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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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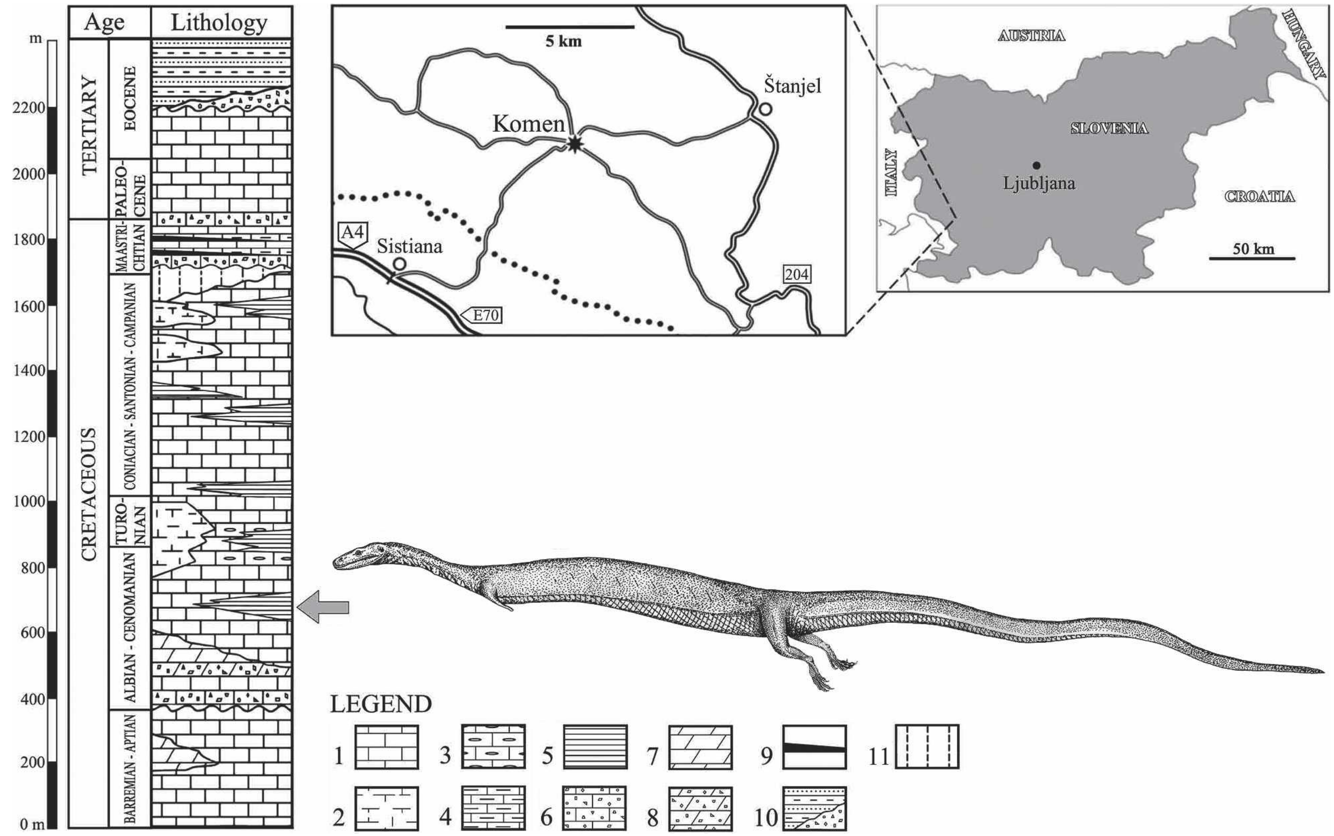

FIGURE 1. Geographic and stratigraphic provenance of *Adriosaurus suessi*, *Adriosaurus microbrachis* and the two specimens of *Adriosaurus* sp. (MCSNT 7793 & MCSNT 9400). Map of area surrounding town of Komen (Comeno), Slovenia, showing main roads and boundary with Italy (dotted line); approximate location of Komen is indicated on map of Slovenia. Stratigraphic column of Trieste-Komen Plateau (carbonate rocks ranging in age from Lower Cretaceous [Barremian] to Eocene) showing horizon producing specimens of *Adriosaurus* sp.; animal reconstructed is *Adriosaurus microbrachis.* Legend: 1, bedded limestone; 2, thick bedded to massive limestone; 3, limestone with chert; 4, marly limestone; 5, platy limestone with chert; 6, limestone breccia; 7, dolomite; 8, dolomite breccia; 9, coal; 10, Flysch (sandstones, marls and breccias); 11, emersion.

teroposteriorly short and broad, only slightly constricted at midlength.

ADRIOSAURUS MICROBRACHIS, sp. nov.
(Fig. 2)

Holotype—MCSNT 7792, an articulated specimen missing the skull, and part of the cervical and caudal skeleton.

Etymology—From the Greek words "*micro*," meaning small, and "*brachis*," meaning arm, referring to the vestigial forelimb composed of only the humerus.

Locality and Horizon—Same as generic type (Jurkovšek et al., 1996; Cavin et al., 2000).

Species Diagnosis—Distinct U-shaped anterior coracoid emargination; forelimbs vestigial; ventral shaft of pubis straight, narrow, not expanded distally.

Description—The type and only known specimen of *Adriosaurus microbrachis* (MCSNT 7792) is exposed in ventral view (Fig. 2A). There are 2 cervicals, 28 to 29 dorsals, and 7 to 8 caudal vertebrae. The first 5 dorsal vertebrae are well-preserved and the centra and neural arches are short and broad; the bone of the remaining dorsals and ribs are sheared through the element (Fig. 2A,B). The articular faces of the prezygapophyses are inclined medially at about 20° from the horizontal; zygosphenes are present (Fig. 2C). All dorsal vertebrae and ribs are pachyostotic (Fig. 2A), similar to many secondarily adapted aquatic tetrapods (Nopcsa, 1923; Kaiser, 1966; Scanlon et al., 1999; Lee and Caldwell, 2000; Bejder and Hall, 2002). The proximal heads of both humeri are broad while the distal tips are very narrow; there is a fine vascular network on the external surface and a small but well-developed deltopectoral crest. The coracoids are ovate, the foramen is large, and there is a well-defined anterior coracoid emargination. The scapulae are small, and hatchet-shaped; the clavicles and interclavicle are not present. The hindlimb and girdle are well developed although poorly preserved. The left pubis is expanded proximally with a tubercle near the acetabulum; the ventral shaft is elongate and narrow. The femur is relatively short and has an unossified distal epiphysis. The tibia is expanded proximally while the fibula is expanded distally. The pes displays the plesiomorphic squamate phalangeal formula (2-3-4-5-[4?]) and the right astragalus is preserved.

DISCUSSION AND CONCLUSION

Biology vs. Taphonomy

The cornerstone of this study is our consideration that the preserved anatomy of *Adriosaurus microbrachis* is not an artifact of preservation/taphonomy, but rather is the result of biologic processes, in this case, limb reduction. Our rationale for concluding that the preserved anatomy is not taphonomic follows.

The head and tail were lost due to breakage along the margins of the block during quarrying, while the poor preservation of the axial skeleton and hindlimbs is due to splitting of the block, not pre-burial taphonomy. The pectoral girdle and forelimbs were not exposed at the time of collection. Preparation of the specimen (Figs. 2A, B; 3B) revealed tiny, perfectly symmetrical, right

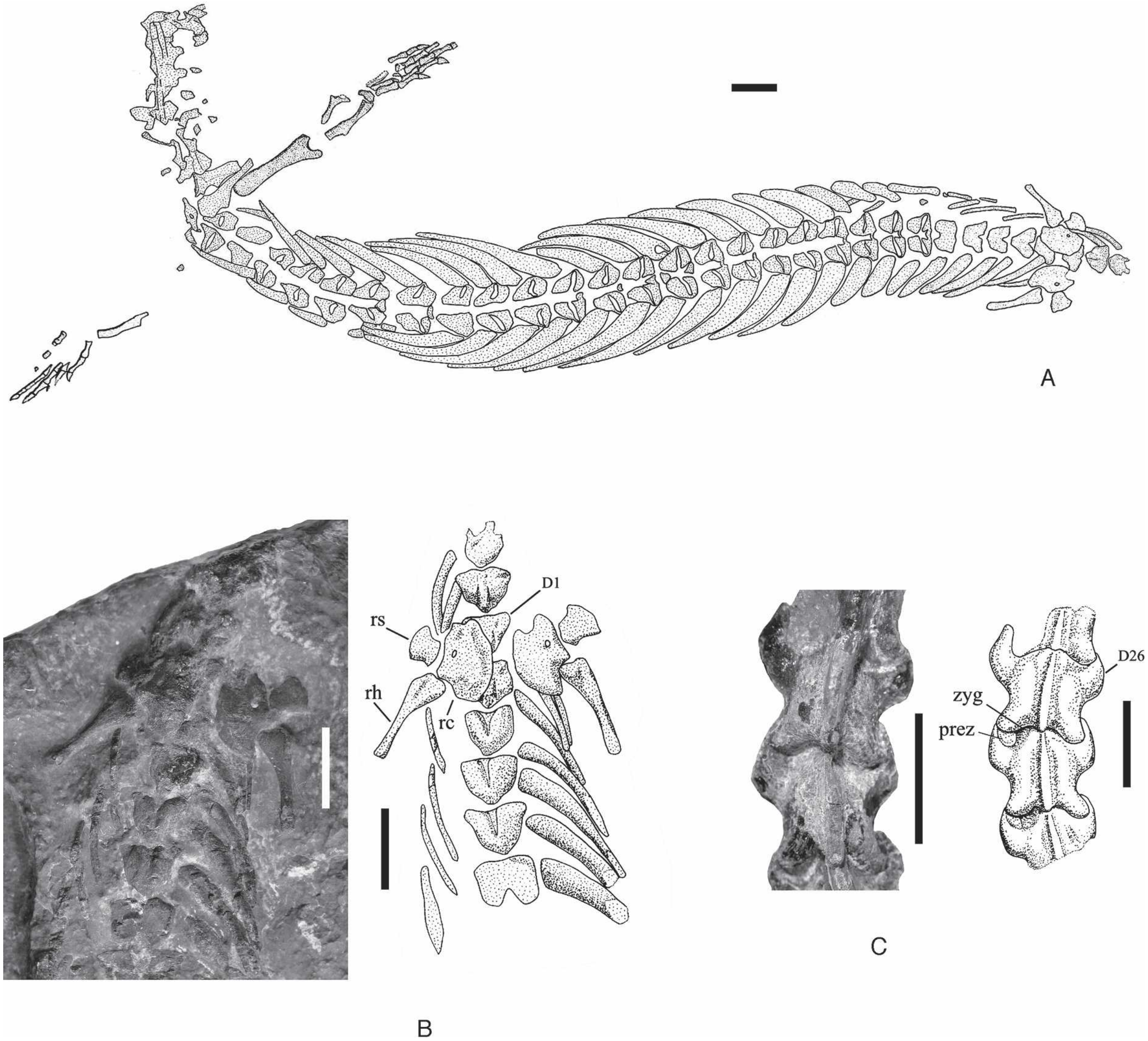

FIGURE 2. *Adriosaurus microbrachis* (MCSNT 7792). **A**, preserved portion of skeleton in ventral view. Note horizontally sectioned dorsal vertebrae exposing neural canal. **B**, photo and drawing of pectoral girdle, anteriormost dorsal and cervical vertebrae. **C**, photo and drawing of neural arches of posterior dorsal vertebrae. **Abbreviations**: **D1**, first dorsal vertebra; **D26**, twenty-sixth dorsal vertebra; **prez**, prezygapophysis; **rc**, right coracoid; **rh**, right humerus; **rs**, right scapula; **zyg**, zygosphene. Scale bar equals 5mm.

and left humeri, both of which taper distally instead of being expanded distally as are the femora (Fig. 2A) or other typical adriosaur humeri (Fig. 3A–D). The bone surface is so well preserved that very fine wrinkles are visible on the periosteum. Preparation distal to the humeri did not recover a single limb element from either side. Additionally, more proximal elements are present, that is, the very small, unfused coracoids and scapulae, but very much reduced in size. Dermal elements such as the clavicles and interclavicle are absent, as are the costal cartilages and calcified sternum (Fig. 2A). Finally, the anteriormost two to three ribs and vertebrae show reduced pachyostosis as compared to the remaining ribs (compare Fig. 2A, B with Fig. 3A–D). The significance of this latter phenomenon is difficult to interpret by comparison to extant limb-reduced squamates because none of them are known to display skeletal pachyostosis.

Form and Function

Based on these observations, we conclude that the anatomy of *Adriosaurus microbrachis* preserves evidence of evolutionary developmental loss of forelimb and girdle elements. This is the first known example of extreme forelimb reduction in a fossil squamate where only a vestige of the humerus is retained. Two additional specimens of *Adriosaurus* sp. (MCSNT 9400 and MCSNT 7793) confirm the presence of significant limb element variation within the genus (see Fig. 3). The humeri of *Adriosaurus* sp. (MCSNT 7793; Fig. 3C) are stouter, larger, and more pachyostotic than those of *A. suessi* (BMNH R2867; Fig. 3A); the largest individual, MCSNT 9400 (Fig. 3D), possesses a gracile humerus similar to BMNH R2867 and thus indicates that humeral robustness is not allometrically related to increasing size. We consider this variation to be demonstrative of species-level differences between closely related forms and relate it to the variation observed in the speciose living scincid genera, *Lerista* (Greer, 1987; 1990) and *Hemiergis* (Shapiro, 2002), where closely related species show a full spectrum of limb reduction to limblessness.

In terms of their function, the vestigial limbs of *Adriosaurus microbrachis* appear to have been too small to be of use in typi-

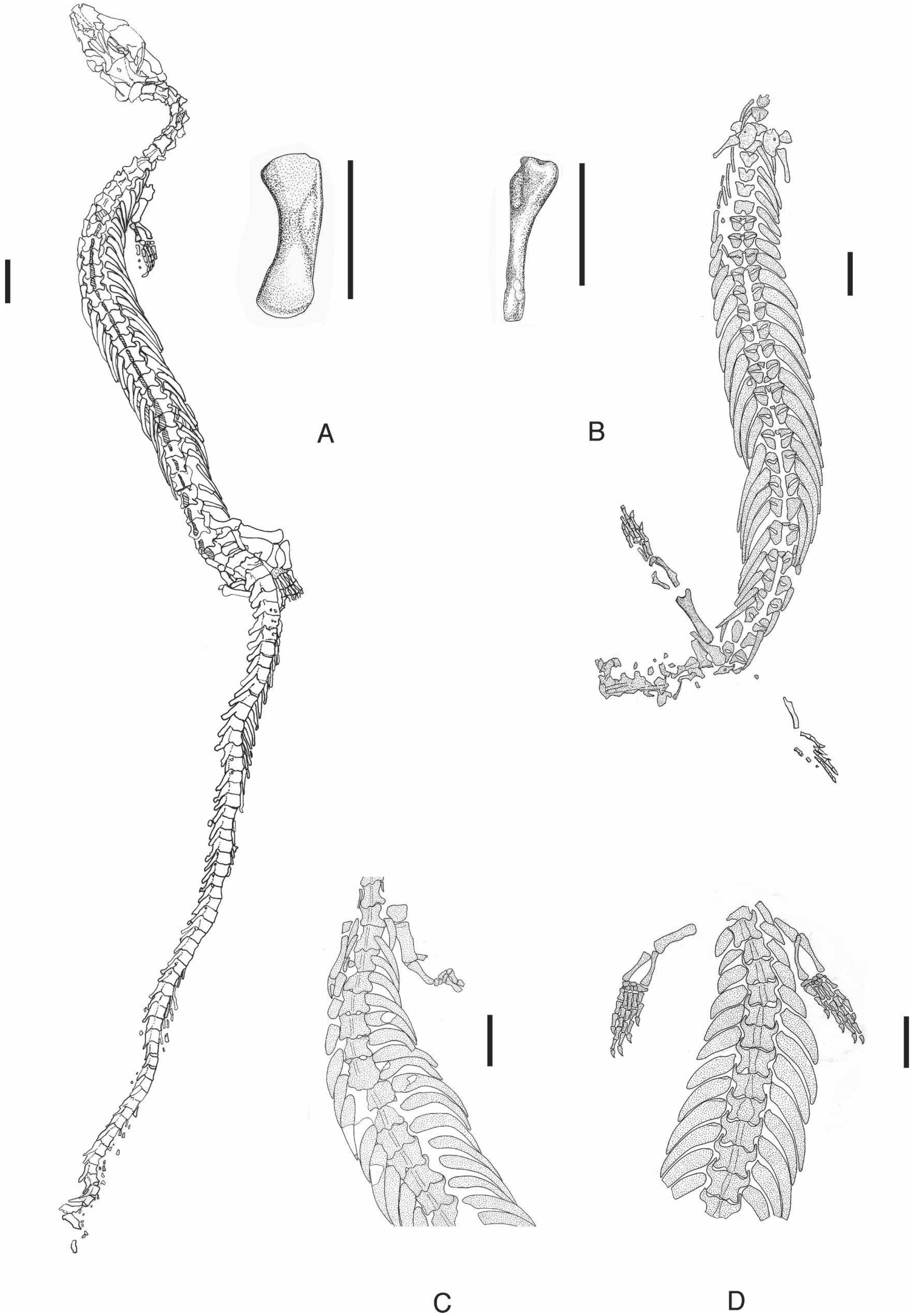

FIGURE 3. Comparison between *Adriosaurus suessi*, *Adriosaurus microbrachis*, and the two other specimens of *Adriosaurus* sp. **A**, *Adriosaurus suessi* (BMNH R2867) and magnification of right humerus. **B**, *Adriosaurus microbrachis* (MCSNT 7792) and magnification of right humerus. **C**, *Adriosaurus* sp. (MCSNT 7793). **D**, *Adriosaurus* sp. (MCSNT 9400). Note: *Adriosaurus suessi* (**A**) has a very stout and well-developed humerus as compared to slender and tapered humerus of (**B**) *Adriosaurus microbrachis*. Scale bar is 1 cm for all images except two magnified humeri, which is 5 mm.

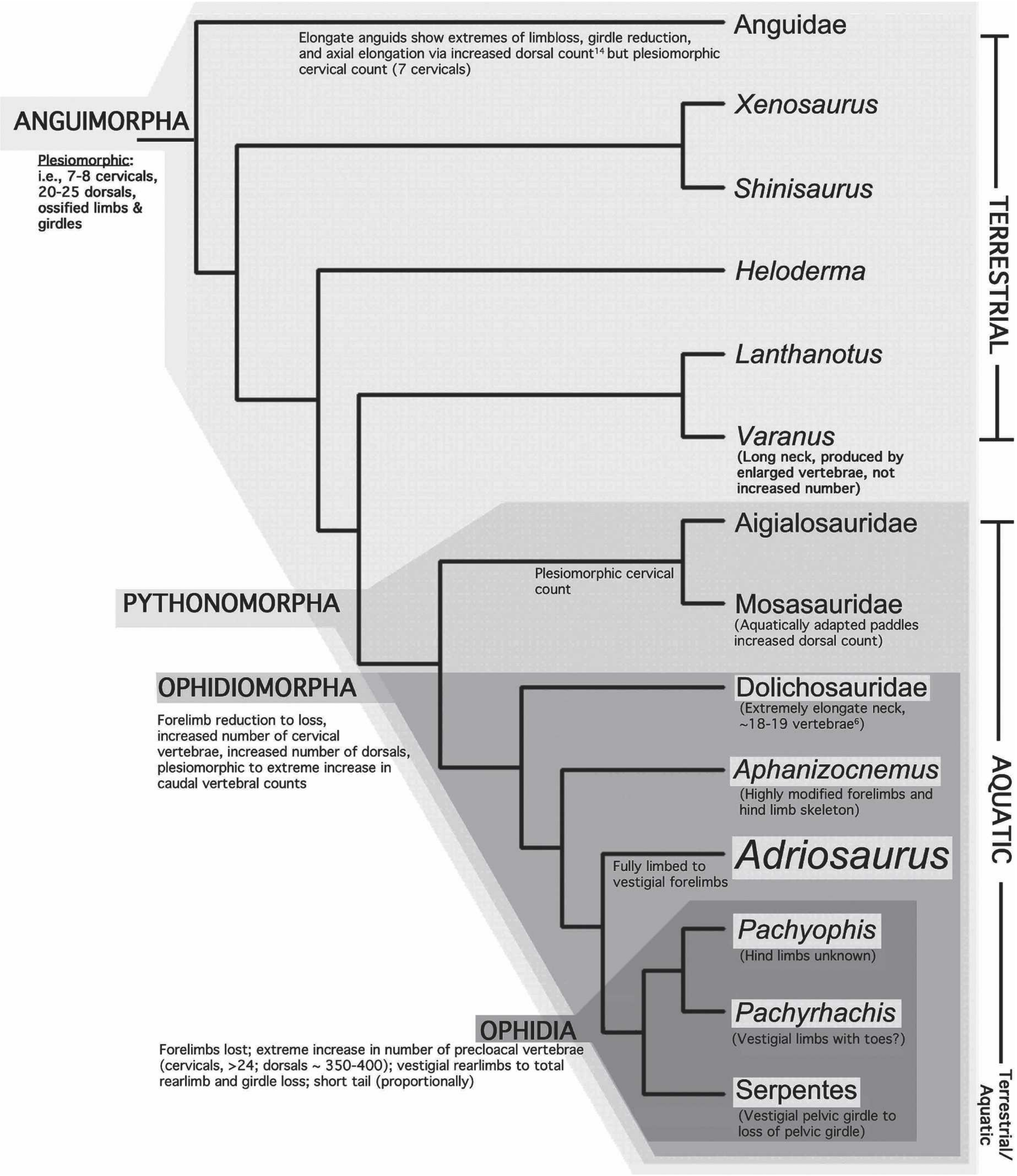

FIGURE 4. Limb, girdle and axial skeleton evolution within Anguimorpha. Phylogeny is derived by consensus from several recent studies (Lee and Caldwell, 2000; Lee and Scanlon, 2002). Distributions of plesiomorphic limb and axial states, and derived states for limb reduction, limblessness, and axial elongation, are mapped onto phylogeny. For Anguidae (the only non-ophidiomorph anguimorphs in which there are limbed and limbless forms), we include notations describing their morphology; for elongate neck of *Varanus*, it is noted that this is due to a doubling in size of cervical vertebrae. Additionally we identify a new clade, Ophidiomorpha, inclusive of Dolichosauridae (*Dolichosaurus*, *Coniasaurus* and *Pontosaurus*), *Aphanizocnemus*, *Adriosaurus*, and Ophidia (*Pachyrhachis*, *Pachyophis*, and Serpentes).

cal limb assisted tetrapodal locomotion and so had lost its original function (see Hall, 2003). In modern snakes that possess a remnant pelvic girdle and femoral spur, these anatomies are often overdeveloped in males and used to assist in maintaining cloacal position during intromission (we judge it unlikely that the humeral spikes of *A. microbrachis* performed a similar function). *A. microbrachis* likely spent most of its time in the water, locomoting in an angulliform manner with all of limbs pressed close to the body (Caldwell and Dal Sasso, 2004). When out of the water, it likely locomoted in a similar manner to modern scincids such as *Lerista* (Greer, 1987; 1990), which display a range of forelimb reduction from absent to fully limbed; these animals are cryptic, often use the large hindlimbs as friction points, and locomote using angulliform undulations of the entire body.

Evolutionary Patterns

While the anatomy of *Adriosaurus microbrachis* does not directly address the complex question of snake origins, the phylogenetic hypothesis finding adriosaurs and snakes to be sister taxa within a monophyletic Pythonomorpha allows inferences on the evolution of axial elongation and limb reduction/limbloss (see Fig. 4). In this context we recognize a unique form of axial elongation shared by ophidiomorph pythonomorphs: an increased number of vertebrae in both the neck and trunk (anterior to the cloaca), and a reduction of the forelimb and girdle leading to complete loss.

While the complete cervical series is not known for *Adriosaurus microbrachis*, we infer it to have at least 10 (cf. *A. suessi* BMNH R2867), and thus a precloacal vertebral count of 38 to 39. The fully limbed Cenomanian marine squamate, *Dolichosaurus longicollis*, possesses 32 dorsals, and 17 to 19 cervicals, for a total of 49–51 presacrals and is approaching the maximum number of 60 presacrals observed among elongate tetrapods still possessing a forelimb and pectoral girdle (Caldwell, 2003). Importantly, for all known fossil and extant snakes, the pectoral girdle is absent, the neck appears to be very long (based on osteological characters), and the total precloacal count is significantly greater than 100 vertebrae. Complete loss of the forelimb and girdle appears to have been essential to the extreme elongation of the precloacal region of snakes.

Again, basal ophidiomorphans provide some insights on the evolution of the forelimb and girdle reduction and loss. In *Dolichosaurus longicollis* and *Pontosaurus kornhuberi* (Caldwell, 2006) the calcified sternum only possesses three facets for ribs, while in *Adriosaurus microbrachis* there is no sternum and thus no sternal ribs. This contrasts with the condition on *Carsosaurus marchesetti*, a basal mosasauroid, where there are five sternal ribs, and with mosasaurs, where there are as many as seven. Examined phylogenetically (Fig. 4), basal ophidiomorph and snake anatomy strongly suggests that complete loss of the forelimb and girdle appears to have been essential to the evolution of extreme axial elongation.

Molecules and Musculature

It is critical to note that our hypothesis that snakes have a long neck (see also Caldwell, 2000; 2003; Scanlon, 2004) is dependent on osteological criteria describing the presence, number and type of anguimorph-like hypapophyses and peduncles (intercentra). However, as the conventional osteological landmark for demarcating the posterior terminus of the neck is the pectoral girdle (specifically the vertebra bearing the first sternal rib), the neck of snakes remains problematic despite the presence of hypapophyses (Hoffstetter and Gasc, 1969).

In attempting to find other criteria for addressing the evolution of elongate axial skeletons, Cohn and Tickle (1999), using molecular genetic data, proposed that the neck is absent in snakes. They found that in *Python*, the *Hox* gene, HoxC8, normally expressed axially just posterior to the pectoral girdle (i.e., in limbed tetrapods), was expressed anteriorly up to the first or second vertebra. In addition, it was noted that anterior vertebrae have ribs, and that a large number of vertebrae, far posterior to the tetrapodal pectoral girdle, possess ventral hypapophyses (a neck character). The authors concluded that anterior ribs indicated that thoracic identity had been overprinted onto the snake 'neck', and that the trunk resembles an elongated thorax (Cohn and Tickle, 1999). However, the presence of ribs on anterior vertebrae (cervical ribs and cervical vertebrae) is a primitive character of tetrapods (Caldwell, 2003; Scanlon, 2004). Thus the overprint of regional identity appears to be cervical, not thoracic.

A third, and very recent hypothesis based on data homologizing the lizard m. episternocleidomastoid (ESCM) with the snake m. cervicoquadratus (CQ), is that snakes have a comparatively short neck (no more than 11 vertebrae) (Tsuihiji et al., 2006). This conclusion is interesting but problematic because 11 vertebrae actually constitute a long squamate neck, and is consistent with the value of 10 or more as a synapomorphy for Ophidiomorpha. The origin of the snake CQ is in the dermis or fascia while its insertion is on the quadrate. In contrast, the origin (pectoral girdle elements) and insertion (cranial elements including the quadrate) of the lizard ESCM is very complex. Additionally, the ESCM is, with the exception of amphisbaenids, innervated by cranial nerve XI (spinal accessory), which is absent in snakes and amphisbaenids. The only similarities between CQ and ESCM are the quadrate insertion and innervation by two to three spinal nerves, rendering the hypothesis of homology by Tsuihiji and colleagues (2006) as very problematic. Recognizing this, the authors note that osteological, myological and molecular data present three different patterns for identifying the neck in snakes.

Conclusions

Whether the patterns of limbloss and axial elongation observed in Upper Cretaceous aquatic snakes and lizards are convergent or homologous remains controversial. To properly address this problem, the synergistic efforts developing between evolutionary developmental biology and paleontology must be directed toward addressing the criteria for defining anatomical regions with developmental boundaries. Otherwise, any attempts to understand the evolution of anatomy, such as that displayed by *Adriosaurus microbrachis*, will be brought up short by the limitations of a static system, that is, the limits of an individual, when the real goal is to understand the transformation of those systems within populations, and between species and other higher taxa.

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