

HELEOSAURUS SCHOLTZI FROM THE PERMIAN OF SOUTH AFRICA: A VARANOPIID SYNAPSID, NOT A DIAPSID REPTILE

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Recent descriptive and phylogenetic work on varanopids, carnivorous basal synapsids ('pelycosaurs' of previous systematic studies), have demonstrated that they are one of the most diverse, widespread, and geologically long-lived group of early amniotes. The oldest known member is *Archaeovenator hamiltonensis* from Upper Carboniferous rocks of central North America (Reisz and Dilkes, 2003), whereas the youngest described members are the Middle Permian *Mesenosaurus romeri* and *Pyozia mesenensis* from Russia, and *Elliotsmithia longiceps* from South Africa (Anderson and Reisz 2003; Dilkes and Reisz, 1996; Reisz et al., 1998; Modesto et al., 2001).

The monitor lizard-like aspect of some varanopids has generated some confusion with regards to their taxonomic affinities. *Mesenosaurus romeri* was first recognized as a varanopid (Efremov, 1940), but was later identified as an archosaurian diapsid reptile (Ivachnenko and Kurzanov, 1979); a detailed description and reappraisal has affirmed the original taxonomic assessment (Reisz and Berman, 2001). The holotype of *A. hamiltonensis* was heralded as a new, early diapsid (Reisz, 1988), one that was suspected to be a more crownward taxon (Laurin, 1991) than the Pennsylvanian diapsid *Petrolacosaurus kansensis* (Reisz, 1977). The formal description of *A. hamiltonensis* by Dilkes and Reisz (2003) demonstrated that it was a varanopid.

All of the above mentioned varanopids were relatively small carnivores, equivalent to or slightly smaller in size than *Mycterosaurus longiceps*, known from Lower Permian rocks in Texas and Oklahoma (Reisz et al., 1997). However, Varanopidae also includes larger predators, members of the clade Varanodontinae: *Aerosaurus*, *Varanops*, *Varanodon*, and *Watongia* (Reisz and Laurin, 2004). All of these larger varanopids, ranging in size from 1.5 to greater than 2 m in total length, are restricted to North American strata.

A century ago, Robert Broom (1907) described *Heleosaurus scholtzi*, a small amniote from Permian rocks of South Africa. Whereas diapsids were recognized as a major group by Osborn (1903), varanopids were not recognized as a distinct group until Romer & Price (1940). Not surprisingly, Broom (1907) classified *Heleosaurus* as an early diapsid reptile. It was placed with outwardly similar taxa from the Permian and Triassic periods into Eosuchia, which was thought by early workers to be the evolutionary 'stock' from which living diapsid reptiles (tuataras, lizards, snakes, and crocodiles) and their fossil relatives were derived (Carroll, 1976). *Heleosaurus* was regarded as a member of the eosuchian family Younginidae (Carroll, 1976), and it was proposed (Carroll, 1976) that the genus was an ideal ancestor for Archosauria (= Archosauriformes of recent authors, e.g., Dilkes, 1998). The presence of dermal armor; a femur with a

sigmoidal, diapsid-like curvature; and teeth with serrations were cited as the principal reasons for this assignment. Currie (1982) expressed reservations that *Heleosaurus* was a younginid, and Benton (1985) classified it simply as a stem diapsid. A cladistic analysis of basal archosauromorph phylogeny (Dilkes, 1998) reveals that none of the 'archosaurian' characters identified in *Heleosaurus* by Carroll (1976) were present in the basal members of Archosauromorpha. *Heleosaurus* has not figured in the latest investigations of basal diapsid phylogeny (Laurin, 1991; Dilkes, 1998; Müller, 2004), and it now appears to be a taxonomic enigma.

Recent advances in our understanding of varanopid anatomy and evolution (Reisz et al., 1998; Reisz and Berman, 2001; Modesto et al., 2001) have prompted our reassessment of the taxonomic affinities of *Heleosaurus scholtzi*. Most conspicuously, *Heleosaurus* shares with *Mesenosaurus*, *Mycterosaurus* and *Elliotsmithia* the presence of serrations on mesial and/or distal edges of the marginal teeth, and it shares with *Elliotsmithia* the presence of small, rounded postcranial dermal ossicles. We reexamine the holotype of *Heleosaurus* here in order to ascertain its systematic position among amniotes.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; FMNH-UC, The Field Museum, Chicago; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; SAM, Iziko: South African Museum, Cape Town.

Anatomical Abbreviations—aco, anterior coronoid; alv, alveoli; an, angular; ar, articular; ax, axis; bp, basiptyergoid process; ch, ceratohyal; cl, clavicle; cp, cultriform process; cv, crista ventrolaterales; d, dentary; ec, ectopterygoid; fe, femur; is, ischium; icl, interclavicle; j, jugal; m, maxilla; os, dermal ossicle(s); pal, palatine; pbs, parabasisphenoid; pco, posterior coronoid; pu, pubis; q, quadrate; qj, quadratojugal; sa, surangular; sc, scapuloacoid; v, vomer.

MATERIALS AND METHODS

The following redescription of the specimen, SAM-PK-1070, is based on latex casts made by R. L. Carroll from part and counterpart blocks that preserve the impression of the greater part of the skeleton. The illustrations shown in Figures 1 and 2 are from Carroll (1976).

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA Osborn, 1903
VARANOPIIDAE Romer and Price, 1940
HELEOSAURUS SCHOLTZI Broom, 1907

Diagnosis—*Heleosaurus scholtzi* is distinguished from other varanopids by distinctive ornamentation on the angular and the

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