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NOTE

THE ANTIQUITY OF AFRICAN TORTOISES

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Tortoises (Testudinidae) are a diverse and highly specialized clade of terrestrial turtles that currently inhabit five continents. The global radiation of tortoises in the Paleogene, part of an explosive radiation of testudinoid turtles out of Asia, is poorly understood. The oldest known tortoises are from the late Paleocene of Mongolia (Parham, pers. obs. at PIN), and early in the Eocene they are known to have colonized North America and Europe (e.g., Hutchison, 1998; Lapparent de Broin, 2001). At some point in the early Paleogene they marched or floated to Africa. Today, the ancestors of those first invaders have evolved into the most diverse tortoise fauna in the world; Africa is home to 10 of the 13 extant genera (Iverson, 1992; Lapparent de Broin, 2000).

One of the most poorly understood episodes in the early testudinid range expansion is the dispersal of tortoises into Africa. Fossil tortoises have been known from Africa since the beginning of the last century, when Andrews (1902) noted that a ''gigantic land-tortoise'' had been found by H. J. L. Beadnell. However, the age of these tortoises has never been firmly established, because early collecting records were not precise with regard to the specific quarries from which they were collected. Three species of *Testudo* were described (Andrews and Beadnell, 1903; Andrews, 1906) as having come from the upper Eocene ''Fluviomarine'' deposits of the Jebel Qatrani Formation in the Fayum Province of Egypt. In the intervening years, the Jebel Qatrani Formation came to be regarded as early Oligocene in age (e.g., Simons, 1968), then partly late Eocene and partly early Oligocene (Kappelman, 1992; Kappelman et al., 1992). No further testudinids have been reported from Egypt, although fragmentary testudinid fossils possibly close to the Egyptian taxon have been recovered from lower Oligocene sediments in Oman (Thomas et al., 1989; Lapparent de Broin, 2000). Most recently, Lapparent de Broin (2000) reviewed the African fossil record of turtles and conservatively reported the age of the Fayum tortoises as early Oligocene.

Resolution of the age of Africa's oldest tortoises has been difficult because specimens housed in European institutions (Natural History Museum, London, and Staatliches Museum, Stuttgart) lack detailed locality data, and more recent fieldwork in the area by E. L. Simons and crews (materials housed at Yale Peabody Museum, Cairo Geological Museum, and Duke University Primate Center, Durham, North Carolina) has not yielded remains of these comparatively rare reptiles. Reevaluation of older collections from the Jebel Qatrani Formation has uncovered the only African tortoise with associated stratigraphic data indicating a late Eocene age, allowing us to place this taxon in an updated geochronologic context and providing us with the opportunity to resolve several taxonomic issues regarding these specimens.

Abbreviations Used—**AMNH**, American Museum of Natural History, New York; **BMNH**, The Natural History Museum, London; **CGM**, Cairo Geological Museum, Cairo; **PIN**, Paleontological Institute, Moscow.

SYSTEMATIC PALEONTOLOGY

Order CHELONII Brongniart, 1800 (Latreille, 1800)
Suborder CRYPTODIRA Cope, 1869
Superfamily TESTUDINOIDEA Batsch, 1788
Family TESTUDINIDAE Batsch, 1788
Genus *GIGANTOCHERSINA* Chkhikvadze, 1989
GIGANTOCHERSINA AMMON
(Andrews *in* Andrews and Beadnell, 1903)
(Fig. 1)

Testudo ammon Andrews *in* Andrews and Beadnell, 1903:6; Andrews, 1904:527, 1906:278.
Testudo beadnelli Andrews, 1906:285.
Testudo isis Andrews, 1906:286.
Geochelone (*Geochelone*) *ammon* Auffenberg, 1974:154.
Geochelone (*Geochelone*) *beadnelli* Auffenberg, 1974:154.
''*Testudo*'' *ammon* Thomas et al., 1989:108.
Gigantochersina ammon Chkhikvadze, 1989:429; Lapparent de Broin and van Dijk, 1999:154; Lapparent de Broin, 2000:59.
Geochelone (s.l.) Roset et al., 1990:80.

Holotype—CGM C8130, nearly complete carapace and plastron.

Previously Described Material—CGM specimen numbers C8772, C8773 (type of *Testudo beadnelli* Andrews, 1906), C8774 (type of *Testudo isis* Andrews, 1906), C9008, C9240, BMNH specimen numbers R3097, R3273, R3099, R3351, R3098, R3098a. Lapparent de Broin (2000) noted the presence of additional specimens in the Staatliches Museum in Stuttgart, but these have not been formally reported.

Newly Referred Material—AMNH 5091, a partial pelvis.

Locality—AMNH Quarry B, lower sequence, Jebel Qatrani Formation, Fayum Province, Egypt.

Description—AMNH 5091 (Fig. 1) is a partial pelvis that includes parts of the right ilium, right ischium, and right pubis in articulation. Almost the entire right ilium is preserved. In posterior view (Fig. 1A) the dorsal process of the ilium is medially directed, while in anterior view a strong ridge is visible (Fig. 1B). The ischium is largely missing; only the dorsolateralmost portion (that helps form the acetabulum) is present. Most of the lateral portion of the right pubis is preserved, including part of the pubic plate. Anteriorly, the lateral process is separated from the pubic plate by an obtuse angle. In life, both the lateral process and the pubic plate would have had an oblique, loose articulation with the xiphiplastron.

DISCUSSION

Taxonomy—We can assign AMNH 5091 to *Gigantochersina ammon* based on its similarities to BMNH R3097, a pelvis found in association with a distorted carapace and plastron, and illustrated by Andrews (1906:fig. 90). Furthermore, the other turtles known from the Jebel Qatrani Formation are pleurodires (Andrews, 1903, 1906; Lapparent de Broin, 2000). Those taxa have pelves that are diagnostically distinguishable from AMNH 5091. In pleurodires the pubis and ischium are fused to the xiphiplastron and the pubic plate is absent. AMNH 5091 (Fig. 1) possesses a pubic plate. Also, the lateral process of the pubis in AMNH 5091 is less ventrally directed than in pleurodires and lacks the ventral suture seen in pleurodires. Finally, the overall appearance of the pelvis, including the medially directed dorsal processes of the ilium (to meet the sacral vertebrae) and the circular shape of the thyroid fenestra, conforms to that of other Testudinidae, rather than Pleurodira.

In reporting above the authority and synonymies associated with this species, we follow Andrews (1906) and Chkhikvadze (1989) in recognizing Andrews *in* Andrews and Beadnell (1903) as the first valid publication of the name. Auffenberg (1974) regarded the use of ''*Testudo*'' *ammon* in Andrews and Beadnell (1903) as a nomen nudum and designated Andrews (1904) as the authority for the species, probably because the specimen number of the holotype was not reported in the 1903 publication and the words ''holotype'' or ''type'' were not used in the text. The phrase ''type-specimen'' was used in Andrews (1904) to describe this same specimen, but no catalog number was given for

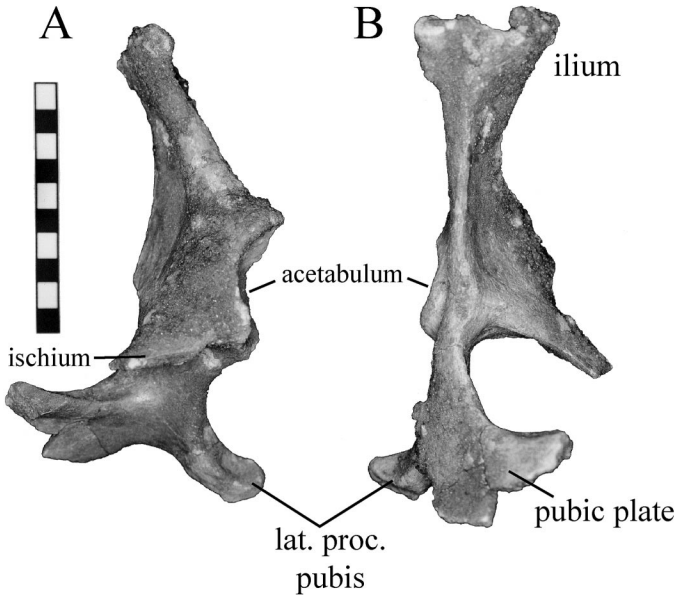

FIGURE 1. AMNH 5091, pelvis of *Gigantochersina ammon* Andrews, 1903. **A**, posterior view. **B**, anterior view.

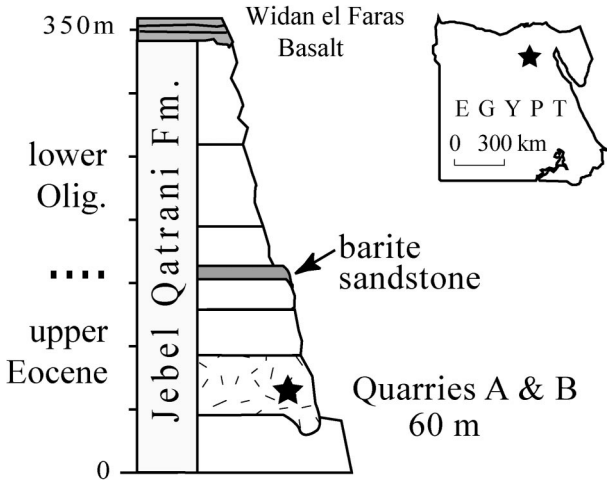

FIGURE 2. Locator map and schematic stratigraphic section for the Jebel Qatrani Formation, Fayum Province, Egypt.

it until Andrews (1906). However, the illustration of a specimen clearly labeled ''Testudo ammon, n. sp.'' (Andrews and Beadnell, 1903:11) combined with discussion of it as the then sole known specimen of the taxon would appear to fulfill the requirements of Article 73 of the International Code of Zoological Nomenclature, and the fact that the specimen number was not reported until Andrews (1906) does not affect the name authority for the taxon. Lapparent de Broin (2000) lists the authority as Andrews and Beadnell (1903); however, although this is the publication in which *Testudo ammon* is first reported, the section of the paper describing the specimen is clearly designated as having been authored by Andrews alone, and both Andrews (1904, 1906) and Beadnell (1905) subsequently reported Andrews as the sole author of the taxon. In our synonymies, we also follow Lapparent de Broin's (2000) suggestion that *Gigantochersina beadnelli* (Andrews, 1906) and *G. isis* (Andrews, 1906) are likely junior synonyms of *G. ammon* and formalize that synonymy above.

Age—The Jebel Qatrani Formation (Fig. 2) comprises approximately 360 m of sediment and has been divided into three parts: 1) the 153 meter-thick lower sequence; 2) the barite sandstone, a wide-ranging, 4–10 meter-thick marker bed that delimits the upper and lower sequences; and 3) the 190 meter-thick upper sequence. Quarry B lies within the lower sequence, which is dominated by three gravelly sandstone sequences of large sand bodies formed by coalesced channel deposits containing abundant silicified wood (Bown and Kraus, 1988). Based on paleomagnetic reversal stratigraphy, Kappelman (1992) and Kappelman et al. (1992) produced a series of dates for deposits in the Jebel Qatrani Formation, concluding that most of the vertebrate fossil localities occur in Chrons C13–C15r, spanning the Eocene–Oligocene boundary. Based on the time scale of Cande and Kent (1992), the 34 Ma Eocene–Oligocene boundary lies slightly below the barite sandstone dividing the upper and lower sequences of the formation. The estimated age of Quarry B in the lower sequence is between 35.40 and 35.56 Ma.

It is highly likely that most, if not all, the previously described specimens of *Gigantochersina* come from the middle gravelly sandstone of the lower sequence of the Jebel Qatrani Formation. There are only seven shells and a few postcranial remains of *Gigantochersina* known. Andrews (1907:305) remarks that the shells of ''a gigantic land-tortoise . . . are comparatively numerous.'' Although precise locality data are not listed on specimen tags of the type specimens, the discovery of only this small number of these immense animals was sufficiently remarkable that Beadnell (1905) explicitly included them in his stratigraphic sections. In a stratigraphic section running from the base of the Jebel Qatrani Formation at a point 2.5 km NNW of the Qasr el Sagha Temple to Widan el Faras, Beadnell identified his lowest stratigraphic unit as ''grey sandstones and loose false-bedded sandy clays with many silicified trees and remains of [mammals described by Beadnell and/or C.W. Andrews] . . . and large and numerous tortoises (*Testudo Ammon* [sic], Andr.) . . . '' (p. 59). He notes that although all the vertebrates he listed were not found at the point where the actual line of section was taken, most were obtained in this bed at ''some distance'' to the west. These localities correspond to the ''Bone Pits'' shown in several locations on Plate XXI of that same publication. All of these occur within the part of the formation termed the lower sequence by Bown and Kraus (1988), and some of the bone pits mapped by Beadnell are those that eventually came to be called Quarries A and B by AMNH and Yale University crews (see Gagnon, 1997, for a quarry map). The mammal species reported by Beadnell (1905) as having come from the same horizon as the tortoises are those now known to come from this part of the section, also informally referred to as ''Fayum Faunal Zone 2'' (Rasmussen et al., 1992).

The presence of large tortoises at this stratigraphic level may reflect a combination of taphonomic factors and environmental factors. Massive fossil logs (up to 44 m in length; Bown and Kraus, 1988) and most of the very large mammal specimens (e.g., *Arsinoitherium* and proboscidean skulls) have been recovered from the middle gravelly sandstone, where conditions apparently favored the preservation (or at least recovery) of larger animal and plant remains. Gagnon (1997) also presented ecologic inferences drawn from the analysis of mammalian paleoecology suggesting that this portion of the formation may reflect more open habitats, with a subsequent return to more closed forested habitats higher in the stratigraphic section. The presence of a large, high-domed tortoise is consistent with interpretations of a more open habitat.

The discovery of a tortoise specimen from the upper Eocene portion of the Jebel Qatrani Formation demonstrates that testudinids had spread to at least four continents by the end of the Eocene. In Europe, the group is known from the middle Eocene (Lapparent de Broin, 2001) and in North America from the early Eocene (Holroyd et al., 2001). In each instance, an Asian origin has been presumed, but we currently lack data that could allow us to determine if this biogeographic hypothesis is correct. The true time of arrival for tortoises as well as many Fayum mammals to Africa is likely to be older, but our knowledge suffers from a dearth of older fossil-bearing strata (see e.g., Holroyd and Maas, 1994). Now, nearly a century after its discovery, *Gigantochersina ammon* is still the only tortoise from the Paleogene of Africa and can finally be recognized as the oldest African member of this clade.

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