsal reaches the astragalus, nor are there signs of an astragalar posterior groove or an ascending process.

The astragalus of *Anhanguera piscator*

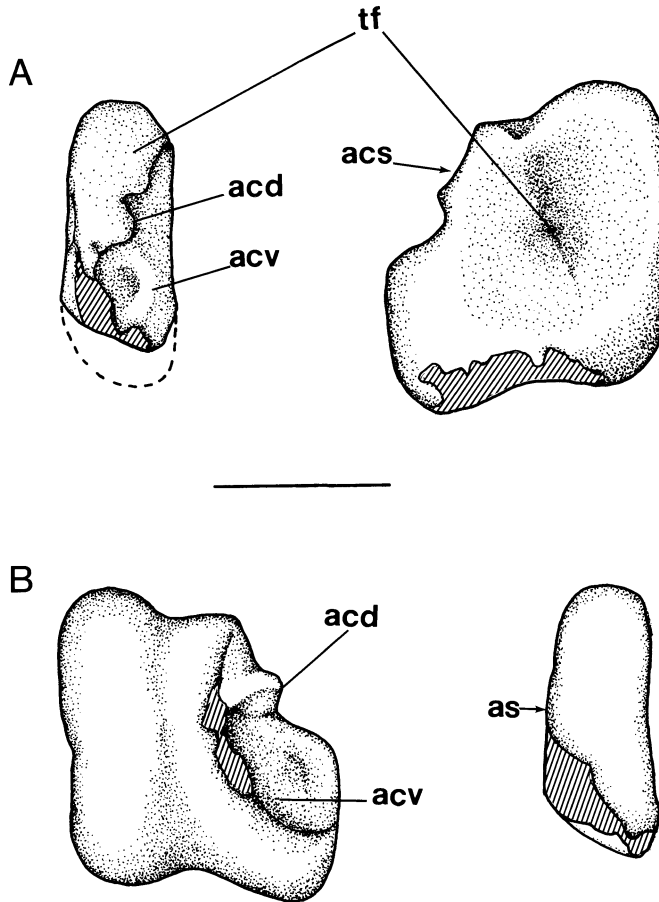


Fig. 2.2. Left astragalus and calcaneum of *Tapejara* sp. (MN 6532-V) in (A) proximal and (B) distal views. Scale bar: 5 mm. Abbreviations: **acd**, dorsal portion of the astragalocalcaneal articulation surface; **acs**, astragalocalcaneal articulation surface; **acv**, ventral portion of the astragalocalcaneal articulation surface; **as**, articulation surface for the astragalus; **tf**, tibial facet.

(figs. 2.6, 2.7) is similar to that of *Tapejara* sp. and also forms the largest element of the tarsus. The main difference lies in the medial surface, which is rounded and projected medially in *A. piscator* (flat in *Tapejara* sp.), and lacks nutrient foramina but shows a depression (fig. 2.6A) on the anterior corner (posterior corner in *Tapejara* sp.). Moreover, the proximodistal ridge positioned in the proximal portion of the astragalocalcaneal articulation surface is less developed in *A. piscator* (fig. 2.7).

The calcaneum is a smaller element (figs. 2.2, 2.3). Distally this bone is broad, smooth, and convex, and forms the anterolateral por-

tion of the lateral condyle of the tibiotarsus. Proximally it has contact with the tibia only on a slightly concave articulation surface (the fibula in both specimens does not reach the tarsus). In *Tapejara* sp. the astragalocalcaneal articulation surface can be divided into two main portions that make a perfect counterpart to the astragalus (fig. 2.3B). The proximal portion shows a small recess bordered by two projections that fit the ridge and depressions of the corresponding part of the astragalus. The distal portion of the astragalocalcaneal articulation surface of the calcaneum is formed by a broad process that fits a concavity in the astragalus. The lateral sur-

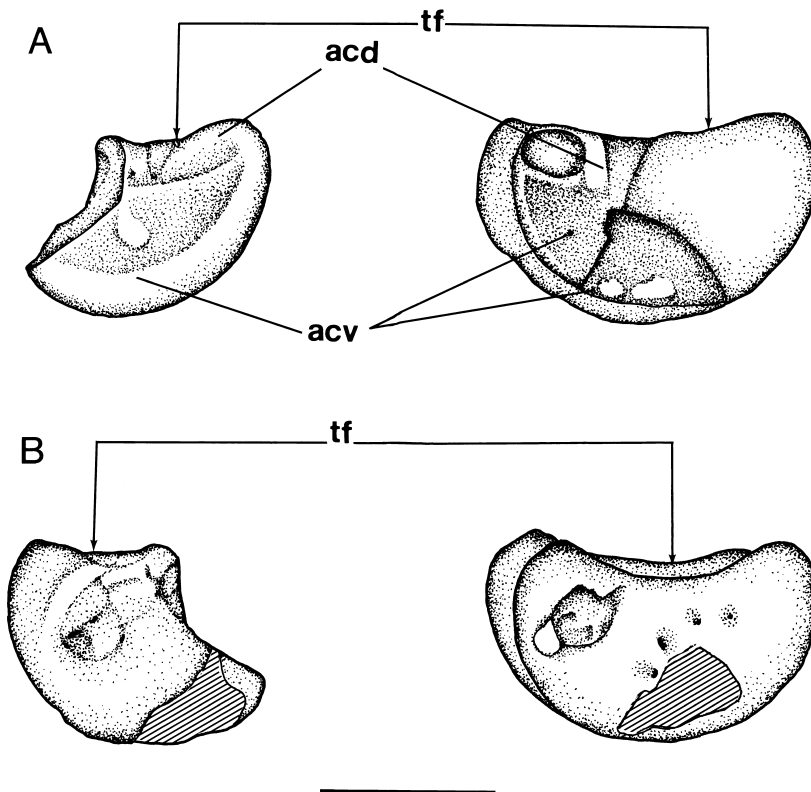


Fig. 2.3. Left astragalus and calcaneum of *Tapejara* sp. (MN 6532-V) in (A) calcaneum in medial view and astragalus in lateral view and (B) calcaneum in lateral view and astragalus in medial view. Scale bar: 5 mm. Abbreviations as in figure 2.2.

face of the calcaneum is flat and shows a comparatively large cavity pierced by several foramina. No calcaneal tuber is developed.

The calcaneum of *Anhanguera piscator* shows the same basic features, differing from *Tapejara* sp. mainly by being comparatively more developed proximodistally. *A. piscator* also lacks the large cavity present in *Tapejara* sp., showing in this region only a shallow oval depression and no foramina.

In *Tapejara* sp., the distal tarsals are subequal in size, both smaller than the proximal tarsals (figs. 2.4, 2.5). Distal tarsal 3, positioned medially, has an irregular shape. Essentially, it is an anteroposteriorly elongate bone with anterior and posterior areas expanded (the former more developed). The proximal part is concave and articulates with the astragalus. The distal part shows a diagonal mediolateral depression. The anterior surface is convex and smooth, receiving

metatarsals 1 to 3. The posterior surface is slightly convex. The contact surface with the distal tarsal 4 is flat and shows a cavity with a comparatively large foramen.

Laterally positioned and elongate anteroposteriorly, distal tarsal 4 has a more uniform shape compared with distal tarsal 3. The proximal articulation surface (contacting both proximal tarsals) is smooth and slightly concave but the distal part shows a more complex shape with a large and deep central depression bearing two foramina. The anterior surface that articulates with metatarsal 4 and 5 is expanded and presents a convex smooth surface. The articulation with metatarsal 5 is well marked and situated on the lateral surface of this bone, facing ventrolaterally. The posterior portion is flat.

In *Anhanguera piscator*, the distal tarsals are not well preserved (not figured). Only

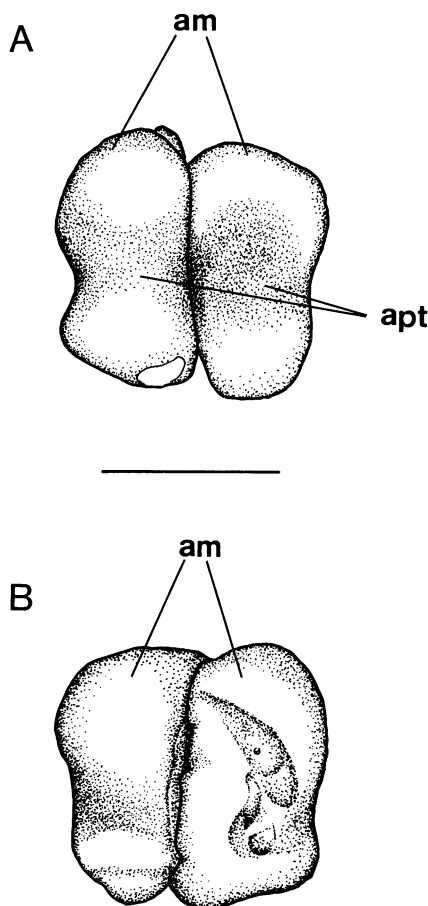


Fig. 2.4. Left distal tarsals of *Tapejara* sp. (MN 6532-V) in (A) proximal and (B) distal views. Scale bar: 5 mm. Abbreviations: **am**, articulation surface for metatarsals; **apt**, articulation surface for proximal tarsals.

distal tarsal 4 can be identified and it shows similar shape to that of *Tapejara* sp.

Distal tarsals are known in detail only for *Dimorphodon* (Padian, 1983a) and *Pteranodon* (Bennett, 2001). In the more basal pterosaur *Dimorphodon*, the distal tarsals are thin and wedge-shaped, with two ridges on the distal face of the distal tarsal 3 to receive metatarsals 1 to 3. This condition differs markedly from the distal tarsals of *Tapejara* sp., particularly distal tarsal 3, which is more elongate and lacks ridges. The distal tarsals of *Pteranodon* are more similar to those of *Tapejara* sp., with the former differing essentially by their lack of foramina that are

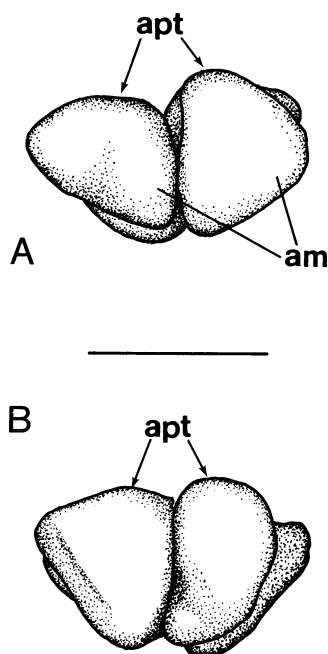


Fig. 2.5. Left distal tarsals of *Tapejara* sp. (MN 6532-V) in (A) anterior and (B) posterior views. Scale bar: 5 mm. Abbreviations as in figure 2.4.

present in the latter. In all three taxa, the articulation surface on tarsal 4 for metatarsal 5 faces ventrolaterally.

DISCUSSION

As pointed out, pterosaur specimens with tarsal elements are rare; having them unfused and preserved in three dimensions is even more exceptional. In most specimens, the proximal tarsals are fused with each other and with the tibia, forming a tibiotarsus. Wellnhofer (1970, 1975) reported unfused proximal tarsals in a few skeletons of *Rhamphorhynchus* and *Pterodactylus*, but they were not sufficiently preserved (or prepared) to be described in detail. Only *Tapejara* sp. (MN 6532-V) and the type of *Anhanguera piscator* (NSM-PV 19892) have unfused, three-dimensionally preserved, proximal tarsals.

In most pterosaur specimens the tarsus is composed of four elements: two proximal and two distal tarsals. Wellnhofer (1970, 1975) mentioned the existence of three distal tarsals in some ontogenetically immature

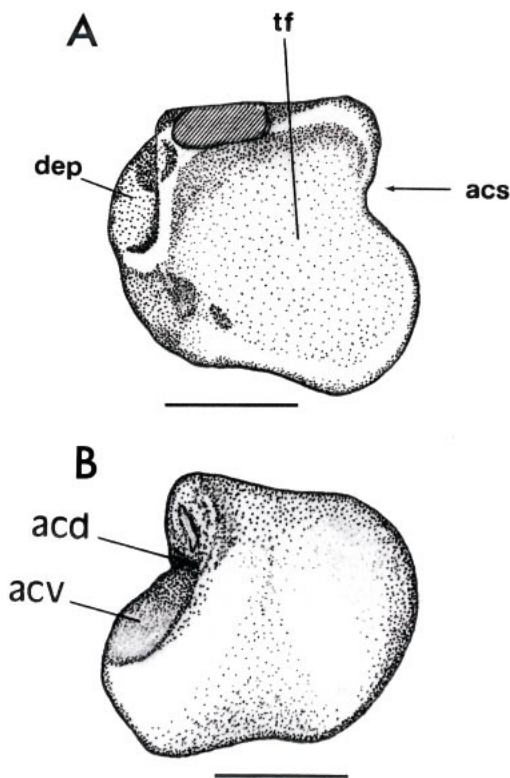


Fig. 2.6. Right astragalus of *Anhanguera piscator* (NSM-PV-19892) in (A) proximal and (B) distal views. Scale bar: 5 mm. Abbreviations: **dep**, depression; and as in figure 2.2.

specimens of *Rhamphorhynchus* (Rhamphorhynchidae) and *Pterodactylus* (Archaeopterygoidea sensu Kellner, 1996, 2003; fig. 2.1). This condition was not observed in *Tapejara* sp. and *Anhanguera piscator* and is not known in any derived pterodactyloid (Dsungaripteroidea sensu Young, 1964). It is likely that this third distal element was lost during the evolutionary history of pterosaurs.

According to the phylogenetic hypothesis of pterosaur interrelationships proposed by Kellner (1996, 2003), *Tapejara* (Tapejaridae) and *Anhanguera* (Anhangueridae) are distantly related pterodactyloid taxa (fig. 2.1), yet the tarsus of each shows essentially the same basic structure. Therefore, it is not unreasonable to assume that most, if not all, pterodactyloid taxa might have developed the same basic ankle joint, at least at the level of Ornithocheiroidea. The difficulty lies in whether or not this condition is present in the

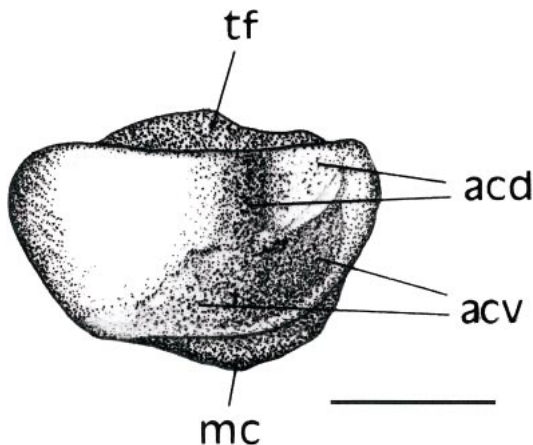


Fig. 2.7. Right astragalus of *Anhanguera piscator* (NSM-PV-19892) in lateral view. Scale bar: 5 mm. Abbreviations: **mc**, medial condyle; and as in figure 2.2.

more basal members of this group of flying reptiles.

Among the most outstanding features observed in *Tapejara* sp. and *Anhanguera piscator* is the astragalocalcaneal articulation surface that can be divided into two parts. The proximal portion shows a small ridge on the astragalus bordered by two shallow concavities that have a perfect counterpart in the calcaneum. This indicates that there was no movement between the proximal tarsals and that both fuse with each other and with the tibia forming a tibiotarsus in ontogenetically more mature animals. Although very little is known about pterosaur ontogeny, it is assumed that this fusion is reached early in life (Kellner and Tomida, 2000), with the proximal tarsals fusing first with each other and then with the tibia (based on the observation of other specimens like *Pterodactylus*). The hinge between foot and leg passes through the proximal and distal tarsals, a condition known as mesotarsal, which can be considered as plesiomorphic for the group (Wellnhofer, 1978).

In both tarsi described herein, the calcaneum is extremely reduced and confined to the anterolateral portion of the lateral condyle. One reason that could explain the small size of the calcaneum is the reduction of the fibula, which is generally splintlike, tapering distally, and not reaching the tarsus. This is

the condition observed in all pterodactyloids (Dsungaripteridae + Archaeopterodactyloidea) for which those bones are known, and in the Rhamphorhynchidae (Wellnhofer, 1975), *Dimorphodon* (Padian 1983a), *Dorygnathus* (SMNS 51827, personal observation), and *Sordes* (Sharov, 1971). For some basal pterosaurs the distal expansion of the fibula is not known (e.g., *Eudimorphodon*, Anurognathidae) and the only exception noted so far is *Campylognathoides* (e.g., SMNS 9787; Wellnhofer, 1974) in which the fibula shows a distal expansion and reaches the tarsus. Unfortunately no detailed information of the proximal tarsals is known for the specimens attributed to this taxon, but it is possible that in *Campylognathoides* (and perhaps in more basal forms) the calcaneum was larger and probably more projected posteriorly, building most of the lateral condyle of the tibiotarsus. Even if this were the case, there is no reason to suppose that the calcaneum would form the posterior portion of the lateral condyle and that the basic astragalocalcaneal contact surface would be different from the condition observed in *Tapejara* sp. and *Anhanguera piscator* since all the remaining observable features (e.g., lack of calcaneal tuber, lack of ascending process, hinge between proximal and distal tarsals) are the same. Therefore the pterosaur ankle joint (PAJ) described here is considered as representative of the Pterosauria.

Long held in the literature, there are basically two main types of ankle structure in archosaurs, crocodile-normal (CN) and crocodile-reverse (CR) joints, both thought to be derived from the primitive mesotarsal (PM) condition found in taxa such as *Proterosuchus* (e.g., Cruickshank, 1979). According to some authors (e.g., Sereno, 1991: 41), the main difference between these two basic types of ankle joint is found in the ventral portion of the astragalocalcaneal articulation that is concavo-convex, with the concavity in the calcaneum in the CN joint and the reverse in the CR joint. In this respect, the PAJ shows the condition found in the CR joint.

There is another aspect to be considered when discussing ankle joints: the movement of the foot relative to the crus. As pointed out several times in the literature (e.g., Krebs, 1963; Cruickshank, 1979; Chatterjee, 1982),

in both CR and CN the movement between foot and crus occurs essentially between the proximal astragalus and calcaneum, with the former tightly connected to the crus and the latter forming another unit with the distal tarsals and metatarsals. This is clearly not the case of the PAJ described here, where the interlocking system, particularly on the proximal portion of the astragalocalcaneal articulation surface, precludes any movement between astragalus and calcaneum.

The ankle joint in more derived archosaurs differs from the CN and CR types and is functionally similar to the PM condition since the hinge movement occurs between the proximal and distal tarsals. According to Chatterjee (1982), this ankle type, which received the designation advanced mesotarsal joint (AM), differs from the previous by having an mediolaterally elongated hemicylindrical astragalus with an ascending process, a reduced calcaneum lacking a "heel", and the absence of a perforating foramen. Furthermore, this condition is present in *Lagosuchus* and in all dinosaurs. Chatterjee (1982) also observed that the astragalocalcaneal articulation surface is concavo-convex and recognized two "sub-types" of this ankle joint: AM-normal, with the concavity in the calcaneum, and AM-reversed (AM-R), with the concavity in the astragalus.

The PAJ shows more affinities with the AM-R condition, based on the general shape of the astragalus, a mediolaterally elongated hemicylinder, and the concavity of the astragalus that receives the distomedial portion of the calcaneum. However, the PAJ differs by lacking a calcaneal tuber (which, according to Sereno, 1991, can be rudimentary in some dinosaurs), by the extreme reduction of the calcaneum (that is posteriorly bounded by the astragalus), and especially by the lack of an ascending astragalar process.

Regarding movement, the particular construction of the articulation surface between the proximal and distal tarsal series indicates a great degree of mobility, allowing pterosaurs to turn the distal tarsal from 90° (when the foot was on the ground) up to 240° during flight.

Several authors have tried to determine posture based on the ankle structure, pointing out that early ornithodirans were bipedal and digitigrade and that their evolution was char-

acterized by the improvement of locomotor capabilities (e.g., Gauthier, 1986; Novas, 1996). It was suggested that pterosaurs in particular were derived from agile, cursorial archosaurs, and that the early members of this clade adopted a bipedal posture on the ground (e.g., Padian, 1983b). The PAJ does not add anything substantial to this debate. It should be noted, however, that increasing evidence challenges the hypothesis that pterosaurs, including the more basal forms, must have been obligate bipeds. Quite the contrary, it seems that some basal members were quadrupeds (e.g., Unwin and Bakhurina, 1994), while some might have had an upright posture (e.g., Bennett, 1997). The analyses of the relation between the articulation of the metatarsal-phalangeal joints of some primitive forms (Clark et al., 1998) and of *Tapejara* sp. indicate that pterosaurs were plantigrade, rather than digitigrade, which is also corroborated by pterosaurian footprints (e.g., Mazin et al., 1995).

Assuming that the PAJ is representative of Pterosauria, it adds support to a close relationship of this clade of volant reptiles and Dinosauromorpha. The lack of an astragalar posterior groove and the reduction of the calcaneal tuber (absent in Pterosauria) are some of the features shared among members of both clades. It is also interesting to note that the basal dinosauromorph *Lagosuchus* has a rudimentary peg in the calcaneum that fits into a depression in the astragalus (Chatterjee, 1982). As this condition is similar to the PAJ, it may be an ornithodiran synapomorphy. Furthermore, at least one feature regarded as a synapomorphy of Dinosauromorpha by Novas (1996), calcaneal distal articulation surface less than 35% of astragalar width, is also present in the pterosaur ankles studied herein, and therefore constitutes a potential ornithodiran diagnostic feature.

Several authors criticized the sole employment of the ankle structure to elaborate hypotheses of archosaur ingroup relationships (e.g., Gauthier, 1988; Sereno and Arcucci 1990). Dyke (1998) took this criticism a step further considering "ankle and pedal" characters "unimportant" in reconstructing the "broad shape of archosaur phylogeny". Although it is clear that phylogenetic hypotheses should not be limited to a subset of char-

acters of the organism, it has been shown that the ankle structure (a complex of characters) is important in establishing the relationships of archosaurian taxa. The fact that some archosaur phylogenies have relied heavily on ankle and foot characters (e.g., Sereno and Arcucci, 1990; Sereno, 1991; Parrish, 1993) demonstrates that this character complex, indeed, has a strong phylogenetic signal.

Perhaps ankle and pedal characters should be seen for what they are, characters like any other from an animal's body that have the potential to provide useful data in phylogenetic reconstructions. Archosaurs have been extensively studied—from skull to tail—and if a comparatively large number of synapomorphies come from one part of the body, it only illustrates the importance of that part and should not be a reason to have such information excluded from the analysis. Furthermore, a large number of characters from one region have relative importance, because one does not know a priori where they will fall out in the cladogram.

CONCLUSIONS

The morphology of the ankles of the tapejarid *Tapejara* sp. and the anhanguerid *Anhanguera piscator* exhibit the following characteristics:

- mediolaterally elongated hemicylindrical astragalus;
- astragalocalcaneal contact separated into two parts: a dorsal contact surface characterized by a ridge bordered on each side by a small depression on the astragalus that has a perfect counterpart in the calcaneum, and a ventral contact, larger than the former and concavo-convex, with the concavity present in the astragalus, a condition usually referred to as "crocodile-reverse" (CR);
- extremely reduced calcaneum that does not reach the posterior portion of the tarsus;
- lack of astragalar posterior groove, perforating foramen, calcaneal tuber, and astragalar ascending process;
- presence of a joint between the proximal and distal tarsal that is highly movable in an anteroposterior direction;
- proximal tarsals fused very early in ontogeny, forming a tibiotarsus.

Except for the calcaneum, which might have been more elongated posteriorly in basal

forms, the PAJ is regarded as representative of the Pterosauria. The main movement between the crus and foot in the PAJ occurs between the proximal and distal tarsals that are associated with the ventral astragalocalcaneal articulation surface, showing a condition similar to the advanced mesotarsal-reversed joint (AM-R) described by Chatterjee (1982). The main difference, making the PAJ unique, is the lack of an ascending process and the extreme reduction of the calcaneum that does not reach the posterior portion of the tarsus.

Some features of the PAJ reinforce the hypothesis that pterosaurs are basal ornithomirans and therefore closely related to the Dinosauromorpha. Although criticism of reliance solely on the ankle structures (a complex of characters) in archosaurian phylogenies is pertinent, it has been demonstrated that this anatomical region is an important source of information and should not be dismissed a priori as has been suggested.

ACKNOWLEDGMENTS

I am indebted to D.A. Campos, P. Sereno, J. Clark, S. Chatterjee, and J.G. Maisey for several stimulating discussions about the ankle structure in archosaurs. For access to specimens, I would like to thank M. Norell and E. Gaffney (American Museum of Natural History, AMNH), P. Sereno (University of Chicago), Rupert Wild (Staatliches Museum für Naturkunde Stuttgart, SMNS), and Y. Tomida (National Science Museum, Tokyo). G.C. Gould and S.K. Bell are thanked for the invitation to contribute to this volume and Maurílio de Oliveira for skillfully rendering the illustrations published here.

I also wish to express my gratitude to Malcolm McKenna for his support while I was working on my Ph.D. dissertation at the Columbia University-AMNH joint graduate program. It is not easy for a "mammal-person" to advise someone working on fossil reptiles, particularly flying, toothless ones! (At least they had ankles. . . .)

This research was partially supported by CNPq (Ph.D. fellowship 1992–1996), American Museum of Natural History and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Rio de Janeiro (FAPERJ, grant: E-26/172.280/2000) and is a contribution to the

project "Mesozoic Archosaurs from Brazil" (SID 37010221003–9) that is coordinated at the Museu Nacional by the author.

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