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FEATURED ARTICLE

VESTIGIAL FORELIMBS AND AXIAL ELONGATION IN A 95 MILLION-YEAR-OLD NON-SNAKE SQUAMATE

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A new species of 95-million-year-old snake-like marine lizard, *Adriosaurus* sp. nov., shows complete loss of the manus and zeugopodium in association with elongation of the axial skeleton. The fossil was collected during the 19th century from Upper Cenomanian-aged (Upper Cretaceous) platy limestone quarries located near Komen, Slovenia (Fig. 1) (Jurkovšek et al., 1996; Cavin et al., 2000), and remained in collections at the Museo Civico di Storia Naturale in Trieste, Italy (MSCNT) until recent preparation revealed its unique anatomy (Fig. 2A; MCSNT 7792). The Komen squamate fauna includes the fully limbed adriosaur type species, *Adriosaurus suessi*, a number of undescribed adriosaurs, acteosaurs, eidolosaurs, and at least two taxa of aigialosaurs.

The anatomy of this new species of *Adriosaurus* is informative regarding evolution within adriosaurs, but more importantly, when examined within the context of a resolved phylogeny of all squamates, illuminates broader evolutionary patterns of limb reduction and axial elongation within Squamata. In this study, we examine the transformation of the limb and axial skeleton using the phylogenies that find adriosaurs to be the sister taxon to snakes within a clade of pythonomorph squamates (e.g., Caldwell and Lee, 1997; Lee and Caldwell, 1998; Lee and Caldwell, 2000; Rage and Escuillié, 2000; Caldwell and Dal Sasso, 2004; Caldwell and Lee, 2004; Pierce and Caldwell, 2004). Despite the large number of claimed falsifications of the pythonomorph hypothesis (e.g., Zaher and Rieppel, 1999; Tchernov et al., 2000; Rieppel et al., 2003; Apesteguia and Zaher, 2006), the balance of these studies (excepting Rieppel and Zaher [2000] and Vidal and Hedges [2004]) have presented hypotheses of the ingroup relationships of snakes or have been focused on problems of character similarity without presenting an alternative snake sistergroup hypothesis and thus are of no comparative value for this study.

Rieppel and Zaher's (2000) phylogeny, produced by analysis of a selected subset of Lee's (1998) characters and taxa, is also problematic for our purposes because they found amphisbaenians and dibamids, usually allied with lacertoids and scincids, respectively, to form a clade with snakes nested within Anguimorpha. Rationalizing amphisbaenians and dibamids as anguimorphs is problematic and so we have excluded the Rieppel and Zaher (2000) phylogeny. The molecule-based analysis of squamate phylogeny by Vidal and Hedges (2004) was ostensibly a falsification of the pythonomorph hypothesis. However, as was shown by Lee (2005), the empiricism of a total evidence analysis (taxa and characters) is the only suitable manner for inserting fossil taxa into a phylogenetic analysis. We follow Lee's (2005) phylogeny as opposed to Vidal and Hedges' (2004) inductive inference of the phylogenetic relationships of fossil snakes and mosasaurs.

Therefore, we examine the evolutionary patterns and processes of squamate limblessness and axial elongation using the phylogenies produced by parsimony analysis of the morphology and/or molecules of fossil and modern squamates (e.g., Caldwell and Lee, 1997; Lee, 1997; Caldwell, 1999; Lee and Caldwell, 2000; Lee, 2005). We also discuss the phylogenetic distribution of limb reduction and elongation characters for snakes and lizards as they relate to the genetics of limb and body axis development in squamates (Cohn and Tickle, 1999; Weins and Slingluff, 2001; Adrianens et al., 2002; Shapiro, 2002; Sanger and Gibson-Brown, 2004).

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811
PYTHONOMORPHA Cope, 1869
OPHIDIOMORPHA, new clade

Definition—The most recent common ancestor of Dolichosauridae, *Aphanizocnemus*, adriosaurs, all Ophidia (fossil and extant), and all of its descendants (a node-based definition [see DeQueiroz and Gauthier, 1992]).

Diagnosis—Fossil and extant pythonomorph squamates differing from other fossil pythonomorphs in possessing an elongate neck (10 or more cervical vertebrae or anterior precloacal vertebrae with cervical-like features), elongate trunk (>35 cervical + dorsal/precloacal vertebrae), zygosphenes/zygantra throughout the entire presacral/precloacal region, and reduction to loss of forelimb elements.

ADRIOSAURUS Seeley, 1881

Holotype—The "Vienna" specimen (missing), Geological Museum, University of Vienna, Vienna. Slab with posterior trunk region, pelvis, hindlimb, and tail.

Locality and Horizon—Upper Cretaceous (Upper Cenomanian) platy limestones of the Trieste-Komen Plateau, Komen (Comeno), Slovenia (Jurkovšek et al., 1996; Cavin et al., 2000).

Emended Generic Diagnosis—Small marine squamate with elongate neck, body, and tail; 10 cervical, 29 dorsal, and at least 65 caudal vertebrae; zygosphenes/zygantra present in presacral region; tail deep, laterally compressed; limbs reduced in size; forelimbs much shorter than hindlimbs; strongly expanded distal end of fibula; laterally compressed trunk region; pachyostotic dorsal vertebrae and ribs; neural arches on dorsal vertebrae an-

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