On the Origin and Evolution of the Ophidia

by

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ABSTRACT

With well over 3,400 described species, snakes undoubtedly represent one of the most successful groups of reptiles. Much has been written about their ecology, behavior, anatomy, relationships and evolution. However, despite the debate about the origin of this taxonomic group dating back to the second half of the XIX century, no consensus has been reached, yet. Scenarios that portray the first snakes as evolving from aquatic lacertilian ancestors are countered with others that see the first snakes as the result of long-term adaptations to a burrowing, cryptic lifestyle. The supporters of the first type of scenario found their evidence mostly in osteological comparisons of non-burrowing snakes with extinct aquatic lizards (e.g., mosasaurs, dolichosaurs and adriosaurs), while the supporters of the second type of scenario base their conclusions mostly on anatomical comparisons between modern legless squamates and burrowing snakes. The debate is further complicated by the scarcity of well-preserved fossil remains that may help elucidate the origin of the group, and by the contradictory interpretations that different authors have provided after examination of the same fossil specimens. Therefore, the goal of this work was that of analyzing all the evidence that has been put forward so far in support of the two main origin scenarios, critically evaluate the contradictory evidence provided by different researchers, examine first-hand all the pivotal extant and fossil taxa that have been used in the formulation and support of each scenario, and provide a phylogenetic analysis of snakes within squamate reptiles that is based both on molecular and morphological data. The examination of over 400 specimens of squamates, including both extant and fossil species, lead to the following results: (1) the redescription of several important fossil taxa (*Pachyrhachis*, *Eupodophis*, *Haasiophis*, *Najash*, and *Dinilysia*), and the identification, in some of them, of anatomical features never reported before (e.g., chevron bones in *Haasiophis*, mental foramina and a sacral vertebra in *Pachyrhachis*); (2) the discovery of new material (a pelvic girdle) attributable to the fossil species *Wonambi naracoortensis*, a snake whose pelvic anatomy was previously unknown; (3) the retrieval of evidence that supports a reinterpretation of the circumorbital bones of snakes, with particular regard to the “postorbital” and the “supraorbital”, here reinterpreted as primary homologues of the jugal and postfrontal, respectively; (4) a detailed assessment of what constitutes the “crista circumfenestralis” of snakes and how this anatomical feature varies within the Ophidia; (5) new hypotheses regarding the ingroup relationships of snakes, which imply a possible convergent evolution of the macrostomatan skull condition, and the possibility that scolecophidians may represent an aberrant lineage of alethinophidian snakes.

PREFACE

Some of the research conducted for this thesis forms part of an international research collaboration, led by Professor Michael W. Caldwell at the University of Alberta. The literary reviews in chapters one and two, as well as the phylogenetic analyses in chapter eight, are entirely the product of my original work, with some minor edits from my supervisor (M. W. Caldwell).

Chapter three of this dissertation has been published as Palci, A., M. W. Caldwell, and R. L. Nydam (2013), Reevaluation of the anatomy of the Cenomanian (Upper Cretaceous) hind-limbed marine fossil snakes *Pachyrhachis*, *Haasiophis*, and *Eupodophis*, *Journal of Vertebrate Paleontology*, vol. 33, issue 6, 1328–1342. I was responsible for the collection of the data and part of its interpretation, manuscript composition, figures, and phylogenetic analyses. M. W. Caldwell and R. L. Nydam contributed to manuscript edits and some of the interpretations. R. L. Nydam also contributed to enhancing the contrast and sharpness of some of the figures.

Chapter four of this dissertation has been published as Palci, A., M. W. Caldwell, and A. M. Albino (2013), Emended diagnosis and phylogenetic relationships of the Upper Cretaceous fossil snake *Najash rionegrina* Apesteguía and Zaher, 2006, *Journal of Vertebrate Paleontology*, vol. 33, issue 1, 131–140. I was responsible for the collection and interpretation of the data, manuscript composition, figures, table, and phylogenetic analyses. M. W. Caldwell and A. M. Albino contributed to manuscript edits.

Chapter five of this dissertation has been published as Palci, A., M. W.

Caldwell, and J. D. Scanlon (2014), First report of a pelvic girdle in the fossil snake *Wonambi naracoortensis* Smith, 1976, and a revised diagnosis for the genus, *Journal of Vertebrate Paleontology*, vol. 34, issue 4, 965–969. I was responsible for the collection and interpretation of the data, manuscript composition, and figure. M. W. Caldwell and J. D. Scanlon contributed to manuscript edits.

Chapter six of this dissertation has been published as Palci, A., and M. W. Caldwell (2013), Primary homologies of the circumorbital bones of snakes. *Journal of Morphology*, vol. 274, issue 9, 973–986. I was responsible for the collection and interpretation of the data, manuscript composition, figures, and tables. M. W. Caldwell was involved with concept formation and contributed to manuscript edits.

Chapter seven of this dissertation has been published as Palci, A., and M. W. Caldwell (2014), The Upper Cretaceous snake *Dinilysia patagonica* Smith-Woodward, 1901, and the crista circumfenestralis of snakes, *Journal of Morphology*, vol. 275, issue 10, 1187–1200. I was responsible for the collection and interpretation of the data, manuscript composition, figures, and tables. M. W. Caldwell was involved with concept formation and contributed to manuscript edits.

Chapter nine of this dissertation provides the general conclusions to the whole dissertation, and as such, it represents the product of my original work, with the only exception of portions of text that were adapted from the abstracts of the above-mentioned published chapters, which may include minor edits from my co-authors.

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Institutional Abbreviations

AMNH, American Museum of Natural History, New York, NY; **ANSP**, Academy of Natural Sciences of Philadelphia, Philadelphia, PA, USA; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, PA, USA; **FMNH**, Field Museum of Natural History, Chicago, IL; **GBA**, Austrian Geological Survey, Wien, Austria; **HUI-Pal** Hebrew University of Jerusalem, Paleontology Collections; **LACM**, Los Angeles County Museum, Los Angeles, CA, USA; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; **MCSNT**, Museo Civico di Storia Naturale di Trieste, Trieste, Italy; **MCZ**, Museum of Comparative Zoology, Cambridge, MA; **MLP**, Museo de La Plata, La Plata, Argentina; **MSNM**, Museo di Storia Naturale di Milano, Milano, Italy; **NHML**, Natural History Museum, London, England; **QM**, Queensland Museum, Brisbane, Australia; **Rh-E.F.**, Natural History Museum of Gannat, Gannat, France; **FHSM**, Fort Hays Sternberg Museum, Fort Hays, Kansas, USA; **SMF**, Senkenberg Museum, Frankfurt, Germany; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; **UAMZ**, University of Alberta Museum of Zoology, Edmonton, Alberta, Canada; **UF**, University of Florida, Gainesville, FL; **USNM**, United States National Museum of Natural History, Washington, DC; **YPM**, Yale Peabody Museum, New Haven, CT; **ZFMK**, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Anatomical Abbreviations

Because of the great variability of the abbreviations used in this work (sometimes the same abbreviation was applied to different features) the reader is referred to the list of abbreviations contained in each figure caption.

CHAPTER ONE

GENERAL INTRODUCTION: WHAT IS A SNAKE?

HISTORY OF THE SYSTEMATICS OF THE OPHIDIA

Snakes are a unique group of organisms that in one way or another have always had a special role in human history and culture, from the mythical snake of the Garden of Eden to the adder that killed Queen Cleopatra. Some people may find snakes terrifying and repulsive, others beautiful and fascinating, but what everybody has in common is a reverent respect and admiration for these creatures, which have thrived on this planet for millions of years, long before humans made their appearance. Perhaps it is because of their prehistoric appearance, supple bodies and magnetic reptilian eyes that many of us find them so captivating and interesting, while it's likely the potent venom of some of their representatives that causes fear and repulsion in others.

Snakes are so deeply entwined into human culture that no matter which part of the world one may live in, if snakes are part of the local fauna they also have an important role in local folklore, myths and legends; be it the Basilisk or the Hydra of ancient Greece, the Quetzalcoatl of the Aztecs, the Nagas of India, or the of sea serpent Midgard of Scandinavian mythology (Fourcade, 1994).
All of these myths, legends and historical anecdotes have in common creatures that are referred to as "snakes" or "serpents".

People all seem to know what a snake is even though their definition of 'snake' seems to differ somewhat. This leads to a more biological question - what is a snake? The first scholar who is known to have tried to provide a definition of what is a snake was the Greek philosopher Aristotle in his "History of the Animals", which dates back to ~ 350 B.C. Here is his definition:

"*An animal that is blooded and capable of movement on dry land, but is naturally unprovided with feet, belongs to the serpent genus; and animals of this genus are coated with the tessellated horny substance. Serpents in general are oviparous; the adder, an exceptional case, is viviparous*." [Aristotle, History of the Animals, Book I, Chapter VI]

Interestingly, Aristotle was also the first to propose a classification scheme for organisms that constitutes the basis for modern systematics. In particular, he introduced the concepts of "*Genos*" and "*Eidos*", or "genus" and "species" (Serafini, 1993). According to Aristotle the "genus" was a general, more inclusive, category of organisms, and genera could be nested within each other. For example he considered "quadrupeds" (basically what we would call tetrapods in modern systematics) to be a genus, and "tessellates" (animals with scales or scutes) to be another genus included within quadrupeds. Serpents would constitute yet another genus within tessellates, while the viper and the adder would be two species within the genus serpents.

Aristotle was also one of the first scholars to realize that snakes most closely resemble lizards, and that the main distinguishing features are represented by axial elongation of the body and limb loss in the former group of organisms:

"*The serpent genus is similar and in almost all respects furnished similarly to the saurians among land animals, if one could only imagine these saurians to be increased in length and to be devoid of legs. That is to say, the serpent is coated* *with tessellated scutes, and resembles the saurian in its back and belly; only, by the way, it has no testicles, but, like fishes, has two ducts converging into one, and an ovary long and bifurcate. The rest of its internal organs are identical with those of the saurians, except that, owing to the narrowness and length of the animal, the viscera are correspondingly narrow and elongated, so that they are apt to escape recognition from the similarities in shape. Thus, the windpipe of the creature is exceptionally long, and the oesophagus is longer still, and the windpipe commences so close to the mouth that the tongue appears to be underneath it; and the windpipe seems to project over the tongue, owing to the fact that the tongue draws back into a sheath and does not remain in its place as in other animals. The tongue, moreover, is thin and long and black, and can be protruded to a great distance. And both serpents and saurians have this altogether exceptional property in the tongue, that it is forked at the outer extremity, and this property is the more marked in the serpent, for the tips of his tongue are as thin as hairs*." [Aristotle, History of the Animals, Book II, Chapter XII]

The years that followed Aristotle's classificatory efforts did not see much progress in systematics until the works of the Swiss botanist Kaspar Bahuin and the first introduction of "binomial nomenclature" at the end of the 16th century, a classification system that would be further elaborated and popularized by the Swedish naturalist Carolus Linnaeus (Latinized version of Carl von Linné) about two centuries later (Serafini, 1993).

After Aristotle, Linnaeus is the next scholar known to have provided a tentative scientific definition of what is a snake. Linnaeus (1735) first introduced the term "Serpentia" as a synonym of what we would today call amphibians and reptiles, his first use of the 'Ordo Serpentia' in a less inclusive and a more modern sense can be found in the second edition of his Systema Naturae, published in 1740. Linneaus (1740) grouped under the name "serpents" several axially elongated and limbless organisms, which apart from snakes proper (i.e., as intended today) also included legless lizards, and caecilians. Later, in the edition published in 1756, consistent with his original diagnosis, Linnaeus also added amphisbaenians to his Serpentia.

According to Linnaeus (1740, 1756), serpents were "Amphibia" (defined by him as having "*corpus nudum aut squamosum, dentes molares nulli, omnes acuti, pinnae nullae radiate*" = "body either naked or covered in scales, lack of molar teeth, all teeth are pointed, absence of ray fins), and the basic feature that was considered diagnostic of snakes among other "amphibians" consisted in the absence of limbs (his original diagnosis simply read "*pedes nulli*" = "lack of feet"); Linneaus (1758) slightly modified his definition for this latter group in the tenth edition of the Systema Naturae. In this volume Linneaus used the term "Serpentes" rather than "Serpentia", introducing the taxonomic term that is still used in modern systematics. His new definition of Serpentes read as follows: "*os respirans, pes pinnaeue* [note of the author: most likely "*pinnaeque*"] *nullae*" = organisms that breath from their mouth and lack feet or fins". However, despite the new definition, Linneaus still included his Ordo Serpentes within his Classis

"Amphibia" and the former was again inclusive of not only snakes, but also caecilians, amphisbaenians and legless lizards.

In the years that followed the pioneering works of Linneaus, several scholars tried to refine the concept of what is a snake. The first of them was Brongniart (1800a,b), who proposed the name "Ophidiens" to be used instead of Linnaeus' Serpentes, a term that would later be latinized into "Ophidia" and be used interchangeably with Serpentes. Brongniart's (1800a) "Ophidiens" was defined as reptiles that, like crocodilians, chelonians and lizards, have long curved ribs, are capable of internal fertilization, that lay eggs with a calcareous shell, and whose hatchlings are similar to their parents in all respects (this point was made mostly to highlight the differences between the two main groups that in modern systematics would be called reptiles and amphibians). The main differences between Brongniart's "Ophidiens" and other Saurians (i.e., crocodilians and lizards, according to his classification scheme) consisted in the fact that the former have only one ventricle (Brongniart used the improper term "oreillette", which translates into "atrium"; however, all tetrapods are known to have two atria [Kardong, 2002]) in their heart, lack a sternum, the males have a paired penis, the females lay eggs with a soft calcareous shell, and they have no legs. Similarly to Linnaeus' definition of Serpentes, Brongniart (1800b) included in his "Ophidiens" amphisbaenians and legless lizard along with snakes. Caecilians were tentatively placed in this order, but with a note explaining that their anatomy was still too poorly known at the time to allow the accurate systematic placement of this taxon. Brongniart's (1800a) definition of his Order

"Ophidiens" is no less problematic than the preceding ones by Linnaeus, because it fails to point out anatomical features that are really unique to the group and also contains errors in the differential part of the diagnosis (e.g., limbed lizards have one ventricle and a paired penis as well [Kardong, 2002], and some of them lay eggs with soft calcareous shells [Kohring, 1995]).

Oppel (1811) was the first to realize that caecilians should be better placed in a distinct order (note: Oppel referred to this order as "Nuda", after the terminology of Klein, he did not recognize Linneaus' taxonomic term "Amphibia") as well as legless lizards, which he placed in the Saurii (i.e, lizards and crocodilians according to Oppel's classification). Amphisbaenians and snakes were still both in the Ophidii, and both Ophidii and Saurii were placed within his Squamata (note: Oppel's [1811] Class Reptilia included the Orders Testudinata [turtles and tortoises], Squamata [snakes, lizards and crocodilians] and Nuda or Batrachia [amphibians]; Linneaus, on the other hand, considered the category "Reptilia" to be part of his "Amphibia", this might explain why he grouped the caecilians with legless squamates).

Oppel's (1811:53) definition of Ophidii was as follows: "*corpus elongatum, cylindricum, pedibus, sterno, pelvique carens, squamis obtectum. Penis duplex*", which in English translates as "body elongate and cylindrical, lacking feet, sternum and pelvis, covered with scales. Paired penis".

Merrem (1820) agreed with Oppel (1811) in the removal of legless lizards from the Ophidii or Serpentes. Merrem (1820:9) defined his Tribus Serpentia (a subdivision of the Ordo Squamata) as having the following features: "*Pedibus,* *Scapulis, Sterno et Pelvi omnes omnino carent. Condylus occipitis trifidus. Vertebrae colli 0; dorsi 50–300. lumbales et sacrales 0. Pulmo unus, siepissime cum secondi rudimento. Lingua bifida, extensilis. Aures latentes. Membrana tympani nulla. Canales semicirculares membranacei. Oculi cute communi tecti, absque palpebris et membrana nictitante*”, which in English reads as “feet, scapulae, sternum and pelvis are all completely absent. Occipital condyle is tripartite. Cervical vertebrae 0. Dorsal vertebrae 50–300; lumbar and sacral vertebrae 0. One lung, rarely with a rudiment of a second lung. Bifid, extensile tongue. Ears concealed. Tympanic membrane absent. Membranous semicircular canals. Eyes are covered by a scale, without eyelids or nictitating membrane”.

Shortly after, Gray (1825) removed amphisbaenians from the order, however, along with them he also removed blind snakes (i.e., scolecophidians, a group that at the time was classified under the family name Typhlopsidae) and placed both with skinks and anguids in his Saurophidii. Gray (1825) considered snakes, his Ordo Ophidii, simply as reptiles that lack both legs and ears and at this point one may wonder why the author placed his Typhlopsidae (i.e., scolecophidian snakes) outside of this group. The answer probably lies in the personal opinion of the author, who saw amphisbaenians as intermediate forms between Typhlopsidae and Chalcidae (i.e., skinks) and for this reason thought it natural to group these organisms together.

We have to wait a few more years before Wagler (1830) finally defines Serpentes in the modern sense, i.e., as including scolecophidian snakes but excluding legless lizards and amphisbaenians. Here follows the brief but incisive diagnosis proposed by Wagler (1830:165) for the order Serpentes: "*tomia mandibulae in apice ligamento connexa*", which in English translates as "mandibles connected by a ligament at their apex".

After a universal agreement on what should be considered a snake was reached with Wagler (1830), a series of works bent on putting some order among the different groups of snakes were published. The principal works on this matter were certainly those of Müller (1831), Duméril and Bibron (1844), Duméril (1853), Cope (1864), Nopcsa (1923) and Hoffstetter (1939).

Müller (1831) proposed a division between snakes capable of large gapes, what he called the Macrostomata, and snakes with limited gape sizes, the Microstomata; the latter taxon consisted of two groups of snakes that modern taxonomists would call the Scolecophidia (i.e., Typhlopidae, Leptotyphlopidae and Anomalepididae) and the Anilioidea (i.e, *Anilius*, *Cylindrophis*, and Uropeltidae), and, despite Gray (1925), Müller (1831) also placed amphisbaenians within this taxon. The inclusion of amphisbaenians within Müller's (1831) Microstomata was probably the reason why the taxon name was abandoned shortly after.

Duméril and Bibron (1844) were the first to provide a taxonomic name that refers to all blind snakes, their "Scolecophides", a name that was later latinized into Scolecophidia and formally introduced as a taxon by Cope (1864).

Cope (1864) is also notable for having added to Wagler's (1830) diagnosis of snakes a second unequivocal feature that can be used to distinguish the taxa Lacertilia and Ophidia. The Ophidia are characterized by Cope (1864) not only as having a ligamentous connection at the tips of their dentaries (a feature already pointed out by Wagler [1830] but not unique to snakes), because it is also found in mosasauroids and dolichosaurs [Russell, 1967; Carroll and DeBraga, 1992; Pierce and Caldwell, 2004; Caldwell, 2006]. Cope (1864) also noted that snakes have the lateral descending walls of the parietal which meet the sphenoid in a close contact. This last feature is typical of all snakes, and other squamates typically have a more or less large gap between parietal and sphenoid. This holds true even when the descending flanges of the parietal are extremely well developed (e.g., in Dibamidae, *Anniella*, *Acontias*, and most Amphisbaenia; pers. obs.). However, a contact between the descending flanges of the parietal and the basisphenoid can be observed in *Amphisbaena* (pers. obs).

Duméril (1853) used dental features to further subdivide snakes into Opoterodontes (snakes that lack teeth on either maxilla or mandible, a group redundant with Duméril and Bibron's [1844] Scolecophides), Aglyphodontes (snakes that have teeth on both upper and lower jaws, but whose crowns lack grooves), Opisthoglyphes (snakes that have teeth on both upper and lower jaws, and have grooved teeth at the back of their maxillae), and Solenoglyphes (snakes that are characterized by a single large hollow fang on each maxilla).

Following the work of Duméril and Bibron's (1844) were the monumental monographs on snake classification by Boulenger (1893, 1894 and 1896) and Cope (1900). After the Scolecophidia, the other major group of snakes was named by Nopcsa (1923), who divided snakes into the two main categories Angiostomata (a junior synonym of Scolecophidia) and Alethinophidia (i.e., all other living snakes). Moreover, Nopcsa grouped all fossil snakes known at that time (i.e, *Archaeophis*, *Pachyophis*, *Palaeophis* and *Simoliophis*) into the Cholophidia, which he believed to be an ancestral stock of snakes from which both his Angiostomata and Alethinophidia would have originated.

The most recent major contribution to the taxonomy of snakes was made by Hoffstetter (1939), who divided Nopcsa's (1923) Alethinophidia into primitive forms, what he called the Henophidia (anilioids, boas and pythons), and more derived taxa (*Acrochordus* and colubroids), that he called the Caenophidia.

Important revisions to the classification of snakes were later made by Romer (1956), Underwood (1967), McDowell (1974, 1975, 1979) and Rieppel (1979), but these works mostly dealt with smaller taxonomic subdivisions and rearrangement of genera within the major taxa discussed above. It should be noted that Romer (1956) used the terms Typhlopoidea, Booidea and Colubroidea instead of the equivalent terms Scolecophidia, Henophidia and Caenophidia respectively; however, the term Typhlopoidea was shortly after abandoned in favor of the more widely used Scolecophidia, the term Booidea was made equivalent with a subset of Hoffstetter's (1939) Henophidia (i.e., Booidea = Henophidia – Anilioidea) and the Colubroidea became a subset of the Caenophidia (i.e., Colubroidea = Caenophidia – *Acrochordus*) (Underwood, 1976; Rieppel, 1979).

In more recent years, with the advent of cladistics methods of phylogenetic analysis, several studies tried to identify the closest relatives of snakes among lizards, (e.g., Estes et al., 1988; Wu et al. 1996; Caldwell and Lee, 1997; Lee, 1997, 1998, 2000, 2005a, 2005b, 2009; Lee and Caldwell, 1998; Reinoso, 1998; Zaher, 1998; Caldwell, 1999; Townsend et al., 2004; Vidal and Hedges, 2004, 2005; Evans et al., 2005; Evans and Wang, 2005; Conrad 2008; Albert et al., 2009; Wiens et al., 2010; Müller et al., 2011; Gauthier et al., 2012). These studies were based on morphological data, molecular data or both. Of note among these studies is the first morphology-based phylogeny of Squamates by Estes et al. (1988), where the authors identified 6 unique derived features that typify snakes:

1) Supraoccipital excluded from the margin of the foramen magnum by the exoccipitals (rare exceptions).
2) Crista circumfenestralis present, surrounding the fenestra ovalis.
3) Dentaries loosely united at symphysis.
4) Opthalmic branch of trigeminal nerve enclosed within braincase by lateral downgrowths of parietal, usually entering orbit through orbit foramen.
5) No muscles in ciliary body of the eye.
6) Left systemic arch larger than the right (some exceptions) (note: as pointed out by Lee and Scanlon [2002] this should read: “right systemic arch larger than the left”).

However, it is interesting to note that Estes et al. (1988) did not include any fossil taxa in their analysis. If they had, then their list of unique features of snakes may have been shorter. For example, the lack of a bony symphysis (character 3 in the list above) is not a unique trait defining snakes, but also occurs in mosasaurs and dolichosaurs, two fossil groups that were not included in Estes et al's (1988) phylogenetic analysis of squamates. Also the presence of a crista circumfenestralis as a unique feature defining snakes may be argued against, for two reasons: 1) a very similar structure (i.e., a bony crest originating from contributions of the prootic and opisthotic and surrounding the stapedial footplate) can be observed also in the scincid genus *Acontias*; 2) some snakes lack a crista circumfenestralis (e.g., *Acrochordus*, *Xenopeltis*, *Dinilysia*).

More recently, Lee and Scanlon (2002) provided a more comprehensive list of anatomical features that may be considered unique to snakes:

1) Descending flanges of frontal and parietal meet parabasisphenoid (and enclose ophthalmic branch of the trigeminal nerve)
2) Crista circumfenestralis.
3) Long ventral process of postorbital.
4) Vomer medial to palatine.
5) Palatine has anterior dentigerous process.
6) Dentary has deep posterolateral notch.
7) Two or fewer mental foramina in dentary.
8) Teeth ankylosed to rims of sockets,

9) Vertebral zygapophyses inclined less than 30°
10) Hypapophyses present at least up to tenth presacral vertebra.
11) Epiphyses absent on axial and appendicular (hind limbs) skeleton.
12) Shoulder girdle and forelimbs completely absent.
13) Maxilla barely, if at all, overlapping the lateral surface of the prefrontal.
14) Mobile maxilla-premaxilla contact.
15) Skull platytrabic (trabeculae cranii do not fuse in orbital region, no interorbital septum).
16) Rods primitively present in retina (lizards have only cones).
17) Ciliary body of eye lacking muscles.
18) Gall bladder lies far behind liver, with the connecting (cystic) duct being long.
19) Right systemic arch much larger than left. (note: opposite of Estes et al., [1988]).
20) Right kidney distinctly anterior to left kidney.

So far, this is the most exhaustive list of synapomorphies that can be used to define the clade Ophidia; however, as pointed out by Lee and Scanlon (2002), some of these characters have been modified or lost in some aberrant lineages. Even so, some characters remain problematic, and for example, as already pointed out above for Estes et al. (1988), the presence of a crista circumfenestralis can arguably be used to define snakes as a group, especially if it is absent from the likely primitive snake *Dinilysia patagonica* (Estes et al.

1970; but see Zaher and Scanferla, 2012). The fact that this feature may be primitively absent in snakes refutes Lee and Scanlon's (2002) assumption that it would be secondarily lost only in some highly derived lineages. Also the position of the vomer medial to the palatine is problematic, as is the presence of a dentigerous process on the latter element; in fact, these two features are correlated, because it is the anterior dentigerous process of the palatine that extends lateral to the vomer; however, such a process is absent in the fossil snake *Dinilysia patagonica*, and consequently the palatine does not occupy a position lateral to the vomer in this taxon. The mobile articulation between maxilla and premaxilla is another feature that is not really unique to snakes among Squamates, as it is observed also in the dolichosaur *Pontosaurus korhuberi* (Caldwell, 2006). Last but not least, the platytrabic skull is a condition also found in the semiaquatic lizard *Lanthanotus borneensis* (Rieppel, 1983).

At present, the most comprehensive morphological study of squamate reptiles is that of Gauthier et al. (2012), who compiled a data matrix consisting of 192 taxa and 610 characters. Despite the large number of characters used, these authors retrieved a smaller number of synapomorphies for the clade Ophidia (i.e, the clade inclusive of all fossil and living snakes) than Lee and Scanlon (2002). However, this could be due to the fact that Gauthier et al. (2012) included several fossil taxa that can break up long branches in the phylogeny. The synapomorphies retrieved by Gauthier et al. (2012) are listed below, with some comments provided in brackets where necessary:

1) Parietal overlaps supraoccipital on midline (modified in some derived snakes).
2) Supratemporal lengthens (i.e., extends anteriorly) anterior to level of parietal notch (however, snakes lack a parietal notch).
3) Quadrate does not overlap pterygoid, ligamentous connection only.
4) Braincase not fused in adult (i.e., prootic, basioccipital and otooccipitals remain separate).
5) Supraoccipital origin of temporal muscles spread onto supraoccipital contacting nuchal crest in roughly T-shaped outline (Y-shaped in some derived forms; crest absent in Scolecophidia).
6) Supraocciptal nuchal crest extends laterally (partially redundant with previous character).
7) Anterior margin of trigeminal foramen/foramina enclosed by descending flange of parietal.
8) Long cultriform process.
9) Basipterygoid process present and formed by outgrouwth from parabasisphenoid, no basitrabecular process known (this character is problematic because it is impossible to know if in fossil snakes the basipterygoid process had a basitrabecular process as a precursor or not).
10) Apophyseal ossification (element X) absent (the “element X” is an ossification unique to the Amphisbaenia, therefore the lack of this

element would be a valid synapomorphy for snakes only if the latter actually evolved from the former).

11) Dentary anterodorsal edge of dental parapet tipped ventromedially.
12) Dentary has two mental foramina on its lateral surface.
13) Cervical pedicle (outgrowth of pleurocentrum to which intercentrum may attach) projecting ventrally with discrete fore and aft margins.
14) Zygosphene-zygantrum accessory intervertebral articulations present and separate facets set on distinct pedicle and facing ventrolaterally.
15) Caudal autotomy septum/septa absent.
16) Pubis symphysial process thin (however, it is unclear what this means with respect to other squamates).

Although there is some overlap in the characters listed by Lee and Scanlon (2002) and Gauthier et al. (2012), these authors provided a number of independent synapomorphies to define snakes as a clade (i.e., the Ophidia). Interestingly, snakes are a mosaic of anatomical traits, none of which apply to all snakes to the exclusion of other squamates. So, there is no short simple answer to the question “what is a snake?”. This is probably the reason why the very concept of “snake” has been so volatile in the history of animal classification (see review above). What defines snakes is a unique combination of physical and behavioural traits that is absent in other reptiles, as well as a lack of features that are used to define some similar groups (e.g., amphisbaenians, legless lizards, caecilians). A given animal is readily identified as a snake because it is an axially elongated creature, with a body covered in scales, no forelimbs, a modified kinetism of the skull where the maxillae are moveable with respect to the rigid braincase (with the exceptions of leptotyphlopids and uropeltids), and that lacks features that are used to define other limbless groups (e.g.: dermis subdivided into annuli, typical of amphisbaenians; presence of external ear openings, retained in most limbless lizards; presence of eyelids, typical of most lizards).

INGROUP STUDIES OF SNAKES PHYLOGENY

While some works were devoted to placing snakes among lizards, another series of publications tried to investigate the interrelationships within the clade Ophidia itself (e.g., Cundall et al. 1993; Heise et al. 1995; Lee and Scanlon; 2002; Slowinski and Lawson 2002; Vidal and Hedges 2002, 2004; Wilcox et al. 2002; Lawson et al. 2004; Townsend et al. 2004; Lee 2005a; Lee et al. 2007; Vidal et al. 2007; Douglas and Gower 2010; Wiens et al. 2010; Zaher and Scanferla, 2012), and each one of them had some sort of impact on the taxonomic ranks proposed by earlier authors, which have been either supported or tentatively discarded (e.g., Anilioidea, Henophidia and Macrostomata). However, there is still no consensus regarding the relationships within this group of reptiles. Although most researchers are finding support for the two main clades Scolecophidia (Typhlopidae, Leptotyphlopidae and Anomalepididae) and Alethinophidia (i.e., all other living snakes) the relationships of the taxa within each of these groups still remain unresolved due to conflicting hypotheses (e.g., Scanlon and Lee, 2000; Lee and Scanlon, 2002; Slowinski and Lawson, 2002; Lawson et al., 2004; Vidal and Hedges, 2004, 2005; Lee et al., 2007).

For example, the Scolecophidia is a taxonomic group that was erected by Cope (1864) based on morphological data alone, and many researchers agree that these snakes represent a monophyletic assemblage (e.g., Smith et al., 1977; Cundall et al., 1993; Greene, 1997; Mattison, 2007); however, very few phylogenetic studies included representatives of all three families so that the monophyly of the clade could be tested (e.g., Scanlon and Lee, 2000; Tchernov et al., 2000; Lee and Scanlon 2002; Lee et al. 2007). Moreover, some molecular phylogenies cast doubt on their monophyletic status: Heise et al. (1995), He et al. (2010), and Wiens et al. (2010, 2012) retrieved a paraphyletic Scolecophidia in their analyses, while Vidal and Hedges (2002) found only weak statistical support for this clade to be monophyletic.

THE DEBATE ON THE ORIGIN OF SNAKES

After the Aristotelian concept of the immutability of species was openly challenged first by Lamarck (1809) and later by Darwin (1859), several scholars started wondering about the possible evolutionary origin of snakes. The realization that snakes had to be derived from lizards was soon widely accepted (e.g., Herdman, 1878); however, the question about which group of lizards should be considered ancestral to snakes was not agreed upon so easily. One of the first phylogenetic hypotheses for the origin of the group was that of Cope (1869), who proposed a close relationship between mosasaurs (his Order

Pythonomorpha) and snakes (Order Serpentes). Despite the fact that Cope (1869) did not intend to propose an evolutionary scenario where mosasaurs are directly ancestral to snakes, his idea of a close relationship between these two taxa was interpreted in that sense by several herpetologists of the time, and resulted in a hot debate on snake origins (e.g., Owen, 1877; Cope, 1878, 1895a, 1895b, 1896; Marsh, 1880; Boulenger, 1891; Baur, 1895, 1896; Osborn, 1899; Williston, 1904; Janensch, 1906).

In the course of this debate, Owen (1877) was the first to suggest that the fossil semiaquatic dolichosaurs, rather than mosasaurs, represent the best candidates as the organisms ancestral to snakes. Owen's (1877) idea of a close relationship between dolichosaurs and snakes was supported by Boulenger (1891), although the latter author considered dolichosaurs as ancestral to all squamates (mosasaurs, lizards and snakes).

Nopcsa (1903, 1908) agreed with Cope (1869) that snakes were closely related to mosasauroids (i.e., aigialosaurs and mosasaurs), but he also argued that, as first suggested by Owen (1977), dolichosaurs should be considered ancestral to snakes, while mosasaurs would simply represent a side branch of the evolutionary radiation that originated from the same unknown group of basal platynotans. Besides the fact that dolichosaurs, like snakes, show axial elongation and limb reduction, Nopcsa's (1903, 1908) idea was mostly based on the observation that snakes have a large number of hypapophyses (a cervical feature in lizards) and their heart and lung/s are positioned quite far back along the axial skeleton; according to Nopcsa (1908) these features indicate that snakes, like dolichosaurs, underwent a considerable elongation of the neck via an increase in the number of cervical vertebrae.

Nopcsa (1923) modified in part his evolutionary hypothesis to suggest that snakes are closely related to dolichosaurs, rather than their direct descendants, and proposed that both groups would have originated from within the Aigialosaurinae. Cope (1869, 1895, 1896), Owen (1877) and Nopcsa (1903, 1908, 1923) laid the foundations of the evolutionary scenario according to which snakes would be the result of a secondary adaptation of squamates to an aquatic lifestyle, the so-called "aquatic origin scenario".

According to Cope's (1869) definition the "Pythonomorpha" was intended to include the two families Mosasauridae and Clidastidae; however, after the mosasaur genus *Clidastes* was placed within the family Mosasauridae and the family name Clidastidae was abandoned, the taxonomic term "Pythonomorpha" became redundant with Mosasauridae and was consequently abandoned as well. In recent years, the term Pythonomorpha was resurrected by Lee (1997) with a new meaning; Lee (1997) reintroduced the term to refer to a clade inclusive of both mosasauroids (= mosasaurs and aigialosaurs) and snakes. Later, Palci and Caldwell (2007) built on Lee's (1997) classificatory scheme by introducing the term Ophidiomorpha, which is meant to refer to a clade consisting of both dolichosaurs (e.g., *Dolichosaurus*, *Adriosaurus*, *Pontosaurus*, and *Aphanizocnemus*) and snakes (Ophidia). The Ophidiomorpha would be the sister group of mosasauroids and the two clades together would constitute a more inclusive Pythonomorpha (Palci and Caldwell, 2007, 2010; Caldwell and Palci, 2010).

An alternative evolutionary scenario considers snakes as derived from an unknown group of cryptic/burrowing terrestrial lizards (e.g., Janensch, 1906), and is therefore known as the “terrestrial origin scenario” (as opposed to the “aquatic origin scenario”) or as the “burrowing origin scenario”. This hypothesis gained much support with the publication of Walls’ (1940, 1942) studies on the eye anatomy of vertebrates. Walls (1940, 1942) noticed several important differences between the eye structure of snakes and that of other squamates. In particular he noticed that the eye anatomy of snakes looks like a simplified version of the eye anatomy of lizards, where some features appear to have re-evolved from vestigial structures. Walls (1940, 1942) argued that the simplified eye anatomy of snakes might be the result of degeneration that occurred during a prolonged subterranean evolutionary phase, and that the eyes of non-burrowing (i.e., not blind) snakes would have re-evolved a functional structure after these taxa reacquired above-ground lifestyles. However, as argued convincingly by Caprette et al. (2004), the unique eye anatomy of snakes might easily be the result of a secondary aquatic adaptation.

The “burrowing origin scenario” found support in studies that retrieved evidence for a close relationship of snakes to burrowing scincid lizards (e.g., Brock, 1941; Conrad, 2008), amphisbaenians (e.g., Rage, 1982), dibamids (Senn and Glenn-Northcutt, 1973), or both amphisbaenians and dibamids (e.g., Wu et al., 1996; Rieppel and Zaher, 2000; Kearney, 2003; Gauthier et al., 2012).

However, it is important to note that, unless skinks, amphisbaenians and dibamids all represent a monophyletic group, the above-mentioned publications present conflicting evidence about the sister group relationships of snakes.

Several other possible sister groups have been proposed for snakes. Snakes have been considered as closely related to the Anguimorpha (Estes et al. 1988; Schwenk, 1988; Lee, 1997, 1998, 2000, 2005a; Reynoso, 1998), the Iguania (Vidal and Hedges, 2004; Bohme et al., 2007; Albert et al., 2009) or both (Townsend et al., 2004; Vidal and Hedges, 2005; Wiens et al., 2010). Interestingly, a close relationship between snakes and anguimorph lizards is based on both morphological and molecular data, and is further consolidated when representatives of the extinct Pythonomorpha (= aigialosaurs, mosasaurs and dolichosaurs) are included in the analysis (Lee 1998, 2005a, 2005b, 2009). On the other hand, at present the sister group relationship between snakes and iguanians is only supported by molecular data and there are no morphological intermediates between these two taxonomic groups.

Considering the lack of general consensus regarding the closest relatives of snakes among lizards, it is not surprising that some herpetologists even suggested that perhaps snakes are not derived from within lizards, but rather both of these groups originated independently from some pre-lacertilian ancestor (Fejervary, 1918; Hoffstetter, 1955; Underwood, 1957, 1970; Kochva, 1978; Rieppel, 1978, 1983, 1988; Evans, 1984). This scenario lost popularity after the works of Gauthier et al. (1988) and Estes et al. (1988), who together provided a list of 84 syapomorphies in support of the monophyletic status of Squamata.

Two hind-limbed fossil snakes from the Cenomanian (Upper Cretaceous) of the Middle East, namely *Pachyrhachis problematicus* and *Eupodophis descouensi*, have been used to support the marine origin of snakes (Caldwell and Lee, 1997; Lee and Caldwell, 1998; Caldwell, 2000a, 2007; Rage and Escuillié, 2000). In these studies the above mentioned taxa were placed at the base of the evolutionary radiation of snakes, and they were presented as ideal intermediates between dolichosaurs (i.e., anguimorphs) and more advanced snakes. In their evolutionary reconstruction Lee and Caldwell (1998) also proposed to restrict the term Serpentes to their crown-group snakes (i.e., Scolecophidia and Alethinophidia) and to use the term Ophidia in a more general sense to include all extant and extinct snakes (i.e., the most recent common ancestor of *Pachyrhachis* and Serpentes, and all of its descendants). However, Zaher (1998), Zaher and Rieppel (1999), Rieppel and Zaher (2000), and Zaher and Rieppel (2002) argued about the anatomical interpretations provided by Caldwell and Lee (1997), Lee and Caldwell (1998) and Caldwell (2000a), and consequently questioned the phylogenetic position of these taxa within the evolutionary radiation of the Ophidia. When a third fossil snake with well-developed hind limbs was discovered, *Haasiophis terrasanctus*, Tchernov et al. (2000) and Rieppel et al. (2003) used it to support their view of a derived macrostomatan condition for this and all other hind-limbed snakes from the Cenomanian of the Middle East (i.e., supratemporals that project posteriorly beyond the otooccipitals are considered a derived adaptation of some alethinophidian snakes that allows ingestion of large prey items, hence “Macrostomata”, which means “large mouths”).

In truth, all of these hind-limbed fossil snakes present a serious problem of character conflict, since they possess a puzzling mosaic of primitive and advanced features. In particular, the presence of well-developed hind limbs is considered as a primitive feature, while the presence of a macrostomatan skull anatomy is considered as a derived adaptation for bulk feeding. If these fossil taxa are really basal snakes, then the presence of a macrostomatan skull anatomy should be considered as secondarily lost in scolecophidians, anilioids and fossil snakes like *Dinilysia*; a hypothesis that is not completely unreasonable, because multiple losses of the macrostomatan skull condition has been indirectly suggested by some molecular phylogenetic analyses (Wilcox et al., 2002; Vidal and David, 2004; Vidal and Hedges, 2004). However, if these snakes are basal macrostomatans, then this would imply that hind limbs were either independently lost several times during the evolutionary radiation of snakes or that they were somehow re-evolved in *Pachyrhachis*, *Eupodophis* and *Haasiophis*; the latter hypothesis can hardly be defended, because so far re-evolution of well-developed limbs has never been reported in any organism that experienced their evolutionary loss (Coates and Ruta, 2000).

To make things even more complicated, another snake with well-developed hind limbs was recently described by Apesteguia and Zaher (2006), *Najash rionegrina*, a snake that the authors considered as providing support for the “terrestrial origin scenario”. As a matter of fact *Najash* was found in fluvial deposits, therefore, it cannot be excluded that this taxon was a semiaquatic snake. Moreover, the referral of isolated material to the type specimen of this taxon by Apesteguia and Zaher (2006) and Zaher et al. (2009) may have lead to the creation of a chimera.

GOALS OF THIS PROJECT

Considering the present lack of consensus about the ancestral ecology and the phylogenetic relationships of snakes, both among squamates and within the clade, a series of focal points will be investigated in this dissertation: Chapter two will be devoted to a review of the different origin scenarios so far proposed and to a review of the Scolecophidia (blind snakes), which according to many researchers are representative of the most basal members of the group; Chapter three will be devoted to a revision of the type and referred specimens of the fossil snakes *Pachyrhachis*, *Haasiophis* and *Eupodophis*. The correct understanding of the anatomy of these pivotal fossil taxa is judged fundamental for the proper phylogenetic reconstruction of important character transformations within the evolutionary radiation of snakes (i.e., is the macrostomatan skull anatomy a primitive or a derived feature? Were hind limbs lost more than once in snake evolution?); Chapter four will provide a revision of the type and referred material of *Najash rionegrina*, a fossil snake with hind limbs that in the recent literature has been described as the most basal known snake (Apesteguia and Zaher, 2006; Zaher et al., 2009); Chapter five will provide the first report of a pelvic girdle in the fossil madtsoiid snake *Wonambi naracoortensis*, from the Pliocene and Pleistocene of southern Australia; Chapter six will be a study of the circumorbital bones of snakes and the problem of their homology. This chapter will discuss the evidence put forward in the literature to justify the most broadly accepted interpretation, and will provide an alternative hypothesis of primary homology for what are currently termed the postorbital and the supraorbital; Chapter seven, will analyze the concept of “crista circumfenestralis”, an anatomical term used to refer to a distinctive set of crests that in modern snakes surround the juxtastapedial recess, but that has been inconsistently used in the literature, especially when in reference to fossil forms; Chapter eight will present the results of a large-scale phylogenetic analysis, based on both morphological and molecular data, of extant and fossil snakes inclusive of representatives from all major groups. Because it is not yet clear which group of squamates is the sister group of snakes, in order to retrieve the polarity of character transformations, this study will include several representatives from both extant and fossil lizard groups. These taxa will also provide a broad framework for the placement of snakes within Squamata; the last chapter will provide a summary of the findings and the general conclusions reached during this research project.

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CHAPTER TWO

SNAKE ORIGIN SCENARIOS

INTRODUCTION

Although there seems to be a general consensus that snakes are either nested within, or at least closely related to, the Anguimorpha (e.g., Estes et al. 1988; Lee, 2005, 2009; Vidal and Hedges, 2004, 2005; Gauthier et al., 2012; Wiens et al., 2012), two main alternative evolutionary scenarios have been proposed for the origin of this group of squamates, according to which snakes would have had either an aquatic or a cryptic/burrowing ancestral ecology (see Caldwell [2007] for a detailed review of the topic).

According to the supporters of the aquatic origin, snakes would have originated from a group of semi-aquatic lizards known as dolichosaurs, and fossil snakes like *Pachyrhachis*, *Haasiophis* and *Eupodophis* bridge the morphological gap between the former group of squamates and the earliest snakes (e.g., Caldwell and Lee, 1997; Lee and Caldwell, 1998; Caldwell, 2007).

According to the supporters of the burrowing origin, two groups of extant cryptic/burrowing snakes would alternatively represent the primitive bauplan for the group: either the Anilioidea (i.e., *Anilius*, *Cylindrophis*, *Uropeltis* and *Anomochilus*) or the Scolecophidia (i.e., Leptoptyphlopidae, Typhlopidae, Anomalepididae) (e.g., Mahendra, 1938; Brock, 1941; Walls, 1940, 1942; Stingelin and Senn, 1969; Underwood, 1967; Estes et al., 1970).

Finally, a possible alternative evolutionary scenario will be explored for the origin of the Scolecophidia.

Institutional abbreviations: **AM**, Australian Museum, Sydney, Australia; **AMNH**, American Museum of Natural History, New York, USA; **HUI-Pal**, Hebrew

University of Jerusalem, Paleontology Collections, Jerusalem, Israel; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **USNM**, United States National Museum of Natural History, Washington DC, USA; **UAMZ**, University of Alberta Museum of Zoology; **ZFMK**, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

THE AQUATIC ORIGIN SCENARIO

According to the aquatic origin scenario as first proposed by Nopcsa (1908), mosasauroid lizards like dolichosaurs, adriosaurs and pontosaurs (here referred to as “dolichosauroids”, a group of long-necked, axially elongated, limb-reduced, semi-aquatic lizards) would be the closest relatives of snakes (Hoffstetter, 1955; Lee and Caldwell, 2000; Fig. 2-1A). In modern phylogenetic studies that support Nopcsa’s hypothesis these fossil lizards form a stem group to the Ophidia (e.g., Lee, 2005; Palci and Caldwell, 2010). In this scenario the fossil hind-limbed snakes *Pachyrhachis* (Fig. 2-2), *Haasiophis* and *Eupodophis* would represent ideal intermediates between the long-necked, axially elongated, limb-reduced semi-aquatic lizards of the Upper Cretaceous and some of the most basal snakes, most notably pythons and boas for what concerns the skull anatomy (Caldwell and Lee, 1997; Lee and Caldwell, 1998; Rage and Escuillié, 2000; Tchernov et al., 2000; Rieppel and Head, 2004) (Fig. 2-3). Interestingly, this hypothesis is in agreement with the work of early herpetologists, who considered boids as the most primitive of living snakes (e.g., Boulenger 1893;

Cope, 1900; Gadow, 1901; Beddard, 1904; Schmidt, 1950; List, 1966, Dowling and Duellman, 1978); this conclusion was based on the fact that boids (i.e., boas and pythons) retain several primitive features, including: presence of a large left lung (the left lung in all other snakes is either lost or strongly reduced); a duplex retina (i.e., inclusive of both rods and cones; most other snakes have either rods or cones); presence of teeth on the premaxilla of pythons (this is also true of the anilioid *Anilius*); and presence of vestigial hindlimbs (femoral spurs, Fig. 2-3D; also present in Leptotyphlopidae, *Anilius*, and *Cylindrophis*).

The posterior extension of the supratemporal bone to form a suspensorium for the quadrate (likely an adaptation to engulf large prey items) observed in the skull of *Pachyrhachis*, *Haasiophis* and *Eupodophis* is also seen in modern pythons and boas, so that some authors (e.g., Zaher, 1998, Zaher and Rieppel, 1999; Tchernov et al., 2000; Zaher and Scanferla, 2012) considered the former taxa to be the sister group of the Macrostomata (i.e., all alethinophidian snakes more derived than anilioids). However, the postcranial anatomy of these fossil hind-limbed snakes, in particular the presence of well-developed hind limbs, suggests that they may represent a much more primitive offshoot of the Ophidia (for reviews of this problem see Caldwell, [2007] and Palci et al. [2013]).

Palci and Caldwell (2010) listed a series of synapomorphies to illustrate the morphological changes involved in the evolution of snakes from within the Pythonomorpha (sensu Lee, 1997), or in other words, from their most recent common ancestor with mosasauroids and dolichosauroids. According to Palci and Caldwell (2010), the main synapomorphies of the Pythonomorpha (i.e., mosasauroids, dolichosauroids and snakes) are:

1) Anterior tip of dentary smoothly rounded, no distinct symphysial area.
2) Splenial-angular articulation.
3) Ectopterygoid does not contact the palatine, maxilla enters the suborbital fenestra.
4) Presence of prominent parietal flanges that are sutured to the prootics.
5) Entire anterodorsal edge of the supraoccipital meets the parietal in a sutural contact.
6) Zygosphene and zygantra.
7) Pelvic elements reduced and weakly connected together.
8) Astragalus and calcaneum separate (no astragalocalcaneum).
9) Dorsal body and cranial osteoderms absent.

Interestingly, as noted by Palci and Caldwell (2010), the morphological changes involved in the origin of the Pythonomorpha are mostly related to increased skull-kinesis, reinforcement of the braincase, and adaptations for aquatic locomotion (e.g., limb reduction, reduced ossification in the limbs and girdles, strengthening of the axial column).

A second stage in the evolution of pythonomorphan squamates would be represented by the ophidiomorphan grade (Palci and Caldwell, 2007, 2010), where the anatomical features linked to limb reduction, axial elongation and skull kinesis were further developed. Importantly, axial elongation at this stage was achieved not only through an increased number of trunk vertebrae, but also though an increase in the count of cervical vertebrae. A list of synapomorphies for the Ophidiomorpha is provided by Palci and Caldwell (2010), the most notable of which are reported below:

1) Premaxilla-maxilla contact mobile, not sutural.
2) Hypapophyses/hypapophyseal peduncles extending to the 10th presacral/precloacal vertebra or beyond (i.e., 10 or more cervical vertebrae).
3) Reduction of limbs and girdles.

Finally, the Ophidia would have arisen from an ophidiomorphan ancestor that was characterized by the following anatomical features:

1) Upper temporal arch incomplete.
2) Ventromedial processes of frontals contact parabasisphenoid below olfactory tracts.
3) 120 or more presacral vertebrae.
4) Presence of lymphapophyses.
5) Loss of scapulocoracoid and forelimbs.

According to this model, the origin of snakes would have encompassed a series of morphological transformations involving increased skull kinesis, reinforcement of the braincase, axial elongation (with an increase in the number of both trunk and cervical vertebrae), and reduction to complete loss of the limbs and girdles.

Although the presence of a relatively long neck in snakes has been a long-debated topic (see Palci and Caldwell [2007] for a review of the arguments and methods used to define the extension of the neck in snakes), a recent paper that analyzed the cervical muscles of squamates provided evidence for the presence of an elongated cervical region in snakes (Tsuihiji et al., 2012). Therefore, this new data seems to lend support to the hypothesis that dolichosauroids are the closest relatives of snakes; however, Tsuihiji et al. (2012) suggest that axial elongation involving an increased number of cervical vertebrae may not be unique only to dolichosauroids and snakes, but is also observed in amphisbaenians and dibamids; elongation of the neck in amphisbaenians had been previously recognized also by Bellairs and Underwood (1951) based on the position of the heart.

THE TERRESTRIAL/BURROWING SCENARIOS

Bellairs and Underwood (1951) listed the following similarities between burrowing lizards (e.g., *Acontias* and *Anniella*) and snakes:

1) presence of extensive parietal downgrowths.
2) Loss of the metakinetic joint.
3) Reduction or loss of the interorbital septum and orbital cartilages.
4) Reduction or loss of the upper temporal arch.
5) Reduction or loss of the epipterygoid.
6) Loss of the Eustachian tubes and tympanic membranes.
7) Regression of the pineal eye.

8) Extreme degeneration of the limbs.

According to the burrowing origin scenario two groups of extant snakes with burrowing habits, anilioids and scolecophidians, are considered representative of the bauplan of the earliest snakes (Fig, 2-1B).

Scenario 1: Anilioids as Representatives of the Earliest Snakes

Based on the fossil record, and in particular on isolated vertebrae attributed to the fossil genus *Coniophis* (an anilioid snake according to Rage, 1984), anilioids (represented today by *Anilius*, *Cylindrophis* [Fig. 2-4], Uropeltids, and *Anomochilus*) would be the oldest group of extant snakes. Consequential to this fact, and to the anatomy of living representatives, is the belief that anilioids can be taken as the most primitive group of extant snakes (Bellairs and Underwood, 1951). This idea was strengthened further by the fossil snake *Dinilysia patagonica* Woodward (1901), a snake that was initially considered to be a fossil anilioid (Fig 2-5). As a matter of fact, the skull of *Dinilysia patagonica* shows a very interesting combination of anatomical features, some of which are definitely lizard-like or believed to be ancestral for snakes (Estes et al., 1970; Caldwell and Albino, 2002; Caldwell, 2007; Zaher and Scanferla, 2012). These features include:

1) Lack of a crista circumfenestralis.
2) Lack of medial pillars of the frontals separating the olfactory tracts.
3) Lack of a dentigerous process on the palatine.

4) Deep choanal grooves.
5) Lack of a laterosphenoid (bony bridge that separates the exit for the trigeminal nerve into an anterior and a posterior opening).
6) Presence of jugal and postfrontal.

It is important to point out that there is disagreement about whether or not the jugal would be present in this fossil snake, and some authors prefer to refer to the element that forms the posterior margin of the orbit as the postorbital (e.g., Zaher and Scanferla, 2012). However, as discussed by McDowell (2008) and Palci and Caldwell (2013), the interpretation of this ossification as the homolog of the jugal of lizards would be more parsimonious.

The skull of *Dinilysia* objectively looks more lizard-like than the skull of any other known living or fossil snake. This is particularly evident in the palatal region, where the palatine lacks an anterior dentigerous process and bears a row of relatively small teeth, and in the otic region, where there is complete lack of a crista circumfenestralis.

Last but not least, it is interesting to point out that Dowling and Duellman (1978) considered the Scolecophidia as derived from within anilioids, and more in particular from uropeltid snakes. However, these two authors also believed that booids (i.e. pythons and boas) and not anilioids represent the primitive bauplan for snakes.

Scenario 2: Scolecophidia as Representatives of the Earliest Snakes

The idea that the Scolecophidia would represent the ancestral condition for snakes is largely based on the arguments put forward by Mahendra (1938) and Brock (1941), who see similarities with burrowing lizards, and the findings of Walls (1940, 1942), who realized that the eyes of snakes appear to be highly modified with respect to the eyes of lizards. Walls (1940, 1942) concluded that such radical modifications of the structure and anatomy of the eyes of snakes would find explanation only if we consider snakes as having re-evolved their eyes starting from rudiments that likely resulted from a prolonged subterranean existence. Because the eyes of the scolecophidians are the most strongly reduced among all living snakes, this lead Walls (1940, 1942) to consider this group as likely the most primitive. The hypothesis of a basal position of the Scolecophidia within the evolutionary radiation of snakes found support in several other studies that identified what appear to be lizard-like anatomical features in this group of snakes (e.g., high coronoid process; pleurodont dentition; tropitrabic skull [i.e., presence of a trabecula communis]; lack of teeth on the palate and lack of a dentigerous process on the palatine; quadrates slanting anteroventrally; frontals lack medial pillars; lack of a prokinetic joint; lack of laterosphenoid; possible presence of a jugal in Anomalepididae; lack of gastrosteges [i.e., enlarged ventral scales]; maxilla firmly attached to the prefrontal in leptotyphlopids; replacement teeth that arise vertically; presence of an ischiadic symphysis in some leptotyphlopids; parietals paired in several taxa) (Bellairs and Underwood, 1951; McDowell and Bogert, 1954; List, 1966; McDowell, 1967, 1974; McDowell, 1987; Rieppel et al., 2009; Cundall and Irish, 2008), and more recently in molecular phylogenies (e.g., Vidal and Hedges, 2004; Wiens et al., 2010, 2012; interestingly, according to the latter authors the Scolecophidia may be paraphyletic). However, as previously stated by List (1966), the Scolecophidia may be a highly derived group of snakes, whose adaptations to a subterranean lifestyle made them aberrant. In order to illustrate how peculiar Scolecophidian snakes are, a brief review of their anatomy is provided below.

A REVIEW OF THE ANATOMY OF THE SCOLECOPHIDIA

Several detailed studies have been published on the osteology and soft tissue anatomy of the Scolecophidia (e.g., Evans, 1955; Haas, 1964, 1968; McDowell and Bogert, 1954; List, 1966; McDowell, 1967, 1974; Rieppel, 1979; Kley, 2006; Cundall and Irish, 2008; Rieppel et al., 2009), so here only a general review will be presented. First, some general anatomical features that are common to all representatives of the group will be discussed, and after that, the distinctive aspects of each family (i.e., Leptotyphlopidae, Typhlopidae and Anomalepididae) will be reviewed.

The fossil record of Scolecophidian snakes goes back to the lower Eocene of Belgium (Rage, 1984), and today this group includes more than 300 species of small (usually < 30 cm in total length) burrowing snakes found in temperate and intertropical habitats, in both humid and arid environments (List, 1966; Greene, 1997; Cundall and Irish, 2008). They feed exclusively on invertebrates, typically ants, termites or earthworms (Greene, 1997). Their cylindrical trunks and short (1–18% of total length) tails are covered in equal-sized polished scales, while their heads bear enlarged scales that cover their rudimentary eyes (hence the common name “blindsnakes”) (List, 1966; Greene, 1997).

Most scolecophidians have rounded heads, but some species of typhlopids and leptotyphlopids have pointed snouts (e.g., *Acutotyphlops kunuaensis*); all scolecophidians have an enlarged rostral scale at the tip of their snout (Greene, 1997).

Rieppel (1988) lists the following synapomorphies for Scolecophidia:

1) Retina composed only of rods (this feature is also observed in the uropeltid snake *Rhinophis* and seems to be correlated with burrowing habits and reduction of the eyes).
2) Juxtastapedial recess closed off laterally by extensive development of the crista circumfenestralis, with the exception of *Anomalepis* (a similar enclosure of the juxstastapedial recess is also observed in the colubroid snake *Atractaspis* and could be correlated with burrowing habits).
3) The hyomandibular branch of the facial nerve (VII) is enclosed in an intracranial course through the otic capsule, with the exception of *Liotyphlops* (but see also Rieppel et al., 2009).
4) Third type of fundic (gastric) glands (i.e., glands lack specialized neck cells and cyanophilic cells; unique within Squamata).
5) Multilobed liver (unique within Squamata).

6) Presence of m. geniomucosalis (a throat muscle derived either from the m. genioglossus of lizards or the m. geniotrachealis of other snakes, Groombridge [1979]; interestingly a similar muscle is found in the seasnake *Aipysurus eydouxi*, McCarthy [1987]).

Five more features may be added to the list of potential synapomorphies proposed by Rieppel (1988):

1) A single oviduct, with the exceptions of *Liotyphlops* and *Typhlophis* (this feature is also observed in the colubroid *Tantilla*; McDowell, 1974; Rieppel 1988; Greene 1997).
2) Lack of lacrimal foramen on prefrontal (Cundall and Irish, 2008).
3) Optic nerve passes through frontal, i.e., anterior to frontoparietal suture (also observed in most uropeltids) (Cundall and Irish, 2008).
4) Vidian canal reduced to a groove along the lateral margin of the basisphenoid (Cundall and Irish, 2008) (with several exceptions, e.g., *Rhamphotyphlops subocularis* [MCZ 65993], *Rhynotyphlops schlegelii* [MCZ 38551], *Typhlops angolensis* [AMNH R11633], *Typhlops diardi* [NHML 1930.5.8.3], *Typhlops lineolatus* [MCZ 48063], *Typhlops punctatus* [MCZ 7293], *Typhlops reticulatus* [AMNH R3001]).
5) Pouch-like expansion between small and large intestine, with exception of some anomalepidids (Underwood, 1967; Greene, 1997).

6) Nasals and premaxilla perforated by numerous foramina for the ophthalmic branch of the trigeminal nerve (List, 1966; Lee and Scanlon, 2002; Rieppel et al., 2009).
7) Lack of sphenoid wing that extends dorsolateral to course of the carotid artery/palatine nerve (McDowell, 1974).
8) Eye covered by a large head scale (McDowell, 1974).
9) Sebaceous glands at the base of the larger head scales (McDowell, 1974).

Among the features that are shared by all Scolecophidia (some of which may be plesiomorphic) Cundall and Irish (2008) also list:

1) Frontals lacking medial pillars
2) Lack of a laterosphenoid
3) Lack of basipterygoid processes and lateral wings on basisphenoid
4) Toothless palatines and pterygoids.
5) Lack of supratemporal, with exception of *Liotyphlops*.
6) Quadrate directed sharply anteroventrally
7) Mandible shorter than skull.

Scolecophidians are characterized by an interesting mixture of primitive-looking and specialized anatomical traits (List, 1966; Rieppel et al., 2009). Most of the specialized features are clear adaptations to a burrowing lifestyle, like for example the short tail, absence of neural spines, reduced number of hypapophyses, and enlarged nasal region (List, 1966).

The Leptotyphlopidae (e.g., *Leptotyphlops dulcis*, Fig. 2-6), commonly known as slender blindsnakes, threadsnakes or wormsnakes, include about 80 species of very small snakes (total length < 46 cm) (Greene, 1997). Their skulls are peculiar in lacking a temporal bone, in lacking teeth on the maxillae, and for often having paired supraoccipital bones (List, 1966). Their dentaries carry up to 5 functional teeth that are set in a dorsally flared, conch-like dentary (List, 1966). The intramandibular joint typical of snakes, lost in anomalepidids and typhlopids (or primitively absent) is present and very well developed in leptotyphlopids, apparently an adaptation for their particular feeding mechanism, which involves bilateral outward flexion of the lower jaws (Kley, 2006). Leptotyphlopids typically have vestiges of the pelvic girdle (consisting of well differentiated ilium, pubis, and ischium) and hindlimbs, where the latter are represented by strongly reduced femora (the femur is absent in some species, e.g., *L. albifrons*; List, 1966) (Fig. 2-6). These elements can be ossified or cartilaginous, and the hind limbs are generally enclosed within the body; however, occasionally in some species (e.g., *L. nigricans* and *L. dulcis*) the hind limbs can protrude from the body wall in the form of small spurs (List, 1966; Greene, 1997). In some leptotyphlopids the nasals are fused and form a nasal septum (List, 1966), and in some species the parietals are paired ossifications (e.g., *L. albifrons*, *L. longicaudus*, *L. labialis*; Cundall and Irish, 2008), although, like for typhlopids (see below) they may fuse ontogenetically (some species, like *L. scutifrons*, show various degrees of separation of the parietals; Cundall and Irish, 2008). The hyoid apparatus of leptotyplopids is a cartilaginous element having the shape of an inverted Y; uniquely among Squamata (with the only exception of typhlopids), its location is shifted far posteriorly along the axial skeleton (e.g., between the 12th and 17th precloacal vertebrae in *Leptotyphlops melanotermus*, ZFMK 53237), and it does not divide the hyobranchial musculature into anterior and posterior portions (McDowell, 1974). A unique feature observed in the skull of some leptotyphlopids is the presence of accessory ossifications, single or paired, posterior to the parietal/s and anterior to the supraoccipital/s (e.g., *L. nigroterminatus*, *L. longicaudus*; Cundall and Irish, 2008).

The family Typhlopidae (blindsnakes sensu stricto; e.g., *Ramphotyphlops braminus*, Fig. 2-7) includes over 200 species some of which can reach almost 1 m in total length (e.g., *Rhinotyphlops schlegelii*) (Greene, 1997). The skull of typhlopids is characterized by the lack of a supratemporal (with the possible exception of *Typhlops vermicularis*; Rieppel, 1980); presence of rotatable maxillae (with up to 5 functional teeth; McDowell and Bogert, 1954) that are hinged to the prefrontals through a ligamentous connection and are connected to the palatine through a peg-and-socket joint; toothless lower jaws with very long retroarticular processes (List, 1966; Cundall and Irish, 2008); and septomaxillae that laterally, uniquely among squamates, have an extensive sutural contact with the frontals (McDowell and Bogert, 1954; Rieppel et al., 2009). Like leptotyphlopids, typhlopids typically have paired supraoccipitals, and in some species these bones seemingly fuse to the otooccipitals (e.g., *T.*

boettgeri), or to the otocciptals and prootics (e.g., *T. lineatus*) (List, 1966; Cundal and Irish [2008] point out that the supraoccipital/s may be absent altogether in these forms). However, the fact that some specimens of *T. braminus* and *T. richardi* show individual prootics while others have these elements fused to the otooccipitals and supraoccipitals seems to suggest that, at least in some species, the fusion of braincase elements may be the result of ontogeny, inter- or intraspecific variation (Evans, 1955; List, 1966). Also of interest in this regard is the fact that juveniles of *T. punctatus* have paired supraoccipitals, while older specimens show fusion of these bones to each other and to the back of the parietal (Cundall and Irish, 2008). Some typhlopids also have paired parietal bones (e.g., *Ramphotyphlops braminus*, *T. flaviventer*, *T. pusillus*, *T. boettgeri*), although as noted by Evans (1955) these bones clearly fuse ontogenetically in some species (e.g., *T. jamaicensis*). Paired parietals are observed also in some leptotyphlopids (e.g., *Leptotyphlops emini*) and anomalepidids (e.g., *Liotyphlops albirostris*). Interestingly, distinct ectopterygoids are absent in typhlopids and leptotyphlopids; however, in the former group the shape of the pterygoids, which are very elongate and forked anteriorly, may indicate that the ectopterygoids are fused to the pterygoids (List, 1966) (Fig. 2-7); an alternative interpretation was proposed by Dunn and Thien (1944) and later supported by McDowel and Bogert (1954), according to whom the ectopterygoid of typhlopids is likely fused with the palatine. As regards leptotyphlopids, McDowell and Bogert (1954), based on a suture line at the base of the posterior maxillary process of *L. dimidiata*, proposed that the posterior process of the maxilla in these snakes may represent a vestigial ectopterygoid fused to the maxilla (but see List, 1966). Thyphlopids retain a vestigial pelvic gridle not connected to the axial skeleton and constituted by ossified ischia and usually cartilagineous pubes and ilia (pubes and ischia are occasionally ossified in some species) (List, 1966); no typhlopid is known to retain vestiges of the hindlimbs (Evans, 1955; List, 1966). As mentioned above for leptotyplopids, typhlopids also have a cartilaginous hyoid apparatus that is located far posteriorly along the axial skeleton and has the shape of an inverted Y; however, in some species (e.g., *T. platycephalus* and *T. reticulatus*) the Y-shaped anterior portion is articulated posteriorly to two rod-like ossified elements (ceratobranchials I), and in some others (e.g., *T. boettgeri* and *T. schlegelii*) the whole Y-shaped structure is ossified; in yet other species (e.g., *T. lumbricalis* and *T. pusillus*) the anterior Y-shaped cartilaginous portion of the hyoid apparatus is missing and only the two ossified ceratobranchials are present (List, 1966).

The Anomalepididae are the least known of the three groups of scolecophidians, and include only 15 known species grouped in four genera: *Anomalepis* (Fig. 2-8), *Liotyphlops*, *Helminthophis* and *Typhlophis* (McDowell, 1967; Greene, 1997). These snakes have teeth on both maxillae and dentaries, although the number of teeth on the dentary is typically very low (1 in *Anomalepis*, *Helmintophis* and *Typhlophis*, 2 in *Liotyphlops*; List, 1966), and have lost the splenial in their lower jaws (Cundall and Irish, 2008; Rieppel et al., 2009; however, according to List [1966] anomalepidids would lack the angular rather than the splenial). Typhlopids and anomalepidids have the same type of rotatable maxillae, with only a few functional teeth (Cundall and Irish [2008] report 4 functional teeth in *Anomalepis* and 4 in *Liotyphlops*) and long retroarticular processes, but unlike typhlopids the prefrontals of anomalepidids are slender, evenly curved, rod-like structures loosely articulated to the posterolateral corners of the frontals (Haas, 1964, 1968; McDowell, 1974; Rieppel et al., 2009). Unlike typhlopids and leptotyphlopids, but similar to all other squamates, the supraoccipital of *Liotyphlops* and *Anomalepis* is a single element, but the supraocciptals are either absent or paired and fused to the exoccipitals in *Typhlophis*, and their condition is unknown for *Helmintophis* (McDowell and Bogert, 1954; List, 1966; Rieppel et al., 2009). Uniquely among squamates, in *Liotyphlops albirostris* and *Anomalepis aspinosus* (and possibly also all other anomalepidids) the supraoccipital does not contribute to the formation of the otic capsule (Rieppel et al., 2009). According to List (1966) and Rieppel et al. (2009) the parietals are paired in *Liotyphlops* and *Anomalepis*; however a CT-scanned specimen of *Anomalepis flavapices* (AMNH 6966) clearly shows an unpaired parietal, and unpaired parietals were also reported by Haas (1968) for *Anomalepis aspinosus*. As mentioned above for typhlopids, this variation may be the result of ontogenetic change. Rieppel et al. (2009) also mention paired parietals in *Typhlophis squamosus*.

Liotyphlops and *Typhlophis squamosus* retain a vestigial supratemporal (note that according to McDowell and Bogert [1954], Haas [1968] and Rieppel et al. [2009] the supratemporal would be absent in *Anomalepis*; however an element that may represent a supratemporal has been identified in a CT-scanned specimen of *Anomalepis flavapices* [AMNH 6966], Fig. 2-8). List (1966) stated that the prootics are distinct ossifications in *Anomalepis*, and that they are fused with the exoccipitals (otooccipitals) in *Liotyphlops*; however, *Anomalepis flavipices* (AMNH 6966) seems to have prootics that are fused with the exoccipitals (otooccipitals) (Fig. 2-8). In *Anomalepis* the crista circumfenestralis is absent, so that the juxtastapedial recess and the stapes are largely exposed in lateral view. As in leptotyphlopids, also in anomalepidids the nasals can be fused (e.g., *Liotyphlops*, *Anomalepis dentatus*, *Typhlophis squamosus*), and form an internasal septum (List, 1966; Haas, 1968; Rieppel et al., 2009). Uniquely among living snakes, anomalepidids retain an element posteroventral and ventral to the orbit that lies embedded in soft tissues and is not connected to any other bone; this element has been variously interpreted as a postorbital (Dunn and Tihen, 1954; Haas, 1964, 1968; Cundall and Irish, 2008), fused postorbital and postfrontal (Dunn, 1941), fused jugal and postorbital in *Anomalepis* and jugal in *Liotyphlops* (McDowell and Bogert, 1954; List, 1966), and as either jugal or postorbital (Rieppel et al., 2009).

Anomalepidids are thought to lack a pelvic girdle (Tihen, 1945, List, 1966); however, List (1966) described a large specimen of *Liotyphlops albirostris* as having small cartilaginous vestiges of the ilium and pubis disconnected from the axial skeleton. The hyoid apparatus of *Liotyphlops* is cartilagineous and has the shape of an inverted M with its legs partially bent forward (List, 1966). Unlike typhlopids and leptotyphlopids, where the vomeronasal nerve exits the vomeronasal cupola through a space between vomer and septomaxilla, in anomalepidids (*Liotyphlops* and *Typhlophis*; unknown for *Anomalepis* and *Helminthophis*) the nerve exits through a foramen in the posterodorsal surface of the septomaxilla (Rieppel et al., 2009). Rieppel et al. (2009) report the presence of two mental foramina in the dentary of *Liotyphlops albirostris* and three in that of *Typhlophis squamosus*, an unusual condition for snakes, which usually have only one mental foramen (exceptions are represented by the basal caenophidian *Acrochordus*, some specimens of *Python regius* [Fig. 2-2E] and some fossil snakes, e.g., the madtsoiid *Yurlunggur*).

Interestingly, all scolecophidians share the absence of a notch at the posterior end of the dentary (i.e., absence of posterodorsal and posteroventral rami of the dentary) (Rieppel et al., 2009); however, it is not clear if this is a primitive feature, a shared derived feature, or simply a consequence of the high degree of degeneration of their lower jaws.

The axial skeleton of scolecophidian snakes is quite uniform among the three different groups. Scolecophidians show only a few vertebrae bearing hypapophyses (up to 6; List, 1966), and have depressed vertebrae that lack neural spines and have round synapophyses (the vertebrae are slightly less depressed in leptotyphlopids; List, 1966). The centra are depressed and the condyle faces slightly posterodorsally, and the prezygapophyseal processes are very well developed (List, 1966; Lee and Scanlon, 2002). The Scolecophidia have large foramina of irregular size and occurrence (i.e., present on some vertebrae and absent in others, paired or single, larger on one side and smaller or absent on the other) on the ventral surface of the precloacal vertebrae (List, 1966; Lee and Scanlon, 2002). According to Mookerjee and Das (1933) in the anterior portion of the body these foramina are meant for passage of branches of the vertebral artery, while posteriorly they are meant for branches of the dorsal aorta. Similar foramina have been observed in boids and colubroids, among snakes, and in gekkotans, amphisbaenians and scincomorphs, among lizards, although in all these taxa they never appear in a medial position (List, 1966). The caudal vertebrae lack haemal arches (List, 1966). Some species of *Typhlops* (e.g., *T. polygrammicus* and *T. vermicularis*) have a medial rod-like ossification associated to the ventral surface of the last fused caudal vertebrae, these rudimentary structures are embedded in the soft tissues of the tail and appear to have no function (List, 1966).

SCOLECOPHIDIA AS DERIVED CAENOPHIDIANS?

Underwood (1967) pointed out that typhlopids and leptotyphlopids have both a m. protractor and a m. retractor pterygoidei. Typhlopids even retain a m. retractor vomeris, which is quite interesting if we consider that this muscle is absent in the anilioids *Cylindrophis* and *Anilius* (Underwwod, 1967). This implies that these snakes were derived from ancestors that already acquired the mobility of maxillae and palate. Moreover, even if the maxilla of leptotyphlopids is immobile, these snakes retain a large retractor pterygoidei and a protractor pterygoidei, which would imply that this element secondarily lost its mobility; moreover, the caudal process on the maxilla of leptotyphlopids (possibly a fused ectopterygoid according to McDowell and Bogert, 1954) serves as a point of attachment for the m. pterygoideus. Among other snakes, the m. pterygoideus is known to originate on the maxilla only in colubroids (Cundall and Irish, 2008). Other caenophidian-like features of scolecophidians include:

1) Prominent prezygapophyseal processes on vertebrae (List, 1966; McDowell, 1974; Lee and Scanlon, 2002).

2) Hinged erectable maxillae in typhlopids and anomalepidids, a feature also found in Viperidae and Atractaspididae (Cundall and Irish, 2008).

3) Well-developed crista circumfenestralis, which completely encloses the stapedial footplate (McDowell, 1974; Rieppel, 1979).

4) Although a laterosphenoid is generally considered absent in scolecophidians, a bony bridge dividing the trigeminal opening (separating V2 and V3) in *Leptotyphlops cairi* could be interpreted as a structure homologous to the laterosphenoid of more advanced snakes (Abdeen et al., 1991). Cundall and Irish (2008) report that in a specimen examined by them, the V2 and V3 branches would exit the braincase together from the anterior foramen. This may be due to a misinterpretation by Abdeen et al., (1991), but it could also be the result of intraspecific variation. In any case, a laterosphenoid is present, on both sides of the skull, also in a specimen of *Acutotyphlops kunuaensis* (pers. obs. on CT-scan data of AM R123405).

5) *Acrochordus*, a basal caenophidian snake, has two m. levator pterygoidei (a deep muscle that inserts on the pterygoid and a more superficial muscle that inserts on the ectopterygoid) as is the case in Anomalepidids (often considered

as the most primitive of the Scolecophidia) and no other snakes (McDowell, 1987).

6) The fossil record of the Scolecophidia goes back only up to the middle Paleocene of Belgium (Mead, 2013), when the first colubroids also appeared (Rage, 1984); several other snakes showing a generalized (i.e., anilioid-like or boid-like) ophidian appearance were already present in the lower Upper Cretaceous (e.g., *Haasiophis*, *Pachyrhachis*, *Eupodophis*, *Dinilysia*, *Najash*, *Sanajeh*).

7) In all scolecophidians the premaxillae lack teeth, which are present in some non-caenophidian snakes (e.g., *Anilius*, *Python*, *Loxocemus* and *Xenopeltis*) and are clearly a primitive feature for squamata. Similarly to scolecophidians, all caenophidians lack teeth on their premaxillae.

8) Presence of a tracheal lung has also been suggested as a possible shared feature between typhlopids and anomalepidids on one hand and some caenophidians on the other (e.g., Cope 1894); however, the tracheal lung is also present in some non-caenophidian snakes (e.g., *Ungaliophis* and *Tropidophis*) (Wallach, 1998).

Some seemingly primitive features of scolecophidians, like the lack of ossification of the dorsal surface of the parietals in some species of leptotyphlopids (e.g., *Leptotyphlops humilis*) (McDowell and Bogert, 1954; List, 1966) could be the result of neoteny (paedomorphosis), because snakes ossify this region at the end of development (pers. obs. on hatchling of *Thamnophis* *sirtalis*). Rieppel (1979) also mentioned neoteny as an explanation for the disappearance of the lateral wing of the basisphenoid of scolecophian snakes. It is interesting to note that if we keep neoteny in mind as a process that may explain minor anatomical differences (e.g., lack of fusion between bones, minor changes in proportions, orientation of the quadrate, lack of ossification of certain elements), the skull of the Typhlopidae and Anomalepididae (e.g., *Ramphotyphlops* and *Anomalepis*; Figs. 2-7 and 2-8) and that of the burrowing asp *Atractaspis* (Fig. 2-9) share some striking similarities. All of these snakes have a compact cylindrical braincase where parietal and supraoccipital lack a distinct mid-sagittal crest; they possess maxillae that are strongly reduced anteroposteriorly and are capable of rotating against a hinge-like articulation with the prefrontal; the pterygoids are rod-like and toothless; the supratemporals in both *Anomalepis* and *Atractaspis* are strongly reduced and mostly attached to the lateral surface of prootic and otooccipitals (fused in *Anomalepis*; also note that *Anomalepis* is thought to lack a supratemporal, but as mentioned above, AMNH 6966, clearly shows presence of a vestigial supratemporal; the other well-known anomalepidid, *Liotyphlops*, has a similar supratemporal); the dorsal laminae of the nasals are broadly expanded and arch over the nasal cavities; the parabasisphenoid rostrum is mediolaterally expanded into a broad triangular shape; the premaxilla has anterior foramina (2 in *Atractaspis*, several in typhlopids and anomalepidids); the pituitary fossa is shallow and is not bordered posteriorly by a well-developed, overhanging dorsum sellae; the ventral surfaces of parabasisphenoid and basioccipital lack any mid-sagittal crests or ridges; the dentaries are strongly reduced and bear few or no teeth.

This quite extensive list of similarities is certainly intriguing, but the resemblance may simply be the result of convergence towards a similar burrowing lifestyle. As a matter of fact, a similar degree of convergence in skull anatomy can also be observed between the basal non-caenophidian snake *Cylindrophis* and the elapid *Micrurus*, both of which are burrowers (e.g., they both show a broadened parasphenoid rostrum, long and narrow parietal, triangular roof of the frontals, trapezoidal prefrontals pointing anterolaterally, quadrate short and robust, and finger-like anterolateral processes of the parietal).

Features that make the hypothesis of scolecophidians as derived caenophidians problematic are the retention of a coronoid and a pelvic girdle in the former. These elements are clearly primitive and are consistently absent in all caenophidians with no exceptions.

CONCLUSIONS

Scolecophidian snakes lack many of the derived traits that characterize the Alethinophidia (e.g., frontal pillars, laterosphenoid ossification, extensive skull kinesis, large number of hypapophyses in the precloacal region, dorsoventrally expanded synapophyses, quadrate vertical or tilted posteriorly), but also possess a series of traits that are clearly derived with respect to many other snakes or to the general lepidosaurian condition (e.g., strongly reduced eyes that lack cones in the retina, lack of basipterygoid processes, supraoccipital and parietal often paired, lack of premaxillary teeth, morphology of dentary [in Leptotyphlopidae] and maxilla [in Typhlopidae and Anomalepididae] that strongly deviates from the plesiomorphic lepidosaurian condition, multilobed liver, third type of fundic glands). This mixture of primitive and derived traits makes scolecophidians very problematic in evolutionary scenarios that try to reconstruct the origin of the ophidian body plan from phylogenies that place them as the most basal members of the Ophidia. This is because even if they represent an early offshoot of the Ophidia, this does not mean that they represent the actual ancestral body plan of snakes (as suggested by their many autapomorphic traits). No extant or fossil lizard, either burrowing or not, present a morphology that could easily be seen as the precursor of that of scolecophidian snakes, and scolecophidans themselves do not possess a morphology that could be seen as ancestral to that of other snakes. For example, the jaws of scolecophidians would have had to be considerably transformed to give origin to the jaws of other snakes, which possess plesiomorphic-looking maxillae and dentaries (i.e., similar to those of lizards). Moreover, the argument that the eyes of snakes had to re-evolve from those of a half-blind burrowing snake (Walls, 1942) is weakened by the simple consideration that some snakes (e.g., boas, pythons, vipers) still retain rods and cones in their eyes (cones would have had to re-evolve from a scolecophidian-like most recent common ancestor). Therefore, it is very unlikely that the most recent common ancestor of scolecophidians and alethinophidians was very similar to modern representatives of the former group. Importantly, some of the autapomorphic features observed in scolecophidians are clearly linked to their burrowing lifestyle and diet (e.g., reduction of the eyes, strengthening of the snout region, highly modified feeding apparatus), and there are no grounds to believe that the most recent common ancestor of all snakes shared the same habits. Origin scenarios and ecological inferences can only be based on broad phylogenetic analyses that include not only representatives of the group of interest, but also an exhaustive number of successive sister taxa. If the phylogeny shows a series of burrowing forms as successive sister taxa for a group of organism, then and only then, some conclusions on the ecological drivers for the evolution of that group can be speculated upon. The problem in the case of snakes is that there is no consensus regarding the closest sister group of snakes, and the proposed sister groups all have very different ecologies (e.g., dolichosaurs were marine, amphisabenians and dibamids are burrowers, iguanians are terrestrial, and anguimorphs can be terrestrial, semi-aquatic or cryptic).

FIGURES

FIGURE 2-1. Phylogenies depicting the two main alternative evolutionary scenarios of snakes. **A**, the closest successive sister groups of snakes are all marine lizards (mosasauroids, dolichosaurs and adriosaurs), and the marine snakes *Pachyrhachis* and *Haasiophis* represent the most basal members of the clade. The relationships in this phylogeny provide support to the marine origin of snakes (blue box highlights marine taxa) (tree modified from Lee and Scanlon [2002] and Lee [2005]); **B**, the closest successive sister groups of snakes are burrowing squamates (*Anniella*, amphisbaenians and dibamids), and scolecophidians and anilioids (burrowing snakes) are the most basal snakes. The relationships in this phylogeny provide support to the burrowing origin of snakes (orange box highlights burrowing taxa). In this phylogenetic hypothesis the fossil snakes *Haasiophis* and *Pachyrhachis* are included within the clade labeled “other snakes” (tree modified from Gauthier et al. [2012]). Fossil taxa like *Dinilysia*, *Najash* and madtsoiid snakes can be placed basal to the Scolecophidia or in a more derived position depending on the data set and tree searching criterion (e.g., Lee [2005], Wiens et al. [2010], Gauthier et al. [2012]).

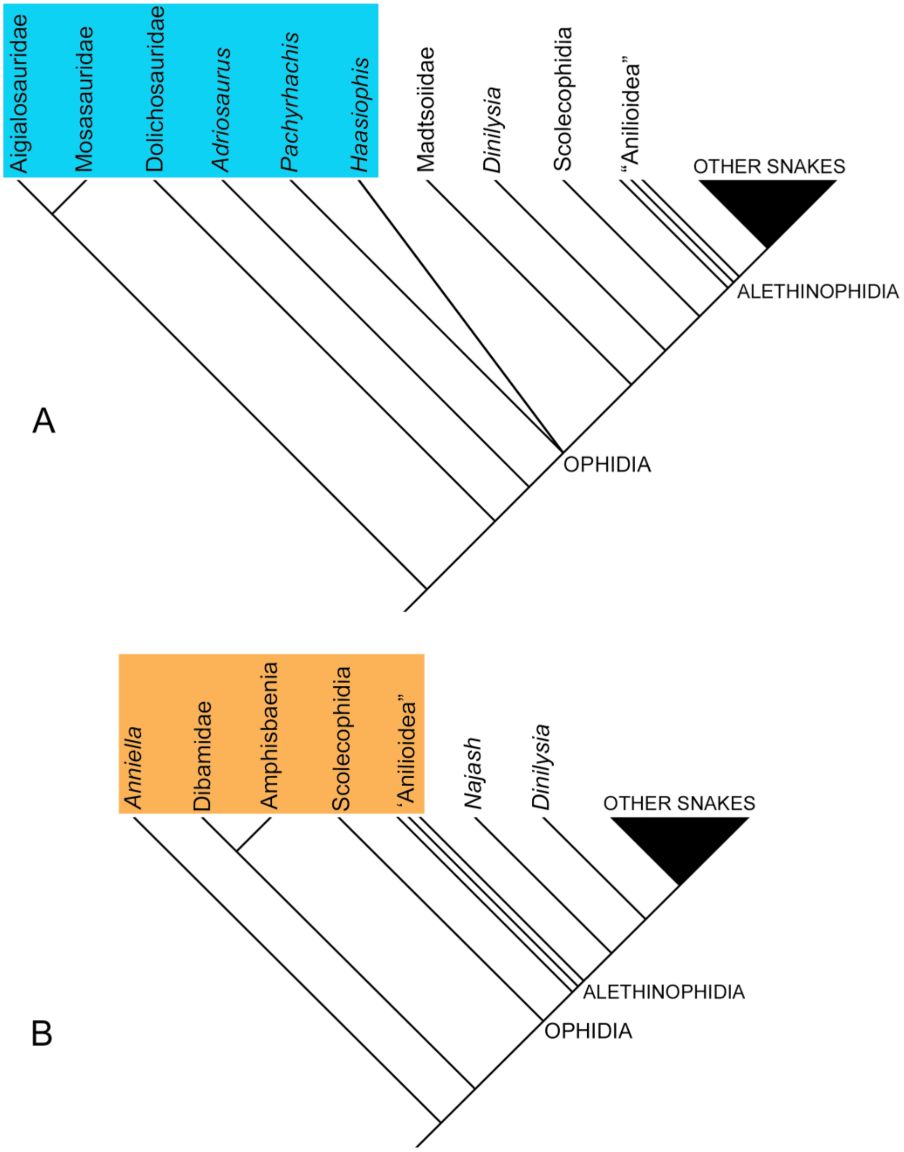
Aigialosauridae
Mosasauridae
Dolichosauridae
Adriosaurus
Pachyrhachis
Haasiophis
Madtsoiidae
Dinilysia
Scolecophidia
"Anilioidea"
OTHER SNAKES
ALETHINOPHIDIA
OPHIDIA
A
Anniella
Dibamidae
Amphisbaenia
Scolecophidia
'Anilioidea"
Najash
Dinilysia
OTHER SNAKES
ALETHINOPHIDIA
OPHIDIA
B

FIGURE 2-2. Skull and pelvic region of *Pachyrhachis problematicus*. **A**, interpretative drawing of the skull of HUJ-Pal 3659, dorsal view; **B**, interpretative drawing of the skull of HUJ-Pal 3659, ventral view; **C**, reconstruction of the skull of HUJ-Pal 3659, left lateral view. Hatched areas indicate unknown regions of the skull; **D**, interpretative drawing of the pelvic region of HUJ-Pal 3775, right lateral view. **Abbreviations**: **a**, angular; **as**, astragalus; **at**, atlas; **ax**, axis; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **ca**, calcaneum; **co**, compound bone; **d**, dentary; **dr**, dorsal rib; **e**, ectopterygoid; **ex**, exoccipital-opisthotic; **f**, frontal; **fe**, femur; **fi**, fibula; **il**, ilium; **is**, ischium; **j**, jugal; **m**, maxilla; **n**, nasal; **o**, optic fenestra; **p**, parietal; **pa**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pof**, postfrontal; **pt**, pterygoid; **pu**, pubis; **q**, quadrate; **s**, stapes; **so**, supraoccipital; **sp**, splenial; **sr**, sacral rib; **st**, supratemporal; **ti**, tibia; **v3**, third vertebra; **?**, unidentifiable element. A, B and C share the same scale bar. Scale bars equal 5 cm.

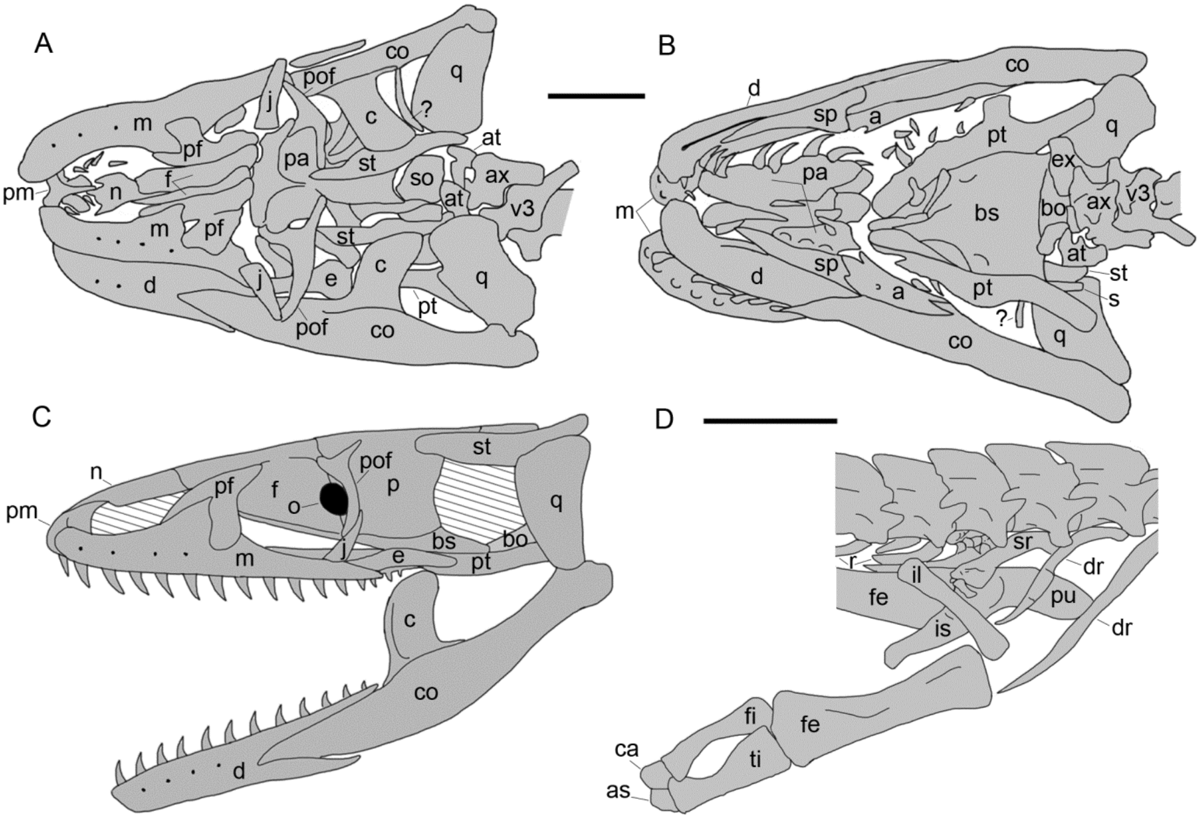
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FIGURE 2-3. Skull and pelvic region of Python. **A**, Python regius, skull in left lateral view (UAMZ 3818); **B**, *Python regius*, skull in ventral view (UAMZ 3818); **C**, *Python regius*, skull in dorsal view (UAMZ 3818); **D**, *Python regius*, lower jaw in medial view (UAMZ 3818); **E**, *Python regius*, lower jaw in lateral view (UAMZ 3818); **F**, *Python sebae*, pelvic region in left lateral view (based on radiograph of ZFMK 35527). **Abbreviations**: $\mathbf{V_2}$, foramen for maxillary branch of trigeminal nerve; $\mathbf{V_3}$, foramen for mandibular branch of trigeminal nerve; **VII**, foramen for facial nerve; **a**, angular; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **co**, compound bone; **d**, dentary; **e**, ectopterygoid; **ex**, exoccipital-opisthotic; **f**, frontal; **fe**, femur; **j**, jugal; **m**, maxilla; **n**, nasal; **o**, optic fenestra; **p**, parietal; **pa**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pof**, postfrontal; **pr**, prootic; **pt**, pterygoid; **pu**, pubis; **pv**, posterior opening of vidian canal; **q**, quadrate; **s**, stapes; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **st**, supratemporal; **v**, vomer. All images are drawn to the same scale. Scale bar equals 5 mm.

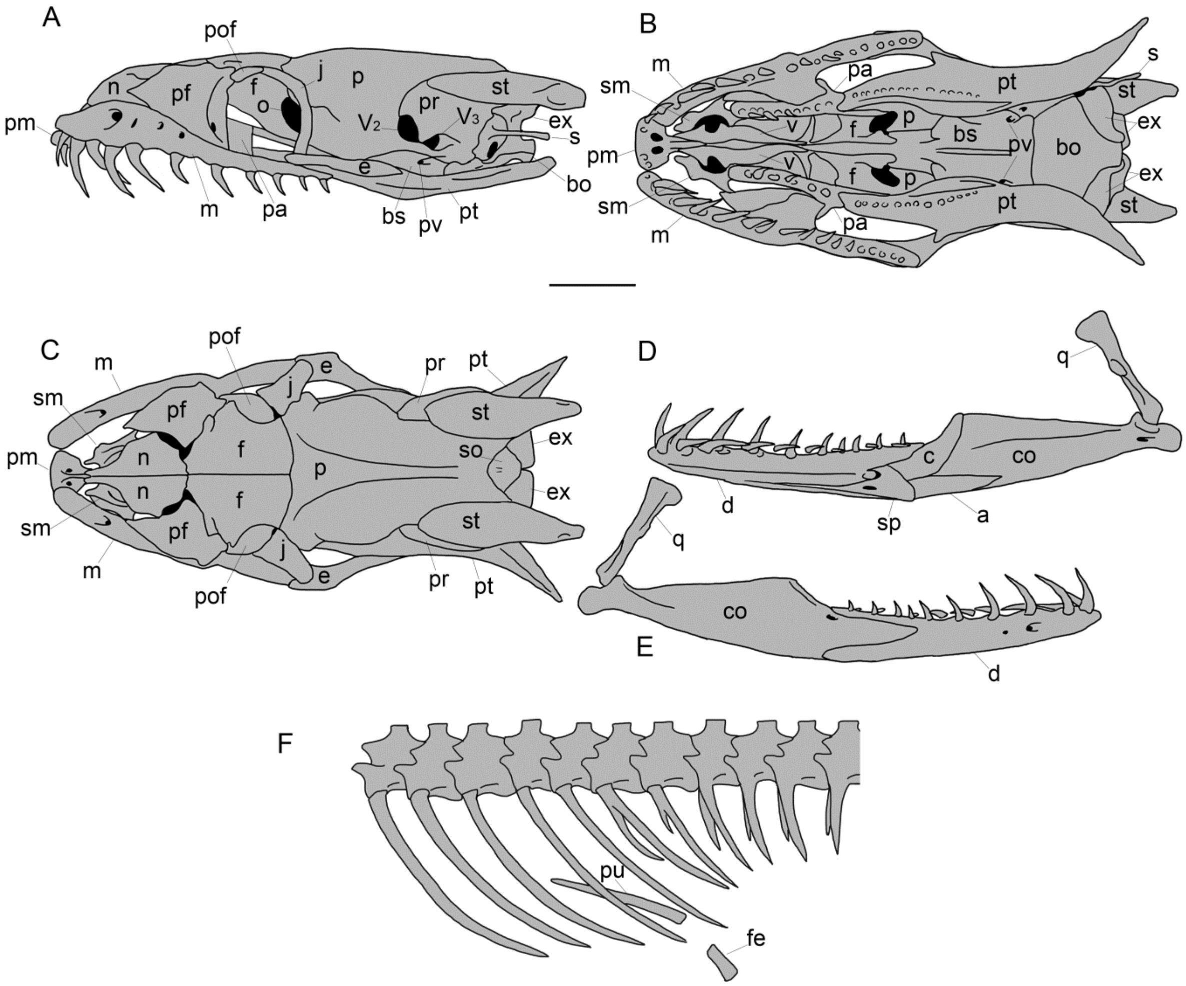
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FIGURE 2-4. Skull and pelvic region of *Cylindrophis*. **A**, *Cylindrophis rufus*, skull in left lateral view (USNM 297456); **B**, *Cylindrophis rufus*, skull in ventral view (USNM 297456); **C**, *Cylindrophis rufus*, skull in dorsal view (USNM 297456); **D**, *Cylindrophis rufus*, lower jaw in medial view (USNM 297456); **E**, *Cylindrophis rufus*, lower jaw in lateral view (USNM 297456); **F**, *Cylindrophis maculatus*, pelvic region in left lateral view (based on radiograph of ZFMK 33609). **Abbreviations**: $\mathbf{V_2}$, foramen for maxillary branch of trigeminal nerve; $\mathbf{V_3}$, foramen for mandibular branch of trigeminal nerve; **VII**, foramen for facial nerve; **XII**, foramen for hypoglossal nerve; **a**, angular; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **co**, compound bone; **d**, dentary; **e**, ectopterygoid; **ex**, exoccipital-opisthotic; **f**, frontal; **fe**, femur; **il**, ilium; **is**, ischium; **j**, jugal; **m**, maxilla; **n**, nasal; **o**, optic fenestra; **p**, parietal; **pa**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pof**, postfrontal; **pr**, prootic; **pt**, pterygoid; **pu**, pubis; **pv**, posterior opening of vidian canal; **q**, quadrate; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **st**, supratemporal; **v**, vomer. All images are drawn to the same scale. Scale bar equals 5 mm.

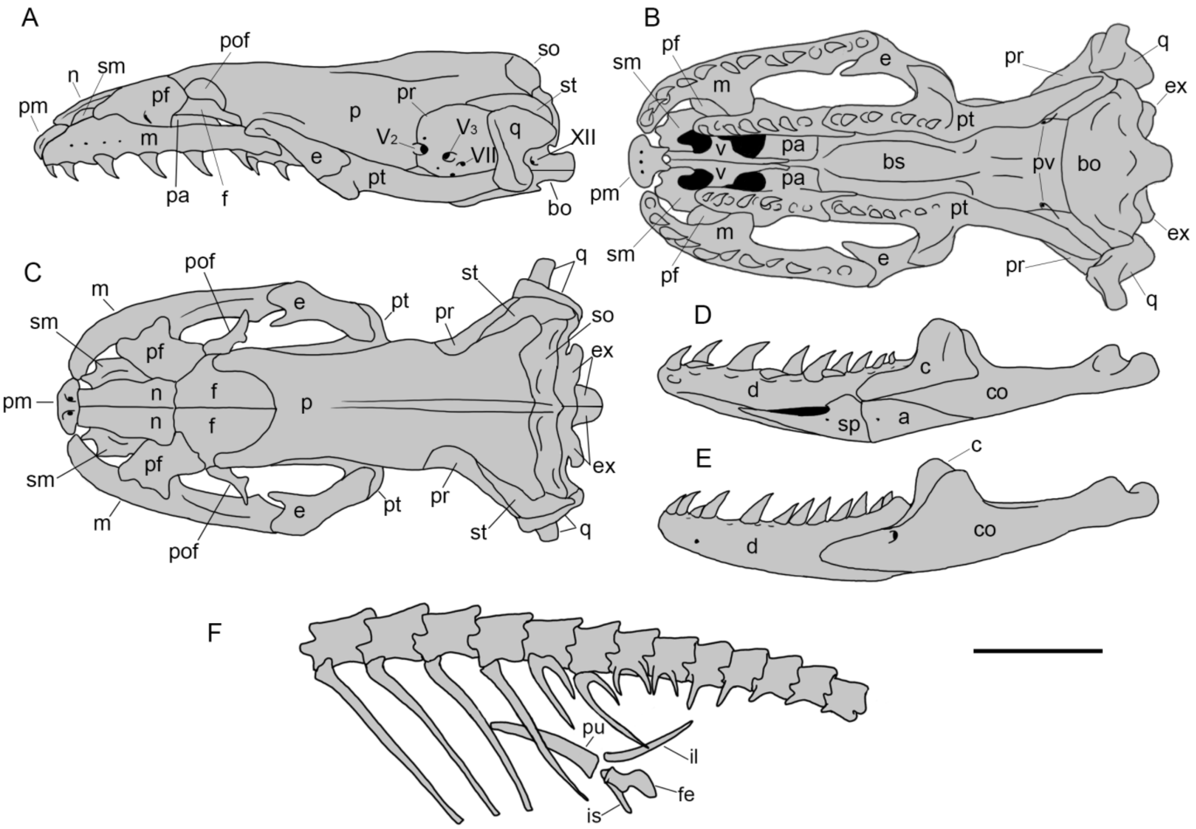
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FIGURE 2-5. Reconstruction of the skull of *Dinilysia patagonica* (drawings based on MLP 26-410, MACN RN-976, MACN RN-1013, MACN RN-1014). Note that the premaxilla (hatched) and most of the septomaxilla are unknown. **A**, skull in left lateral view; **B**, skull in ventral view; **C**, skull in dorsal view; **D**, lower jaw in lateral view; **E**, lower jaw in medial view. **Abbreviations**: $\mathbf{V_2{+}V_3}$, common foramen for maxillary and mandibular branches of trigeminal nerve; **VII**, foramen for facial nerve; **a**, angular; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **co**, compound bone; **d**, dentary; **e**, ectopterygoid; **ex**, exoccipital-opisthotic; **f**, frontal; **j**, jugal; **m**, maxilla; **n**, nasal; **o**, optic fenestra; **p**, parietal; **pa**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pof**, postfrontal; **pr**, prootic; **pt**, pterygoid; **pv**, posterior opening of vidian canal; **q**, quadrate; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **st**, supratemporal; **v**, vomer. All images are drawn to the same scale. Scale bar equals 1 cm.

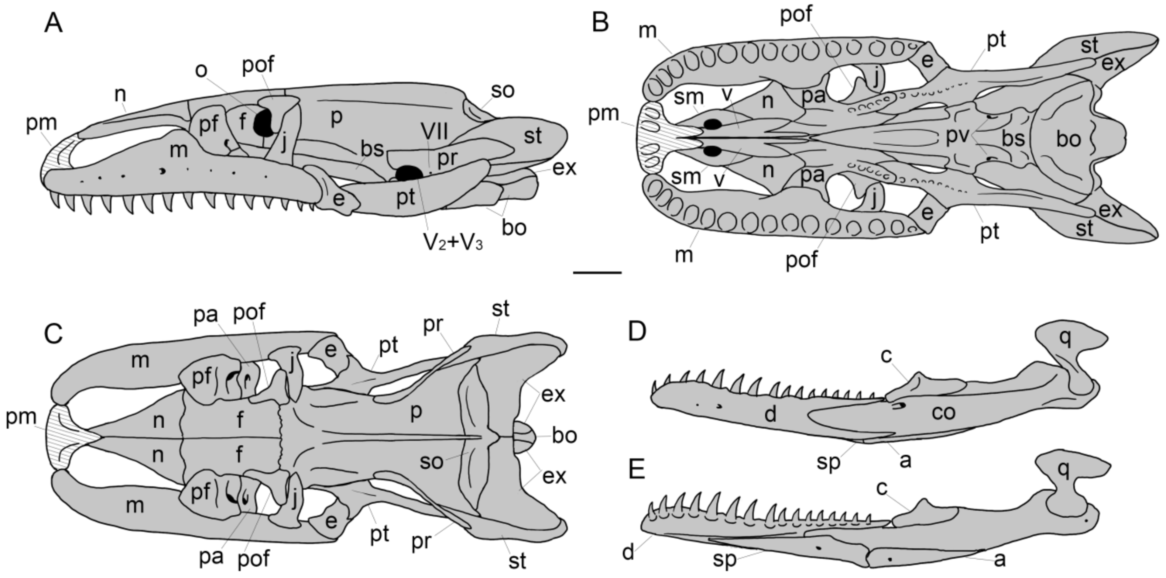
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FIGURE 2-6. Skull and pelvic region of *Leptotyphlops dulcis* (drawings based on computer tomography of UAMZ 343). **A**, skull in left lateral view; **B**, skull in dorsal view; **C**, skull in ventral view; **D**, lower jaw in medial view; **E**, lower jaw in lateral view; **F**, pelvic region in left lateral view. **Abbreviations**: $\mathbf{V_2+V_3}$, common foramen for maxillary and mandibular branches of trigeminal nerve; **a**, angular; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **co**, compound bone; **d**, dentary; **ex**, exoccipital-opisthotic; **f**, frontal; **fe**, femur; **il**, ilium; **is**, ischium; **jf**, jugular foramen; **m**, maxilla; **n**, nasal; **o**, optic foramen; **p**, parietal; **pa**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pr**, prootic; **pt**, pterygoid; **pu**, pubis; **pv**, posterior opening of vidian canal; **q**, quadrate; **s**, stapes; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **v**, vomer. Images A-E and F-H are drawn to different scales. Scale bars equal 1 mm.

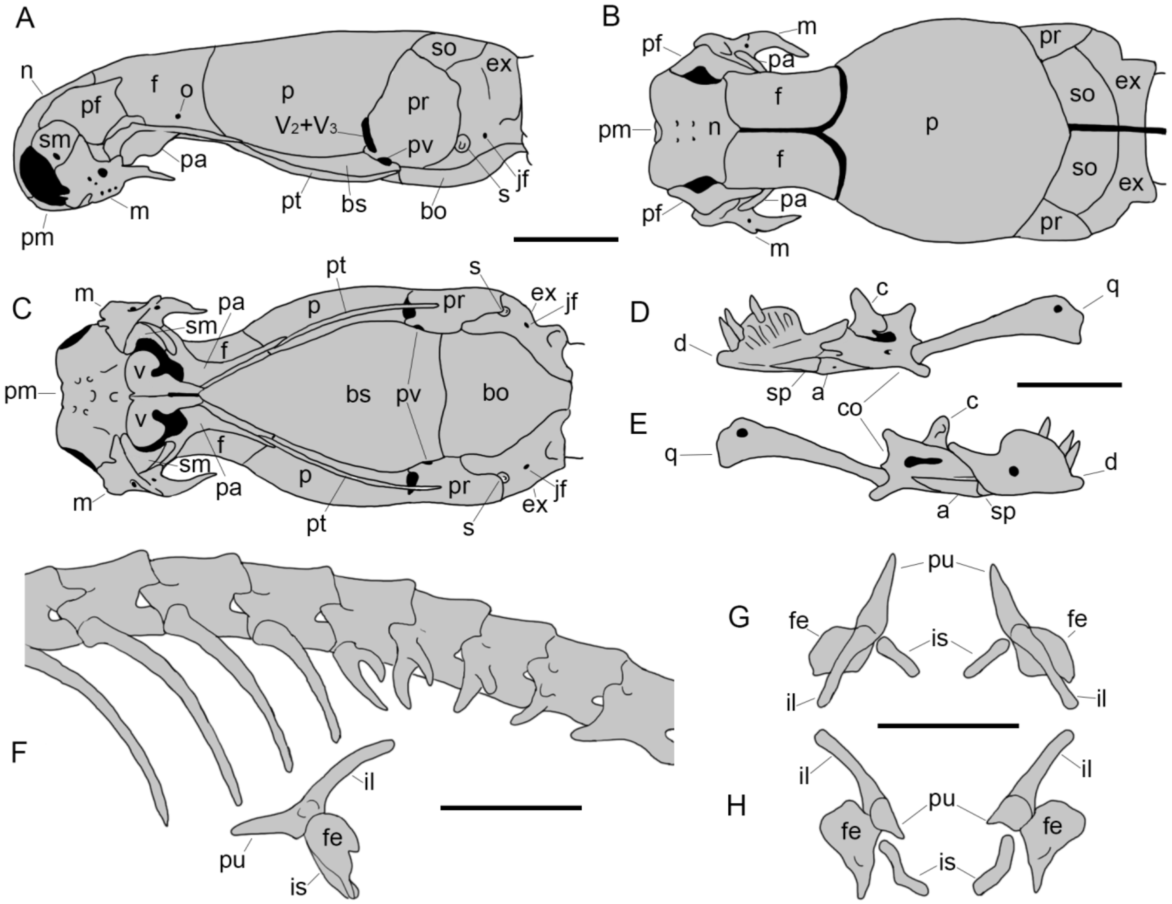
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FIGURE 2-7. Skull and pelvic region of *Ramphotyphlops braminus* (drawings based on computer tomography of UAMZ 553). **A**, skull in left lateral view; **B**, skull in left lateral view, maxilla removed; **C**, skull in dorsal view; **D**, skull in ventral view; **E**, lower jaw in lateral view; **F**, lower jaw in medial view; **G**, pelvic region in left lateral view; **H**, pelvic region in ventral view. **Abbreviations**: $\mathbf{V_2+V_3}$, common foramen for maxillary and mandibular branches of trigeminal nerve; **at**, atlas; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **co**, compound bone; **d**, dentary; **ex**, exoccipital-opisthotic; **f**, frontal; **is**, ischium; **jf**, jugular foramen; **jr**, juxtastapedial recess; **m**, maxilla; **n**, nasal; **o**, optic foramen; **p**, parietal; **pa**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pr**, prootic; **pt**, pterygoid; **q**, quadrate; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **v**, vomer. Images A-F and G-H are drawn to different scales. Scale bars equal 1 mm.

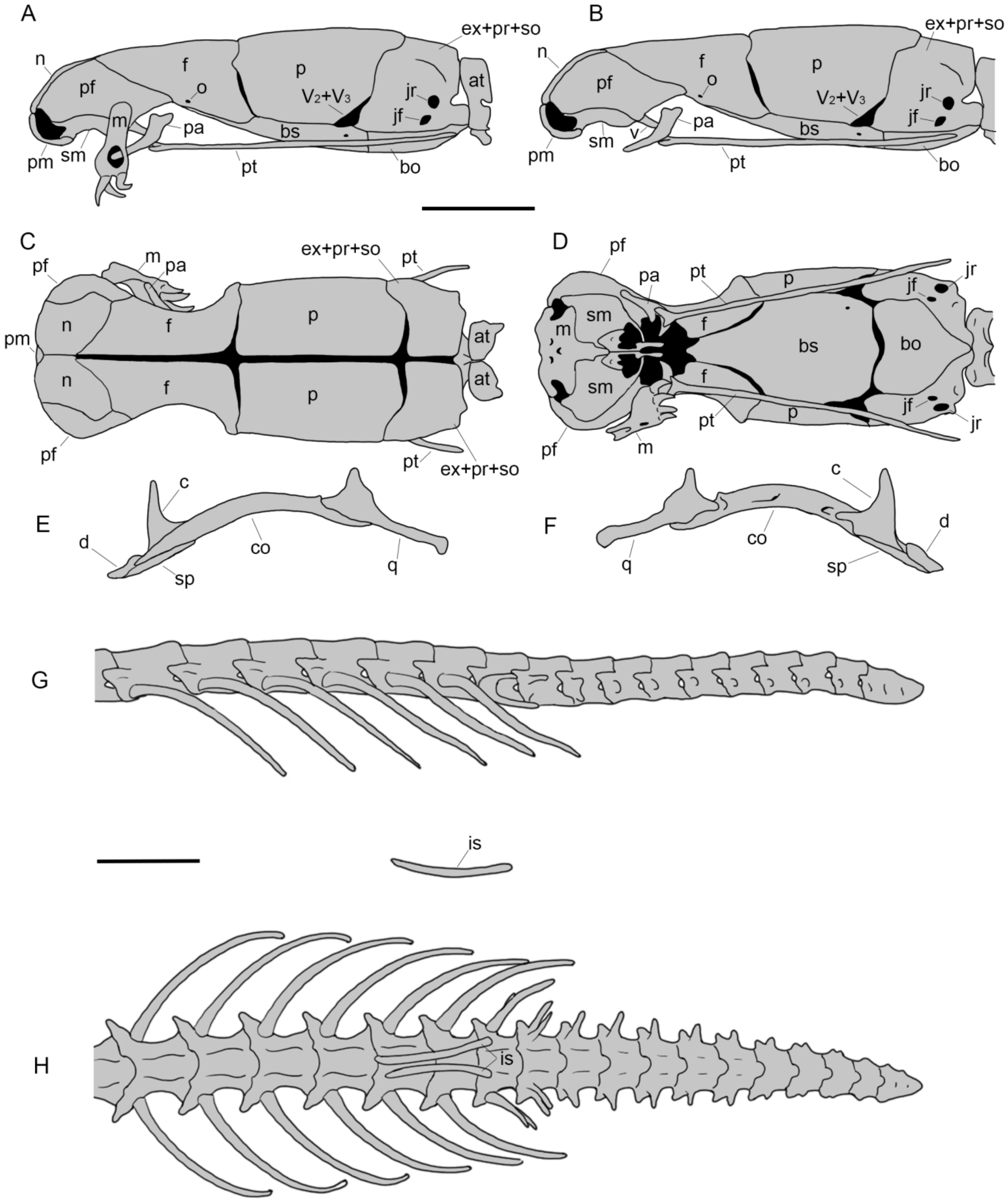
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FIGURE 2-8. Skull of *Anomalepis flavapices* (drawings based on computer tomography of AMNH R-6966). **A**, skull in left lateral view; **B**, skull in left lateral view, maxilla removed; **C**, skull in dorsal view; **D**, skull in ventral view; **E**, lower jaw in lateral view; **F**, lower jaw in medial view. **Abbreviations**: $\mathbf{V_2+V_3}$, common foramen for maxillary and mandibular branches of trigeminal nerve; **a**, angular; **at**, atlas; **av**, anterior opening of vidian canal; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **co**, compound bone; **d**, dentary; **e**, ectopterygoid; **ex**, exoccipital-opisthotic; **f**, frontal; **j**, jugal; **jr**, juxtastapedial recess; **m**, maxilla; **n**, nasal; **o**, optic foramen; **p**, parietal; **pa**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pr**, prootic; **pt**, pterygoid; **pv**, posterior opening of vidian canal; **q**, quadrate; **sm**, septomaxilla; **so**, supraoccipital; **st**, supratemporal; **v**, vomer. Scale bar equals 1 mm.

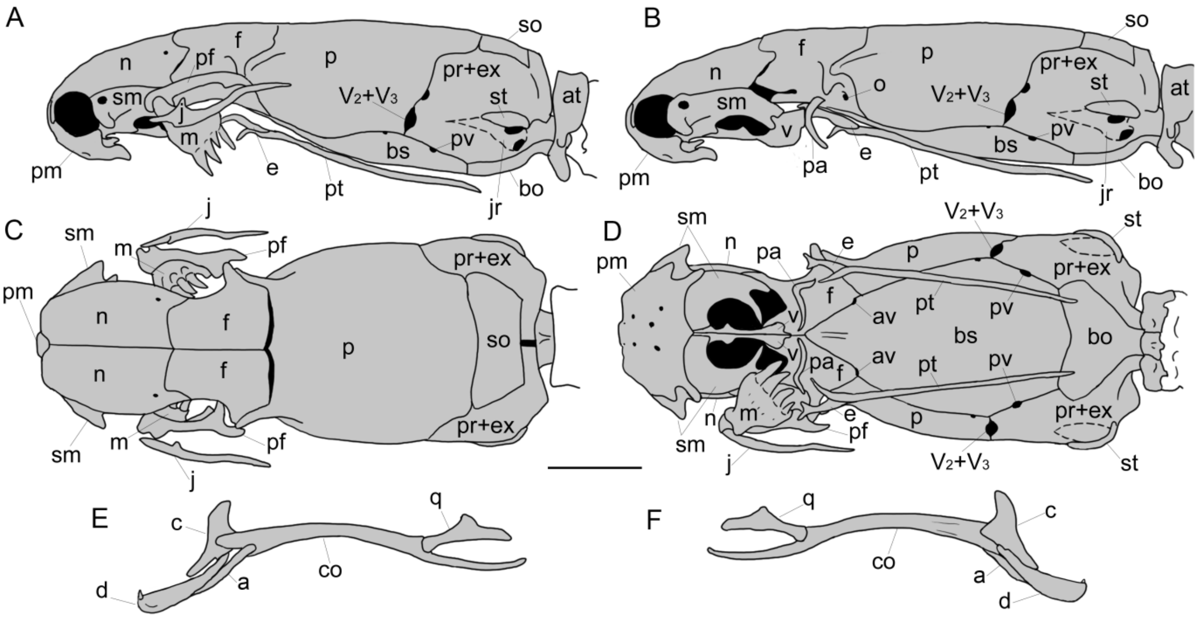

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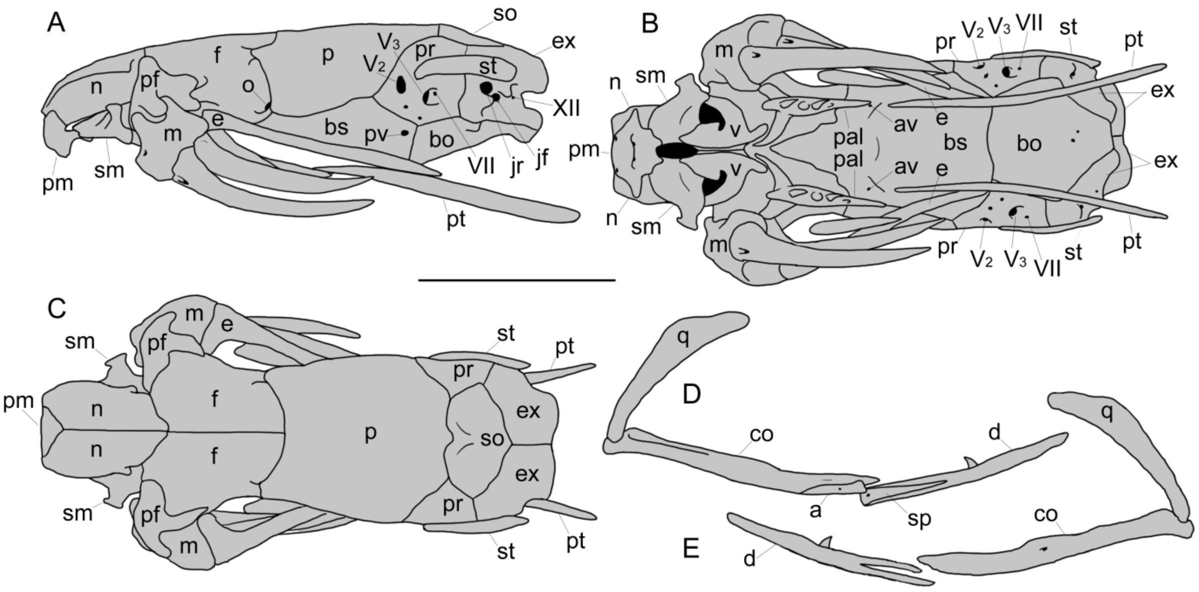
FIGURE 2-9. Skull of *Atractaspis aterrima* (drawings based on computer tomography of AMNH R-12352). **A**, skull in left lateral view; **B**, skull in ventral view; **C**, skull in dorsal view; **D**, lower jaw in medial view; **E**, lower jaw in lateral view. **Abbreviations**: **V_2**, foramen for maxillary branch of trigeminal nerve; **V_3**, foramen for mandibular branch of trigeminal nerve; **VII**, foramen for facial nerve; **XII**, foramen for hypoglossal nerve; **a**, angular; **av**, anterior opening of vidian canal; **bo**, basioccipital; **bs**, basisphenoid; **co**, compound bone; **d**, dentary; **e**, ectopterygoid; **ex**, exoccipital-opisthotic; **f**, frontal; **jf**, jugular foramen; **jr**, juxtastapedial recess; **m**, maxilla; **n**, nasal; **o**, optic foramen; **p**, parietal; **pa**, palatine; **pf**, prefrontal; **pm**, premaxilla; **pr**, prootic; **pt**, pterygoid; **q**, quadrate; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **st**, supratemporal; **v**, vomer. Scale bar equals 1 mm.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CHAPTER THREE

REEVALUATION OF THE ANATOMY OF THE CENOMANIAN (UPPER CRETACEOUS) HIND-LIMBED MARINE FOSSIL SNAKES *PACHYRHACHIS*, *HAASIOPHIS*, AND *EUPODOPHIS*

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INTRODUCTION

Snakes are a fascinating group of organisms made especially intriguing by their highly transformed tetrapod anatomies (extreme axial elongation via increased numbers of somites, limb and girdle reduction to complete limb and girdle loss, internal organ asymmetries, etc.) that confounds the elucidation of their ancestry and origins (Bellairs and Underwood, 1951; Rieppel, 1988; Caldwell, 2007). Thus far, two principal evolutionary scenarios have been proposed, one that envisions snakes as originating from a group of secondarily aquatic lizards, and the other where they originate from an unknown group of cryptic or burrowing squamates (see Bellairs and Underwood [1951], Rieppel [1988], and Caldwell [2007] for detailed reviews).

The first scenario originated after Cope's (1869) assertion that snakes were closely related to a group of marine lizards, the mosasaurs (named 'Pythonomorpha' by Cope [1869] in reference to their resemblance with snakes). Even if Cope's (1869) original intention was not to propose that mosasaurs were ancestral to snakes (Caldwell, 2007), his idea of a close relationship with that extinct group of marine lizards initiated a vitriolic debate between Cope and some of the most preeminent paleoherpetologists of the time (e.g., Owen, 1877; Marsh, 1880; Boulenger, 1891; Baur, 1895, 1896; Cope, 1895a, 1895b, 1896; Osborn, 1899; Williston, 1904; Janensch, 1906). In the course of this debate, Owen (1877) was the first to suggest that, of all extinct varanoid lizards, dolichosaurs rather than mosasaurs would best represent an intermediate stage between limbed terrestrial lizards and snakes. Owen's (1877) idea of a close relationship between dolichosaurs and snakes was further elaborated by Nopcsa (1903, 1908, 1923), who agreed with Cope (1869) that snakes were closely related to mosasauroids (i.e., aigialosaurs and mosasaurs). Nopcsa (1903, 1908) also argued, as was suggested by Owen (1877), that dolichosaurs might represent a better intermediate between a platynotan-like ancestor and modern snakes. Nopcsa later slightly revised his evolutionary hypothesis (Nopcsa, 1923) to depict snakes as the sister group of dolichosaurs, rather than their direct descendants, and proposed both groups to have originated from within his 'Aigialosaurinae.' Cope's (1869, 1895a, 1895b, 1896), Owen's (1877), and Nopcsa's (1903, 1908, 1923) ideas laid the basis for the evolutionary scenario according to which snakes arose from within a group of secondarily aquatic squamates. Cope's (1869) 'Pythonomorpha' was later synonymized with the family name Mosasauridae; however, in recent years, the term Pythonomorpha was resurrected by Lee (1997) to refer to a clade inclusive of both mosasauroids (= mosasaurs and aigialosaurs) and snakes, whereas Palci and Caldwell (2007) introduced the term Ophidiomorpha to refer to a clade consisting of dolichosaurs (either mono- or paraphyletic) and snakes (Ophidia). The Ophidiomorpha would thus be the sister group of mosasauroids and the two clades together would constitute a more inclusive Pythonomorpha (Palci and Caldwell, 2007, 2010).

An alternative to the marine origin scenario sees snakes as derived from some unknown group of cryptic or burrowing terrestrial lizards (e.g., Janensch, 1906). This hypothesis gained strength after Walls' (1940, 1942) studies on the eye anatomy of snakes, where he noted differences between the eye structure of snakes and lizards, and argued that such differences could only be explained if snakes underwent degeneration during a prolonged burrowing stage in their early evolution. The eyes would have been later reevolved or reelaborated in the groups of snakes that secondarily reacquired aboveground ecological habits. However, as shown by Caprette et al. (2004), the unique anatomy of the ophidian eyes might also be the result of adaptation to an aquatic environment.

The hypothesis that snakes may have originated from a burrowing group of squamates was further supported by studies that found evidence for a close relationship of snakes to burrowing scincid lizards (e.g., Brock, 1941; Conrad, 2008), amphisbaenians (e.g., Rage, 1982), dibamids (Senn and Northcutt, 1973), or both amphisbaenians and dibamids (e.g., Wu et al., 1996; Rieppel and Zaher, 2000; Kearney, 2003; Gauthier et al., 2012; Zaher and Scanferla, 2012). However, unless snakes, scincid lizards, amphisbaenians, and dibamids are all closely related to each other, it is clear that the above-mentioned studies present conflicting evidence about snake sister-group relationships and snake origins.

The most recent revival of the burrowing origin hypothesis was presented by Longrich et al. (2012), who attributed some new non-associated, non-articulated materials to the Maastrichtian fossil snake *Coniophis precedens* Cope, 1892 (whose holotype consists of a single vertebra), and combined these various specimens into a single terminal taxon in a phylogenetic analysis of snakes. The results of that analysis were interpreted as suggesting that this ‘snake’ represents the most primitive member of the Ophidia. Longrich et al. (2012) concluded (based on paleoecological context [i.e., fluvial environment], and size and morphology of the vertebrae) that their phylogeny lends support to a terrestrial, and more specifically burrowing, origin of snakes. Although a thorough reanalysis of the Longrich et al. (2012) study is essential, it suffices to state here that their conclusions were based around the results of an ingroup analysis of snake sister-group relationships, similar to previous studies including Tchernov et al. (2000), Apesteguia and Zaher (2006), and Zaher and Scanferla (2012). However, such approaches do not provide the necessary phylogenetic framework from which to justify such conclusions. Valid origin hypotheses can only be derived from the analysis of relationships between the ingroup in question and its potential sister groups within the larger clade (e.g., Caldwell and Lee, 1997; Lee, 2005a; Wiens et al., 2012). For this reason, we reject the burrowing origins conclusion of the recent study by Longrich et al. (2012) and previous studies (e.g., Tchernov et al., 2000; Apesteguia and Zaher, 2006; Zaher and Scanferla, 2012).

At present, the most commonly accepted possible sister-group hypotheses for snakes are those that see them as closely related to the Anguimorpha (Estes et al., 1988; Schwenk, 1988; Lee, 1997, 1998, 2000, 2005a; Reynoso, 1998), the Iguania (Vidal and Hedges, 2004; Bohme et al., 2007; Albert et al., 2009), or both (Townsend et al., 2004; Vidal and Hedges, 2005; Wiens et al., 2010, 2012).

Interestingly, in the case of a close relationship between snakes and anguimorphan lizards, the link between the two groups is usually consolidated by the inclusion of the extinct Pythonomorpha (= aigialosaurs, mosasaurs, and dolichosaurs), which provide support for a marine origin of snakes in the context of a cladistic analysis where character transformations can be followed through a cladogram (i.e., synapomorphies are organized in a hierarchical pattern from more inclusive to less inclusive clades; Lee 1998, 2005a, 2005b, 2009; Palci and Caldwell, 2010). On the other hand, a sister-group relationship between snakes and iguanians is only supported by molecular data; there are no known fossil forms that might act as potential morphological intermediates between these two taxonomic groups. In other words, this scenario tells us nothing about the morphological transformations that may have led to the origin of the ophidian body plan and, as such, has no bearing on the two evolutionary scenarios that see snakes as derived either from aquatic or from burrowing ancestors (neither marine nor burrowing iguanians are known from the fossil record; the marine iguana, *Amblyrhyncus cristatus*, represents a fairly recent [approximately 10 million years] and quite unique evolutionary radiation within Iguania; Rassmann, 1997).

It is in this context of problematic and unresolved sister-group relationships of snakes that two hind-limbed fossil snakes from the Cenomanian (Upper Cretaceous) of the Middle East, namely, *Pachyrhachis problematicus* and *Eupodophis descouensi*, have been introduced as evidence in support of a marine origin of snakes (Caldwell and Lee, 1997; Lee and Caldwell, 1998; Rage and Escuillié, 2000). These snakes would represent almost ideal intermediates between the body plan of dolichosaurs and that of more advanced snakes. However, their phylogenetic position has been questioned repeatedly and no universal consensus has yet been reached (Zaher, 1998; Zaher and Rieppel, 1999, 2002; Caldwell, 2000a; Rieppel and Zaher, 2000). More recently, a third fossil snake with well-developed hind limbs, *Haasiophis terrasanctus*, was added to the debate (Tchernov et al., 2000; Rieppel et al., 2003). Tchernov et al. (2000) and Rieppel et al. (2003) saw the anatomy as supportive of the advanced status (macrostomatan) of this new Cenomanian hind-limbed snake; however, as the specific epithet of *Pachyrhachis* suggests, all of these fossil snakes from the Cenomanian of the Middle East present a serious problem of character conflict, in that they possess a mixture of what are considered primitive (i.e., lizard-like) and advanced (i.e., supposedly derived macrostomatan) features. In particular, the presence of well-developed hind limbs can certainly be considered a primitive feature, whereas the presence of supratemporals that project posteriorly beyond the otooccipitals is usually considered as an adaptation of derived alethinophidian snakes to ingest large prey items. If these fossil snakes are to be considered primitive, then the presence of a macrostomatan skull anatomy should be considered as secondarily lost in scolecophidians, anilioids, and fossil snakes such as *Dinilysia* (Rieppel, 2012). This hypothesis is not totally unreasonable, because, as already pointed out by Rieppel and Head (2004), support for multiple losses of the macrostomatan skull condition comes from some molecular phylogenetic analyses (Wilcox et al., 2002; Vidal and David, 2004; Vidal and Hedges, 2004). On the other hand, if these fossil hind-limbed snakes are to be considered as basal macrostomatans, then the implication would be that hind limbs were either reduced or lost independently several times within snakes. It is also possible, as was suggested by Rieppel et al. (2003), that various lineages of Cenomanian macrostomatan snakes reacquired their limbs (character reversals in their cladograms). However, this hypothesis is problematic because this phenomenon has never been reported for any limbless taxon (Coates and Ruta, 2000).

In this paper, we provide a reevaluation of new and newly interpreted cranial and postcranial anatomies for the three pivotal fossil snakes from the Cenomanian of the Middle East, *Pachyrhachis*, *Eupodophis*, and *Haasiophis*. The data we present are used to rediagnose these three taxa and to revisit the phylogenetic relationships of snakes.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **HUJ-Pal**, Hebrew University of Jerusalem, Palaeontology Collections, Jerusalem, Israel; **MACN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MSNM**, Museo di Storia Naturale di Milano, Milan, Italy; **Rh-E.F.**, Natural History Museum of Gannat, Gannat, France; **SMNH**, Slovenian Museum of Natural History, Ljubljana, Slovenia; **ZFMK**, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

REVISED ANATOMY OF *HAASIOPHIS*, *PACHYRHACHIS*, AND *EUPODOPHIS*

Study of the type and referred materials of *Eupodophis descouensi*, *Pachyrhachis problematicus*, and *Haasiophis terrasanctus* resulted in anatomical identifications and interpretations that are notably different from those given by Tchernov et al. (2000), Rieppel et al. (2003), and Rieppel and Head (2004), and in new observations of previously unreported anatomical features.

Haasiophis and *Eupodophis*: 'Prootic Flange' Absent

In their description of the skull of *Haasiophis terrasanctus*, Tchernov et al. (2000) and Rieppel et al. (2003) interpreted a bony flange on the sides of the posterior region of the skull as a 'prootic flange,' and Tchernov et al. (2000) interpreted this structure as corroborating evidence for the presence of the laterosphenoid (an element considered typical of alethinophidian snakes), which was consequently coded as present in their cladistic analysis of snake interrelationships (their character 65). Following Tchernov et al. (2000), Rieppel et al. (2003:542) included the flange as part of their diagnosis of the taxon: "mandibular nerve foramen underlapped by distinct prootic flange." A similar structure was identified by Rieppel and Head (2004:fig. 10) in one of the referred specimens of *Eupodophis* (MSNM V 4014) and interpreted again as a 'prootic flange.'

Based on our observation of the fossil material, we cannot support the identification of these structures as ‘prootic flanges,’ contra Rieppel et al. (2003) and Rieppel and Head (2004). Instead, we confidently identify these structures as the ectopterygoid processes of the pterygoid bone (see also Lee and Scanlon, 2002). This interpretation is supported by several lines of evidence: (1) they are laterally directed and materially continuous processes arising from the margins of the pterygoid bones (Fig. 3-1; Supplementary Data 3-1); (2) in *Haasiophis* (HUJ-Pal EJ 695), the process on the left side is still in articulation with the ectopterygoid (Fig. 3-1A–C;); and (3) the ‘prootic flanges’ of alethinophidian snakes are located far posteriorly in the skull, very close to the suture line between basioccipital and basisphenoid, and never project far laterally, but rather posteriorly and only slightly, if at all, laterally (Fig. 3-1D). We argue against an interpretation of anatomy that is heavily dependent on taphonomic scenarios; in this case, a scenario requiring dorsoventral compression and anterior displacement in both *Haasiophis* (HUJ-Pal EJ 695) and the referred specimen of *Eupodophis* (MSNM V 4014), that would produce ‘prootic flanges’ in the position of ectopterygoid processes, articulating with the ectopterygoids, projecting at 90◦ from the lateral margin, in a position far anterior to their expected anatomical location (i.e., in the middle of the anterior half of the prootic). Therefore, our observations find no empirical support for the identification of ‘prootic flanges’ in *Haasiophis* and *Eupodophis*, contra Tchernov et al. (2000), Rieppel et al. (2003), and Rieppel and Head (2004). The secondary outcome of our empirical observation is a rejection of the additive and inductive conclusion of the presence of a ‘laterosphenoid’ in these fossil snakes, as well as a rejection of the hypothesis that the presence of a laterosphenoid would be a shared character state (primary homology) of *Haasiophis*, *Eupodophis*, and other higher snakes. The presence or absence of a laterosphenoid ossification in *Haasiophis* and *Eupodophis* can only be confirmed with the recovery of new, better preserved fossil material.

Pachyrhachis and Eupodophis: Jugal Present

Caldwell and Lee (1997), Lee and Caldwell (1998), Lee and Scanlon (2002), and Caldwell (2007) interpreted as jugals the two elements that are located anteroventral to the postorbitofrontals of *Pachyrhachis* (Fig. 3-2A; Supplementary Data 3-1; note: following the argument of Zaher and Scanferla [2012] for *Dinilysia*, we prefer the use of the term ‘postfrontals’ rather than ‘postorbitofrontals’ when referring to the triradiate elements that clasp the frontoparietal suture of *Pachyrhachis*). This interpretation is consistent with the topographical position of the jugals in squamates, which, even when reduced, are consistently articulating with the posterodorsal surface of the maxilla and are located anteroventral to the postorbital, postfrontal, or fused postorbitofrontal (e.g., *Varanus salvator*, *Lanthanotus borneensis*, *Pygopus lepidopus*, *Hemitheconyx caudicinctus*; Estes et al., 1988). Zaher and Rieppel (1999) argued against this interpretation and claimed that the elements identified as jugals in *Pachyrhachis* by Caldwell and Lee (1997) and Lee and Caldwell (1998) were instead parts of the ectopterygoids that had been broken and displaced anteriorly as a result of taphonomic processes. However, such an interpretation is problematic, not only because these ‘ectopterygoids’ would have to have been broken and displaced symmetrically on both sides of the skull without any other of the surrounding elements being similarly affected, but also because similar elements, and in a similar position, have been identified also in one of the referred specimens of *Eupodophis* (MSNM V 3661) (Fig. 3-2B). Rieppel and Head (2004) recognized the fact that these elements in *Eupodophis* (MSNM V 3661) are likely in their natural position and that their posterior margins do not show any sign of breakage whatsoever, which goes against the argument made to support the position taken by Zaher and Rieppel (1999). However, Rieppel and Head (2004) tried to justify the inconsistent topological position of these ‘ectopterygoids’ anterior to what they identified as postorbitals, by suggesting that this had to be the result of a posterior shift (due to development and not to taphonomy) of the latter elements in response to an unusual posterior elongation of the frontals (note: the ‘postorbitals’ of Rieppel and Head [2004] have been alternatively referred to as ‘postorbitofrontals’ by Caldwell and Lee [1997], Lee and Caldwell [1998], and Caldwell [2007]; however, as mentioned above, based on the arguments provided by Zaher and Scanferla [2012] for *Dinilysia*, we conclude that these elements actually represent the homologs of the lacertilian postfrontals). The frontals of both *Pachyrhachis* and *Eupodophis* are indeed quite elongate anteroposteriorly, but even if the shift proposed by Rieppel and Head (2004) had occurred, there should still be a portion of the ‘ectopterygoids’ that project posteromedially to contact the ectopterygoid processes of the pterygoids, a feature that is apparent in the fossil snake *Dinilysia patagonica* despite its similarly long frontals (Fig. 3-2C). This is not the case in either *Pachyrhachis* or *Eupodophis*, and, as already noted above, the well-preserved finished margins of Rieppel and Head's (2004) 'ectopterygoids' are inconsistent with any broken and missing portion. Moreover, the same finished posterior margins of these elements are also inconsistent with the interpretation provided by Polcyn et al. (2005), who considered them (their unidentified elements 'ue1' and 'ue2') as fragments of broken postorbitals.

For all these reasons, we agree with Caldwell and Lee (1997), Lee and Caldwell (1998), and Caldwell (2007) regarding their interpretation of the elements located anteroventral to the postfrontals ('postorbitofrontals' of the above-mentioned authors) of *Pachyrhachis* as jugals, and by extension we also interpret as jugals the elements that share the same topological relationships in *Eupodophis*.

As a final note, it is interesting to point out that both *Dinilysia* (Fig. 3-2C) and *Pachyrhachis* (Fig. 3-2A, D) have a triradiate postfrontal that articulates ventrally with a spatula-shaped jugal, the only difference between the two taxa is that the ventral ramus of the postfrontal of *Pachyrhachis* appears to be more pronounced. Interestingly, Zaher and Scanferla (2012) recognized the homology of the element located posterodorsal to the orbit in *Dinilysia* and *Yurlunggur* as a postfrontal, but concluded that the bone lying ventral to it should be regarded as a postorbital. We disagree with the latter conclusion, and consider the element forming the posterior margin of the orbit of *Dinilysia* and *Yurlunggur* as a jugal, in agreement with the arguments put forward by Caldwell and Albino (2002), Scanlon (2006), McDowell (2008), and Palci and Caldwell (2013).

Haasiophis **and** ***Eupodophis*****: Chevron Bones Present**

Rieppel and Head (2004) described quite unique, ‘ventrally projecting sagittal unpaired keels or pedicels’ in the anteroventral region of the caudal vertebrae of *Eupodophis* (MSNM V4014) (Fig. 3-3A; Supplementary Data 3-1). They used the purportedly unique (neomorphic) nature of these unpaired processes to deny the homologous nature of the chevron bones of *Eupodophis* (see Rage and Escuillé, 2000) to the similar structures of lizards.

However, our examination and analysis of MSNM V 4014 has resulted in the recognition of the ‘neomorphic sagittal pedicels’ of Rieppel and Head (2004) as the typical paired anteroventrally projecting transverse processes found in most snakes (Fig. 3-3C). The chevron bones of *Eupodophis* do not articulate with these processes, but are rather simply overlapped by them locally as a result of diagenetic mediolateral compression, and as a matter of observation, the chevron bones in the type specimen of *Eupodophis* articulate with the posteroventral surface of the caudal centra (Fig. 3-3B).

Interestingly, chevron bones are distinctly present also in the type specimen of *Haasiophis* (Fig. 3-3D), but neither Tchernov et al. (2000) nor Rieppel et al. (2003) reported their presence. The chevron bones of *Haasiophis* are fused distally and articulate proximally to the posteroventral region of the caudal centra via distinct hemapophyseal facets. They do not possess the very elongate hemal spines that are characteristic of *Eupodophis*, but are anteroposteriorly expanded towards their distal extremity, so that they have a spatula-shaped outline in lateral view.

***Haasiophis*: Premaxilla**

Both Tchernov et al. (2000) and Rieppel et al. (2003) described *Haasiophis* as having a strongly reduced and toothless premaxilla. Upon close examination of the type and only specimen (HUJ-Pal EJ 695), we identified an element lying mostly dorsal to the anterior extremities of the two maxillary bones (Fig. 3-4; Supplementary Data 3-1), likely due to some slight postmortem displacement. Immediately posterior to the anterior tips of the maxillae, two triangular lappets are visible that most likely represent the vomerine processes of the premaxilla. If this interpretation is correct, then the premaxilla of *Haasiophis* has fairly large vomerine processes, comparable in shape and relative size to those of modern lizards such as *Varanus* or those of the snakes *Anilius* and *Eunectes*. On the other hand, considering the very limited exposure of the main body of the premaxilla, we were unable to discriminate the presence or absence of premaxillary teeth or of ventral foramina. Although the radiographs published in Rieppel et al. (2003) show an element lying in between and slightly dorsal (i.e., within the matrix) to the two maxillae, these images are too blurry to confidently reconstruct the actual structure of this bone.

***Haasiophis*: Presacral Intercentra Present**

Tchernov et al. (2000) and Rieppel et al. (2003) reported the presence of well-developed hypapophyses on the anterior trunk region of *Haasiophis*. However, upon close examination of the type and only specimen, it is evident that these structures do not represent fused intercentra (i.e., hypapophyses sensu lato [s.l.]), but rather intercentra that retain their individuality and articulate with elongate peduncles (i.e., hypapophyses sensu stricto [s.s.]) at the base of the anterior precloacal vertebrae (Fig. 3-5).

Despite the presence of some fractures in the vertebrae of *Haasiophis*, the length of what we interpret as intercentra does not change randomly, but instead varies very slightly along the vertebral column. Minor stochastic variation in length is due to distortion and breakage of the intercentra, but overall the length of the intercentra is very consistent. Moreover, fractures can be distinguished because of their random orientation, whereas what we interpret as articular surfaces between intercentra and vertebrae retain the same orientation (roughly perpendicular to the long axis of the intercentra) regardless of the orientation of the vertebrae (i.e., whether the vertebrae lie on their dorsal or dorsolateral surface) and their position at the base of the intercentra is very consistent (Supplementary Data 3-1, Fig. 3-7S).

This condition may at first be considered similar to that observed in two groups of lizards, namely, Xantusiidae and Gekkonidae, where some species retain unfused intercentra in the cervical and in the trunk region. However, in these groups, the unfused intercentra are present up to the end of the dorsal series, contrary to what happens in *Haasiophis*, where the presence of unfused intercentra characterizes only the anterior part of the precloacal region. Therefore, the condition of *Haasiophis* is more like that observed in lizards that retain unfused cervical intercentra only (i.e., some iguanids, some cordylids, some lacertids, some scincids, *Heloderma*, *Lanthanotus*, and *Varanus*, and all members of the Pythonomorpha for which the cervical region is known; Russell, 1967; Estes et al., 1988; Carroll and DeBraga, 1992; Caldwell, 2000b; Pierce and Caldwell, 2004; Caldwell and Palci, 2010). An interesting implication to this observation is that the anterior 45 precloacal vertebrae of *Haasiophis* might indeed be homologous to the cervical vertebrae of other squamates. This in turn implies that the cervical region of *Haasiophis* underwent considerable axial elongation by an increase in the number of vertebrae, a phenomenon that occurred also in the fossil dolichosaurs and adriosaurs, two groups of lizards that have long been considered closely related to snakes (Owen, 1877; Nopcsa, 1903, 1908; Caldwell 2000b, 2006; Lee and Caldwell, 2000; Pierce and Caldwell, 2004; Lee 2005a, 2009; Palci and Caldwell, 2007, 2010; Caldwell and Palci, 2010). Furthermore, *Haasiophis* is not the only snake known to possess unfused intercentra posterior to the axis. Their presence was previously reported in the Turonian (Upper Cretaceous) fossil snake *Dinilysia patagonica* (Caldwell and Albino, 2002).

Although some of the long intercentra of *Haasiophis* appear to have been fractured in several places, we have the following reasons to consider that their separation from the centra is not an artifact of preservation: (1) not one of these

45 elements is continuous (i.e., fused) with the adjacent centrum; (2) the discontinuity between intercentrum and centrum is consistently located at the same point; (3) the intercentra decrease regularly in size posteriorly, and even when very small they still retain a discontinuity with the centrum—we find it hard to regard such small and rounded elements as resulting from breakage due to dorsoventral compression; and (4) what we interpret as unfused intercentra in *Haasiophis* are strikingly similar to the unfused intercentra of the fossil lizard *Adriosaurus skrbinensis* (SMNH 2158) in being long, slender, and tapering distally, and in having a long and slender peduncle (hypapophysis s.s.) for attachment to the centrum (Fig. 3-5C). Similarly elongate peduncles (hypapophyses s.s.) are observed in some modern lizards such as *Varanus* (Hoffstetter and Gasc, 1969) and *Lanthanotus* (Rieppel, 1980; A.P., pers. obs.).

***Pachyrhachis*: Mental Foramina**

The dentaries of the referred specimen of *Pachyrhachis problematicus* (HUJ-Pal EJ 3775) show the presence of a series of small foramina aligned in a row, recalling the condition observed in modern lizards (Fig. 3-6; Supplementary Data 3-1). This feature was first noted by Haas (1979:62) on the type specimen of *Pachyrhachis* (HUJ-Pal EJ 3659): "*. . .*there are shallow alveolar depressions for about 10 teeth, caudally growing deeper in succession, and about 6 trigeminal foramina"; however, the same author later retracted his interpretation and wrote: "most probably there was a single mental foramen" (Haas, 1980:95). The uncertainty in Haas' (1980) conclusion is understandable if we consider that the dentaries of the type specimen of *Pachyrhachis problematicus* (HUJ-Pal EJ 3659) show a combination of poor preservation and lack of exposure of their lateral surface (especially after the skull of the type had been embedded in clear resin in order to be prepared on the ventral side; unfortunately, the layer of resin that now lies on top of the dorsal surface of the skull is too thick and murky to allow detailed observations of the surface anatomy of the embedded bones). However, the series of small foramina that Haas (1979) tentatively identified in the dentary of the holotype can be confirmed from examination of the referred material (HUJPal EJ 3775). On the left dentary of HUJ-Pal EJ 3775, these foramina are located in close proximity to a fracture plane that most likely occurred because of the structural weakness imposed by the presence of the canal for the mandibular branch of the trigeminal nerve (V3), and are hard to discern under normal lighting conditions; however, use of lights placed at a low angle to the surface of the fossil reveals their presence (Fig. 3-6A, B). The arrangement of these foramina is strikingly similar to that of modern lizards such as the basal anguimorphan *Ophisaurus apodus* (Fig. 3-6C). Moreover, these features cannot be interpreted as preservational artifacts because they can be observed both on the left and on the right dentary of the referred specimen. Polcyn et al. (2005) also noted the presence of multiple foramina (at least three) in their CAT scan of the type specimen of *Pachyrhachis* (HUJ-Pal EJ 3659); however, they considered only one to represent a true mental foramen and dismissed the rest as preservational artifacts. Their argument was based on the observation that only one of these foramina could be followed inside the dentary through serial sections of the bone, but as noted by Polcyn et al. (2005), the areas of the dentary where the other two foramina occur are crushed, this compression may have easily collapsed the internal passages for the mandibular nerve.

Lastly, we do not consider the asymmetry of the foramina between the left and right dentaries of HUJ-Pal EJ 3775 to be contrary to our interpretation, because the number and position of the mental foramina in lizards are often similarly asymmetrical (Supplementary Data 3-1, Fig. 3-9S).

***Pachyrhachis*: Sacral Vertebra**

Caldwell and Lee (1997) and Lee and Caldwell (1998) described the presence of a sacral vertebra in the referred specimen of *Pachyrhachis problematicus* (HUJ-Pal EJ 3775). Zaher and Rieppel (1999) argued against this interpretation and stated that the free sacral rib of Caldwell and Lee (1997) and Lee and Caldwell (1998) should be more parsimoniously interpreted as the first lymphapophysis. Upon direct examination of HUJ-Pal EJ 3775, we could not conclusively decide what the “sacral rib” portrayed by Lee and Caldwell (1998:fig. 14) really represents, because there is a series of fractures, and minute bone fragments, lying on top and around its dorsal extremity. However, a sacral vertebra is present in *Pachyrhachis*, but was misidentified in previous descriptions of the material. The last ‘dorsal rib’ of Caldwell and Lee (1997) and Lee and Caldwell (1998) clearly has a widely expanded distal extremity that is consistent with it being a sacral rib (Fig. 3-7; Supplementary Data 3-1) (Hoffstetter and Gasc, 1969).

We exclude the possibility that this is simply a presacral rib expanded distally due to taphonomic compression against the pubis, because the preceding rib, which is also compressed against the pubis, does not show the same degree of distal expansion (Fig. 3-7; Supplementary Data 3-1). Moreover, the rib that we interpret as sacral is much wider than the preceding rib also in the region that did not suffer a great deal of compression (i.e., dorsally). Importantly, distally compressed ribs caused by taphonomic distortion have never been reported in any of the other pachyostotic snakes known (i.e., *Haasiophis*, *Mesophis*, *Pachyophis*), despite common overlapping of ribs over other skeletal elements (i.e., other ribs, limb bones, or pelvic elements) (Nopcsa, 1923; Bolkay, 1925; Lee et al., 1999; Tchernov et al., 2000; Rieppel et al., 2003; Houssaye, 2010). Such an expansion is consistent with what should be expected from a sacral rib that retains at least a ligamentous connection with the pelvic girdle. However, what is unusual is the fact that the sacral rib of *Pachyrhachis* articulates with the sacral vertebra rather than being fused to it. Interestingly, according to Hoffstetter and Gasc (1969) and Gauthier et al. (1988), in modern squamates the sacral ribs fuse to their respective centra in the embryo, whereas they fuse post-embryonically only in ancestral lepidosauromorphs such as younginiforms, *Palaeagama*, and rhynchocephalians. Another interesting feature of *Pachyrhachis* is that the sacral rib is not only preceded but also followed by ribs that articulate to their respective vertebrae; in other words, the sacral rib is not immediately followed either by fused forked ribs (i.e., lymphapophyses) or by transverse processes, and the vertebrae located posterior to the sacrum still bear synapophyses like those present in the presacral series.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

OPHIDIA Brongniart, 1800

HAASIOPHIS TERRASANCTUS **Tchernov, Rieppel, Zaher, Polcyn, and Jacobs, 2000 (Figs. 3-1A–C, 3-3D, E, 3-4, 3-5A–C)**

Emended Diagnosis—Snake with well-developed hind limbs consisting at least of femur, tibia, fibula, and mesopodials; ilium, pubis, and ischium present; parietal with well-developed posterolateral processes; ‘V’-shaped suture line between frontals and nasals; dorsal process of coronoid small, much shorter than maximum depth of compound bone; 155 precloacal vertebrae; dorsoventrally elongate intercentra articulate with ventral peduncles (hypapophyses s.s.) located on posteroventral surface of vertebrae in anterior precloacal (cervical?) region; at least 50 caudal vertebrae; chevron bones present on caudal vertebrae and articulate with centra through a pair of posteroventrally located facets; at least 23 tooth positions on maxilla, at least nine on palatine, at least 15 on pterygoid, and at least 25 on dentary.

Type Specimen—HUJ-Pal EJ 695.

EUPODOPHIS DESCOUENSI Rage and Escuillié, 2000 (Figs. 3-1E, F, 3-2B, 3-3A, B)

Emended Diagnosis—Snake with well-developed hind limbs consisting at least of femur, tibia, fibula, astragalus, and calcaneum; ilium, ischium, and pubis present; long and narrow frontals; quadrate expanded dorsally and ventrally, with narrow and almost rod-like shaft; dorsal process of coronoid high, taller than maximum depth of compound bone; retains a jugal; tail short (~20 vertebrae) andmediolaterally compressed; pachyostotic vertebrae and ribs in middle and posterior trunk regions; chevron bones with very long hemal spines articulate to caudal centra posteroventrally; at least 18 tooth positions on maxilla, at least eight on palatine, and at least seven on pterygoid.

Type Specimens—Rh-E.F. 9001, 9002, 9003.

Referred Specimens—MSNM V 3660, 3661, and 4014.

PACHYRHACHIS PROBLEMATICUS Haas, 1979 (Figs. 3-6A, B, 3-7)

Emended Diagnosis—Snake with well-developed hind limbs consisting at least of femur, tibia, fibula, astragalus, and calcaneum; ilium, ischium, and pubis present; long and narrow frontals; quadrate expanded anteroposteriorly and sheet-like; dorsal process of coronoid high, taller than maximum depth of compound bone; retains a jugal; long anterior flange of coronoid extends horizontally along medial surface of dentary; splenialangular joint located far anteriorly, midway between symphysis and coronoid process; numerous (at least four) small mental foramina on dentary; pachyostotic middle trunk vertebrae and ribs; retains a sacral vertebra with sacral ribs articulated to the centrum; at least 13 tooth positions on dentary, at least seven on palatine, and at least six on pterygoid and maxilla.

Type Specimen—HUJ-Pal EJ 3659.

Referred Specimen—HUJ-Pal EJ 3775.

PHYLOGENETIC ANALYSES

In order to test the impact of our observations and character interpretations on the phylogenetic relationships of *Pachyrhachis*, *Haasiophis*, and *Eupodophis*, we conducted a phylogenetic analysis of snakes using the data matrix of Lee and Scanlon (2002) as modified by Palci et al. (2013). Our data set includes 23 ingroup taxa and 212 characters, including the addition of the following two characters: (character 211) sacral vertebra/ae: present (0); absent (1); and (character 212) cervical intercentra posterior to the axis: fused to centrum (0); not fused to centrum (1) (see Supplementary Data 3-2 to 3-5).

The material recently described as *Coniophis precedens* by Longrich et al. (2012) was not included in our phylogenetic analysis, because we have serious concerns regarding the likely chimaeric status of their expanded morphoconcept for this taxon. First, considering that Longrich et al. (2012) reported the presence of three snake taxa from the same localities, we disagree that there is any justification for assigning all the specimens to *Coniophis* to the exclusion of the other two snake types. Secondly, we do not consider it possible to know if any of the skull fragments they describe are from the same taxon as the vertebrae attributed by them to *Coniophis precedens*. We consider their justifications (e.g., co-occurrence, size, abundance, and phylogenetic congruence) insufficient. A third problem, based on tooth implantation (e.g., UCMP 49999) or tooth morphology (e.g., AMNH 22413), is that some of the material described by Longrich et al. (2012) may not belong to a snake, but rather to an anguimorphan lizard. The tooth crowns of UCMP 49999 are very different (much more slender and posteriorly recurved) from those of AMNH 22413, and this casts doubt on their attribution to the same taxon, snake or lizard (ontogenetic differentiation can be excluded based on the similar size of the fragments).

Following arguments presented by Palci et al. (2013), we ran three separate analyses using the following outgroups: (1) varanoid lizards (i.e., *Heloderma*, *Lanthanotus*, *Varanus*, and Mosasauroidea) (Analysis 1); (2) iguanians (*Iguana*, *Agama*, and *Uromastyx*) (Analysis 2); and (3) the skinks *Acontias* and *Corucia*, amphisbaenians, and dibamids (Analysis 3).

The analyses were run in PAUP∗ 4b10 (Swofford, 2002), using heuristic search algorithms, with 1000 random addition replicates, and the branch-swapping algorithm was set to tree-bisection-reconnection (TBR). The characters were left unordered and with equal weights (following the recommendations of Hauser and Presch, 1991). Statistical measures of support for the branches retrieved in the phylogenetic analyses were obtained using 1000 nonparametric bootstrap replicates (Felsenstein, 1983, 1985). Bootstrap values (BS) higher than 70% were considered to provide strong branch support (Hillis and Bull, 1993).

Each analysis retrieved a single most parsimonious tree. Analysis 1 produced a single most parsimonious tree with 620 steps, consistency index (CI) of 0.47, and retention index (RI) of 0.71 (Fig. 3-8A); Analysis 2 produced a single most parsimonious tree with 614 steps, CI = 0.49, and RI = 0.70 (Fig. 3-8B); and Analysis 3 produced a single most parsimonious tree with 641 steps, CI = 0.46, and RI = 0.69 (Fig. 3-8C). Analyses 1 and 2 retrieved identical ingroup relationships, where both the clade Serpentes (i.e., Scolecophidia and Alethinophidia) and the clade Ophidia (i.e., the most recent common ancestor of *Pachyrhachis* and Serpentes, and all of its descendants) were strongly supported (BS >70). Interestingly, Analysis 3 produced a tree where the clades Ophidia and Serpentes as defined by Lee and Caldwell (1998) are no longer supported. Instead, in this tree, scolecophidian snakes (Scolecophidia = Leptotyphlopidae, Typhlopidae, and Anomalepididae) form a clade at the base of the radiation of snakes, and more-derived snakes are divided into two major clades (sister groups), one that includes all fossil forms, and the other that includes all extant alethinophidian snakes (Alethinophidia = most recent common ancestor of *Anomochilus* and the Colubroidea, and all of its descendants). The most parsimonious interpretation for this evolutionary scenario is that the macrostomatan condition does not represent the ancestral condition for snakes, but appeared independently in two very distinct lineages of snakes (i.e., in the common ancestor of *Haasiophis* and *Eupodophis* on the one hand, and in the common ancestor of *Xenopeltis* and the Colubroidea on the other). We find this possibility intriguing, but the relationships between the Scolecophidia and the clade inclusive of all fossil snakes are inverted in the consensus tree derived from the bootstrap analysis of the relevant data set; the bootstrap consensus tree retrieves a monophyletic Ophidia (BS = 69), but the relative position of the Scolecophidia is only weakly supported (BS = 47), and also the node that defines the clade inclusive of all fossil snakes (i.e., *Najash*, *Dinilysia*, Madtsoiidae, *Haasiophis*, *Pachyrhachis*, and *Eupodophis*) has relatively weak support (BS = 51); moreover, most nodes within this latter clade have BS values below 50 (i.e., between 35 and 42, with the only exception of the node joining *Haasiophis*, *Pachyrhachis*, and *Eupodophis* [BS = 68]).

We also conducted three phylogenetic analyses (one for each outgroup) after constraining the relationships of extant taxa according to the results of the molecular phylogeny recently published by Wiens et al. (2012) (the constraint was based on the robustly supported molecular clades with bootstrap values >95%). When the outgroups consisted either of varanoid lizards or dibamids, skinks, and amphisbaenians, the position of all fossil taxa was consistent with our previous unconstrained analyses; however, when the outgroup consisted of iguanians, all the fossil taxa were moved together into a clade like that retrieved in the analysis that had dibamids, skinks, and amphisbaenians as an outgroup (see Supplementary Data 3-1, 3-6 to 3-8). This may suggest that the signal placing the fossil taxa together in a clade that is the sister group to the Alethinophidia may require further investigation, but it should also be kept in mind that molecular analyses of squamate phylogeny are consistently providing signals that are strongly contradicted by morphological studies, and are therefore highly controversial (see Gauthier et al., 2012; Rieppel, 2012).

None of our analyses (either constrained or unconstrained), regardless of the outgroup used, provided support for the placement of the fossil snakes *Haasiophis*, *Pachyrhachis*, and *Euopodophis* as derived alethinophidians, contra Zaher (1998), Zaher and Rieppel (1999), Rieppel and Zaher (2000), Tchernov et al. (2000), Zaher and Rieppel (2002), and Apesteguia and Zaher (2006).

As in the study by Palci et al. (2013), Scolecophidia and the clade inclusive of all derived alethinophidians (i.e., the clade that includes the common ancestor of *Xenopeltis* and Colubroidea, and all of its descendants) were very well supported in all three unconstrained analyses (Fig. 3-8). Interestingly, despite the use of different data sets, this last clade was also retrieved in the recent phylogenetic analysis by Zaher and Scanferla (2012), and the only two differences between their phylogenetic reconstruction for this clade and the one retrieved in this study are that (1) Zaher and Scanferla (2012) did not find support for a sistergroup relationship between *Xenopeltis* and *Loxocemus*, and that (2) Bolyeriidae would be basal to Tropidophiidae rather than vice versa.

In all three analyses, a clade inclusive of *Anilius*, *Cylindrophis*, *Anomochilus*, and Uropeltidae (= Anilioidea) was retrieved, although with low bootstrap support (BS <50).

DISCUSSION AND CONCLUSIONS

Our revision of the Cenomanian fossil marine snakes from the Middle East confirms the presence of a series of primitive anatomical features in all of these taxa. *Haasiophis* and *Eupodophis*, like *Wonambi* and possibly other madtsoiids (Scanlon and Lee, 2000; Scanlon, 2005), are unique among all known snakes in retaining caudal intercentra (i.e., hemal arches and hemal spines) that articulate with hemapophyses (peduncles) on the caudal vertebrae to form true chevron bones (confirming or rejecting this condition in *Pachyrhachis* remains impossible because the tail is incompletely preserved). *Pachyrhachis* and *Eupodophis* retain an identifiable jugal, a feature also present in *Dinilysia patagonica* (Estes et al., 1970; Caldwell and Albino, 2002; Caldwell, 2007; but see Zaher and Scanferla [2012] for an alternative interpretation). The presence of a series of small mental foramina in *Pachyrhachis* is a primitive feature of this taxon, which along with the presence of well-developed limbs suggests a basal position within the clade Ophidia, a position that was confirmed in our phylogenetic analysis.

No evidence for the presence of a ‘prootic flange’ and hence of a laterosphenoid was found by us in either *Haasiophis* or *Eupodophis*, and we have identified the supposed ‘prootic flanges’ as ectopterygoid processes of the pterygoids (contra Rieppel et al. [2003] and Rieppel and Head [2004]).

Interestingly, *Pachyrhachis* also has a unique pelvic girdle anatomy, where the rod-like ilium likely retained a ligamentous connection with an unfused sacral rib. Lack of fusion between the sacral ribs and the centrum has never been reported in any adult squamate so far, but can be observed in the juvenile stages of primitive lepidosauromorphs such as younginiforms, *Palaeagama*, and rhynchocephalians (Hoffstetter and Gasc, 1969; Gauthier et al., 1988). The lack of fusion of the sacral ribs to their respective centrum, as well as the lack of fusion of the ribs posterior to the sacrum, might have been the result of a developmental process that was slowed with respect to the condition found in lizards, so that fusion did not occur embryonically but post-embryonically as in more primitive lepidosauromorphs; in other words, the unfused sacral and postsacral ribs of *Pachyrhachis* are likely the product of a paedomorphic developmental process resulting in local delay of the onset of growth (post-displacement) and/or in the local reduction of the rate of development (neoteny) (McNamara, 1986). Interestingly, Houssaye et al. (2011) reached a similar conclusion for the development of the hind limbs of *Eupodophis descouensi* based on their microanatomical architecture (i.e., their reduced size is likely the result of either local decrease in growth rate or shortening of growth duration). Moreover, Caldwell and Palci (2010), after noticing lack of fusion of the epiphyses to the diaphysis in the femora of *Adriosaurus skrbinensis*, hypothesized a similar delayed developmental mechanism to be responsible for the reduced limb morphology observed in the genus *Adriosaurus*. It is important to point out that reduced ossification of limb and girdle elements (e.g., separate astragalus and calcaneum, poorly ossified or reduced limb elements, loss of a tight sutural connection between ilium, ischium, and pubis) is commonly observed in aquatic squamates (i.e., mosasaurs, adriosaurs, snakes). The lack of fusion between the sacral ribs and the sacral vertebra of *Pachyrhachis* may be caused by the same evolutionary trend. If this hypothesis is correct, paedomorphic patterns of development (especially delayed onset of growth and reduced rates of development) may be responsible for the origin of limblessness in snakes. In order to achieve a better understanding of the mechanisms at the base of limb loss in this group of squamates, further studies on the genes that regulate the onset and speed of developmental processes are required.

Another very interesting anatomical feature is represented by the series of free intercentra located at the base of the anterior precloacal vertebrae of *Haasiophis terrasanctus*. If these intercentra are homologized with the cervical intercentra of limbed squamates, then this would imply that snakes, in their evolutionary history, experienced a considerable amount of axial elongation that involved not only the dorsal but also the cervical region, a point that is supported by the posterior extension of some cervical muscles (e.g., m. rectus capitis anterior) in snakes (Tsuhiji et al., 2012). Interestingly, a similar pattern of axial elongation, where the cervical series makes a substantial contribution to the overall axial elongation of the body, is observed also in dolichosaurs, adriosaurs, and pontosaurs—a group of lizards that have been long considered to be close relatives of snakes (Owen 1877; Nopcsa, 1903, 1908, 1923; Lee and Caldwell, 2000; Pierce and Caldwell, 2004; Lee, 2005a, 2009; Caldwell, 2006; Palci and Caldwell 2007, 2010; Caldwell and Palci, 2010). This is not to say that we consider dolichosaurs, adriosaurs, or pontosaurs to be the ancestors of snakes, but rather that the possibility of a close phylogenetic relationship between these taxa should be carefully considered, because derived developmental mechanisms that are shared between closely related taxa may provide insights on the evolutionary and developmental processes that lead to the origin of snakes.

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FIGURES

FIGURE 3-1. Photos and interpretative drawings of the cranial anatomy of *Haasiophis terrasanctus* (HUJ-Pal EJ 695), *Eupodophis* sp. (MSNM V 4014), and comparison with the extant snake *Cylindrophis ruffus* (AMNH 85647). **A**, skull of *Haasiophis* (HUJ-Pal EJ 695) in ventral view; **B**, close-up ventral view of the right pterygoid and ectopterygoid of *Haasiophis* (HUJ-Pal EJ 695); **C**, close-up dorsal view of the ectopterygoids of *Haasiophis* (HUJ-Pal EJ 695), note how the left ectopterygoid still articulates with the lateral process of the left pterygoid; **D**, skull of *Cylindrophis ruffus* (AMNH 85647); **E**, skull of *Eupodophis* (MSNM V 4014) in ventral view; **F**, close-up of the right pterygoid of *Eupodophis* (MSNM V 4014) in ventral view. **Abbreviations**: **dp**, dentigerous process of pterygoid; **ec**, ectopterygoid; **ep**, ectopterygoid process of pterygoid; **f**, frontal; **pa**, parietal; **pf**, prootic flange; **qr**, quadrate ramus of pterygoid; **?**, unidentified element. All scale bars equal 5 mm.

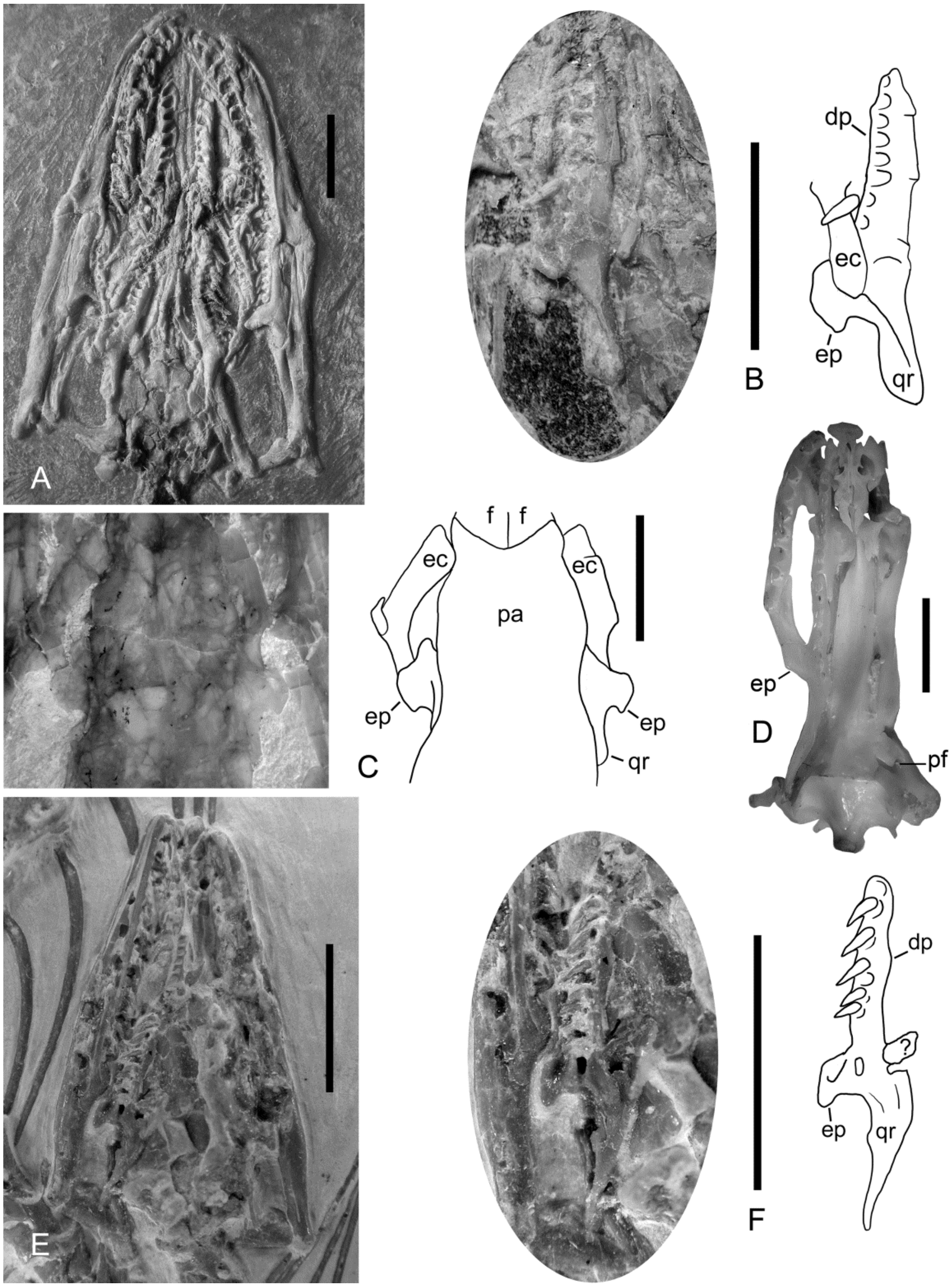
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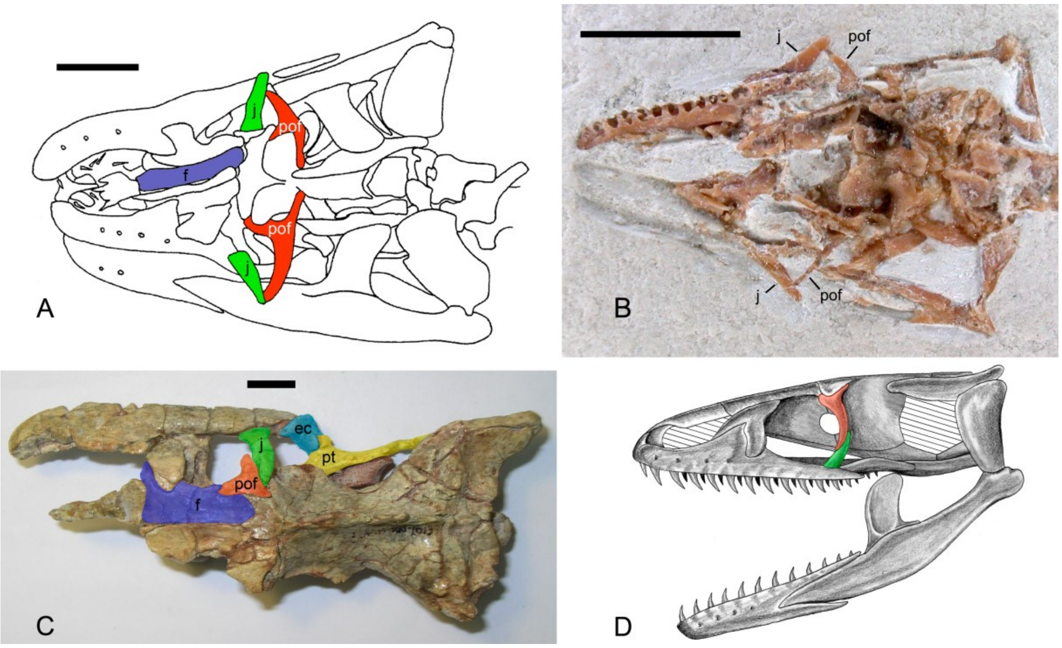
FIGURE 3-2. Topological relationship between postfrontal, jugal, and ectopterygoid in snakes. **A**, interpretative drawing of the skull of *Pachyrhachis problematicus* (HUJ-Pal EJ 3659) in dorsal view (modified from Caldwell, 2007). Note that the jugal (highlighted in green) is located anterior to the ventral end of the postfrontal (highlighted in red). The elongate frontal is highlighted in violet. **B**, photo of the skull of *Eupodophis* sp. (MSNM V3661) showing the same topological relationships of jugal and postfrontal as in *Pachyrhachis*. Note the finished (i.e., unbroken) posterior margin of the jugal. **C**, dorsal view of the skull of the fossil snake *Dinilysia patagonica* (MACN RN-1013). Note the topological relationship between postfrontal (highlighted in red), jugal (highlighted in green), and ectopterygoid (highlighted in blue) and the posteromedial process of the ectopterygoid contacting the pterygoid (highlighted in yellow). Also note the relative length of the frontal (highlighted in violet), comparable to the length of the same element in *Pachyrhachis*. **D**, reconstruction of the skull of *Pachyrachis problematicus* in lateral view, postfrontal is highlighted in red and jugal is highlighted in green. **Abbreviations**: **ec**, ectopterygoid; **f**, frontal; **j**, jugal; **pof**, postfrontal; **pt**, pterygoid. Scale bars equal 10 mm in **A** and **C**, 5 mmin **B**.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f
D

FIGURE 3-3. Caudal vertebrae of the snakes *Eupodophis*, *Morelia*, and *Haasiophis* in lateral view, anterior to the right. **A**, *Eupodophis* sp. (MSNM V 4014); **B**, *Eupodophis descouensi* (Rh-E.F. 9001–3); **C**, the extant snake *Morelia viridis* (ZFMK 53538); **D**, *Haasiophis terrasanctus* (HUJ-Pal EJ 695); **E**, close-up of a chevron bone of *Haasiophis terrasanctus* (HUJ-Pal EJ 695). **Abbreviations**: **ch**, chevron bones; **ha**, hemapophyses; **tp**, transverse processes. Scale bars equal 5 mm in **A**–**D**, and 1 mm in **E**.

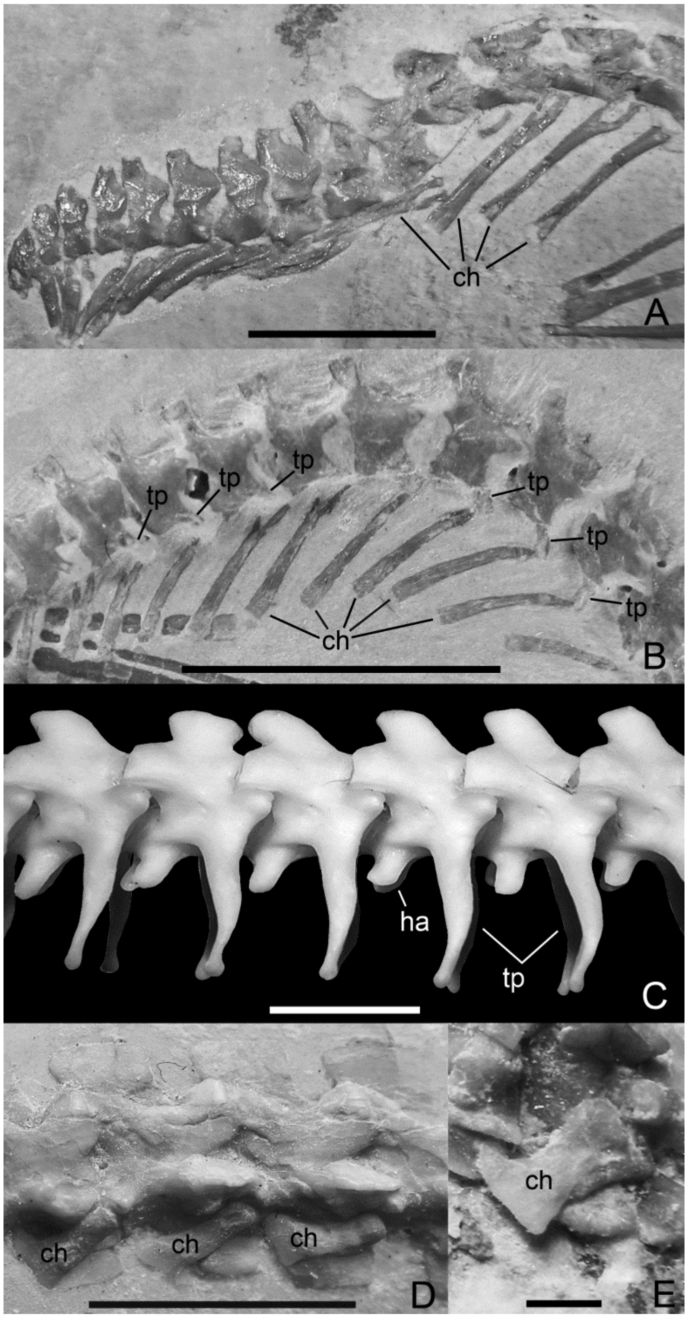

ch
A
tp
tp
tp
tp
tp
tp
ch
B
ha
tp
C
ch
ch
ch
D
ch
E

FIGURE 3-4. Photos and interpretative drawing of the anterior portion of the skull of *Haasiophis terrasanctus* (HUJ-Pal EJ 695) in ventral view.

Abbreviations: **de**, dentary; **ma**, maxilla; **pl**, palatine, **pm?**, putative premaxilla; **v**, vomer. Scale bar equals 5 mm.

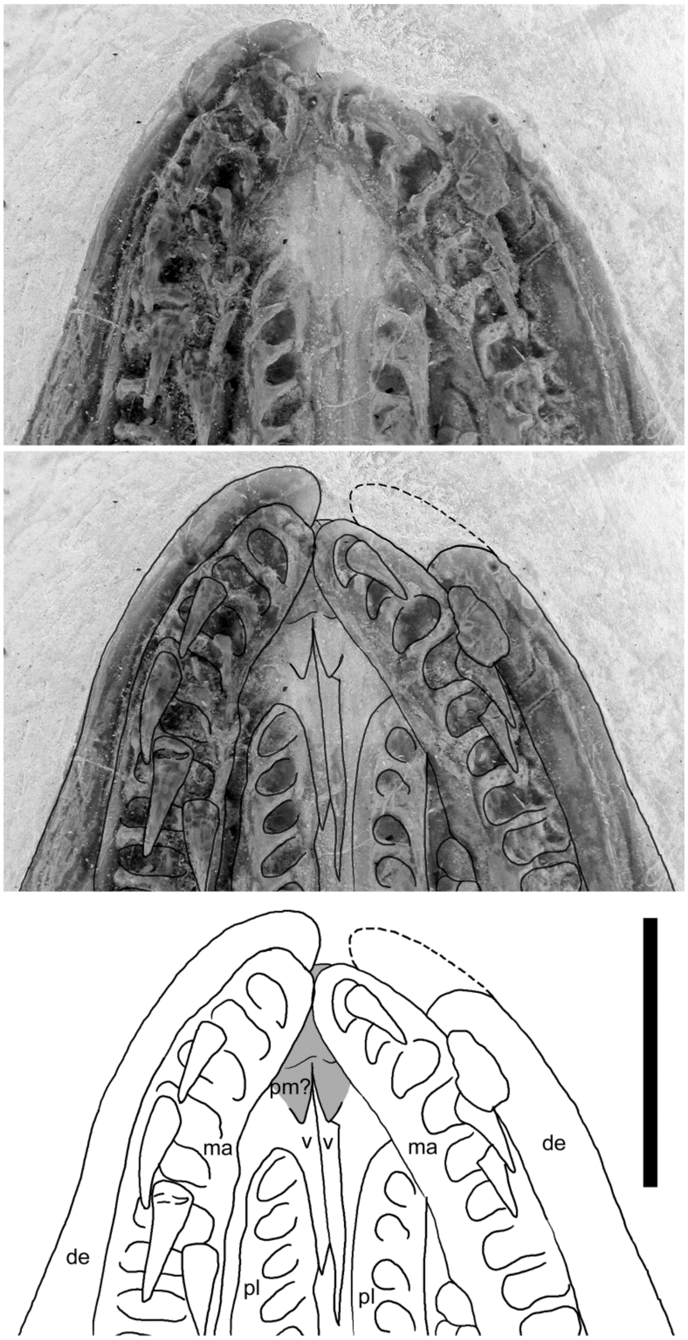

pm?
v
v
ma
ma
de
de
pl
pl

FIGURE 3-5. Comparison between anterior presacral (cervical) vertebrae of *Haasiophis terrasanctus* (HUJ-Pal EJ 695) and cervical vertebrae of the ophidiomorph lizard *Adriosaurus skrbinensis* (SMNH 2158). **A**, anterior cervical vertebrae of *Haasiophis terrasanctus* (HUJ-Pal EJ 695) in ventral view; **B**, close-up on one of the intercentra of *Haasiophis terrasanctus* (HUJ-Pal EJ 695) in ventrolateral view; **C**, posterior cervical vertebrae of *Haasiophis terrasanctus* (HUJ-Pal EJ 695) in ventral view; **D**, anterior cervical vertebrae of *Adriosaurus skrbinensis* (SMNH 2158) in lateral view; Black arrows point at free intercentra. Scale bars equal 10 mm in **A**, **C**, and **D**, 1 mm in **B**.

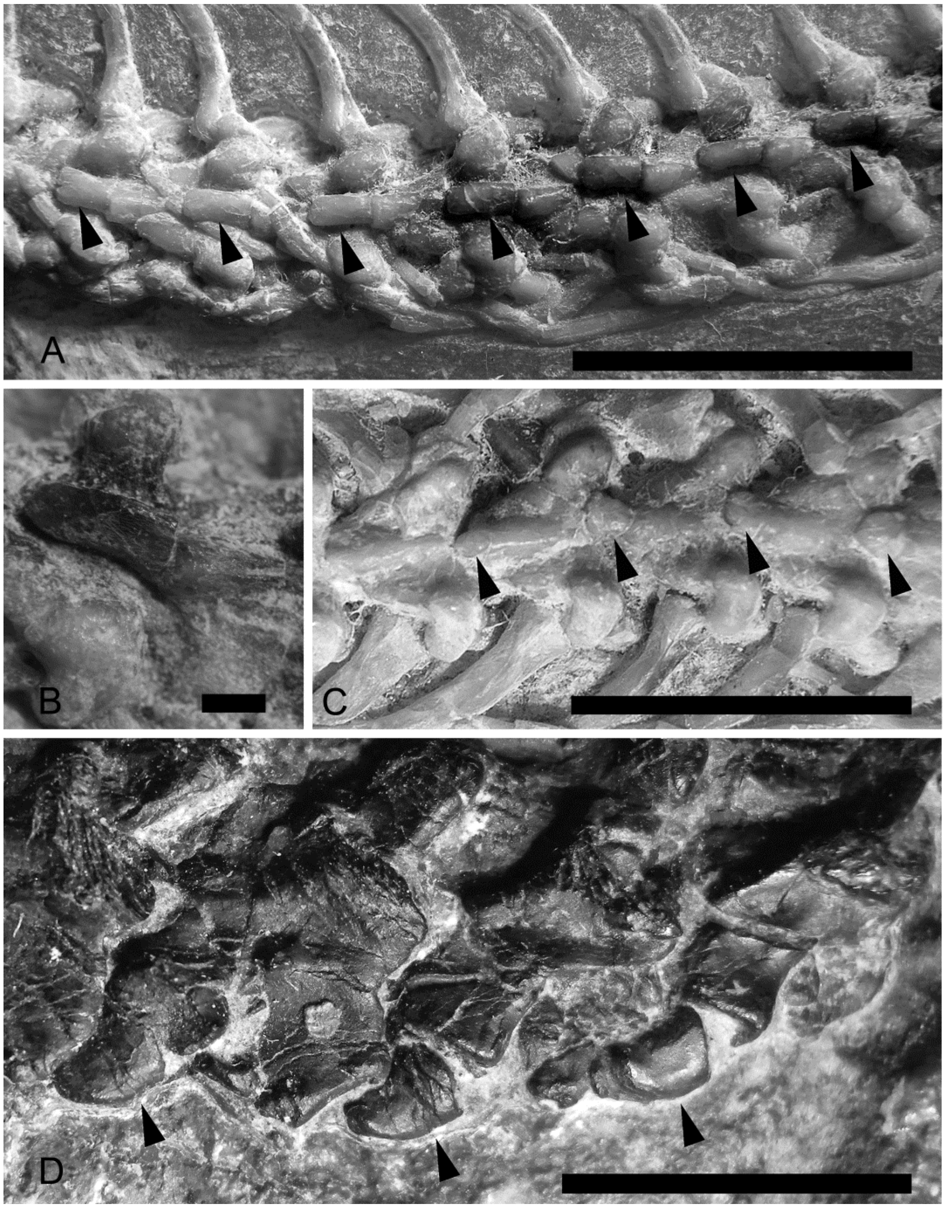

A
B
C
D

FIGURE 3-6. Lower jaws of *Pachyrhachis* and *Ophisaurus*. **A**, left mandibular ramus of *Pachyrhachis problematicus* (HUJ-Pal EJ 3775) in lateral view; **B**, right dentary of *Pachyrhachis problematicus* (HUJ-Pal EJ 3775) in lateral view; **C**, anterior portion of lower jaw of *Ophisaurus apodus* (MCZ 2094) in lateral view. Arrows point at mental foramina. Scale bar equals 5 mm.

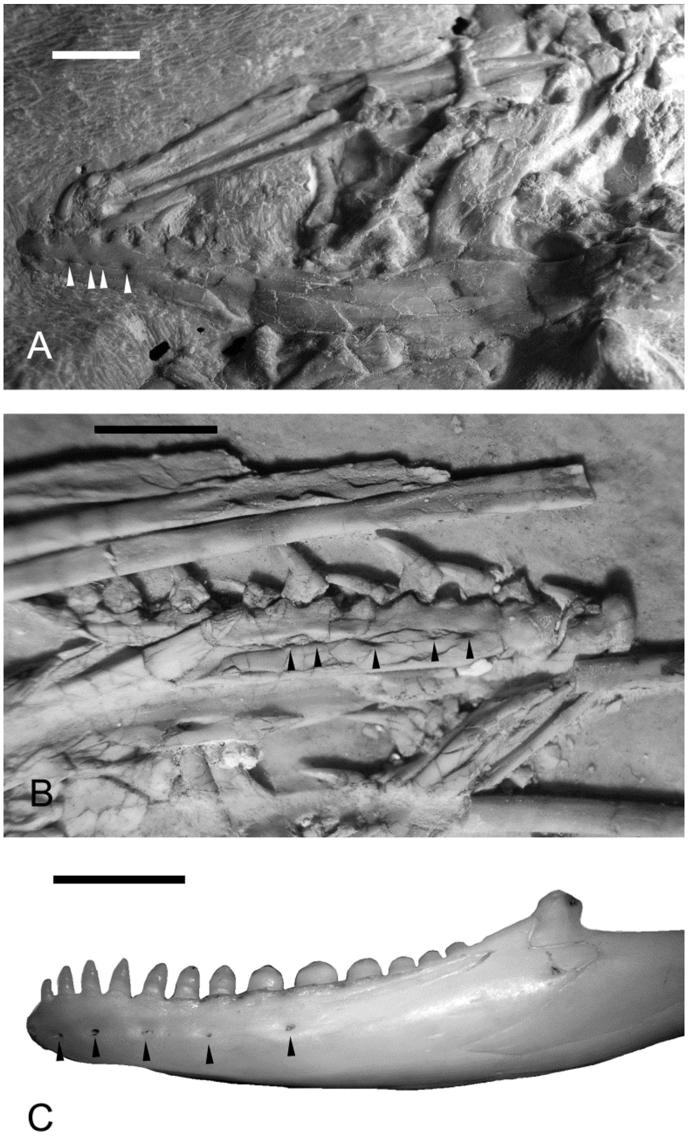

A
B
C

FIGURE 3-7. Photos and interpretative drawing of pelvic region of *Pachyrhachis problematicus* (HUJ-Pal EJ 3775). **Abbreviations**: **dr**, dorsal rib; **il**, ilium; **is**, ischium; **lfe**, left femur; **pu**, pubis; **r**, caudal rib; **rfe**, right femur; **sr**, sacral rib; **?**, unidentified element. Scale bar equals 5 mm.

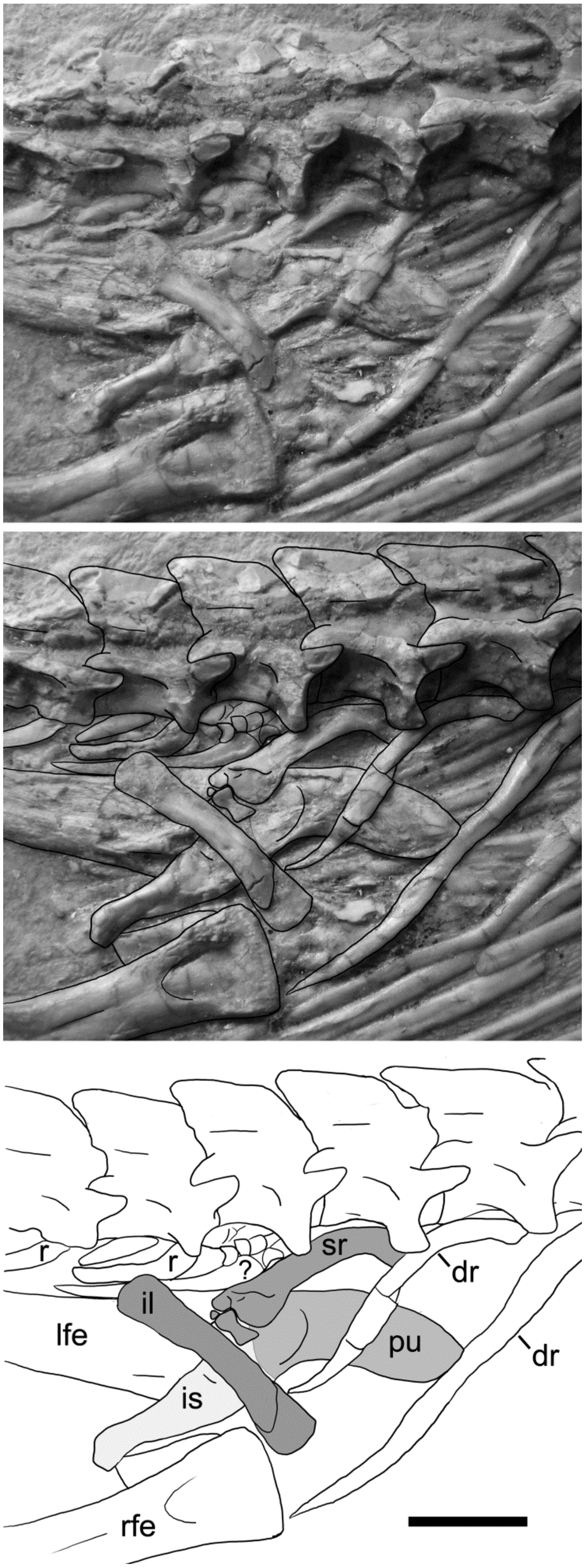
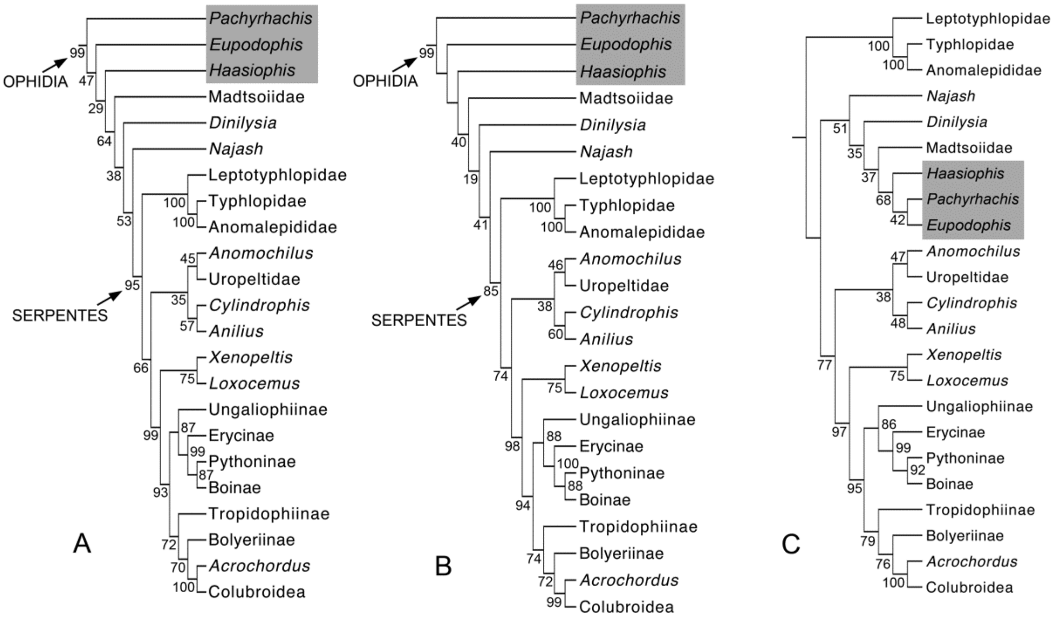

r
r
?
sr
dr
il
lfe
pu
dr
is
rfe

FIGURE 3-8. Most parsimonious trees retrieved in the three phylogenetic analyses of extinct and extant snakes, outgroups not shown. **A**, most parsimonious tree retrieved in the analysis that used varanoid lizards (*Heloderma*, *Lanthanotus*, *Varanus*, and Mosasauroidea) as outgroups; **B**, most parsimonious tree retrieved in the analysis that used the iguanians *Iguana*, *Agama*, and *Uromastyx* as outgroups; **C**, most parsimonious tree retrieved in the analysis that used the skinks *Acontias* and *Corucia*, Amphisbaenia, and Dibamidae as outgroups. The numbers next to the nodes are values of bootstrap support for the branch leading to that node. Note: the consensus tree from the bootstrap analysis relative to the second data set (tree in **B**) recovers a monophyletic clade consisting of (*Haasiophis* (*Pachyrhachis*, *Eupodophis*)) (BS = 47, not shown); the consensus tree from the bootstrap analysis relative to the third data set (tree in **C**) retrieves a monophyletic Ophidia (BS = 69), but where the Scolecophidia (i.e., Anomalepididae, Typhlopidae, and Leptotyphlopidae) and the clade formed by all fossil snakes (*Najash* (*Dinilysia* (Madtsoiidae (*Haasiophis* (*Pachyrhachis*, *Eupodophis*))))) are inverted with respect to their positions in the tree shown in **C**.


A
OPHIDIA
SERPENTES
Pachyrhachis
Eupodophis
Haasiophis
Madtsoiidae
Dinilysia
Najash
Leptotyphlopidae
Typhlopidae
Anomalepididae
Anomochilus
Uropeltidae
Cylindrophis
Anilius
Xenopeltis
Loxocemus
Ungaliophiinae
Erycinae
Pythoninae
Boinae
Tropidophiinae
Bolyeriinae
Acrochordus
Colubroidea
99
47
29
64
38
53
95
100
100
45
35
57
66
75
99
87
99
87
93
72
70
100
B
OPHIDIA
SERPENTES
Pachyrhachis
Eupodophis
Haasiophis
Madtsoiidae
Dinilysia
Najash
Leptotyphlopidae
Typhlopidae
Anomalepididae
Anomochilus
Uropeltidae
Cylindrophis
Anilius
Xenopeltis
Loxocemus
Ungaliophiinae
Erycinae
Pythoninae
Boinae
Tropidophiinae
Bolyeriinae
Acrochordus
Colubroidea
99
40
19
41
85
100
100
46
38
60
74
75
98
88
100
88
94
74
72
99
C
Leptotyphlopidae
Typhlopidae
Anomalepididae
Najash
Dinilysia
Madtsoiidae
Haasiophis
Pachyrhachis
Eupodophis
Anomochilus
Uropeltidae
Cylindrophis
Anilius
Xenopeltis
Loxocemus
Ungaliophiinae
Erycinae
Pythoninae
Boinae
Tropidophiinae
Bolyeriinae
Acrochordus
Colubroidea
100
100
51
35
37
68
42
47
38
48
77
75
97
86
99
92
95
79
76
100

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CHAPTER FOUR

EMENDED DIAGNOSIS AND PHYLOGENETIC RELATIONSHIPS OF THE UPPER CRETACEOUS FOSSIL SNAKE *NAJASH RIONEGRINA* APESTEGUÍA AND ZAHER, 2006

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INTRODUCTION

The fossil record of snakes dates back to the latest part of the Early Cretaceous (Albian) but is represented by only a few isolated vertebrae from the enigmatic early snake taxa *Coniophis* and *Lapparentophis* (Gardner and Ciffelli, 1999; Rage and Escuillié, 2003). Until recently, the Cretaceous snake fossil record of articulated specimens included the non-marine snake *Dinilysia patagonica* (Smith-Woodward, 1901; Estes et al., 1970) and the marine snakes *Pachyophis woodwardi* (Nopcsa, 1923) and *Mesophis nopcsai* (Bolkay, 1925). With the recognition that *Pachyrhachis problematicus* Haas, 1979, was indeed a snake (for a review of that debate, see Caldwell, 2007), a number of new specimens of Cretaceous snakes represented by articulated remains have been described for both marine and non-marine forms. New Cretaceous marine snakes include *Eupodophis descouensi* Rage and Escuillié, 2000, with additional specimens and new details described by Rieppel and Head (2004) and Houssaye et al. (2011), and *Haasiophis terrasanctus* Tchernov, Rieppel, Zaher, Polcyn, and Jacobs, 2000, with a full description published by Rieppel et al. (2003). New Cretaceous non-marine snake taxa include *Najash rionegrina* Apesteguía and Zaher, 2006, followed by the full description by Zaher et al. (2009), and *Sanajeh indicus* Wilson, Mohabey, Peters, and Head, 2010. New specimens and detailed new data for *D. patagonica* have been presented by Caldwell and Albino (2002), Budney et al. (2006), Caldwell and Calvo (2008), and most recently by Zaher and Scanferla (2012).

This study focuses on the holotype and associated specimens of *Najash rionegrina* as reported on by Apesteguía and Zaher (2006) and Zaher et al. (2009). *Najash* was described as a new fossil snake from the Upper Cretaceous (Cenomanian–Turonian) of Argentina that retains a sacrum and robust hind limbs. Apesteguía and Zaher's (2006) original phylogenetic analysis of extant and fossil snakes placed *Najash* at the base of the radiation of all snakes (i.e., basal to the Scolecophidia, the Alethinophidia, and all other well-known fossil snakes from the Cretaceous: *Dinilysia*, *Pachyrhachis*, *Eupodophis*, and *Haasiophis*). Zaher et al. (2009) followed the 2006 study with a detailed description of the type material of *Najash* (MPCA 389–400) and of a series of referred specimens (MPCA 380–388).

Here we present observations of all available materials of *Najash rionegrina* as well as a critique of Zaher et al. (2009). We begin by recharacterizing the holotype specimen and providing arguments to support the rejection of the original composition of that type specimen. We examine the justifications used by Zaher et al. (2009), both anatomical and geological/geographical, to refer additional specimens to *Najash* and emend the diagnosis given by Apesteguía and Zaher (2006). This is followed by a redescription and alternative interpretation of the pelvic anatomy of *Najash rionegrina* (MPCA 400). We use the new data and interpretations presented here to provide a significantly revised and accurately conservative diagnosis of *Najash*, followed by a phylogenetic reanalysis of snakes inclusive of this taxon.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MPCA**, Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina; **MSNM**, Museo di Storia Naturale di Milano, Milan, Italy; **Rh-E.F.**, Natural History Museum of Gannat, Gannat, France; **UAMZ**, University of Alberta Museum of Zoology, Edmonton, Alberta, Canada; **USNM**, United States National Museum of Natural History, Washington, D.C., U.S.A.; **ZFMK**, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

HOLOTYPE OF *NAJASH RIONEGRINA*

Composition of the Holotype

The detailed description of *Najash rionegrina* Apesteguía and Zaher, 2006, was given by Zaher et al. (2009) and accompanied by an emended diagnosis of the taxon. In that latter publication, the authors outlined further details of the composition of the holotype specimen (Zaher et al., 2009:4): “Holotype: Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina (MPCA) 389–400. The holotype consists of a series of associated materials, including a large fragment of the left dentary and anterior portion of the corresponding splenial (MPCA 390), and a nearly complete and articulated postcranial skeleton, composed of 16 sections bearing a total of at least 122 articulated vertebrae (109 presacrals, two sacrals, and 11 caudals), a pelvic girdle, and hind limbs."

Below we provide comments on some elements that Zaher et al. (2009) referred to the holotype of *Najash* and that we consider problematic.

Postcranium—Apesteguía and Zaher (2006) did not include MPCA 399 (a series of disarticulated fragmentary presacral vertebrae) in the composition of the type specimen, but these fragments were later added by Zaher et al. (2009). If these fragmentary remains were indeed found in close association with the articulated type specimen (Zaher et al., 2009), then it is unclear as to how this association was recognized three years after it was missed in the original description (Apesteguía and Zaher, 2006). We agree that based on morphological features these vertebrae can be referred to the taxon *Najash rionegrina*, but disagree that there is sufficient evidence to justify assigning them to the type specimen. The same argument can be raised for another series of fragmentary remains labeled MPCA 398.

We therefore reject the holotype composition of postcranial remains inclusive of MPCA 398 and 399 because of the lack of articulation or direct association.

Dentary and Splenial—The most notably unjustified association for the holotype composition is the inclusion of an isolated and fragmentary dentary and splenial (MPCA 390; Zaher et al., 2009, refer to this element both as MPCA 390 and 391, but considering that MPCA 391 is also used to refer to the first five presacral vertebrae of the type specimen, we conclude that MPCA 390 is the appropriate specimen number for the fragments of the dentary and splenial).

As noted above, the claim of Zaher et al. (2009) is that the 16 sections of postcranium were collected together in a state of articulation or association. However, MPCA 390 (dentary/splenial) was certainly not found in articulation with the rest, because there are no intermediate elements preserved between it and the anterior-most element retrieved for the postcranium (the axis). Simple association, as loose as the term may be, is not compelling enough evidence for assigning it to the postcranium as the associated remains of a single individual snake specimen. Although we cannot dispute the statement by Zaher et al. (2009) that the dentary fragment was found at area Med4, we do reject the inclusion of this dentary in the holotype simply because it shows snake-like characteristics. There is no overlap between the articulated postcranium (i.e., the holotype) and these isolated fragments of dentary and splenial that supports their inclusion in the holotype. Zaher et al. (2009) argue that the 'oligotypicity' of the vertebrate assemblage of La Buitrera indicates that there is only one snake in the assemblage and that this snake can be unequivocally diagnosed as *N. rionegrina*. We reject this form of circularity and the data used to support it. Should future specimens of fossil snakes from La Buitrera present overlapping anatomies with the postcranium of *Najash rionegrina*, then and only then can the diagnosis of this taxon be emended with empirical confidence by adding new materials. We have therefore removed the dentary from the composition of the holotype of *Najash rionegrina* and will present our emended diagnosis of the taxon later in this study.

Localities and Stratigraphy—Apesteguía and Zaher (2006) and Zaher et al. (2009) refer to the geographical categories of 'locality,' i.e., the La Buitrera locality, and 'area,' i.e., Med4, the site of discovery of the holotype; the areas are thus smaller subunits within the larger unit known as La Buitrera. Although we prefer the term locality to refer to the spot of discovery for a specimen, for the purpose of consistency in critically assessing and revising the conclusions and interpretations of Apesteguía and Zaher (2006) and Zaher et al. (2009), here we will use the same terminology, i.e., locality and area.

The holotype area within La Buitrera, is an ". . . area called Med4, (39°36.436'S, 68°42.427'W), whereas the larger specimen and basicranium were found in the area called Hoyada deMuñoz (39°36.755'S, 68°40.234'W)" (Zaher et al., 2009:3), which from our observation of the specimens presents lithofacies that preserve both mixed assemblage lag deposits (dentary and splenial elements), and event-deposited sediments with articulated, undisturbed whole-body fossils (holotype postcranium). As we will detail below, this aspect of the Med4 area is neither described nor justified in Apesteguía and Zaher (2006) and Zaher et al. (2009), but is in fact important data bearing on the provenance of the assigned type materials.

SPECIMENS REFERRED TO *NAJASH RIONEGRINA*

Apesteguía and Zaher (2006) as well as Zaher et al. (2009) referred five other specimens to *Najash rionegrina*. However, only one of these specimens is represented by a series of articulated vertebrae (MPCA 386) that are comparable to the vertebrae of the type specimen (MPCA 389, 391–397, 400). The remainder of the referred specimens include isolated vertebrae, a single isolated quadrate, fragments of two dentaries (one of which was added to the holotype in the original composition—see above), and an isolated, partial cranium. These five elements or groups of elements were all found at geographically widely separated 'areas' within the La Buitrera locality in a disconnected series of mixed-assemblage lag deposits (5–30 km distant from the holotype locality) (Zaher et al., 2009). From Zaher et al. (2009:3): "The La Buitrera locality is composed of patches of outcrops that are basically at the same level and bear the same fauna. The holotype of *N. rionegrina* comes from the area called Med4 (39°36.436'S, 68°42.427'W), whereas the larger specimen and basicranium were found in the area called Hoyada de Muñoz (39°36.755'S, 68°40.234'W). The latter find was close to other isolated snake vertebrae, also referred to *Najash*. The prospection of other localities of equivalent stratigraphic levels provided specimens of the same flag species (i.e., *Kaikaifilusaurus*, *Araripesuchus*, and *Najash*), which act as useful guides for stratigraphic purposes. This was clear for localities that were either 5 km (Cerro Bandera, 39°37.909'S, 68°42.374'W) or 30 km (Cerro Policía, 39°43.410'S, 68°29.534'W) distant from each other (Apesteguía et al., in press)."

We consider the geographic disparity of these sites/areas to be extremely problematic because of the absence of any reporting of outcrop stratigraphy, described in Zaher et al. (2009:3) as “basically the same level,” and any information on the stratigraphic position of specimens being attributed to *Najash rionegrina*. The integrity of the taxon diagnosed by non-associated elements, in particular the isolated cranial remains, suggests that the taxon *Najash*, not just the holotype composition, is a possible chimera resulting from loose associations of isolated skeletal elements that appear to be those of a snake, correlated against poorly defined stratigraphy.

Cranium and Quadrate—The isolated cranium (MPCA 385) was found in the area referred to as Hoyada de Muñoz, approximately 3 km to the east and slightly south of Med4, the type specimen area within La Buitrera. Although we do not doubt that the partial cranium referred to *Najash rionegrina* is a snake, there is no logical rationale (e.g., overlap of skeletal elements) for referring it to the postcranial remains of the holotype. Although admittedly convenient for scoring character states for a single terminal taxon in a phylogenetic analysis, there is no support for such a taxonomic and phylogenetic chimera from the available empirical data. We therefore have removed the partial cranium from the diagnosis of *N. rionegrina.*

The same rationale is applied here to the isolated quadrate (MPCA 387) that was also collected from a lag deposit (area unknown) along with five other presacral vertebrae referred to *N. rionegrina*. Because there is no skull associated with the holotype, and no quadrate with MPCA 385, the rationale that the quadrate is referable to *N. rionegrina* because it co-occurred in the lag with five *Najash* vertebrae is rejected. We have thus excluded the quadrate from the list of referred specimens and from our emended diagnosis of *Najash*.

Dentaries—As discussed above, we do not find the arguments provided by Apesteguía and Zaher (2006), and more recently by Zaher et al. (2009), compelling as regards the reference of the dentary numbered MPCA 390 to the type specimen of *Najash rionegrina*. As a direct consequence of this, we also do not agree with the referral of another dentary fragment (MPCA 380) to *N. rionegrina*. Moreover, even accepting MPCA 390 as belonging to *N. rionegrina*, the dentary referred to as MPCA 380 and portrayed in Zaher et al. (2009:fig. 2) does not bear any striking resemblance to the dentary originally assigned to be part of the type specimen (MPCA 390). In our view, ontogeny is not sufficient to explain such differences. The arguments that follow are meant to support the possibility that, contrary to what has been assumed so far by Apesteguía and Zaher (2006) and Zaher et al. (2009), there might be more than one snake taxon at La Buitrera.

The referred dentary (MPCA 380) shows tooth sockets that are widely expanded mediolaterally, a condition reminiscent of what is observed in *Dinilysia* (Caldwell and Albino, 2002; Budney et al., 2006; Caldwell and Calvo, 2008), whereas the dentary of MPCA 390 has alveoli that are subcircular in shape (Fig. 4-1). Moreover, the dentary previously included in the type (MPCA 390) bears an almost straight tooth row, whereas that of the referred specimen (MPCA 380) has a distinct anteromedial curvature that starts at the level of the fourth tooth socket. We concede that the curvature of the dentary might be acquired as a consequence of ontogenetic change, as in *Eunectes murinus* (cf. AMNH R-54158 and AMNH R-29349); however, the presence of the symphysial facet should be expected to be present in the juvenile as well (i.e., in MPCA 390), at least as a small eminence, but such a feature is completely lacking in the smaller specimen. We reject the possibility that the facet was simply abraded away in MPCA 390, because the delicate anterior portion of the splenial could not have been preserved so well under abrasive conditions. Moreover, a change in the shape of the alveoli, which in the larger specimen (MPCA 380) are mediolaterally expanded in dorsal view, has never been previously reported to occur as the result of ontogenetic change in any snake.

A further reason to doubt the referral of MPCA 380 to the same taxon as MPCA 390 resides in the fact that the mental foramina on the former dentary are located in different positions compared with those in the latter. In particular, the dentary of MPCA 380 has two foramina located below the fourth and the sixth alveoli, respectively, whereas the dentary of MPCA 390 has two foramina located under the second and fifth alveoli. We have reason to doubt that such a large difference (i.e., a shift of the foramen that spans the space of two tooth positions) can be the result of ontogenetic change or intraspecific variation. We examined the position of the mental foramen/foramina in 12 randomly selected species (for a total of 54 specimens) of alethinophidian snakes and we observed that even if shifts are relatively common (observed in about one-third of the specimens), their range of variability is always very limited within the same species; in the specimens examined by us, shifts of the mental foramen never extended beyond one tooth position (Table 4-1).

Because of these differences, we conclude that MPCA 380 and MPCA 390 likely represent individuals that do not belong to the same species and possibly not even to the same genus. A similar line of reasoning could be applied to other isolated elements that were referred to *N. rionegrina* simply on the basis of their being associated with vertebrae that undoubtedly belong to this taxon (i.e., MPCA 385 and MPCA 387). Our position is that simple associations of disarticulated elements sorted and deposited together in taxonomically mixed assemblages (Rogers et al., 2007; Sankey and Baszio, 2008) should never be a criterion for classification in the same taxon, despite the claim by Zaher et al. (2009:3) that *N. rionegrina* is “the only known snake to occur in La Buitrera.” It only makes sense that if you characterize one chimeric snake taxon from a composite of articulated and disarticulated elements, found at disparate localities and stratigraphic intervals, then there can only be ‘one’ snake at La Buitrera.

HOLOTYPE: REVISIONS TO ANATOMICAL INTERPRETATIONS

The Sacrum

Our interpretation of the pelvic anatomy of the type material of *Najash rionegrina* (MPCA 389–400) contrasts with that proposed by Apesteguía and

Zaher (2006) and more recently by Zaher et al. (2009). According to the latter authors, the holotype specimen of *Najash* possesses two sacral vertebrae, each bearing a pair of fairly long and narrow pleurapophyses that taper distally. Furthermore, in their description, the two sacral vertebrae would be followed by at least three vertebrae bearing lymphapophyses.

In our interpretation of the anatomy of *Najash*, the long and slender appearance of what Apesteguía and Zaher (2006) and Zaher et al. (2009) call 'sacral pleurapophyses' is not consistent with the morphology of such processes, which are typically robust, expanded distally and relatively broad in all amniotes still retaining a sacrum (Romer, 1956). Those processes are much more like the fused ribs present in the last presacral vertebrae of *Sphenodon punctatus* (UAMZ 405) and some squamates such as *Agama agama* (MCZ 173367) or *Dibamus novaeguineae* (USNM 305916), and are here interpreted as such, i.e., as structures that show primary homologies to presacral fused ribs. According to our interpretation, the single and only sacral vertebra would be the one following the two vertebrae bearing presacral fused ribs; the single true sacral vertebra has fairly short and stocky transverse processes that have an expanded distal extremity, consistent with processes that serve as attachment points for the pelvic girdle (Figs. 4-2, 4-3).

Apesteguía and Zaher (2006) and Zaher et al. (2009) interpreted the transverse processes of this vertebra as lymphapophyses based on the presence of what looks like a distally forked extremity on the left side. In fact, the extremity of these processes is not forked, but simply expanded anteroposteriorly as well as dorsoventrally. Following this reinterpretation of the cloacal region, there are only two vertebrae behind the sacrum that clearly bear lymphapophyses. Due to incomplete preparation on the ventral side of the specimen, it is not clear whether there are more vertebrae that bear lymphapophyses.

Pelvic Girdle and Hind Limbs

Apesteguía and Zaher (2006) and Zaher et al. (2009) described *Najash* as possessing ischia that were broken into two pieces on both sides. However, this is inconsistent with the fact that the right ischium is completely preserved and has unbroken, finished margins (Fig. 4-3). This element retains the general appearance of the squamate ischium, i.e., almost rectangular in shape, with a robust acetabular head, and with slightly concave anterior and posterior margins (Estes et al., 1988). We see no reason to consider as fragments of the ischia the two elements located on the sides of what we interpret as the first vertebra with lymphapophyses. These elements are fairly elongate and bear an expanded bilobed extremity (Fig. 4-3). It is not clear what anatomical feature these poorly preserved elements represent, but they might be the slightly disarticulated left and right fibulae. In support of this interpretation, it is clear that the putative fibula on the left side shows a pathology (likely a healed fracture) as does the femur on the same side. This would be consistent with both of these elements being part of the same injured limb. Moreover, the distally expanded and bilobed morphology of the putative fibula of *Najash* is also reminiscent of the morphology of the fibula of the extinct anguimorph lizard *Adriosaurus* (Lee and Caldwell, 2000). This interpretation is in conflict with what Apesteguía and Zaher (2006) and Zaher et al. (2009) consider to be the right fibula of this specimen. We agree with the authors that the element they describe shows a strong resemblance with a typical squamate fibula, but we also note that the whole specimen lies in almost perfect articulation on the same sedimentary layer, whereas the element identified as a fibula by Apesteguía and Zaher (2006) and Zaher et al. (2009) is about one centimeter below and within the sediment, and for this reason might well be an isolated element from a different animal, and perhaps not even a snake.

With regard to the hind limbs of *Najash*, we noted an additional element that was not mentioned by either Apesteguía and Zaher (2006) or Zaher et al. (2009). This element lies next to the articular head of the left femur, and consists of a rod-like bone slightly expanded at the extremities (Fig. 4-3). These extremities show the same kind of mediolateral compression that is typical of phalangeal and metapodial elements. Because of its relatively large size compared with the femur and because of the fact that both extremities are similarly expanded (phalanges in squamates typically have a distal end that is clearly smaller than the proximal), we interpret this bone as an isolated metatarsal rather than a phalanx.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

OPHIDIA Brongniart, 1800

NAJASH RIONEGRINA Apesteguía and Zaher, 2006

Revised Type Material—MPCA 389, MPCA 391–397, MPCA 400.

Emended Diagnosis—Medium-sized snake retaining hind limbs, which are complete at least up to the metatarsals; femur robust with well-developed ventromedial process along midshaft (trochanter); ilium elongate and rod-like, slightly curved dorsoventrally and tapering posteriorly; pubis long and rod-like, slightly bent mediolaterally with distinct obturator foramen near proximal head; ischium short and square with slightly concave anterior and posterior margins; two vertebrae with fused short ribs anterior to sacrum; single sacral vertebra with pair of short and square transverse processes for articulation with ilium; at least two vertebrae with fused lymphapophyses; precloacal vertebrae with parazygantral foramina and neural spines mediolaterally expanded posterodorsally, teardrop- or 'Y'-shaped in dorsal view; neural arches of presacral vertebrae with parasagittal ridge joining lateral edge of zygosphene and posterior margin of postzygapophysis; hypapophyses present only on anterior precloacal vertebrae; caudal vertebrae bear a pair of rounded and knob-like haemal processes.

PHYLOGENETIC ANALYSES

Apesteguía and Zaher (2006) proposed a phylogeny of snakes where *Najash rionegrina* occupies the most basal position within the clade, and this view was recently supported by Zaher and Scanferla (2012). We wanted to test if this phylogenetic hypothesis could be affected by the removal of the information based on the most problematic referred material (MPCA 380, 385, 387, and 390), which cannot be unequivocally assigned to *N. rionegrina*. Moreover, in order to have a more stringent test of Apesteguía and Zaher's (2006) hypothesis, we decided to base our analysis on an independent osteological data set derived from that used by Lee and Scanlon (2002). The new data set consisted of a total of 23 ingroup taxa (with the addition of *Najash* and *Eupodophis*) and 210 characters. Two characters were removed from the original data set of Lee and Scanlon (2002), namely characters 7 and 209. Character 7 was removed because it was considered redundant with our character 7 (Lee and Scanlon, 2002: character 6) after the latter was modified from its original description. With regard to character 209, this character tries to define the presence or absence of a cervical region in squamates, but the only way this region can be defined in both extant and fossil forms, and in both limbed and limbless forms, is by referring to the presence of anteriorly located hypapophyses. We consider Lee and Scanlon's (2002) sharp variation in thickness and length between the putative cervical ribs and the dorsal ribs too subjective and not always applicable. However, rewriting this character with reference to the extent and location of the hypapophyses would make it redundant with our character 200 (Lee and Scanlon, 2002: character 201).

Considering that in the literature there is still no consensus regarding the sister group of snakes, we ran three separate analyses using the following outgroups: (1) varanoid lizards (i.e., *Heloderma*, *Lanthanotus*, *Varanus*, and Mosasauroidea), following the hypothesis originated with Cope (1869) and more recently supported by Lee (1997, 1998, 2005, 2009), Lee et al. (1999), and Lee and Caldwell (2000); (2) iguanians (*Iguana* and *Agama*), following relatively recent hypotheses that originated with the molecular phylogenies by Townsend et al. (2004) and Vidal and Hedges (2004, 2005); and (3) a skink (*Corucia*), amphisbaenians, and dibamids, following the hypotheses of Rage (1982) and more recently of Conrad (2008) and Gauthier et al. (2012). The composite 'varanoid outgroup' of Lee and Scanlon (2002) was not used in our analysis, because we preferred to let the analysis retrieve the polarity of character-state transformations at the base of the tree (for more details about our character list and data matrices, see Supplementary Data 4-1 to 4-4). Codings for *Najash* are based on MPCA 386, MPCA 389, MPCA 391–397, and MPCA 400; codings for *Eupodophis* are based on Rh-E.F. 9001–9003, MSNM V-3660, MSNM V-3661, MSNM V-4014, and Houssaye et al. (2011); codings for *Iguana* are based on MCZ 6097, MCZ 10975, andMCZ 83228; codings for *Agama* are based on MCZ 173366 and MCZ 173367; codings for *Corucia* are based on MCZ 68815, MCZ 72918, and MCZ 77375; all other codings follow Lee and Scanlon (2002) unless otherwise specified in Supplementary Data 4-1.

The analyses were run in PAUP∗ 4.0b10 (Swofford, 2002), the search criterion was set to heuristic with 1000 random addition replicates, and the branch-swapping algorithm was set to tree-bisection-reconnection (TBR). The characters were left unordered and with equal weights (Fitch, 1971). Statistical measures of support for the branches retrieved in the phylogenetic analyses were obtained using 1000 nonparametric bootstrap replicates (Felsenstein, 1983, 1985). Bootstrap values higher than 70% were considered to provide strong branch support (Hillis and Bull, 1993).

The analysis that used varanoid lizards as an outgroup retrieved one most parsimonious tree with a length of 617 steps, a consistency index (CI) of 0.47, and a retention index (RI) of 0.71 (Fig. 4-4A); the analysis that had Iguania as the outgroup yielded six most parsimonious trees of 590 steps, CI =0.50, andRI=0.69; and the analysis that had a skink, amphisbaenians, and dibamids as the outgroup retrieved 10 equally parsimonious trees of 617 steps, CI = 0.48, and RI = 0.68.

Bootstrap replicates found strong support for the clades Ophidia and Serpentes (both intended sensu Lee and Caldwell, 1998: Serpentes = Scolecophidia and Alethinophidia; Ophidia = most recent common ancestor of *Pachyrhachis* and Serpentes, and all of its descendants) when the outgroups were varanoids and iguanians, but only low values of support in the third analysis (Fig. 4-4), so that these two clades do not even appear in the respective strict consensus tree. In particular, the analysis that used a skink, amphisbaenians, and dibamids as outgroups was problematic because in 6 of the 10 most parsimonious trees, scolecophidian snakes formed the sister group to a clade constituted by amphisbaenians and dibamids, making snakes polyphyletic. This is likely due to the numerous convergent features linked to skull miniaturization, axial elongation, and limb loss in amphisbaenians, dibamids, and snakes, which may fail to polarize correctly the character transformations.

The clade Scolecophidia (i.e., Leptotyplopidae, Typhlopidae, and Anomalepididae) was always extremely well supported (bootstrap = 100%), and also the clade including all derived alethinopidian snakes (i.e., the clade defined by the common ancestor of *Xenopeltis* and Colubroidea, and all of its descendants) was well supported in all three analyses, both as regards its monophyletic status and its internal relationships (bootstraps ranging between 70% and 100%). The clade commonly referred to as ‘Anilioidea’ (i.e., *Anilius*, *Cylindrophis*, *Anomochilus*, and Uropeltidae) was weakly supported in the analyses that used varanoids and iguanians as outgroups, whereas it was found to be paraphyletic in 2 of the 10 trees retrieved in the third phylogenetic analysis (Fig. 4-4). Interestingly, *Najash* is consistently placed among the most basal snakes, but even despite some uncertainty in the basal relationships of snakes in two of the analyses, none of our trees shows *Najash rionegrina* to be the most basal representative of the clade Ophidia.

DISCUSSION AND CONCLUSIONS

In our phylogenetic analyses of extant and extinct snakes, *Najash rionegrina* was consistently placed within the basal radiation of snakes, but was never retrieved as the most basal member of the group (contra Apesteguía and

Zaher, 2006). The majority of trees (i.e., 11 out of 17 trees) retrieved the taxa *Pachyrhachis problematicus*, *Haasiophis terrasanctus*, and *Eupodophis descouensi*, forming either a monophyletic clade (Fig. 4-4B–C) or a paraphyletic assemblage (Fig. 4-4A) between the lacertilian outgroups and all other snakes.

In 2 of the trees (out of 6) recovered from the second analysis, and 3 of the trees (out of 10) recovered from the third analysis, *Dinilysia patagonica* and the Madtsoiidae were also grouped together with the above-mentioned fossil marine snakes to form a monophyletic clade, and in each analysis one of these trees also included *Najash rionegrina* as a basal representative of the clade. However, we have little reason to believe in the monophyletic status of this clade, because it has low statistical support (boostrap <50%). The Scolecophidia (i.e., Leptotyphlopidae, Typhlopidae, and Anomalepididae) were retrieved at the base of the radiation of all other snakes only in one of the trees produced by our third analysis; this particular tree and the weakly supported trees that retrieved a polyphyletic Ophidia (with *Najash* at the base of the Alethinophidia) are the only exceptions to the consistent placement of *Najash* outside of the radiation of modern snakes (i.e., Serpentes). Consequently, we consider *Najash* as belonging to the early radiation of snakes, but we could find no support for its proper placement within this radiation, nor for saying that it represents the most basal snake.

Interestingly, if we apply the logic of the extant phylogenetic bracket (Witmer, 1995) to our cladogram in Figure 4-4A (even if not all taxa are extant), we can infer the presence of well-developed (i.e., retaining at least a zeugopodium, if not also a partial autopodium) hind limbs in all the snakes placed between their lacertilian ancestors (outgroup) and *Najash*. In other words, based on character optimization, we should expect madstoiids and *Dinilysia* to have possessed hind limbs similar to those of *Najash*.

As pointed out by Hall (2003:411), vestiges are organs or structures "that either are nonfunctional or may have a different function from the fully formed ancestral feature." The hind limbs of snakes fall under this definition, and as such they lost their original function (i.e., as an aid in locomotion) and either acquired a new function or have no function at all. It is hard to imagine that limbs like those of *Najash*, whose femur bears an extremely well developed ventromedial process (trochanter), had no function whatsoever; and it is interesting to note that a strikingly similar morphology of the femur is observed only in the males of the lizard genus *Dibamus*, which possess a strongly developed ventromedial process (Greer, 1985). Other sexual dimorphs of vestigial limb anatomies are observed in modern boas and pythons, where males possess hind limbs (cloacal spurs) that are used in ritualized male combat, during courtship, and during copulation (Carpenter et al., 1978; O'Shea, 2007). Despite the robust femoral head of *Najash*, the acetabular surface formed by its adjoining ilium, pubis, and ischium is not extensive. Considering that the three pelvic bones were only loosely articulated to each other, they cannot have provided a robust attachment point for the femur. Because of the weak connection between femur and axial skeleton, the main function of the femur was likely something other than locomotion. We suggest that the hind limbs of *Najash* were likely used either during courtship or copulation, as is the case in living snakes with vestigial limbs.

All this evidence indicates the presence of evolutionary constraints (developmental, behavioral, functional) that prevented the complete loss of the hind limbs in basal snakes. Cloacal spurs are indeed present in at least some representatives of all basal groups of extant snakes (i.e., scolecophidians, anilioids, *Loxocemus*, boids, ungaliophines, and tropidophiines; McDowell, 1975; Carpenter et al., 1978; Greene, 1997; O'Shea, 2007).

We contest the statement made by Apesteguía and Zaher (2006:1039) that "vertebral (a low neural arch) morphological traits of *Najash* show adaptations to a subterranean life." This statement was clearly made to provide support to the hypothesis of a subterranean origin of snakes as opposed to the hypothesis of an aquatic or semiaquatic origin for this group of squamates. The mid-trunk vertebrae of *Najash* show no particular resemblance in their morphology to those of modern burrowing snakes such as *Anilius* or *Typhlops*, but rather resemble those of large constrictors such as *Python molurus* (Fig. 4-5). Moreover, Zaher et al. (2009) estimated the total length of *Najash* to be about 2m for the largest known specimens, which, as noted by Albino (2011), is inconsistent with a subterranean lifestyle for this snake, especially if coupled with the large diameter of some of its vertebrae. Little can be inferred from the morphology of the vertebrae of *Najash*, allowing only for the exclusion of extreme ecological habits (i.e., obligatorily aquatic or fossorial) (Albino and Caldwell, 2003; Albino, 2011). Inferences about the ecology of an organism should not be simply based on vertebral morphology, because, for example, both *Anilius scytale*, commonly known as a burrower, and *Python molurus*, commonly known as a surface dweller, are also known to be semiaquatic (Frazzetta, 1966; Greene, 1997; Maschio et al., 2010).

In conclusion, we consider the fossil material from Argentina to be of great importance for our understanding of the origin and evolution of snakes; however, we urge caution when attributing isolated elements to any taxon, let alone creating a taxon around such composites. Proceeding with caution in such matters is even more important when the specimens are derived from fluvial deposits such as those at the La Buitrera locality where physical processes leading to fossilization are so taphonomically disruptive. Fluvial deposits are indeed a classic example of sedimentation where elements of similar size, shape, and density are sorted and deposited together in taxonomically mixed assemblages (Rogers et al., 2007; Sankey and Baszio, 2008).

The use of such taxa in cladistic analysis is even more problematic because such artificial terminal taxa have a profound impact on the resultant tree topologies. The importance of using only material that clearly belongs to a robust and properly identified taxon (i.e., found either in articulation or in close association with other elements from the same region of the body) cannot be overemphasized, especially when this material is eventually used to formulate hypotheses on the origin and evolution of a major taxonomic group such as that represented by what we call snakes.

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FIGURES AND TABLES

FIGURE 4-1. Comparison between the two partial dentaries MPCA 380 and MPCA 390. **A**, MPCA 390, medial view; note the fragment of the left splenial still attached to the posteroventral margin of the dentary; **B**, MPCA 390, lateral view; **C**, MPCA 390, dorsal view; **D**, MPCA 380, medial view; **E**,MPCA 380, lateral view; **F**,MPCA 380, dorsal view. Scale bar equals 5 mm.

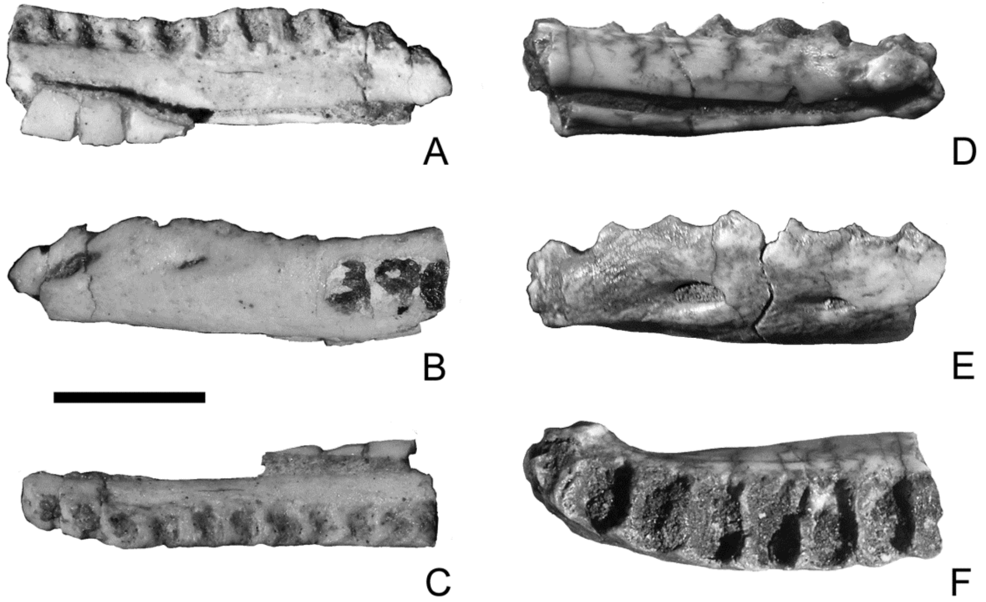

A
D
B
E
C
F

FIGURE 4-2. Photo and interpretative drawing of the sacral region and hind limbs of *Najash rionegrina* (MPCA 400) in dorsal view. **Abbreviations**: **C1**, first caudal vertebra; **lf**, left femur; **lfi**, left fibula; **lis?**, fragment of left ischium?; **lp**, left pubis; **rf**, right femur; **rfi**, right fibula; **ril**, right ilium; **ris**, right ischium; **rp**, right pubis; **rti**, right tibia; **S**, sacral vertebra. Scale bar equals 5 mm.

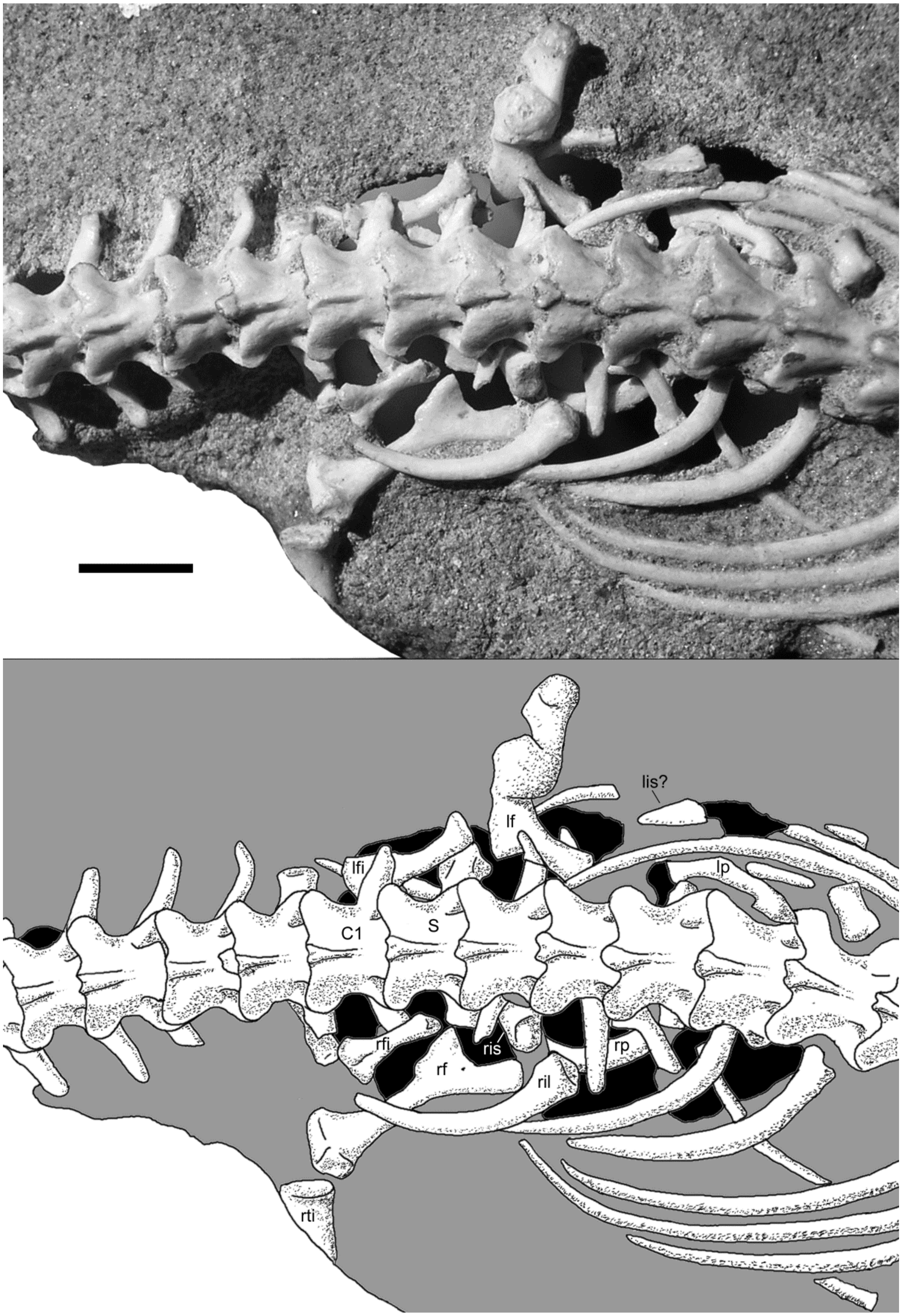

lis?
lf
lfi
lp
C1
S
rfi
ris
rf
ril
rp
rti

FIGURE 4-3. Photo and interpretative drawing of the sacral region and hind limbs of *Najash rionegrina* (MPCA 400) in ventral view. **Abbreviations**: **C1**, first caudal vertebra; **lf**, left femur; **lfi**, left fibula; **lp**, left pubis; **mt**, metatarsal; **rf**, right femur; **rfi**, right fibula; **ris**, right ischium; **rp**, right pubis; **S**, sacral vertebra. Scale bar equals 5 mm.

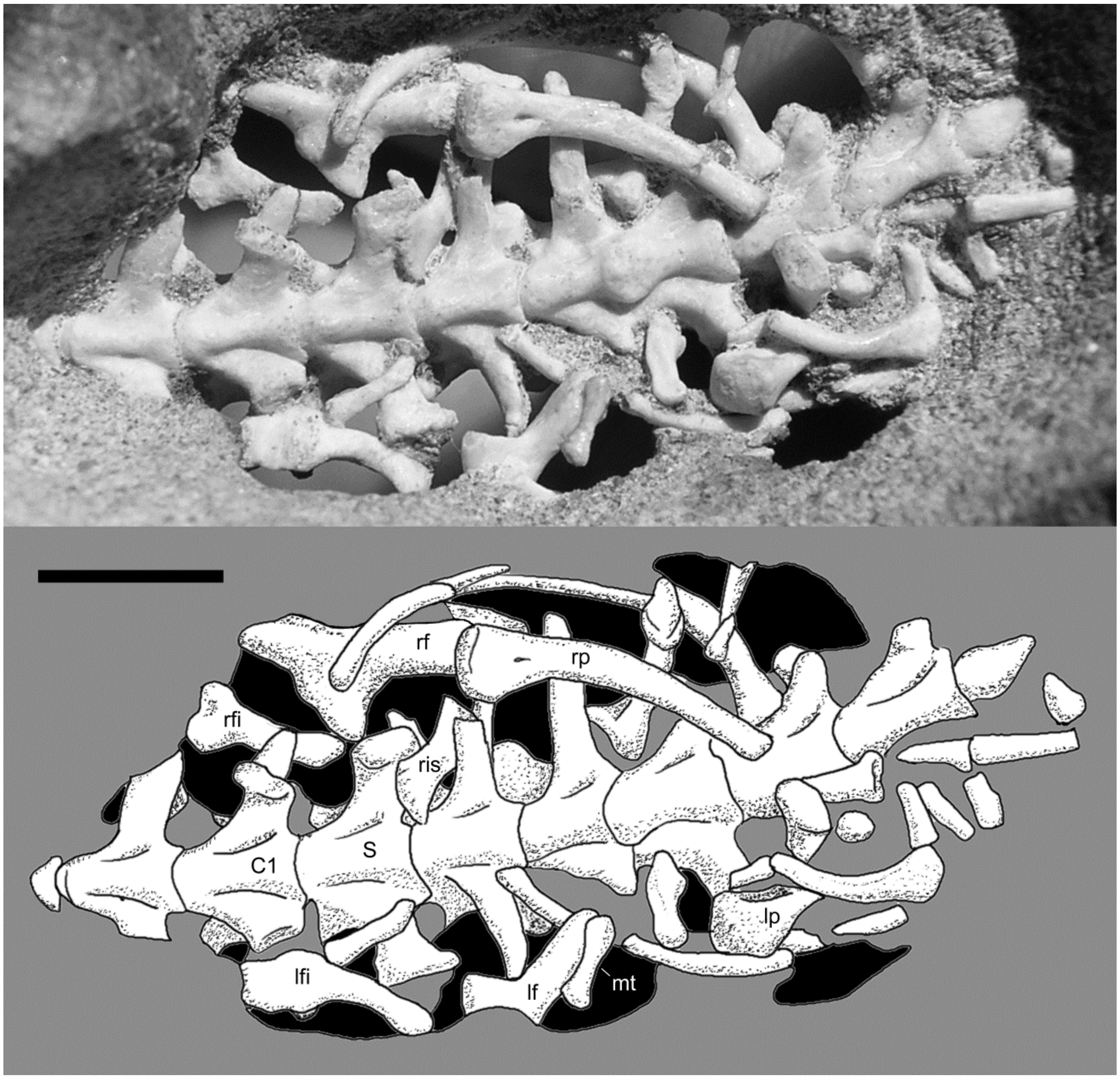
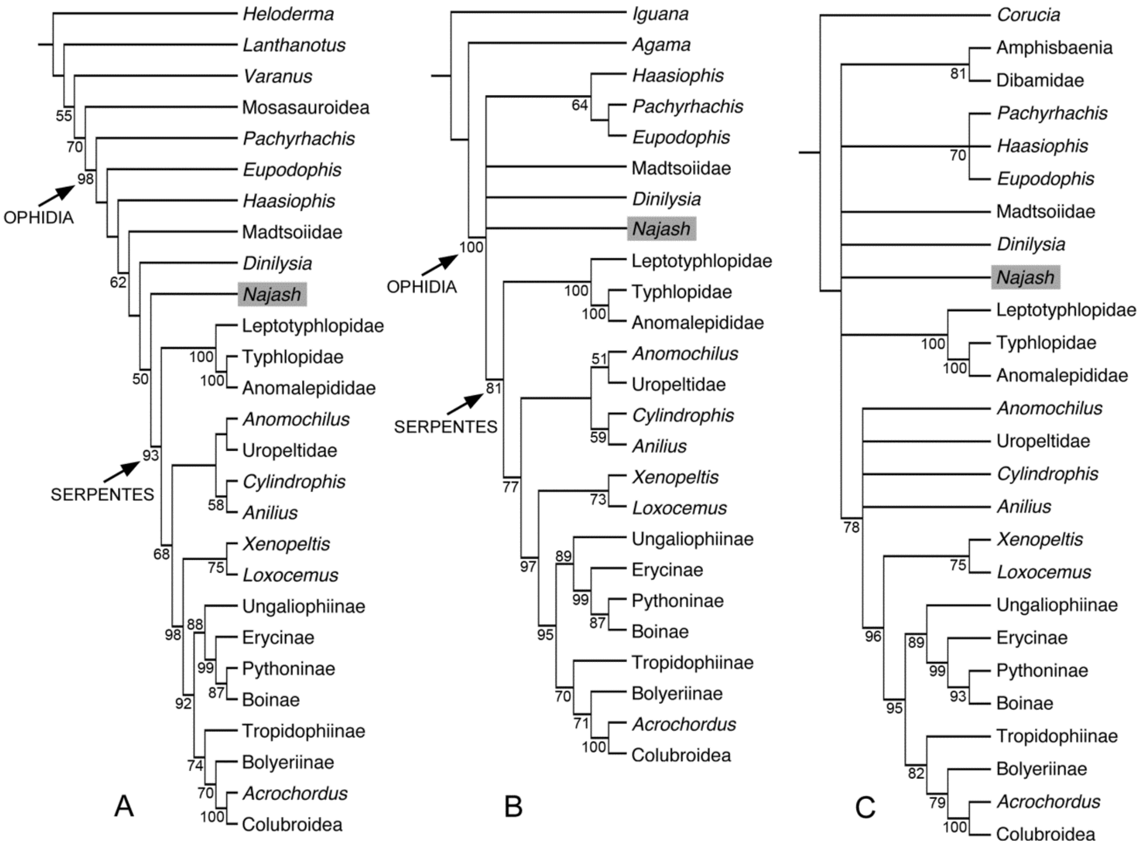

rf
rp
rfi
ris
C1
S
lp
lfi
lf
mt

FIGURE 4-4. Most parsimonious trees retrieved in the three phylogenetic analyses of extinct and extant snakes. **A**, most parsimonious tree retrieved in the analysis that used varanoid lizards (*Heloderma*, *Lanthanotus*, *Varanus*, and Mosasauroidea) as outgroups; **B**, strict consensus of the six most parsimonious trees retrieved in the analysis that used the iguanians *Iguana* and *Agama* as outgroups; **C**, strict consensus of the 10 most parsimonious trees retrieved in the analysis that used the skink *Corucia*, Amphisbaenia, and Dibamidae as outgroups. The numbers next to the branches are values of bootstrap support, values lower than 50% are not shown.



Heloderma
Lanthanotus
Varanus
Mosasauroidea
Pachyrhachis
Eupodophis
Haasiophis
Madtsoiidae
Dinilysia
Najash
Leptotyphlopidae
Typhlopidae
Anomalepididae
Anomochilus
Uropeltidae
Cylindrophis
Anilius
Xenopeltis
Loxocemus
Ungaliophiinae
Erycinae
Pythoninae
Boinae
Tropidophiinae
Bolyeriinae
Acrochordus
Colubroidea
55
70
98
OPHIDIA
62
50
100
100
93
SERPENTES
58
68
75
98
88
99
87
92
74
70
100
A
Iguana
Agama
Haasiophis
Pachyrhachis
Eupodophis
Madtsoiidae
Dinilysia
Najash
Leptotyphlopidae
Typhlopidae
Anomalepididae
Anomochilus
Uropeltidae
Cylindrophis
Anilius
Xenopeltis
Loxocemus
Ungaliophiinae
Erycinae
Pythoninae
Boinae
Tropidophiinae
Bolyeriinae
Acrochordus
Colubroidea
64
100
OPHIDIA
100
100
81
SERPENTES
51
59
77
73
97
89
99
87
95
70
71
100
B
Corucia
Amphisbaenia
Dibamidae
Pachyrhachis
Haasiophis
Eupodophis
Madtsoiidae
Dinilysia
Najash
Leptotyphlopidae
Typhlopidae
Anomalepididae
Anomochilus
Uropeltidae
Cylindrophis
Anilius
Xenopeltis
Loxocemus
Ungaliophiinae
Erycinae
Pythoninae
Boinae
Tropidophiinae
Bolyeriinae
Acrochordus
Colubroidea
81
70
100
100
78
75
96
89
99
93
95
82
79
100
C

FIGURE 4-5. Comparison between the middle dorsal vertebrae of *Najash rionegrina* and those of some extant snakes. **A**, *Typhlops punctatus* USNM 320704, posterior view; **B**, *Typhlops punctatus* USNM 320704, right lateral view; **C**, *Anilius scytale* MCZ 19537, posterior view; **D**, *Anilius scytale* MCZ 19537, right lateral view; **E**, *Python molurus* ZFMK 83431, posterior view; **F**, *Python molurus* ZFMK 83431, right lateral view; **G**, *Najash rionegrina* MPCA 386, posterior view with rocky matrix highlighted in gray; **H**, *Najash rionegrina* MPCA 386, right lateral view with rocky matrix highlighted in gray. Vertebrae are not drawn to scale.

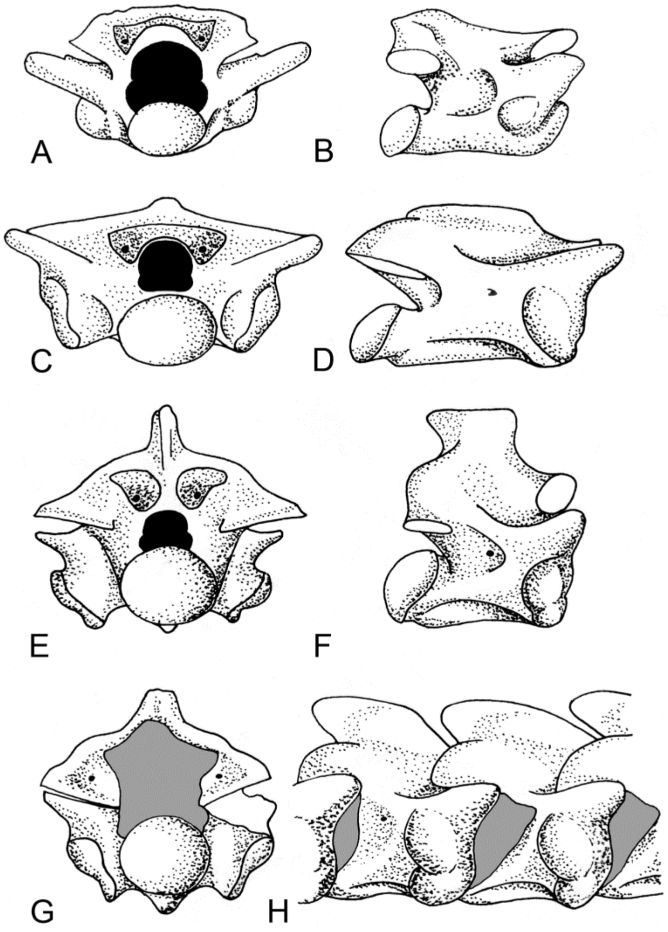

A
B
C
D
E
F
G
H

TABLE 4-1. Variability in the position of the mental foramen/foramina in a series of snake taxa. The numbers in the third column refer to whether the mental foramen is located below a given tooth position (counting from the anterior end of the dentary, i.e., mesial to distal) or below a point located in between two adjacent tooth sockets (e.g., 6th–7th). Note: *Acrochordus javanicus* has two mental foramina.

Species name	Specimen numbers	Location of mental foramen/foramina relative to tooth positions
Anilius scytale	MCZ 19537, MCZ 857, MCZ 2984, MCZ 17645	Below 3rd
Anilius scytale	MCZ 5478	Below 2nd–3rd
Boa constrictor	MCZ 60802, ZFMK 21661, ZFMK 21662	Below 6th
Boa constrictor	MCZ 50234, MCZ 5023, MCZ 19878	Below 6th–7th
Sanzinia madagascariensis	ZFMK 61722, ZFMK 70428	Below 7th
Corallus caninus	AMNH 73347, MCZ 176787, MCZ 53217	Below 5th–6th
Corallus caninus	AMNH 57788, AMNH 155263, ZFMK 21669	Below 4th–5th
Eunectes murinus	AMNH 54158, AMNH 29349, AMNH 29350, AMNH 57474, ZFMK 5179	Below 6th
Morelia spilota	ZFMK 59880, ZFMK 84282	Below 5th
Morelia spilota	MCZ 4279, MCZ 32806	Below 4th–5th
Python sebae	MCZ 30067, ZFMK 5200, ZFMK 21678	Below 5th
Python molurus	MCZ 176780, MCZ 147450, MCZ 176778, ZFMK 21673, ZFMK 5161, ZFMK 83431	Below 5th
Python molurus	MCZ 32219	Below 4th–5th
Acrochordus javanicus	AMNH 46251, AMNH 155254	Below 5th and below 7th
Acrochordus javanicus	AMNH 89839	Below 6th and below 8th
Lampropeltis getulus	AMNH 70097, AMNH 128202, MCZ 39857, ZFMK 54259	Below 7th
Lampropeltis getulus	AMNH 75539, MCZ 15969	Below 6th
Naja naja	AMNH 74833, ZFMK 21704, ZFMK 21706	Below 6th
Bitis gabonica	AMNH 64518, ZFMK 5186	Below 8th
Bitis gabonica	MCZ 131479, ZFMK 21718	Below 7th

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CHAPTER FIVE

FIRST REPORT OF A PELVIC GIRDLE IN THE FOSSIL SNAKE *WONAMBI NARACOORTENSIS* SMITH, 1976, AND A REVISED DIAGNOSIS FOR THE GENUS

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INTRODUCTION

Madtsoiidae is an extinct family of medium-sized to very large snakes whose fossil record extends from the Upper Cretaceous (Cenomanian) to the Pleistocene. So far their remains have been found in Europe, Africa, Madagascar, India, Australia, South America and possibly North America, and therefore they are considered very valuable for paleobiogeographic reconstructions (Albino, 1986; Rage, 1998, Rage and Werner, 1999; Scanlon and Lee, 2000; Scanlon, 2006; Head and Holroyd, 2008; Laduke et al., 2010). Interestingly, by the end of the Eocene, representatives of this group went extinct everywhere except in Australia, where they survived until the Pleistocene as evidenced by the genera *Wonambi*, *Yurlunggur*, and *Nanowana* (Scanlon, 2004).

This group of fossil snakes was initially considered as closely related to extant booids (e.g., Hoffstetter, 1961; Rage, 1984); however, recent phylogenetic analyses suggested that they may represent a very primitive group that originated close to the base of the evolutionary radiation of snakes (Scanlon and Lee, 2000; Lee and Scanlon, 2002; Scanlon, 2006; Lee et al., 2007; Longrich et al., 2012; but see also Rieppel et al., 2003, Wilson et al., 2011, and Zaher and Scanferla, 2012, who place madtsoiids within Alethinophidia).

Wonambi naracoortensis Smith, 1976, is known from Pliocene and Pleistocene deposits in southern and eastern Australia (Barrie 1990; Scanlon and Lee, 2000; Scanlon, 2003, 2005), and its cranial and postcranial anatomy are fairly well known, especially when compared to other madtsoiids (Scanlon and Lee, 2000; Scanlon, 2005, 2006). Regardless of whether *Wonambi* is a basal Alethinophidian or a basal snake, based on the concept of the phylogenetic bracket (Witmer, 1995) it should be expected that this taxon would possess at least some form of vestigial pelvic girdle, if not vestigial hind limbs as well (hind limbs and pelvis are consistently lost in derived Alethinophidia, while most basal families all have at least some representatives that retain at least pelvic vestiges; Dowling [1959], Lee and Scanlon [2002]).

Here we report for the first time the presence of a pelvic girdle in the fossil snake *Wonambi naracoortensis*. The material that we attribute to *Wonambi* consists of a right pelvic girdle where ilium, pubis and ischium are co-ossified. It comes from Victoria Cave, a World Heritage site in the Naracoorte region (about 300 km southeast of Adelaide), South Australia, a locality famous for its richness and diversity of Pleistocene animals (Moriarty et al., 2000; Reed and Bourne, 2000).

Our arguments for attributing this element (SAM P48706) to *Wonambi naracoortensis* are as follows: (1) the element was found in close association with some vertebrae of *Wonambi naracoortensis,* some of which are posterior dorsals (distinguishable from middle and anterior dorsals because of the notched zygosphene tectum); (2) the element has the triradiate structure that is typical of the pelvic girdle of squamates (Fig. 5-1); (3) co-ossification of the pelvic elements, resulting in the lack of sutures between ilium, ischium and pubis, is an unusual trait in squamates, the exceptions are exemplified by *Cordylus cordylus* (MCZ 21570, MCZ 21568), *Xenosaurus grandis* (MCZ 54313, MCZ 54315), some limbless lizards (e.g., *Anguis fragilis*; Stokely,1947) and by some snakes (e.g., *Anilius*, *Cylindrophis*, *Trachyboa*, some Scolecophidia; Essex, 1927; Bellairs, 1950; List, 1966); (4) the obturator foramen (a foramen for the passage of the obturator nerve, a nerve that innervates some of the muscles of the hind limb; Haines, 1935) is absent. This foramen is generally present in lizards (with the exception of limbless forms like *Anguis fragilis*; Stokely, 1947), and typically absent in snakes that retain a vestigial pelvic girdle (Bellairs, 1950). An exception is *Najash rionegrina*, a fossil snake with well-developed hind limbs that still possesses an obturator foramen (Apesteguía and Zaher, 2006). Therefore, this feature is consistent with the animal possessing this pelvic girdle as being either limbless or with strongly reduced limbs; (5) pubis and ischium lack a distinct medial curvature, which is indicative of the lack of a puboischiadic symphysis. Lack of a puboischiadic symphysis is a feature typical of the pelvic girdle of snakes and some limbless lizards (Stokely, 1947; Bellairs, 1950); (6) the lack of an acetabulum suggests that the animal was either limbless or that the limbs had at least lost their weight-bearing function; (7) *Wonambi naracoortensis* is the only locally occurring limbless (or strongly limb reduced) squamate whose size is compatible with the pelvic girdle in question. Furthermore, although pythons (*Morelia*) now occur in the general region, attribution to Pythoninae can be excluded because the morphology of the pelvic girdle in Boidae (i.e., Pythoninae and Boinae) is very distinctive, i.e., they have an anterodorsally directed rod-like process that is considerably longer than the other two processes, which in some forms may be absent altogether (Bellairs, 1950; Gasc, 1966; Boughner et al., 2007). Other limbless squamates (e.g., pygopodids, scincids) can be excluded based both on morphology and size (Stokely, 1947; Stephenson, 1962).

Institutional Abbreviations—MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; **SAM**, South Australian Museum, Adelaide, South Australia.

DESCRIPTION

The pelvic girdle that we refer to *Wonambi naracoortensis* (SAM P48706; Fig. 5-1) consists of a triradiate element where the contributions from ilium, ischium and pubis are very distinct, although no sutures are visible at their junction. There is no acetabulum, and the area where the ilium, ischium and pubis meet is gently convex in lateral view.

The portion corresponding to the pubis slants anteroventrally. It shows a distinct medial curvature towards the ventral end and is broadest at its mid-length. The obturator foramen is absent. There is a distinct ridge along its ventrolateral side, perhaps equivalent to the crest of the processus lateralis of other squamates (e.g., *Gerrhosaurus major*, Fig. 5-1A–C; Russell and Bauer, 2008), and a distinct tapering towards the anterior end, which is especially evident in lateral view. The anterior tip of the pubis is truncated, and this may indicate that the element was originally capped with cartilage, a feature commonly observed in lizards (Russell and Bauer, 2008). The very weak medial inflection of the pubis, which is inconsistent with this element meeting its counterpart along the ventral midline of the body, suggests that a pubic symphysis was absent.

The ischium is represented by a flat trapezoidal process that has a slightly convex and very thin posteroventral margin. Its lateral surface is smooth and gently convex, while its medial side is slightly concave, and shows a distinct step where the excavated surface terminates anterodorsally. Posterodorsal and anteroventral to this step, the excavated surface is bounded by two thin diverging crests. The ventral margin of the ischium is strongly reduced (i.e., lacks a subhorizontal ventral edge), which is consistent with the loss of the ischiadic symphysis, while the posterior subvertical margin and associated ischiadic tubercle are retained.

The ilium consists of a fairly elongate, posterodorsally directed process that tapers at its posterior end. Its ventral half, close to the junction with ischium and pubis, is slightly bent medially, while in its dorsal portion a weak lateral bend is present. This condition can also be observed in the ilium of some lizards (e.g., *Ameiva ameiva*, MCZ 5791; *Diploglossus millepunctatus*, MCZ 130071). A distinct crest runs along the lateral margin of the ilium and extends ventrally to the junction with the ilium and ischium. A round crest runs along the dorsal margin of the ilium, and terminates anteriorly, i.e., close to the junction with the pubis, in a small tubercle that is likely homologous to the iliac tubercle of lizards ("preacetabular process" of Russell and Bauer, 2008). Interestingly, the posterior half of the ilium bears a medial facet that is reminiscent of the facet for articulation with the sacrum observed in limbed lizards (Fig. 5-1). However, the relatively small surface area and ventral orientation of this facet seem to preclude the presence of a strong attachment, if any, to the axial skeleton.

The lack of an acetabulum at the junction between ilium, pubis and ischium, together with the lack of an obturator foramen in the pubis, clearly indicates that the hind limbs were either absent or strongly reduced.

DISCUSSION

There is a distinct ridge along the lateral side of the ilium, and interestingly, a similar ridge in lizards separates the attachment points for the m. iliofemoralis, m. iliofibularis and m. iliotibialis (= m. ambiens pars dorsalis of Herrel et al., 2008) ventrally, and the m. longissimus dorsi and m. iliocostalis, dorsally (Snyder, 1954). Crests that may have provided attachment for other leg muscles are also present on the pubis and ischium (Fig. 5-1). This seems to be inconsistent with the clear absence of an acetabulum, which could be interpreted as evidence for the absence of a femur and therefore of a hind limb. However, it must be pointed out that in snakes that retain vestigial hind limbs the acetabulum is typically very poorly developed (Bellairs, 1950), and this is due to the fact that the limb has completely lost its weight-bearing function, and is no longer in need of a strong connection with the axial skeleton through the pelvis (i.e., there is no longer the need to transmit forces from the limbs to the axial skeleton). Even if the hind limbs of snakes are vestigial, this does not mean that they are useless; indeed, they retain functions that are mostly related to courtship and copulation (Bellairs, 1950; Carpenter et al., 1978; O’Shea, 2007).

It is therefore to be expected that the musculature connecting pelvic girdle and hind limb could be, at least partially, preserved. It is very hard to make conjectures about which muscles are preserved in *Wonambi* and which are not, especially considering that this snake may have represented an intermediate condition between what we see in a typical lizard (e.g., *Basiliscus*; Snyder, 1954) and the highly modified anatomy present in a relatively derived snake that retains hind limbs (e.g., *Trachyboa*; Bellairs, 1950), where the homology of the individual muscles is extremely problematic.

Interestingly, the ilium, when compared to the same element of a typical fully-limbed lizard, is oriented more vertically. This is consistent with a reduced mass for the muscles that connect the ilium to the hind limb, i.e., the m. iliofemoralis, m. iliotibialis, m. iliofibularis, and m. caudifemoralis brevis (Snyder, 1954), and suggests that even if *Wonambi* retained vestigial hind limbs, these were operated by muscles that had lost their full potential for locomotion, and were probably only responsible for the more limited movements involved in courtship and mating, similarly to what we see in modern pythons and boas (Bellairs, 1950). Stokely (1945) mentions that the loss of the puboischiadic symphysis is the first step that marks the beginning of degeneration of the pelvis, and that this can precede any manifest degeneration of the hind limb. This is in agreement with the fact that *Wonambi*, despite showing some level of degeneration of its pelvic girdle, may still have retained the hind limbs. However, it should be kept in mind that in snakes the presence of vestigial hind limbs can be a sexually dimorphic character (Bellairs, 1950; O’Shea, 2007). Only the discovery of new material can help shed some light on whether *Wonambi* did indeed possess hind limbs, and if their presence or absence could have been related to sexual dimorphism. Another interesting feature observed in the pelvic girdle of *Wonambi* is the absence of an obturator foramen. This foramen is typically present in lizards and primitive snakes like *Najash rionegrina* (Apesteguia and Zaher, 2006; Palci et al., 2013), and its absence may suggest that *Wonambi* occupies a phylogenetic position above this taxon (i.e., more derived); however, this can only be determined through the test of congruence of several characters in a phylogenetic analysis.

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811
SERPENTES Linnaeus, 1758
MADTSOIIDAE Hoffstetter, 1961
Wonambi Smith, 1976

Emended Diagnosis—Neural spines of vertebrae well developed and trapezoidal, with slanting anterior and posterior margins; anterior margin of neural spines reaches anterior edge of the zygosphenal tectum; well-developed articulatory facets on stout zygosphene and zygantra; zygosphene tectum deeply notched in posterior precloacal vertebrae; transverse processes extending laterally beyond prezygaphophyses in most trunk vertebrae; synapophyses with concave dorsal edge in lateral view; haemal keel in middle and posterior trunk region narrow and weakly defined laterally, often distinctly bifid on the posterior third of the centrum; pterygoid tooth row near middle of bone, away from medial margin; ectopterygoid process of pterygoid triangular in ventral view; maxilla and dentary depressed; basipterygoid process on basisphenoid well-developed and facing ventrolaterally; basypterygoid facet anteroposteriorly elongate; maxilla with anterolateral trough on suborbital surface; pelvic girdle present; ilium, ischium and pubis present and co-ossified, acetabulum absent, obturator foramen absent.

Differs from *Yurlunggur* in: presence of a single mental foramen on dentary (2 in *Yurlunggur*); oblique trough on suborbital surface of maxilla (flat facet in line with maxilla in *Yurlunggur*); distinct, fan-shaped dorsolateral crest on frontal, posterior to articulation with prefrontal (crest absent or weakly developed in *Yurlunggur*); palatine with wide choanal process that extends medially for about twice the width of the dentigerous ramus, process mostly horizontal (choanal process in *Yurlunggur* narrow, about as wide as dentigerous process, and strongly curved ventromedially); pterygoid teeth along middle of shaft (adjacent to medial edge in *Yurlunggur*); mid-dorsal vertebrae have relatively tall neural spines, distinctly higher than neural canal (neural spines in mid-dorsal vertebrae of *Yurlunggur* are relatively short, about as high as neural canal); haemal keel in middle and posterior trunk vertebrae narrow (relatively broad with parallel margins in *Yurlunggur*).

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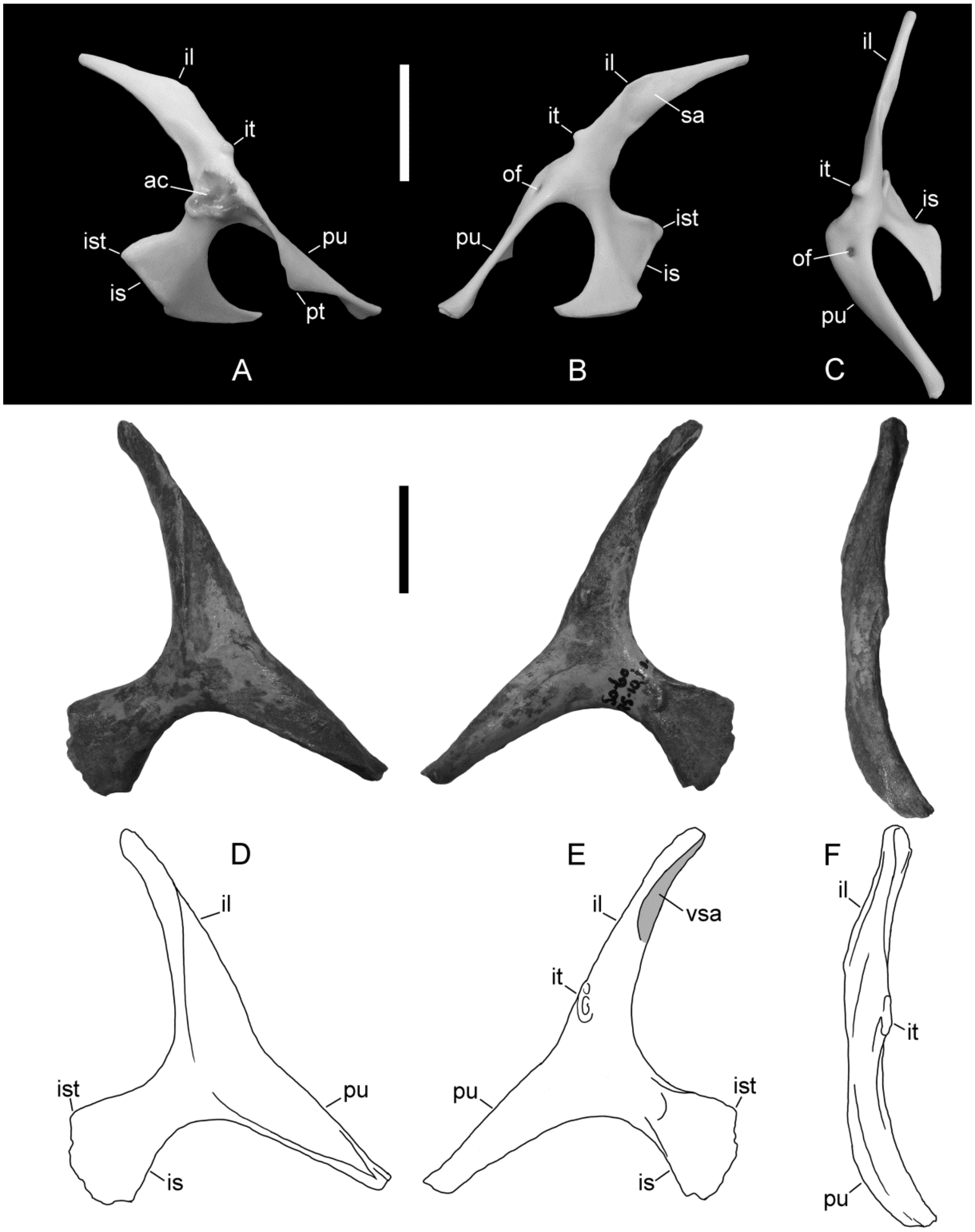
FIGURES

FIGURE 5-1. Comparison between the right pelvic girdle of a lizard (*Gerrhosaurus major*, MCZ 30841) and that of *Wonambi naracoortensis* (SAM P48706). **A**, *Gerrhosaurus*, lateral view; **B**, *Gerrhosaurus*, medial view; **C**, *Gerrhosaurus*, anterodorsal view; **D**, photo and interpretative drawing of right pelvic girdle of *Wonambi*, lateral view; **E**, photo and interpretative drawing of *Wonambi*, medial view; **F**, photo and interpretative drawing of *Wonambi*, anterodorsal view. **Abbreviations**: **ac**, acetabulum; **il**, ilium; **is**, ischium; **ist**, ischiadic tubercle; **it**, iliac tubercle (preacetabular process); **of**, obturator foramen; **pu**, pubis; **pt**, pubic tubercle (extremity of lateral process of pubis); **sa**, sacral articulation; **vsa**, vestigial sacral articulation. Scale bar equals 1 cm.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CHAPTER SIX

PRIMARY HOMOLOGIES OF THE CIRCUMORBITAL BONES OF SNAKES

A nearly identical version of this chapter was published as: Palci, A., and M. W. Caldwell. 2013. Primary homologies of the circumorbital bones of snakes. Journal of Morphology 274:973–986. I was responsible for the collection and interpretation of the data, manuscript composition, figures, and tables. M. W. Caldwell was involved with concept formation and contributed to manuscript edits.

INTRODUCTION

Snakes are a very successful and diverse group of squamate reptiles, numbering about 3,000 living species (Greene, 1997; Caldwell, 2007). A large number of osteological studies have focused on living snakes, but despite these efforts, uncertainty about the homology of many of their highly transformed skeletal elements still persists (e.g., Cundall and Irish, 2008; McDowell, 2008). For example, debate continues regarding the homology of the bone articulating with the dorsal surface of the quadrate, forming the jaw suspensorium of derived alethinophidian snakes, which has been homologized with the tabular, squamosal, and supratemporal of lacertilian squamates and more basal diapsids (Cundall and Irish, 2008; McDowell, 2008). Almost all of these homology problems and their resulting debates revolve around uncertain statements of comparative anatomy arising from inconsistent anatomical nomenclature (e.g., use of the term “tabular”); in other cases, the problem relates to a priori concepts of the plesiomorphic state for snakes as demonstrated by degenerate morphologies [e.g., Walls (1940) and the degenerate snake eye of scolecophidians as primitive for snakes], as opposed to similarities to the lacertilian condition of a character.

Perhaps most critically, there are longstanding issues of primary homology characterizations arising when fossil taxa, which usually present anatomies and combinations of characters not seen among living groups, are assessed for sistergroup relationships using homology concepts developed from the morphologies presented by living taxa and clades. An example of this is the concept that the jugal is absent in all snakes as derived by assessment of living forms, and that any jugal-like element in a fossil snake cannot be a jugal because in all snakes the jugal must be absent (i.e., absence of a jugal is seen as a synapomorphy of snakes). Although this approach to generating conjectures of homology is clearly erroneous, it is important to delineate why: 1) the circularity of this argument is obvious and problematic to any progress whatsoever on the evolution of snakes from lizards, which possess a jugal; 2) such lines of argumentation conflate and confuse the concepts of primary and secondary homology (i.e., synapomorphy). Primary homology statements (i.e., initial conjectures of homology used to construct character matrices) should only be based on anatomical similarity and the test of conjunction, and must be devoid of preconceived ideas of phylogenetic relationships (De Pinna, 1991).

Another example, involving living taxa, is provided by Kluge (1993), who refrains from using the term “basipterygoid process” for snakes because he considers it “. . .likely that such a projection was lost early in snake history” (Kluge, 1993:25), in other words, that it is not homologous with the same structure in lizards based on previous phylogenetic analyses. Such a statement is the result of a methodological error where there is no distinction made between concepts of primary and secondary homology. Once again, primary homology concepts must be based only on similarity (topological and structural) that passes the test of conjunction, and not on preconceived ideas based on previous phylogenetic analyses (Patterson, 1982; De Pinna, 1991). Although it seems obvious, the formulation of hypotheses of homology (primary homology) cannot be biased by previous phylogenetic analyses because the phylogenetic analysis must follow the conceptualization of primary homologies and provide a test of their nature [i.e., verify, by virtue of the test of congruence, whether the observed similarity is homologous or homoplastic for a given group of organisms (De Pinna, 1991)]. To base the formulation of primary homology concepts on previous phylogenies and then test those conjectures of homology in a new phylogenetic analysis would inevitably be a circular process.

Debates concerning the homology hypotheses of the circumorbital bones in fossil snakes are longstanding, although they were most vigorously revived by Caldwell and Lee (1997) and countered by Zaher and Rieppel (1999) concerning *Pachyrhachis*, and most recently by Zaher and Scanferla (2012) concerning *Dinilysia* as compared to Estes et al. (1970), Caldwell and Albino (2002), and Caldwell (2007). Therefore, in this study, we focus our critiques and reinterpretations as a response to Zaher and Scanferla (2012) on the topological relationships and problematic homology assessment of the circumorbital bones in squamates, living and fossil.

The principal purpose of this study is to address the primary homology hypothesis that the posterior orbital element (POE) of many snakes is a postorbital and that the jugal is absent in snakes. We take an explicitly taxic approach to elucidating primary homology, utilizing the tools of comparative anatomy and the explicit rigor of the test of similarity as proposed by Patterson (1982), and seconded most recently by Rieppel and Kearney (2002). In proposing rigorous comparative anatomical boundaries to primary homology statements for snake circumorbital elements, we recognize the implications for subsequent statements of secondary homology arising from the test of congruence, and explore these implications.

MATERIALS AND METHODS

To understand the topological relationships among the circumorbital bones of squamate reptiles, we examined a series of skeletonized, cleared, and stained, or computer tomography (CT)-scanned specimens belonging to both living and fossil taxa, for a total of 32 species of lizards (76 specimens) and 81 species of snakes (151 specimens). Two species of snakes (*Python breitensteini* and *Calabaria reinhardtii*) were dissected to evaluate the presence and anterior insertion points of the quadratomaxillary ligament. Comparisons between snakes and other lizards are justified methodologically against lepidosaur phylogenies (e.g., Estes et al., 1988) that find extant snakes to be derived squamate lizards; we therefore use the non-snake lizard configuration of circumorbital elements as the plesiomorphic pattern against which snakes are more derived.

The specimens examined in this study belong to the collections of the following institutions: American Museum of Natural History, New York, NY (AMNH); Carnegie Museum of Natural History, Pittsburgh, PA (CMNH); Field Museum of Natural History, Chicago, IL (FMNH); Hebrew University of Jerusalem, Paleontology Collections (HUJ-PAL); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina (MACN); Museum of

Comparative Zoology, Cambridge, MA (MCZ); Museo de La Plata, La Plata, Argentina (MLP); Museo di Storia Naturale di Milano, Milano, Italy (MSNM); Natural History Museum, London, England (NHML); Queensland Museum, Brisbane, Australia (QM); Natural History Museum of Gannat, Gannat, France (Rh-E.F.); Senkemberg Museum, Frankfurt, Germany (SMF); University of Alberta Museum of Zoology (UAMZ); University of Florida, Gainesville, FL (UF); United States National Museum of Natural History, Washington, DC (USNM); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK).

Photographs of the figured specimens were taken using a NIKON Coolpix s8200 and CT-scan data for *Cylindrophis ruffus* (USNM 297456) were acquired using a Skyscan 1174. The CTscan data for *Tupinambis teguixin* (FMNH 22416), *Calabaria reinhardtii* (FMNH 117833), and *Lanthanotus borneensis* (YPM 6057, curated at the Yale Peabody Museum, New Haven, CT) were acquired under the Deep Scaly Project (NSF grant EF-0334961) and kindly provided by M. Kearney and O. Rieppel.

The lizards examined in collections include (list organized systematically): *Iguana delicatissima* MCZ 10975, MCZ 6097, MCZ 83228; *Phrynosoma solare* FMNH 22415, FMNH 98395, FMNH 98396; Agama agama MCZ 173366, MCZ 173367; *Uromastyx acanthinurus* MCZ 27377, MCZ 27381, MCZ 27382; *Chamaeleo gracilis* MCZ 22559, MCZ 41654; *Gekko gecko* MCZ 43738, MCZ 131538, MCZ 173377; *Lialis burtonis* MCZ 59105, MCZ 59106; *Acontias meleagris* FMNH 187063, MCZ 21416, NHML 63-2-21-21; *Acontias plumbeus* MCZ 14233, MCZ 21452, NHML 94-6-29-38; *Chalcides ocellatus* FMNH

164674, FMNH 167941; *Corucia zebrata* MCZ 68815, MCZ 77375; *Cordylus cordylus* MCZ 21568, MCZ 21570; *Gerrhosaurus major* MCZ 30841, MCZ 147438; *Ameiva ameiva* MCZ 5791, MCZ 131788, MCZ 165368, MCZ 173127; *Tupinambis teguixin* FMNH 140193; *Bachia heteropus* MCZ 9006, MCZ 79737; *Bachia trinasale* ZFMK 81766 (X-rayed specimen); *Xantusia riversiana* MCZ 9177, CMNH 56451, CMNH 56457; *Lacerta lepida* FMNH 22098, MCZ 15733, MCZ 15736, MCZ 29977; *Anniella pulchra* FMNH 213666, MCZ 8855, MCZ 8858, MCZ 11798; *Diploglossus millepunctatus* MCZ 130070, MCZ 130071; *Ophisaurus apodus* MCZ 2094, MCZ 32249; *Gerrhonotus liocephalus* MCZ 19062, MCZ 24514, MCZ 24514; *Xenosaurus grandis* MCZ 54311, MCZ 54313, MCZ 54315; *Shinisaurus crocodilurus* UF 71623; *Heloderma horridum* MCZ 5008, MCZ 5009, MCZ 5010; *Lanthanotus borneensis* FMNH 134711, MCZ 8305, SMF 66188; *Varanus bengalensis* MCZ 33453, MCZ 43073, MCZ 43739; *Dibamus novaeguineae* USNM 305916, USNM 305914; *Rhineura floridana* MCZ 4337, MCZ 55615; *Amphisbaena alba* MCZ 32256, MCZ 32257, MCZ 165208; *Bipes biporus* MCZ 83227, MCZ 145823, NHML 1454; *Trogonophis wiegmanni* NHML 94-3-22-4, NHML 1920-9-20-653, NHML 1964-1831. Additional information on the cranial osteology of lizards was obtained from Estes et al. (1988) and Evans (2008).

The snake species, extant and fossil, examined in collections include (list organized systematically): *Eupodophis descouensi* Rh-E.F. 9001, 9002, 9003, MSNM V-3661; *Haasiophis terrasanctus* HUJ-PAL 659; *Pachyrhachis problematicus* HUJ-PAL 3659, HUJ-PAL 3775; *Dinilysia patagonica* MLP 26-

410, MACN-RN-1013; *Yurlunggur* sp. QM 45391; *Anomalepis aspinosus* MCZ 14785 (cleared and stained); *Anomalepis flavapices* AMNH R-6966 (CT-scanned specimen); *Typhlophis squamosus* AMNH R-25051 (cleared and stained); *Leptotyphlops dulcis* AMNH R-160152; *Leptotyphlops humilis* AMNH R-73716, USNM 222795; *Leptotyphlops scutifrons* MCZ 54515 (cleared and stained), MCZ 68781 (cleared and stained); *Rhamphotyphlops braminus* USNM 509423; *Rhamphotyphlops subocularis* MCZ 65993, MCZ 65997, MCZ 72084; *Rhinotyphlops schlegeli* MCZ 29174 (cleared and stained), MCZ 70064 (cleared and stained), MCZ 38551; *Typhlops angolensis* AMNH R-11633; *Typhlops diardi* NHML 1930-5-8-3; *Typhlops lineolatus* MCZ 48063; *Typhlops punctatus* MCZ 7293, MCZ 2249, NHML 1911-6-9-2, NHML 1975-567, USNM 320704; *Typhlops reticulatus* AMNH R-3001; *Anilius scytale* MCZ 19537, MCZ 2984, MCZ 17645, NHML 58-8-23-48; *Cylindrophis maculatus* NHML 1930-5-8-50; *Cylindrophis ruffus* AMNH R-85647, NHML 1930-5-8-47, USNM 297456; *Rhinophis planiceps* NHML 1930-5-8-69; *Rhinophis sanguineus* NHML 1930-5-8-62; *Uropeltis ocellatus* MCZ 3873; *U. pulneyensis* MCZ 3870; *U. rubrolineatus* MCZ 47101; *Loxocemus bicolor* AMNH R-110151, AMNH R-44902, AMNH R-19393, NHML 82-8-17-16; *Xenopeltis unicolor* AMNH R-29969, AMNH R-71531, NHML 1947-1-1-10, NHML 1947-1-1-12, USNM 287277; *Tropidophis canus* AMNH R-45839, AMNH R-73066; *Tropidophis pardalis* FMNH 233; *Ungaliophis panamensis* AMNH R-58845, AMNH R-62639, MCZ 56051; *Boa constrictor* ZFMK 21661, ZFMK 54844; *Calabaria reinhardtii* ZFMK 89190, AMNH R-10092, NHML 1911-10-28-17, UAMZ R937 (dissected); *Charina bottae* FMNH 1218, FMNH 22348, FMNH 31300; *Corallus caninus* AMNH R-57788, AMNH R-63587, AMNH R-73347, AMNH R-155263; *Eryx colubrinus* ZFMK 50246; *E. conicus* NHML 1930-5-8-14; *E. jaculus* FMNH 19624; *E. johni* NHML 1930-5-8-34; *Eunectes murinus* AMNH R-54158, AMNH R-29349, AMNH R-29350, AMNH R-57474; *Messelophis variatus* SMF ME-1828; *Messelophis ermannorum* SMF ME-759; *Liasis albertisi* ZFMK 5165, ZFMK 70427; *Morelia spilota* AMNH R-59880, AMNH R-79043, FMNH 22234, FMNH 22380, ZFMK 84282; *Palaeopython fisheri* SMF ME-1002; *Python breitensteini* UAMZ R938 (dissected); *Python molurus* NHML 1972-21-78, ZFMK 5161, ZFMK 83431; *Python reticulatus* FMNH 15678, FMNH 51631, NHML 1972-2169, ZFMK 5175, ZFMK 70207; *Acrochordus javanicus* AMNH R-46251, AMNH R-140814, AMNH R-155254; *Pareas carinatus* NHML 1964-1092, NHML 1964-1094, NHML 1964-1098; *Xenodermus javanicus* FMNH 67427; *Atractaspis aterrima* NHML 95-5-3-58, AMNH R-12352 (CT-scanned specimen); *Atractaspis bibroni* AMNH R-82071; *Atractaspis corpulenta* MCZ 4826; *Atractaspis irregularis* FMNH 142994, MCZ 53534, AMNH R-12355; *Atractaspis microlepidota* FMNH 58397; *Homoroselaps lacteus* FMNH 187420, FMNH 187421, FMNH 204893, FMNH 206416; *Agkistrodon piscivorus* ZFMK 21724, AMNH R-81544, AMNH R-57801; *Azemiops feae* FMNH 218628; *Causus rhombeatus* FMNH 2268, FMNH 51692, FMNH 51693, FMNH 164744; *Bitis gabonica* ZFMK 21718, AMNH R-64518, AMNH R-57792, AMNH R-137177; *Cerastes cerastes* ZFMK 53537, ZFMK 5181; *Vipera russelli* AMNH R-75739, AMNH R-74818, ZFMK 5187; *Bungarus fasciatus* AMNH R-56198, AMNH R-76574; *Laticauda colubrina* FMNH 236242,

FMNH 234147, FMNH 234149, FMNH 236242, FMNH 236243; *Micrurus fulvius* FMNH 34282, FMNH 229600; *M. nigrocintus* FMNH 210092; *Naja naja* AMNH R-57807, AMNH R-74833, ZFMK 21704, ZFMK 21705; *Pelamis platurus* FMNH 171628, FMNH 171632, FMNH 216510, MCZ 7084, MCZ 131501; *Cerberus rhynchops* NHML 58-9-21-3, NHML 1964-10-20; *Homalopsis buccata* NHML 111-18-1-e, NHML 1930-5-8-630, NHML 1930-5-8-631, NHML 1964-11-25; *Coluber caspius* ZFMK 5221; *Coluber viridiflavus* AMNH R-67896; *Dasypeltis scabra* MCZ 30208, MCZ 54894; *Heterodon platyrhinos* AMNH R-63590, AMNH R-69647, AMNH R-155313; *Lampropeltis getulus* AMNH R-70097, AMNH R-75539, AMNH R-128202, ZFMK 54259, ZFMK 5205; *Malpolon monspessulanus* ZFMK 5197; *Natrix natrix* ZFMK 42502; *Oxyrhabdium modestum* FMNH 96532; *Pseudoxenodon macrops* NHML 1930-5-8-271, NHML 1930-5-8-273, NHML 1930-5-8-274; *Thamnophis sirtalis* AMNH R-74849, AMNH R-148084; *Thamnophis validus* AMNH R-62287.

Information concerning the cranial osteology of Scolecophidia was complemented by reference to the works of List (1966), Cundall and Irish (2008), and Rieppel et al. (2009). Data for the rare snakes *Anomochilus leonardi* and *Casarea dussumieri* were obtained from the works of Rieppel and Maisano (2007) and Maisano and Rieppel (2007), respectively. Data on uropeltid snakes were complemented with the work of Olori and Bell (2012). A useful source of information was also the series of CT-derived animations available on DigiMorph.org for both lizards and snakes.

RESULTS

The general condition of circumorbital elements (plesiomorphic condition) in a lizard includes the following individual bones: frontal; prefrontal; lacrimal; jugal; maxilla; postorbital; and postfrontal. The frontal forms, to varying degrees, the dorsal margin of the orbit (i.e., it can be excluded from the margin of the orbit in forms where the postfrontal and prefrontal meet dorsal to the orbit; e.g., *Heloderma*, some Chamaeleonidae, Pygopodidae, Scincidae and Anguidae; Estes et al., 1988), whereas the prefrontal and lacrimal form the anterior margin. The orbit is framed posteriorly by the postfrontal, jugal and, in some cases, the postorbital (Fig. 6-1; Table 6-1). However, with the exception of iguanians (i.e., Iguanidae, Agamidae, Chamaeleonidae; e.g., *Iguana delicatissima*, Fig. 6-1A), the postorbital bone rarely forms a major contribution to the bony arch that borders the orbit posteriorly. Moreover, the postorbital never makes contact with the maxilla, and contacts the ectopterygoid only in Agaminae and Chamaeleonidae (as previously noted by Gauthier et al., 2012, who named this new clade “Chamaeleonoidea”); however, the contact we observed in *Agama* is a very weak point-contact between the posterolateral corner of the ectopterygoid and the anteroventral corner of the postorbital, and in some specimens (e.g., *Agama agama* MCZ 173367) the two bones may fail to meet, leaving a small gap between them. In all other lizards with a distinct postorbital (i.e., neither lost nor fused with the postfrontal), this bone either barely enters the orbital margin with a very small contribution between jugal and postfrontal [e.g., *Diploglossus millepunctatus* (Fig. 6-1B) and *Tupinambis teguixin* (Fig. 6-2A)] or is completely excluded from the posterior margin of the orbit [e.g., *Anniella pulchra*, *Eumeces obsoletus*, *Ophisaurus apodus* (Fig. 6-1C), and *Tropidophorus misaminius*] (Table 6-1). Importantly, the loss of the upper temporal bar (a strut of bone formed by postorbital and squamosal) in lizards is typically correlated with loss or extreme reduction of the postorbital [e.g., lost in *Heloderma*, and *Lanthanotus* (Fig. 6-2B), vestigial in *Anniella pulchra*]; In some Gekkota the postorbital may still be present, in very reduced form, if it is indeed fused with the postfrontal, a matter of some debate (Daza et al., 2008). When present, the postfrontal of lizards typically straddles the frontoparietal suture, with the only exception being iguanians, where the bone, if present, is located anterior to the aforementioned suture (Fig. 6-1A). In a few lizards (i.e., *Varanus*, anguids, lacertids, xenosaurids, cordylids, and scincids; Estes et al., 1988; Evans, 2008), there are additional bones that form the dorsal margin of the orbit, namely palpebrals or supraorbitals placed near the suture of the prefrontal and frontal, or lateral to the frontal, respectively.

In all snakes, three of the lizard circumorbital elements are always retained: the frontal, the prefrontal, and the maxilla. The frontal generally forms a major component of the dorsal margin of the orbit, unless excluded by a supraorbital ossification (as in pythons, for example), whereas the prefrontal is always present and forms the anterior margin of the orbit (the only exception being Anomalepididae, where this element is highly modified and lies mostly above the orbit). The maxilla is elongate posteriorly and usually forms the major portion, if not the complete ventral margin, of the orbit; exceptions include taxa where the maxillae have been strongly reduced (e.g., Scolecophidia, Viperidae, *Aspidelaps*, and *Atractaspis*; Cundall and Irish, 2008). A fourth element, the lacrimal, is also agreed upon to be absent in all known snakes, fossil and living, with the possible exceptions of *Casarea* and *Bolyeria* (McDowell, 2008).

Non-scolecophidians can present one, two, or no posterior circumorbital bones. The two-element condition is observable in a number of basal snakes such as pythons, *Loxocemus*, and *Calabaria*, where one element frames the orbit posteriorly and the other dorsally. Their possible homology with the generalized lizard postfrontal, postorbital, and jugal is extremely problematic. Therefore, in this study, when referring to these elements, we will use the terms "posterior orbital element" (POE), in the sense that it is posterior to the orbit, and "dorsal orbital element" (DOE), simply because it lies dorsal to the orbit. In general, the POE can be in contact ventrally with the maxilla and/or the ectopterygoid, or can fall short of contacting either, so that the connection between these bones is only achieved via one or more ligaments (Table 6-2); this element has been referred to in the past as the "postfrontal" (for a review, see McDowell, 2008) and more recently as the "postorbital" (Rieppel, 1977).

In both *Loxocemus* and *Calabaria*, the DOE straddles the frontoparietal suture, as does the postfrontal of most lizards that retain this bone; however, in pythons, the DOE is located anterior to the frontoparietal suture, as in iguanians that retain this ossification.

The topological relationships of the POE and DOE of the fossil snakes *Dinilysia* and *Yurlunggur* (Fig. 6-2C,D) are identical to those observed for the jugal and postfrontal of some lizards (e.g., *Ophisaurus apodus* and *Lanthanotus borneensis*), where the jugal/POE forms most of the bony arch that frames the orbit posteriorly and makes contact with the postfrontal (=DOE) dorsally and the maxilla ventrally. Moreover, in *Dinilysia* and *Yurlunggur*, the DOE straddles the frontoparietal suture, as does the postfrontal of lizards (with iguanians being the only exception). The only difference between the jugal of lizards and the POE of *Dinilysia* and *Yurlunggur* is that the latter element does not make contact with the ectopterygoid, but this is clearly a consequence of the posterior elongation of the maxillae that is typical of snakes, which force the ectopterygoid articulation with the maxilla to shift posteriorly. Only in some of the living snakes is a contact (ligamentous, not sutural) between the POE and ectopterygoid reestabilished as a consequence of the lengthening of this latter element anteriorly and its interposition between the maxilla and POE (Table 6-2). Importantly, the POE of *Yurlunggur* shows a posteroventral process that was likely a point of attachment for a superior head (jugal head) of the quadratomaxillary ligament (Fig. 6-3A); a similar process is present also in some extant lizards like *Lacerta lepida* and *Gerrhonotus liocephalus* (Estes et al., 1988; Fig. 6-3B). It is important to note that, although the posteroventral process of the jugal can be absent in some lizards (e.g., *Ophisaurus apodus*, *Lanthanotus borneensis*, *Varanus salvator*; Estes et al., 1988) despite the presence of a quadratomaxillary/quadratojugal ligament, the presence of such a process is clear indication that the ligament inserts in that position.

The POE and DOE of the extant snake *Calabaria* maintain the same topological relationships as in the fossil snakes *Dinilysia* and *Yurlunggur*, where the DOE straddles the frontoparietal suture and the POE bridges the gap between the latter element and the maxilla/ectopterygoid complex. The only difference between *Calabaria* and these two fossil snakes is that the ectopterygoid of *Calabaria* is sandwiched between the posterior portion of the maxilla (ventrally) and the POE (dorsally), likely as a result of the shortening of the skull of this burrowing snake and because of the anterior lengthening of the ectopterygoid itself (Fig. 6-2E).

In most lizards, there is a ligament, the quadratojugal, or quadratomaxillary ligament, that extends between the lateral side of the condylar region of the quadrate posteriorly and the posterior tip of the maxilla and posterior margin of the jugal anteriorly (Iordansky, 1996). Snakes retain the homologue to this ligament, usually referred to as the quadratomaxillary ligament (Frazzetta, 1966), and while in some species (e.g., *Python breitensteini*, UAMZ R398), the ligament extends only between the condylar region of the quadrate posteriorly and the posterior tip of the maxilla anteriorly, in *Calabaria reinhardtii* (UAMZ R937), the same ligament attaches anteriorly to the maxilla, the ectopterygoid, and extends a distinct bundle of contiguous ligament fibers to the posteroventral margin of the POE (Fig. 6-4). In *Corallus caninus* (Fig. 6-2F), the POE lies in front of the ectopterygoid in a way that is reminiscent of the condition in *Dinilysia* and *Yurlunggur*, but fails to contact the maxilla ventrally and so a distinct gap persists between the two elements.

The same condition is observed in some specimens of *Morelia spilota* (e.g., AMNH R-59880, FMNH 22234); however, other specimens of the same species (e.g., FMNH 22380, ZFMK 84282) show a POE that clearly makes contact with the ectopterygoid. This observation suggests that there is a degree of plasticity in the length of the POE of snakes. In this regard, another interesting case of intraspecific variation is observed in *Python reticulatus*, where ventrally the POE can contact the ectopterygoid (e.g., ZFMK 5175), the maxilla (e.g., FMNH 51631, ZFMK 70207), or neither element (e.g., FMNH 15678). In colubroid snakes, the POE generally fails to make contact with either maxilla or ectopterygoid ventrally, and an individual DOE is always absent; however, in some colubroid snakes (e.g., *Bungarus* and *Dasypeltis*), the frontal has a lateral expansion that is separated from the medial portion of the bone by a series of small foramina. The shape of this lateral expansion resembles the DOE of Pythoninae and it may therefore represent a DOE that fused to the frontal early in ontogeny; however, no developmental data are currently available to support this hypothesis.

Some snakes have the orbit bounded posteriorly and dorsally by an element that has the shape of an inverted "L". It is not clear whether this condition simply corresponds to an anterodorsally expanded POE or to a POE that fused with a reduced DOE, but when the dorsal ramus of this inverted L-shaped element extends for a considerable length along the lateral margin of the frontal, it is plausible that it may indeed represent a DOE that has fused with the POE (e.g., *Acrochordus javanicus*; Fig. 6-2G; Table 6-2).

Burrowing forms (e.g., *Anilius*, *Anomochilus*, Uropeltidae, *Micrurus*, *Homoroselaps*, *Atractaspis*) have typically lost the bones that form the posterior orbital arch (i.e., both DOE and POE), with the exception of *Cylindrophis* (Fig. 6-2H; Table 6-2), which still retains an element of uncertain homology posterodorsal to the orbit. It is not clear whether this element is equivalent to the DOE or the POE of other snakes, because it straddles the frontoparietal suture (especially evident in juveniles), as does the DOE of *Dinilysia*, *Yurlunggur*, *Calabaria*, and *Loxocemus*, but it also extends ventrally as more typical of the POE of other snakes. These burrowing forms also typically have anterolateral finger-like processes of the parietal that extends to the posterolateral margin of the frontals, and this may be of functional importance as a burrowing adaptation. It is very unlikely that these processes are homologous, because they appear in very distantly related lineages (e.g., uropeltids and a few colubroids) that share a burrowing behavior.

Anomalepidids are the only scolecophidians that retain a posterior orbital ossification in the shape of a rod-like element embedded in soft tissues and lacking any contact with the surrounding bones (Fig. 6-5). This element typically frames the orbit ventrally and posteriorly, but in *Anomalepis flavapices* (AMNH R-6966) it also produces a dorsal process that frames the orbit anteriorly, and extends a little further posteriorly than the POE of *Liotyphlops* and *Typhlophis*.

DISCUSSION

It is commonly accepted that snakes, both fossil and living, are a large and successful clade of limb-reduced to limbless lizards (Greene, 1997); this concept of sistergroup relations, though nonspecific in terms of the closest lizard sistergroup to snakes, is constraining in terms of homology concepts for the circumoribital elements and their plesiomorphic states. In snakes, the condition of the circumorbital series is significantly different from that of a generalized lizard, both in terms of the degree of transformation of the elements present and their topological relations, and in terms of the number of elements. Identifying primary homologies is difficult for most snakes, and entirely problematic for some highly derived groups such as the blind, burrowing clades inclusive of typhlopids, leptotyphlopids, and anomalepidids (i.e., Scolecophidia) who have lost a well-defined orbit altogether along with a number of the circumorbital elements present in the plesiomorphic lizard condition.

The homologies of the POE and DOE are longstanding matters of debate in snake evolution (McDowell, 2008). Romer (1956) was aware of the problem in identifying the POE either as a postfrontal or as a postorbital and chose the latter term out of the necessity of having an anatomical term to refer to this ossification, but without providing any clear justification for his choice [as a matter of fact, this author sometimes used the terms postorbital and postfrontal interchangeably in the same study when writing about snakes; e.g., Romer (1956:127) and Romer (1956:569)]. Romer (1956) considered the DOE of pythons as a neomorph, largely because this element is absent in most other snakes.

If snakes are considered to be the sister group of iguanians, as has been hypothesized from molecular phylogenetic analyses (e.g., Vidal and Hedges, 2004), then it may be tempting to interpret the large postorbital bone of these lizards as homologous to the POE of snakes. This conclusion would be based on the resemblance in the topological position of these elements, that is, posterior to the orbit and failing to make contact with the maxilla ventrally. However, the contact between ectopterygoid and postorbital as observed in snakes cannot be considered homologous to the contact observed in Agaminae and Chamaeleonidae for three reasons: 1) Iguaninae are placed at the base of the clade Iguania (Gauthier et al., 2012) and show the plesiomorphic condition of the lack of a contact between ectopterygoid and postorbital, which implies that the most recent common ancestor of snakes and Iguania (if we accept the hypothesis of a sistergroup relationship between these two clades) lacked a postorbital-ectopterygoid contact and this contact evolved independently in derived snakes and derived iguanians (i.e., Agaminae and Chamaeleonidae); 2) the nature of the contact between ectopterygoid and postorbital in the Chamaeleonoidea (sensu Gauthier et al., 2012) is different from what can be observed in snakes; while in these lizards the postorbital contacts a posterior process of the ectopterygoid, in snakes, when the POE contacts the ectopterygoid, it always makes contact with its anterior end; 3) the lack of contact between POE and maxilla is a condition observed only in some of the extant species of snakes (Table 6-2). In the fossil snakes *Dinilysia* and *Yurlunggur*, the POE does not contact the ectopterygoid; instead it contacts the maxilla, and as reported above, the postorbital of lizards never makes contact with the maxilla. All these observations make the homology between the postorbital of Chamaeleonoidea, and more generally of lizards, and the POE of snakes, very unlikely.

In complete contrast to the observations presented here, Rieppel (1977) presented an elaborate transormational argument for the identification of the snake POE as the postorbital rather than the jugal. Rieppel's (1977) primary homology conclusions where derived while revisiting the results of a much earlier study made by Baumeister (1908). Rieppel (1977) concluded that the presumed postfrontals (DOE) of *Rhinophis* (a uropeltid snake) ontogenetically fused with the anterolateral margins of the parietal to form distinct anterolateral projections (Fig. 6-6). Distinct DOE's are rarely observed in uropeltids, as even Rieppel (1977) claimed to have seen only two such elements in the 19 specimens he examined (one specimen of *Rhinophis* and one of *Melanophidium*). Further confirmation of the rarity of these separate DOEs is presented in the comprehensive study of uropeltid snakes made by Olori and Bell (2012), who did not report the presence of such elements. In any case, anterolateral processes of the parietal that are similar to those observed in uropeltids can be observed in the basal snake *Cylindrophis*. By analogy with *Rhinophis*, Rieppel (1977) extrapolated further that these processes must represent postfrontals that are fused to the parietals. Rieppel (1977) noted that similar anterolateral processes of the parietal, although in reduced form, can also be observed in other snakes (e.g., *Anilius*) and concluded that they must have been reduced in snakes that retain an anteriorly concave frontoparietal suture line, and lost in some of the more derived snakes (e.g., Boidae). In other words, according to Rieppel (1977), the frontoparietal suture of most derived snakes would be shaped as it is (i.e., anteriorly concave) as a consequence of the fusion of the postfrontals to the parietal. The observations and conclusions of Baumeister (1908) and Rieppel (1977) might be more conservatively interpreted as unusual, perhaps even pathological, conditions of the anteroventral processes of a few isolated specimens rather than as a general condition of uropeltid snakes, and certainly not snakes in general.

Following on his conclusions regarding the postfrontal of many snakes, Rieppel (1977) hypothesized a transformational scenario for the DOE of pythons, *Calabaria* and *Loxocemus*, which induced from his logic could not be a postfrontal, but could only be a neomorphic supraorbital. Therefore, the POE could only be considered homologous to the postorbital based on its relationships with the frontal, parietal, and postfrontal (which in his interpretation is fused to the parietal and represented by an anterolateral process of this bone). The idea that the DOE of snakes could represent a neomorphic ossification had been proposed before Rieppel (1977), although it was based on different arguments (e.g., Haas, 1930; Romer, 1956; Frazzetta, 1966), even though many other contemporary authors still used the term postfrontal to refer to this ossification (e.g., Williston, 1925; McDowell and Bogert, 1954; Estes et al., 1970; McDowell,1975). Rieppel (1977) based his argument on the assumption that *Rhinophis* represents a primitive condition with respect to all other living snakes, and that the putative element that ontogenetically fuses to the parietal is the primary homolog of the squamate postfrontal. Rieppel's (1977) interpretation of the DOE of snakes as a neomorph (supraorbital) and of the POE as a postorbital has since become broadly accepted (e.g., Rage, 1984; Cundall and Irish, 2008).

McDowell (2008) was the first to argue that, when compared to lizards, the POE of snakes extends too far ventrally along the orbit to be considered a postorbital. With reference to lizards, no living species, nor known fossil species, have a postorbital that forms the posteroventral margin of the orbit; this margin is always defined by the jugal. As demonstrated by the anguimorphans *Diploglossus* (Fig. 6-1B) and *Ophisaurus* (Fig. 6-1C), as well as by the teiid *Tupinambis* (Fig. 6-2A), the postorbital of lizards, with the exception of iguanians, is typically an element that contributes to the formation of the upper temporal arch, and has little or no role in forming the posterior rim of the orbit, which instead is formed mostly by the postfrontal (posterodorsally) and the jugal (posteroventrally). Following this line of argumentation further, it should be noted that in lizards the loss of the upper temporal arch typically results in the loss or extreme reduction of the postorbital, and because all snakes lack the upper temporal arch as a plesiomorphic condition, it is highly unlikely that either the DOE or the POE would represent the homolog of the postorbital. The question should then be whether the POE of snakes is homologous to the postfrontal or to the jugal. This question is best addressed by reference to the topological relationships between the circumorbital bones of extant lizards, for example, *Lanthanotus borneensis* (Fig. 6-2B), and of the fossil snakes *Dinilysia* and *Yurlunggur* (Fig. 6-2C,D).

Like snakes, *Lanthanotus* lacks an upper temporal arch and hence a postorbital, and as a result of this loss the jugal has an extensive contact with the posteroventral margin of the postfrontal, extending dorsally to almost contact the parietal. *Dinilysia* (Fig. 6-2C) has a very similar configuration of the elements that form the posterior and posterodorsal margin of the orbit, and based on their topological relationships (i.e., the DOE clasps the frontoparietal suture, as is generally the case for the postfrontal of lizards, and the POE extends between postfrontal and maxilla, as does the jugal of *Lanthanotus*), we consider them to be the primary homologs of the jugal (POE) and postfrontal (DOE). One difference between the jugal of *Dinilysia* and that of *Lanthanotus* is that *Dinilysia* lacks the anteroventral process that extends anteriorly along the dorsal margin of the maxilla (in *Lanthanotus* and other lizards this anteroventral ramus of the jugal typically extends so far anteriorly as to contact the lacrimal). The reduced contact between the jugal and maxilla (hence a reduced anteroventral process of the jugal) in *Dinilysia* is probably of functional importance in achieving some degree of cranial kinesis, a kineticism that has been further refined in living snakes (Frazzetta, 1966). A second notable difference between the jugal of *Dinilysia* and that of *Lanthanotus* is that in the former the jugal contacts the parietal dorsally. As noted by McDowell (2008), this is mainly the result of the anterolateral expansion of the parietal, a feature that is typical of snakes, and which in turn is linked to the appearance of a crest for attachment of the m.

levator pterygoidei. Contact between the jugal and parietal has more to do with the novel morphology acquired by the parietal of snakes than with any apparent aspect of the jugal itself. As a matter of fact, apart from the aforementioned lack of an anteroventral process, the jugal of *Dinilysia* still remains very close to the lacertilian morphology as represented by *Lanthanotus*, and in the case of *Yurlunggur* the topological relationships of jugal, maxilla, postfrontal, and parietal are identical to those in *Lanthanotus* (i.e., there is no contact between the jugal and the parietal in *Yurlunggur*; Scanlon, 2006; Fig. 6-2D).

Comparing *Dinilysia* (Fig. 6-2C) and the extant snake *Calabaria* (Fig. 6-2E) further aids in identifying and characterizing the POE and DOE in snakes. Rieppel (1977) was aware of the similarity between *Dinilysia* and *Calabaria*, but in spite of this he interpreted the former as having a postorbital (our jugal) and a postfrontal, and the latter as having a postorbital and a neomorphic supraorbital. This conclusion was based on his argument that the postfrontal of all snakes more derived than *Rhinophis* should be expected to have fused with the parietal, and therefore, that any DOE should be considered as a neomorph (i.e., a supraorbital). Although such fusions are possible in uropeltids, especially considering that these snakes lack both a DOE and a POE, we see no reason to extrapolate this condition to all other snakes in the absence of evidence. We caution against transformationist arguments for primary homology determinations, and favour the tests of similarity and their boundary constraints as professed by Patterson (1982), De Pinna (1991), and Rieppel and Kearney (2002). In addition, there is no conclusive evidence to support the idea that

Rhinophis is more primitive than *Anilius* and *Cylindrophis* (e.g., Lee and Scanlon, 2002; Wiens et al., 2012), and there is no embryological evidence to support the idea that the anterolateral parietal processes of snakes other than *Rhinophis* are the result of fusion of a postfrontal ossification to the parietal. As previously noted by Zaher and Scanferla (2012), the weakness of Rieppel's (1977) argument is made very clear by the condition in the fossil snake *Yurlunggur*, where the interpretation of the anterolateral processes of the parietal as structures homologous with the postfrontals clearly fails the test of conjunction (Patterson, 1982; De Pinna, 1991). In *Yurlunggur*, the DOE and the POE (Fig. 6-2D) are clearly homologous to the same elements in *Dinilysia* (based both on topology and structural similarity), and therefore can only represent the postfrontal and the jugal, respectively (Scanlon, 2006). Even if we agree with Zaher and Scanferla (2012) on the interpretation of the DOE of *Dinilysia* and *Yurlunggur* as a postfrontal, we disagree with their interpretation of the POE as a postorbital for the reasons provided above and because the POE of *Yurlunggur* possesses a posteroventral process for attachment of the quadratomaxillary ligament, a feature typical of the jugal of lizards (Fig. 6-3).

Thus, if *Yurlunggur* has a distinct postfrontal, then the anterolateral processes of the parietal (and the semicircular frontoparietal suture) can have nothing to do with an ontogenetic fusion of the postfrontal with the parietal. Conjectures of homology (primary homology) should be devoid of interpretations based on phylogenetic assumptions (i.e., that *Yurlunggur* cannot have a jugal because its absence is supposedly a synapomorphy of snakes), and should only be based on topological and structural similarities that pass the test of conjunction (Patterson, 1982; De Pinna, 1991). The topological relationships and structure of the POE of *Yurlunggur* are consistent with its interpretation as the primary homologue of the jugal of lizards and it should therefore be coded as such in phylogenetic analyses. As pointed out by McDowell (2008), there is no compelling reason to assume that any extant snake should have any ossification around the orbit that was not already present in the fossil snake *Dinilysia*, especially if it is possible to match all the elements in the former with those in the latter. *Calabaria* (Fig. 6-2E) clearly shows a DOE that straddles the frontoparietal suture, a feature typical of the postfrontal of lizards that retain such an ossification (with the only exception of iguanians); there is no reason not to consider this element as homologous to the postfrontal unless we prefer to base our interpretation on preconceived ideas of phylogenetic relationships and weakly supported evolutionary scenarios. It is more parsimonious to consider the DOE of *Calabaria*, and by extension of all extant snakes that possess such an ossification (i.e., pythons and *Loxocemus*), as a postfrontal, rather than as an adhoc neomorph ossification [contra Rieppel (1977)]. Similarly, the POE of *Calabaria* is clearly homologous to the same element in *Dinilysia* (they share the same topological position), and therefore it can only be interpreted as a jugal. Importantly, the POE of *Calabaria* also provides an attachment point for a dorsal expansion of the quadratomaxillary ligament (Fig. 6-4), as is typically the case for the jugal of lizards (Iordansky, 1996). Consequently, snakes that have lost the postfrontal (DOE, i.e., most extant snakes; e.g., *Corallus*, Fig. 6-2F; Table 6-

2) would retain the jugal to form the posterior margin of the orbit. In these snakes, the jugal typically extends from the parietal (dorsally, often involving a suture along the lateral margin of the crest for the m. levator pterygoidei; Frazzetta, 1966) to the ectopterygoid and/or maxilla ventrally. In some forms (e.g., many colubroids), the jugal does not ossify in its ventral portion, and the connection between this element, the maxilla, and the ectopterygoid is ligamentous (McDowell, 2008; a notable exception among colubroids is represented by *Fimbrios*, where the POE reverted to the plesiomorphic morphology of the lacertilian jugal, i.e., has an anteroventral ramus that extends dorsal to the maxilla and almost contacts the prefrontal; Underwood, 1967); this is likely an adaptation that allows for a greater degree of mobility of the palatomaxillary arch during feeding (Frazzetta, 1966), and simply represents a further modification of the already reduced (compared to lizards) contact between jugal and maxilla that is observed in *Dinilysia*. This adaptation is not dissimilar to the loss of a sutural contact between premaxilla and maxilla in many snakes and its substitution with a ligamentous connection. Pythons represent a slightly modified condition with respect to *Calabaria* and *Loxocemus*, because the DOE does not straddle the frontoparietal suture as it does in these two snakes and most lizards. In pythons, the DOE is located just anterior to the frontoparietal suture, with its posterior margin forming a continuation of that line. This could be seen as evidence against its interpretation as a postfrontal; however, in iguanians, the postfrontal lies just in front of the frontoparietal suture, and this suggests that this element can occupy both positions in

squamates. The interpretation of the DOE of pythons as a homologue of the DOE of *Calabaria*, *Loxocemus*, *Yurlunggur*, and *Dinilysia*, and therefore as a postfrontal rather than as a neomorph ossification, would also be more parsimonious. Importantly, the interpretation of the POE of pythons as the homologue of the jugal of lizards is also supported by developmental data. In their study of embryos of *Python sebae*, Boughner et al. (2007:fig. 6A) reported that the POE (their "postorbital") of this snake starts ossifying from a membranous precursor that is located posterior to the orbit and that does not contact any of the surrounding bones; the same developmental pattern was reported by Brock (1941:fig. 5) for the jugal of the lizard *Acontias meleagris*. Although there is variation in the morphology and topological relationships of the jugal precursors in lizards (e.g., Rieppel, 1994a; Hugi et al., 2010; Roscito and Rodrigues, 2012), the fact that the developmental patterns for the jugal of a lizard (*Acontias*) and the POE of a snake (*Python*) are extremely similar should not be overlooked. This observation is consistent with the interpretation that the POE of snakes represents the primary homologue (based on topological relationships, structural similarity, and embryological data) of the jugal of lizards.

The derived alethinophidian (i.e., caenophidian) snake *Acrochordus* (Fig. 6-2G) represents an interesting case where fusion between the jugal and the postfrontal likely occurred. This fusion is suggested not only by the morphology of an element that in this taxon forms both the posterior and the dorsal margin of the orbit, but also by the fact that this bone has been observed to develop, at least in one specimen, from the union of two centers of ossification (Rieppel and

Zaher, 2001). Coossification of the postfrontal and the jugal can be easily explained if we consider that these elements in the lizard *Podarcis sicula* ossify within an originally homogenous cell condensation (Rieppel, 1987). A similar condition, where a single bone is the result of the coossification of jugal and postfrontal, may be expected in all those snakes where the orbit is bordered both posteriorly and dorsally by a single element that has the shape of an inverted “L” and where the dorsal ramus extends anteriorly along the lateral margin of the frontal (e.g., *Casarea dussumieri*). The condition of *Cylindrophis* (Fig. 6-2H) appears somewhat more problematic, because the POE is in contact with the frontoparietal suture, which is typical of the postfrontal, but extends ventrally for quite a distance along the posterior margin of the orbit, which is typical of the jugal. However, if we examine the morphology of the postfrontal of the fossil snake *Pachyrhachis problematicus* (“postorbitofrontal” of Caldwell and Lee, 1997; Palci et al., 2013; Fig. 6-2I), we can see that it extends ventrally well beyond the center of the orbit, and therefore a conjecture of homology between the POE of *Cylindrophis* and the postfrontal is not unreasonable. Alternatively, if we agree with Rieppel’s (1977) hypothesis that the postfrontals of *Cylindrophis* are fused to the parietal to form the anterolateral processes of the latter element (as in *Rhinophis*, but this hypothesis still lacks embryological evidence), then the POE of *Cylindrophis* may represent a jugal that, as in several more derived snakes, has lost its ventral portion and its connection with the maxilla and ectopterygoid has become fully ligamentous. This interpretation would not explain why the POE of *Cylindrophis* extends so far anteriorly as to contact the frontoparietal suture, but on the other hand a point-contact between the POE (jugal) and frontoparietal suture is observed in pythons. Yet another possibility is that this element may represent the fusion of both postfrontal and jugal; this hypothesis is supported by the morphology of the element in question in juveniles of *Cylindrophis* (Cundall and Irish, 2008), where it has the shape of an inverted "L" whose anterodorsal ramus extends anteriorly beyond the frontoparietal suture and along the lateral margin of the frontal.

Another taxon where the homology of the element located posteroventral to the eyeball seems problematic is Anomalepididae (a family of scolecophidian snakes; Fig. 6-5). In these snakes, the element in question lies embedded in soft tissue and has no sutural contact with any other bone; for this reason, its identity is problematic and it has been variably referred to as a neomorphic ossification ("suborbital"; Dunn and Tihen, 1944), a postorbital (Haas, 1964, 1968; Rage, 1984; Cundall and Irish, 2008), fused postorbital, and postfrontal (Dunn, 1941), fused jugal and postorbital in *Anomalepis* and jugal in *Liotyphlops* (McDowell and Bogert, 1954; List, 1966), and as either jugal or postorbital (Rieppel et al., 2009). However, McDowell and Bogert's (1954) proposition that *Anomalepis* may retain the anterior portion of the upper temporal arch, and hence a postorbital, was based on an erroneous reconstruction of the skull of this taxon, where the POE had been placed too far posteriorly; in particular, in their reconstruction the POE of *Anomalepis* was placed so that its dorsal process was located posterior to the orbit, while in truth it is located in front of it (Haas, 1968; McDowell, 2008; Fig. 6-3C).

Because snakes lack an upper temporal arch, there is no reason to consider that the postorbital is or could be present in any snake. We agree with McDowell (2008) that the location of this element ventral and posterior to the orbit of anomalepidids is consistent with it representing a jugal, because that is the position that this element occupies in lizards (Figs. 6-1A,B). In the absence of embryological evidence, the unique morphology observed in *Anomalepis*, where the POE deviates from a simple rod-like shape and exhibits an additional process, is more parsimoniously interpreted as a specialization in the shape of this element rather than it representing the fusion of two or more elements.

The morphology of the prefrontal of anomalepidids clearly suggests that the skull bones of these snakes are prone to acquiring aberrant morphologies that are not directly comparable to their plesiomorphic counterparts. The interpretation of the POE of anomalepidids as a jugal is in agreement with the idea that this bone is primitively present in snakes and is retained in most living lineages.

In conclusion, we believe that comparisons between fossil and extant taxa, as well as developmental studies and the inspection of soft tissue elements, are key to our understanding of the topological correspondence of the circumorbital elements of snakes. We suggest that when referring to the POE of snakes, the term “postorbital” should be abandoned and replaced with the term “jugal,” and we suggest that the DOE of snakes should not be considered as a neomorphic ossification but as the homolog of the lacertilian postfrontal. These alternative interpretations for the dorsal and posterior orbital ossifications of snakes are based on topological relationships and structural similarity, two criteria that must be at the base of any conjecture of homology (Patterson, 1982; De Pinna, 1991; Rieppel, 1994b; Rieppel and Kearney, 2002).

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FIGURES AND TABLES

FIGURE 6-1. The orbital region of lizards. **A**, *Iguana delicatissima* (MCZ 10975), lateral view; **B**, *Diploglossus millepunctatus* (MCZ 130071), lateral view; **C**, *Ophisaurus apodus* (MCZ 2094), lateral view. **Abbreviations**: **fr**, frontal; **j**, jugal; **l**, lacrimal; **max**, maxilla; **pf**, postfrontal; **po**, postorbital; **prf**, prefrontal.

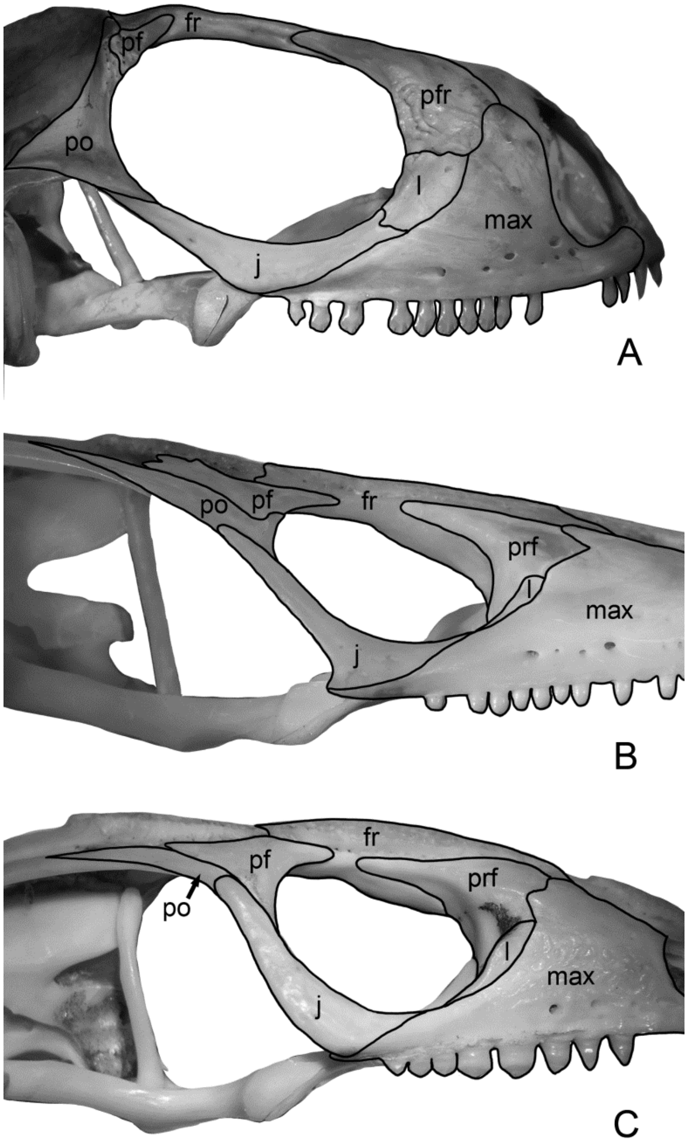
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FIGURE 6-2. Comparison of the orbital regions of different squamates. **A**, *Tupinambis teguixin*, dorsolateral view (FMNH 22416; CTscan); **B**, *Lanthanotus borneensis*, dorsolateral view (YPM 6057; CT-scan); **C**, *Dinylisia patagonica*, dorsolateral view (MACN RN-1013); **D**, *Yurlunggur* sp., dorsal view of skull, right maxilla in lateral view (QM 45391); **E**, *Calabaria reinhardtii*, dorsolateral view (FMNH 117833; CT-scan); **F**, *Corallus caninus*, dorsolateral view (ZFMK 21667); **G**, *Acrochordus javanicus*, dorsolateral view (AMNH 155254); **H**, *Cylindrophis ruffus*, dorsolateral view (USNM 297456; CT-scan); **I**, reconstruction of *Pachyrhachis problematicus*, lateral view. Interpreted Jugal, postorbital, and postfrontal are highlighted in red, yellow, and green, respectively; the frontoparietal suture is highlighted in blue. An element that may result from fusion of jugal and postfrontal in *Acrochordus* is outlined in blue. CT-scan data for *Tupinambis*, *Lanthanotus*, and *Calabaria* are courtesy of M. Kearney and O. Rieppel, Deep Scaly Project.

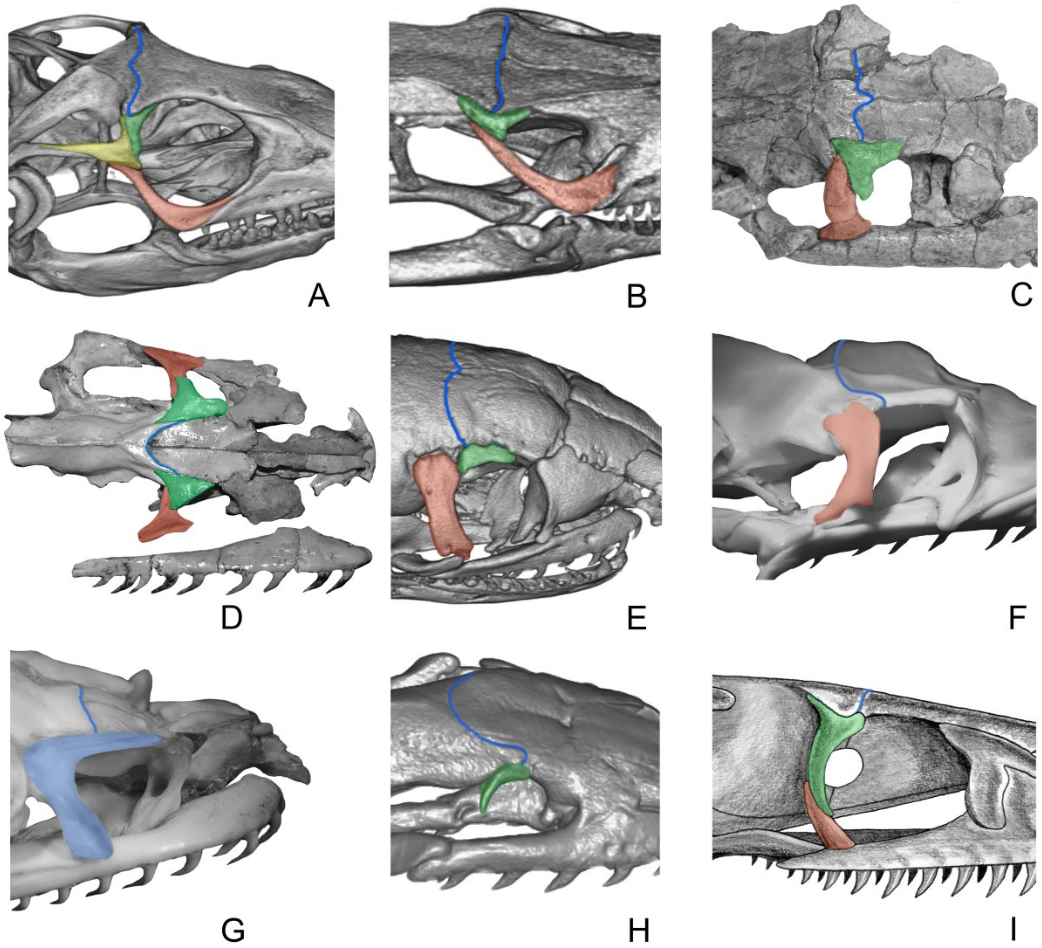
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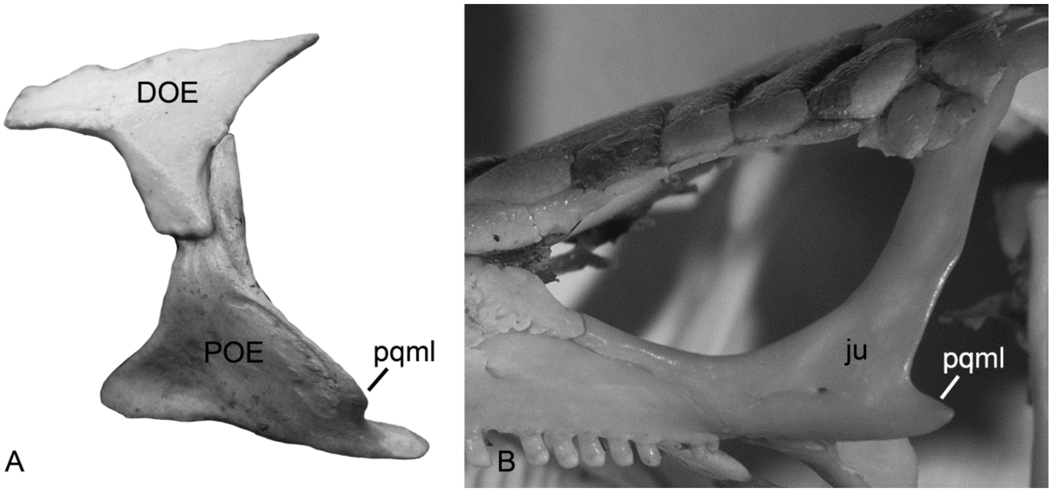
FIGURE 6-3. Comparison between the POE of *Yurlunggur* and the jugal of a lizard. **A**, POE of *Yurlunggur* sp. (QM 45391) in posterolateral view; **B**, lateral view of the orbital region of *Gerrhonotus liocephalus* (MCZ 19062). **Abbreviations**: **DOE**, dorsal orbital element; **ju**, jugal; **POE**, posterior orbital element; **pqml**, process for attachment of quadratomaxillary ligament.


DOE
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A
ju
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FIGURE 6-4. *Calabaria reinhardtii* (UAMZ R937). **A**, dissection of the head (top) and line drawing of the relevant structures (bottom); **B**, close-up of the anterior area of attachment of the quadratomaxillary ligament (top) and line drawing of the relevant structures (bottom). Note the collagen fibers of the quadratomaxillary ligament attaching to maxilla, ectopterygoid, and POE. **Abbreviations**: **E**, eye; **ec**, ectopterygoid; **max**, maxilla; **POE**, posterior orbital element; **q**, quadrate; **qml**, quadratomaxillary ligament.

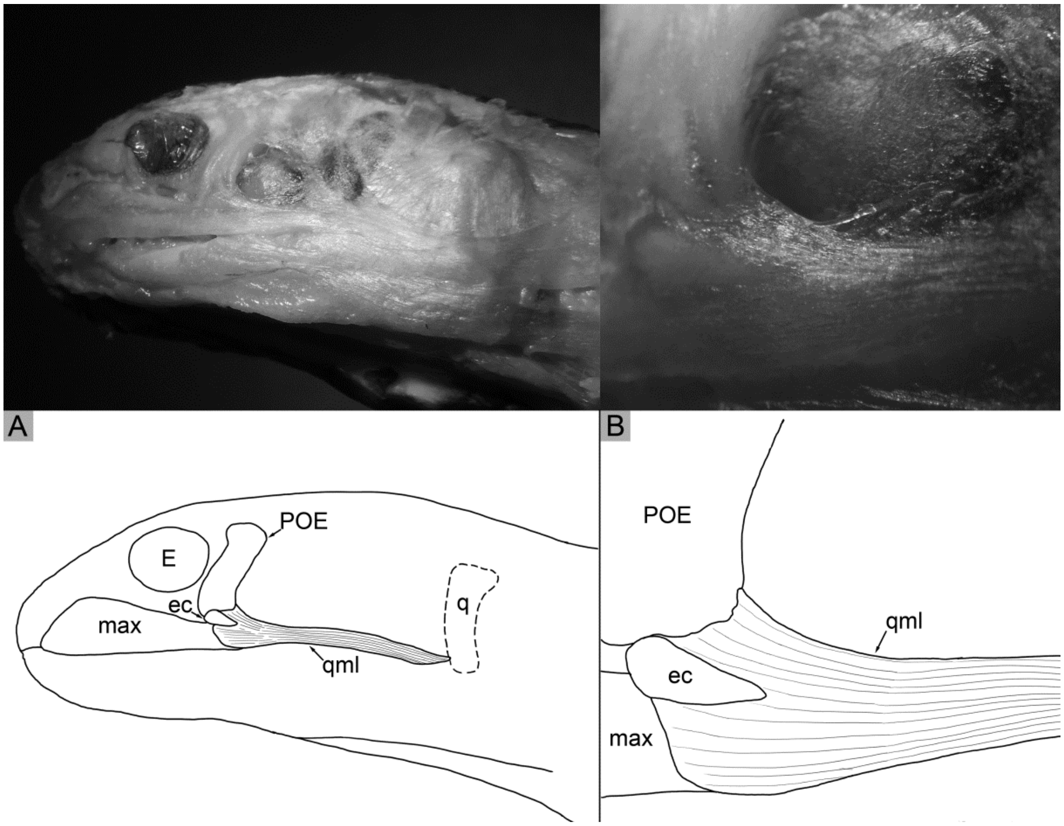
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FIGURE 6-5. Skulls of anomalepidid snakes. **A**, *Liotyphlops albirostris*, lateral view (drawing based on Rieppel et al., 2009); **B**, *Typhlophis scutatus*, lateral view (drawing based on Rieppel et al., 2009); **C**, *Anomalepis flavapices*, lateral view (AMNH R-6966). POE is highlighted in red, blue circle indicates the position of the eye.

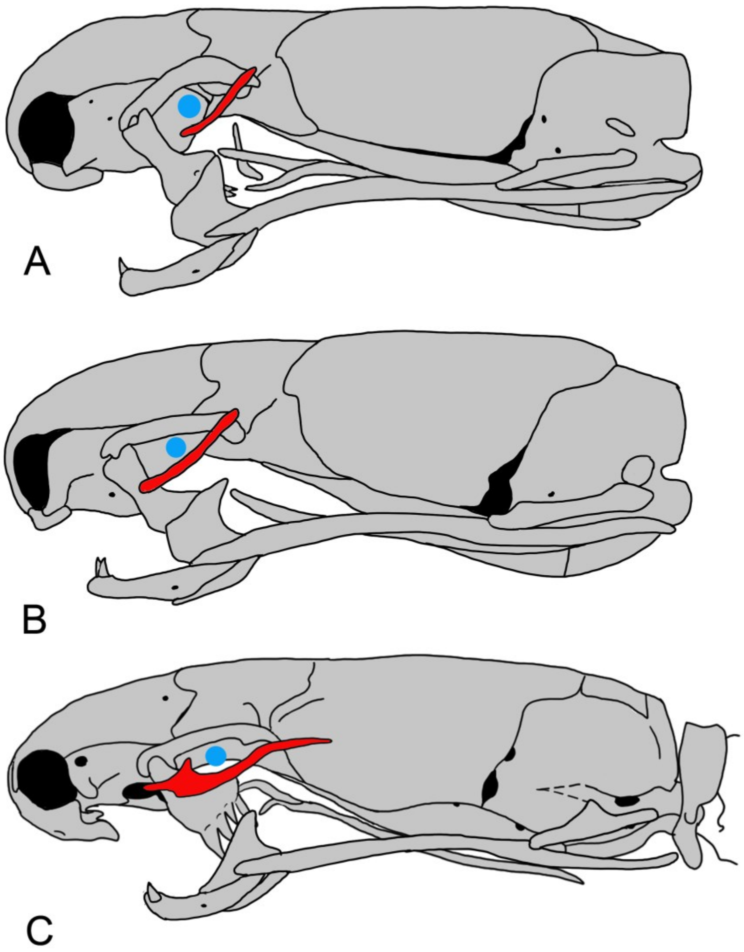
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FIGURE 6-6. Skull of the uropeltid snake *Rhinophis drummondhayi* (redrawn from Olori and Bell, 2012). **A**, Left lateral view; **B**, dorsal view. Anterolateral processes of the parietal are highlighted in grey. **Abbreviations**: **fr**, frontal; **pa**, parietal; **prf**, prefrontal.

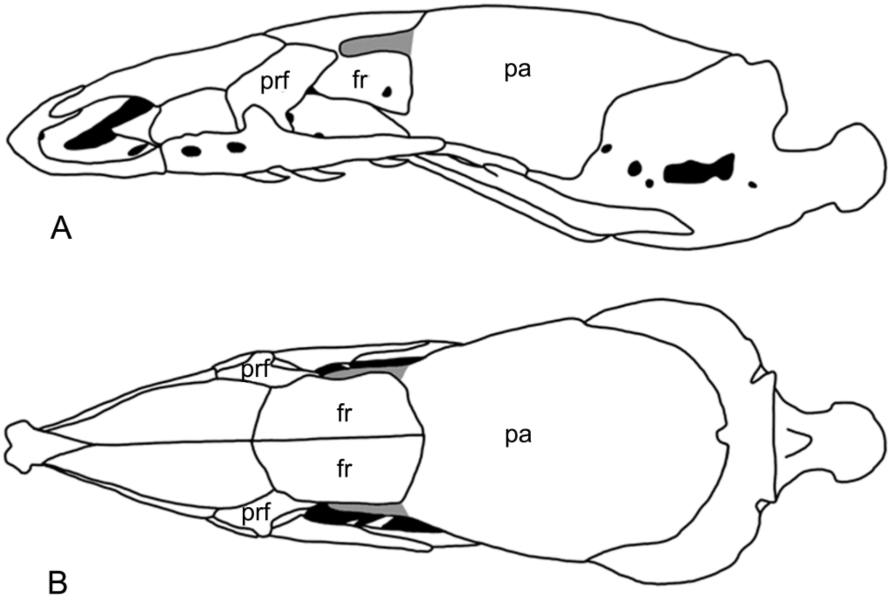
prf
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TABLE 6-1. Elements that form the posterior margin of the orbit in lizards. **Abbreviations**: **J**, jugal; **Li**, ligament; **Pf**, postfrontal; **Po**, postorbital; **Pof**, postorbitofrontal (i.e., fused postorbital and postfrontal).

Taxon	Orbit framed posteriorly by:	Po enters margin of orbit (unknown if Pof)
Iguana delicatissima	Pf/Po/J	Yes
Agama agama	Po/J	Yes
Uromastyx acanthinurus	Po/J	Yes
Chamaeleo gracilis	Po/J	Yes
Gekko gecko	Pof/Li/J	?
Pygopus lepidopus	Pof/Li/J	?
Tupinambis teguixin	Pf/Po/J	Yes, barely
Ameiva ameiva	Pof/J	?
Bachia trinasale	Pf/Po/J	Yes, barely
Cordylus cordylus	Pf/Po/J	Yes, barely
Gerrhosaurus major	Pf/Po/J	Yes, barely
Acontias plumbeus	Pof/J	?
Corucia zebrata	Pof/J	?
Tropidophorus misaminius	Pf/J	No
Eumeces obsoletus	Pf/J	No
Lacerta lepida	Pf/Po/J	Yes, barely
Xantusia riversiana	Pof/J	?
Anniella pulchra	Pf/Li/J	No
Diploglossus millepunctatus	Pf/Po/J	Yes, barely
Ophisaurus apodus	Pf/J	No
Xenosaurus grandis	Pof/J	?
Shinisaurus crocodilurus	Pof/J	?
Gerrhonotus liocephalus	Pf/Po/J	Yes, barely
Heloderma horridum	Pof/J	?
Lanthanotus borneensis	Pf/J	—
Varanus bengalensis	Pof/Li/J	?
Rhineura floridana	J	—
Amphisbaena alba	—	—
Bipes biporus	—	—
Trogonophis wiegmanni	—	—
Dibamus novaeguineae	—	—

TABLE 6-2. Distribution and topological relationships of the circumorbital elements (POE and DOE) in a selection of snakes representative of all major taxonomic groups. **Abbreviations**: **Ec**, ectopterygoid; **Fr**, frontal; **Pa**, parietal; **Max**, maxilla; **N**, neither maxilla nor ectopterygoid; **—**, not applicable.

Taxon	DOE	POE	DOE straddles Fr/Pa suture	DOE + POE (L-shaped element that extends lateral to the Fr)	POE contacts Max/Ec/N	Anterolateral finger-like processes of parietal
Yurlunggur sp.	Yes	Yes	Yes	—	Max	Yes
Dinilysia patagonica	Yes	Yes	Yes	—	Max	No
Leptotyphlopidae	No	No	—	—	—	No
Typhlopidae	No	No	—	—	—	Yes
Anomalepis flavapices	No	Yes	—	—	N	Yes
Liotyphlops albirostris	No	Yes	—	—	N	Yes
Typhlophis squamosus	No	Yes	—	—	N	No
Anomochilus leonardi	No	No	—	—	—	Yes
Anilius scytale	No	No	—	—	—	Yes
Cylindrophis ruffus	?	?	—	?	N	Yes
Uropeltidae	?	No	?	—	—	Yes
Loxocemus bicolor	Yes	Yes	Yes	—	N	Yes
Xenopeltis unicolor	No	No	—	—	—	Yes
Boa constrictor	No	Yes	—	—	Ec	No
Corallus caninus	No	Yes	—	—	N	No
Eunectes murinus	No	Yes	—	—	Ec	No
Calabaria reinhardtii	Yes	Yes	Yes	—	Ec	No
Eryx johni	No	Yes	—	—	Ec	No
Morelia spilota	Yes	Yes	No	—	Ec/N	No
Python reticulates	Yes	Yes	No	—	Ec/Max/N	No
Liasis albertisi	Yes	Yes	No	—	N	No
Casarea dussumieri	?	?	—	Yes	N	No
Tropidophis canus	No	Yes	—	—	Ec	No
Ungaliophis panamensis	No	Yes	—	—	N	No
Acrochordus javanicus	?	?	—	Yes	N	No
Xenodermus javanicus	?	?	—	Yes	N	No
Pareas macularius	No	Yes	—	—	N	No
Atractaspis aterrima	No	No	—	—	—	Yes
Azemiops feae	No	Yes	—	—	N	No
Bitis gabonica	No	Yes	—	—	N	No
Vipera russelli	No	Yes	—	—	N	No
Naja naja	No	Yes	—	—	N	No
Micrurus nigrocintus	No	No	—	—	—	Yes
Bungarus fasciatus	No	Yes	—	—	N	No
Pelamis platurus	No	Yes	—	—	N	No
Homoroselaps lacteus	No	No	—	—	—	Yes
Dasypeltis scabra	No	Yes	—	—	N	No
Heterodon platyrhinos	No	Yes	—	—	N	No
Lampropeltis getula	No	Yes	—	—	N	No

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CHAPTER SEVEN

THE UPPER CRETACEOUS SNAKE *DINILYSIA PATAGONICA* SMITH-WOODWARD, 1901, AND THE CRISTA CIRCUMFENESTRALIS OF SNAKES

A nearly identical version of this chapter was published as: Palci, A., and M. W. Caldwell. 2014. The Upper Cretaceous snake *Dinilysia patagonica*, Smith-Woodward, 1901, and the crista circumfenestralis of snakes. Journal of Morphology 275:1187–1200. I was responsible for the collection and interpretation of the data, manuscript composition, figures, and tables. M. W. Caldwell was involved with concept formation and contributed to manuscript edits.

INTRODUCTION

The debate on the origin of snakes is one of the longest debates about the origin of a major group of vertebrates in the history of science (Caldwell, 2007), having been initiated by Cope (1869), only one year after Huxley (1868) proposed the origin of birds might be found amongst dinosaurs. Both origins scenarios have been at the center of spirited debates ever since.

The question of snake origins has remained intriguing, if not intractable, for two main reasons: (1) snakes are an extremely derived clade of squamate reptiles that have either lost or extensively modified many of the plesiomorphic features common to their lizard relatives; (2) the fossils that may help us fill in the ‘gaps’ between snakes and their closest relatives amongst lizards are extremely rare and fragmentary. Because snakes represent such a highly derived group of organisms, the identification of homologous features shared with lizards is especially problematic and becomes one of the main sources of conflict when reconstructing squamate phylogeny. Phylogenetic analyses are based on characters that are tentative statements of primary homologies (Patterson 1982; Rieppel, 1988a, 1994; De Pinna, 1991; Brower and Schawaroch, 1996; Wägele, 1996; Hawkins et al., 1997; Rieppel and Kearney, 2002); however, if the characters are poorly conceptualized and/or the interpretations of the same anatomical features are not consistent, then the results of the phylogenetic analyses will be in conflict. The problems afflicting character conceptualization/selection have been dealt with in several publications (e.g., Hawkins et al., 1997; Poe and Wiens, 2000; Wagner, 2001;

Rieppel and Kearney, 2002) and will not be further discussed here. The focus of this paper is on the second main source of conflict in phylogenetic analyses: the inconsistent interpretation and lack of clear definition of anatomical features used to formulate statements of primary homology as exemplified by the crista circumfenestralis (CCF).

Anatomical nomenclature underpins empirical statements that are used as transformed metadata statements in the form of characters and states; these statements are then tested via congruence to hypothesize synapomorphies that support sistergroup relationships and thus define the constituents of clades. Because anatomical data is key to hypotheses of homology and thus clade structure, it is critical that translation of empirical observations of anatomy into character statements and states, be as rigorous as possible in reflecting the observed anatomical variation.

We present here the results of our investigation of the anatomical characterizations of the crista circumfenestralis (CCF) of snakes. This ‘crista’ or ‘crest’ is neither a single coherent crest, nor does it arise from a single element. Rather, it is an anatomical feature that is defined by a system of bony crests (crista tuberalis, crista interfenestralis and crista prootica), derived from a number of bones, that converge to surround the fenestra ovalis and lateral aperture of the recessus scalae tympani. The CCF is a composite of a number of elements and structures, each of which potentially develops and evolves independent of the others. Therefore, even superficial examination of the CCF in a small sample of fossil and modern snakes shows a remarkable degree of variation that does not merit the use of single term from which to develop an absence versus presence character concept. We will show here that the CCF is a poorly defined anatomical feature that depends on subjective evaluations of the size of its individual components, and that these variations should not be used to define a character concept, contra Zaher and Scanferla (2012).

In order to effectively qualify the morpho-concept of the CCF, the test of topology will be used in an empirical assessment of the individual anatomical features that are used to indicate the presence or absence of the CCF. We will examine and discuss the anatomy of the phylogenetically basal, and arguably very important, Argentinian fossil snake *Dinilysia patagonica* Smith-Woodward, 1901. This Upper Cretaceous fossil snake has been variously interpreted as either having, or lacking, a CCF (Estes et al., 1970; Rage, 1984; Rieppel, 1988b; Caldwell and Albino, 2002; Caldwell and Calvo, 2008; Zaher and Scanferla, 2012; Scanferla and Bhullar, 2014). Conflicting homology statements of this kind demonstrate lack of consensus, not on the presence or absence of a feature, but on what the necessary anatomy is that defines that feature. The result is confusion at the level of primary homology assignments and subsequent chaos in the reconstruction of phylogeny as there is no common language defining a structure at the level of comparative anatomy (e.g., Lee and Scanlon, 2002; Apesteguía and Zaher, 2006; Zaher and Scanferla 2012; Scanferla and Bhullar, 2014).

The problem at the heart of the debate is the lack of a precise definition of what constitutes the so-called “CCF” coupled with a lack of clarity on how this important anatomical feature evolved. Because the characteristics of the CCF were originally defined in extant, highly derived snakes (colubroids) (Baird, 1960), it is not surprising that a highly derived state might show different conditions of form in more basal snakes, or even be completely absent in other living or fossil snakes. For accurate reconstructions of phylogenetic relationships and to understand the evolution of the CCF, it is very important to interpret correctly the condition of fossil forms.

The CCF

In any anatomical discussion geared to revising the understanding of a complex structure, it is critical to establish how a feature is currently defined. Several authors have tried to provide a definition for this unique feature of snakes. Baird (1960), in his treatise on the periotic labyrinth of reptiles, described it as a crest of bone formed by the prootic (anteriorly) and otooccipital (fused opisthotic and exoccipital; posteriorly) that encircles the stapedial footplate and the anterior portion of the lateral aperture of the recessus scalae tympani, the posterior portion of which forms the jugular (vagus) foramen. The periotic sac, an extension of the perilymphatic system of the inner ear, exits through the lateral aperture of the recessus scalae tympani, anterior to the otooccipital component of the CCF (crista tuberalis), and fills the fossa formed by the CCF itself, covering the lateral aspect of the stapedial footplate (Baird, 1960) (Fig. 7-1). This external portion of the periotic sac was referred to as the juxtastapedial sinus by Baird (1960) (equivalent to the “pericapsular sinus” of De

Burlet, [1934]), while the bony cavity it occupies (i.e., the space encircled by the CCF) was termed the juxtastapedial fossa. The juxtastapedial sinus is walled laterally by a thick fibrous layer that attaches to the lateral margin of the CCF medially and to the stapedial shaft laterally; the lateral extension of the periotic sac outside of the otic capsule is a feature typical of snakes and absent in most lizards, which always lack a CCF. Baird (1960), Wever (1973; 1978) and Rieppel (1979a; 1988b) note that amphisbaenians, the anguimorph *Anniella,* the iguanian *Phrynosoma*, and acontine skinks and *Dibamus* possess a periotic sac that extends outside of the otic capsule.

Rieppel and Zaher (2001) refined Baird's (1960) definition of the CCF by dividing this structure into three main components derived from the lizard skull: crista prootica, crista tuberalis, and crista interfenestralis. The crista prootica, as defined by Rieppel and Zaher (2001), would be a posterolateral projection of the prootic that forms the anterior margin of the vestibular fenestra (fenestra ovalis) and often partially overlaps the anterior part of the stapedial footplate. This crest can show various degrees of development in different taxa (e.g., in *Acrochordus* the crista prootica does not extend posteriorly to partially overlap the stapedial footplate); the crista tuberalis is a crest that in lizards extends from the ventral margin of the paroccipital process to the basioccipital tubera, is completely derived from the otooccipital, and in snakes forms the posteroventral portion of the CCF. In both lizards and snakes this crest also serves as an area of insertion for cervical muscles, such as the m. longissimus capitis and/or the m. longus colli lateralis (Al Hassawi, 2007). The crista interfenestralis is another portion of the otooccipital that forms a crest separating the fenestra ovalis from the lateral aperture of the recessus scalae tympani (fenestra rotunda of lizards), and that in some snakes participates in the formation of the ventral margin of the CCF.

Despite the attempts to clearly define the composition of the CCF (Baird, 1960; Rieppel and Zaher, 2001), confusion still persists in the recent literature regarding the presence or absence of the CCF in some snakes (e.g., *Acrochordus*, *Xenopeltis*, *Dinilysia*, *Najash*). This is largely due to uncertainty regarding the necessary height, degree of protrusion, amount of coverage, etc., that one, or all of the constituent crests must have, with respect to the juxtastapedial space, in order for the CCF to be considered as present (note: we will use the term “juxtastapedial space” in order to refer to the space occupied by the fenestra ovalis and lateral aperture of the recessus scalae tympani, regardless of the presence or absence of a CCF, as opposed to “juxtastapedial recess”, which implies presence of a fully developed CCF). For example, is it enough to have one or two of the crests described by Rieppel and Zaher (2001) (e.g., a well-developed crista prootica with or without a well developed crista tuberalis) in order to consider the CCF present? Or should all three crests be present and well-developed? What does “well-developed” mean? And last but not least, should all of these crests be in contact with each other and form a continuous rim around the juxtastapedial space in order to be labeled a CCF?

MATERIALS AND METHODS

To understand the architecture and characteristics of the juxtastapedial space of snakes, we compared this structure with the homologous region of the lacertilian skull. Comparisons between snakes and lizards are justified methodologically against lepidosaur phylogenies (e.g., Estes et al., 1988) that find extant snakes to be derived squamate lizards; therefore, the lacertilian configuration of the elements surrounding the juxtastapedial space can be used to define the plesiomorphic pattern against which snakes are more derived (with caution in all those cases where the skull morphology is heavily modified from the primitive condition, as in several burrowing taxa; Estes et al. [1988], Evans [2008]). We examined 32 species of lizards (76 specimens) and 81 species of snakes (151 specimens), inclusive of both fossil and extant taxa. Data on extant species was retrieved from observation of specimens that were dry (skeletons), cleared and stained, or scanned using X-ray computer microtomography (micro-CT).

The specimens examined in this study belong to the collections of the following institutions: American Museum of Natural History, New York, NY (AMNH); Carnegie Museum of Natural History, Pittsburgh, PA (CMNH); Field Museum of Natural History, Chicago, IL (FMNH); Hebrew University of Jerusalem, Paleontology Collections (HUJ-PAL); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina (MACN); Museum of Comparative Zoology, Cambridge, MA (MCZ); Museo de La Plata, La Plata, Argentina (MLP); Museo di Storia Naturale di Milano, Milano, Italy (MSNM); Natural History Museum, London, England (NHML); Queensland Museum, Brisbane, Australia (QM); Natural History Museum of Gannat, Gannat, France (Rh-E.F.); Senkenberg Museum, Frankfurt, Germany (SMF); University of Alberta Museum of Zoology (UAMZ); University of Florida, Gainesville, FL (UF); United States National Museum of Natural History, Washington, DC (USNM); Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK).

Photographs of the figured specimens were taken using a NIKON Coolpix s8200 and micro-CT data for *Cylindrophis ruffus* (USNM 297456) were acquired using a Skyscan 1174. The micro-CT data for *Tupinambis teguixin* (FMNH 22416), *Calabaria reinhardtii* (FMNH 117833), and *Lanthanotus borneensis* (YPM 6057, curated at the Yale Peabody Museum, New Haven, CT) were acquired under the Deep Scaly Project (NSF grant EF-0334961) and kindly provided by J. Maisano, M. Kearney and O. Rieppel.

The non-ophidian squamates examined in collections include (list organized systematically): Dibamidae – *Dibamus novaeguineae* USNM 305916, USNM 305914; Gekkota – *Gekko gecko* MCZ 43738, MCZ 131538, MCZ 173377; *Lialis burtonis* MCZ 59105, MCZ 59106; Scincoidea – *Acontias meleagris* FMNH 187063, MCZ 21416, NHML 63-2-21-21; *Acontias plumbeus* MCZ 14233, MCZ 21452, NHML 94-6-29-38; *Chalcides ocellatus* FMNH 164674, FMNH 167941; *Cordylus cordylus* MCZ 21568, MCZ 21570; *Corucia zebrata* MCZ 68815, MCZ 77375; *Gerrhosaurus major* MCZ 30841, MCZ 147438; *Xantusia riversiana* MCZ 9177, CMNH 56451, CMNH 56457; Lacertoidea – *Ameiva ameiva* MCZ 5791, MCZ 131788, MCZ 165368, MCZ 173127; *Amphisbaena alba* MCZ 32256, MCZ 32257, MCZ 165208; *Bachia* *heteropus* MCZ 9006, MCZ 79737; *Bachia trinasale* ZFMK 81766 (X-rayed specimen); *Bipes biporus* MCZ 83227, MCZ 145823, NHML 1454; *Lacerta lepida* FMNH 22098, MCZ 15733, MCZ 15736, MCZ 29977; *Rhineura floridana* MCZ 4337, MCZ 55615; *Trogonophis wiegmanni* NHML 94-3-22-4, NHML 1920-9-20-653, NHML 1964-1831; *Tupinambis teguixin* FMNH 140193; Iguania – *Agama agama* MCZ 173366, MCZ 173367; *Chamaeleo gracilis* MCZ 22559, MCZ 41654; *Iguana delicatissima* MCZ 10975, MCZ 6097, MCZ 83228; *Phrynosoma solare* FMNH 22415, FMNH 98395, FMNH 98396; *Uromastyx acanthinurus* MCZ 27377, MCZ 27381, MCZ 27382; Anguimorpha – *Anniella pulchra* FMNH 213666, MCZ 8855, MCZ 8858, MCZ 11798; *Diploglossus millepunctatus* MCZ 130070, MCZ 130071; *Gerrhonotus liocephalus* MCZ 19062, MCZ 24514, MCZ 24514; *Heloderma horridum* MCZ 5008, MCZ 5009, MCZ 5010; *Lanthanotus borneensis* FMNH 134711, MCZ 8305, SMF 66188; *Ophisaurus apodus* MCZ 2094, MCZ 32249; *Shinisaurus crocodilurus* UF 71623; *Varanus bengalensis* MCZ 33453, MCZ 43073, MCZ 43739; *Xenosaurus grandis* MCZ 54311, MCZ 54313, MCZ 54315; Additional information on the cranial osteology of lizards was obtained from Estes et al. (1988) and Evans (2008).

The snake species, extant and fossil, examined in collections include (list organized systematically): basal Ophidia – *Dinilysia patagonica* MLP 26-410, MACN-RN-1013; *Eupodophis descouensi* Rh-E.F. 9001, 9002, 9003, MSNM V-3661; *Pachyrhachis problematicus* HUJ-PAL 3659, HUJ-PAL 3775; *Haasiophis terrasanctus* HUJ-PAL 659; *Yurlunggur* sp. QM 45391; Scolecophidia –

Anomalepis aspinosus MCZ 14785 (cleared and stained); *Anomalepis flavapices* AMNH R-6966 (micro-CT-scanned specimen); *Leptotyphlops dulcis* AMNH R-160152; *Leptotyphlops humilis* AMNH R-73716, USNM 222795; *Leptotyphlops scutifrons* MCZ 54515 (cleared and stained), MCZ 68781 (cleared and stained); *Rhamphotyphlops braminus* USNM 509423; *Rhamphotyphlops subocularis* MCZ 65993, MCZ 65997, MCZ 72084; *Rhinotyphlops schlegeli* MCZ 29174 (cleared and stained), MCZ 70064 (cleared and stained), MCZ 38551; *Typhlophis squamosus* AMNH R-25051 (cleared and stained); *Typhlops angolensis* AMNH R-11633; *Typhlops diardi* NHML 1930-5-8-3; *Typhlops lineolatus* MCZ 48063; *Typhlops punctatus* MCZ 7293, MCZ 2249, NHML 1911-6-9-2, NHML 1975-567, USNM 320704; *Typhlops reticulatus* AMNH R-3001; basal Alethinophidia – *Anilius scytale* MCZ 19537, MCZ 2984, MCZ 17645, NHML 58-8-23-48; *Boa constrictor* ZFMK 21661, ZFMK 54844; *Calabaria reinhardtii* ZFMK 89190, AMNH R-10092, NHML 1911-10-28-17, UAMZ R937 (dissected); *Charina bottae* FMNH 1218, FMNH 22348, FMNH 31300; *Corallus caninus* AMNH R-57788, AMNH R-63587, AMNH R-73347, AMNH R-155263; *Cylindrophis maculatus* NHML 1930-5-8-50; *Cylindrophis ruffus* AMNH R-85647, NHML 1930-5-8-47, USNM 297456; *Eryx colubrinus* ZFMK 50246; *E. conicus* NHML 1930-5-8-14; *E. jaculus* FMNH 19624; *E. johni* NHML 1930-5-8-34; *Eunectes murinus* AMNH R-54158, AMNH R-29349, AMNH R-29350, AMNH R-57474; *Liasis albertisi* ZFMK 5165, ZFMK 70427; *Loxocemus bicolor* AMNH R-110151, AMNH R-44902, AMNH R-19393, NHML 82-8-17-16; *Messelophis variatus* SMF ME-1828; *Messelophis ermannorum* SMF ME-759; *Morelia spilota*

AMNH R-59880, AMNH R-79043, FMNH 22234, FMNH 22380, ZFMK 84282; *Palaeopython fisheri* SMF ME-1002; *Python breitensteini* UAMZ R938 (dissected); *Python molurus* NHML 1972-21-78, ZFMK 5161, ZFMK 83431; *Python reticulatus* FMNH 15678, FMNH 51631, NHML 1972-2169, ZFMK 5175, ZFMK 70207; *Rhinophis planiceps* NHML 1930-5-8-69; *Rhinophis sanguineus* NHML 1930-5-8-62; *Sanzinia madagascariensis*, ZFMK 61722, ZFMK 70428; *Tropidophis canus* AMNH R-45839, AMNH R-73066; *Tropidophis pardalis* FMNH 233; *Ungaliophis panamensis* AMNH R-58845, AMNH R-62639, MCZ 56051; *Uropeltis ocellatus* MCZ 3873; *U. pulneyensis* MCZ 3870; *U. rubrolineatus* MCZ 47101; *Xenopeltis unicolor* AMNH R-29969, AMNH R-71531, NHML 1947-1-1-10, NHML 1947-1-1-12, USNM 287277; basal Caenophidia – *Acrochordus javanicus* AMNH R-46251, AMNH R-140814, AMNH R-155254; *Pareas carinatus* NHML 1964-1092, NHML 1964-1094, NHML 1964-1098; *Xenodermus javanicus* FMNH 67427; Lamprophiidae – *Atractaspis aterrima* NHML 95-5-3-58, AMNH R-12352 (micro-CT-scanned specimen); *Atractaspis bibroni* AMNH R-82071; *Atractaspis corpulenta* MCZ 4826; *Atractaspis irregularis* FMNH 142994, MCZ 53534, AMNH R-12355; *Atractaspis microlepidota* FMNH 58397; *Homoroselaps lacteus* FMNH 187420, FMNH 187421, FMNH 204893, FMNH 206416; *Malpolon monspessulanus* ZFMK 5197; *Oxyrhabdium modestum* FMNH 96532; Viperidae – *Agkistrodon piscivorus* ZFMK 21724, AMNH R-81544, AMNH R-57801; *Azemiops feae* FMNH 218628; *Causus rhombeatus* FMNH 2268, FMNH 51692, FMNH 51693, FMNH 164744; *Bitis gabonica* ZFMK 21718, AMNH R-64518, AMNH R-57792, AMNH R-

137177; *Cerastes cerastes* ZFMK 53537, ZFMK 5181; *Vipera russelli* AMNH R-75739, AMNH R-74818, ZFMK 5187; Elapidae – *Bungarus fasciatus* AMNH R-56198, AMNH R-76574; *Laticauda colubrina* FMNH 236242, FMNH 234147, FMNH 234149, FMNH 236242, FMNH 236243; *Micrurus fulvius* FMNH 34282, FMNH 229600; *M. nigrocintus* FMNH 210092; *Naja naja* AMNH R-57807, AMNH R-74833, ZFMK 21704, ZFMK 21705; *Pelamis platurus* FMNH 171628, FMNH 171632, FMNH 216510, MCZ 7084, MCZ 131501; Homalopsidae – *Cerberus rhynchops* NHML 58-9-21-3, NHML 1964-10-20; *Homalopsis buccata* NHML 111-18-1-e, NHML 1930-5-8-630, NHML 1930-5-8-631, NHML 1964-11-25; Colubridae – *Coluber caspius* ZFMK 5221; *Coluber viridiflavus* AMNH R-67896; *Dasypeltis scabra* MCZ 30208, MCZ 54894; *Heterodon platyrhinos* AMNH R-63590, AMNH R-69647, AMNH R-155313; *Lampropeltis getulus* AMNH R-70097, AMNH R-75539, AMNH R-128202, ZFMK 54259, ZFMK 5205; *Natrix natrix* ZFMK 42502; *Pseudoxenodon macrops* NHML 1930-5-8-271, NHML 1930-5-8-273, NHML 1930-5-8-274; *Thamnophis sirtalis* AMNH R-74849, AMNH R-148084; *Thamnophis validus* AMNH R-62287.

Data on the cranial osteology of Scolecophidia were also obtained from the works of List (1966), Cundall and Irish (2008), and Rieppel et al. (2009). Data for the rare snakes *Anomochilus leonardi* and *Casarea dussumieri* were obtained from the works of Rieppel and Maisano (2007) and Maisano and Rieppel (2007), respectively. The works of Rieppel and Zaher (2002) and Olori and Bell (2012) provided useful information on the anatomy of uropeltid snakes.

A useful source of information was also the series of micro-CT-derived animations available on www.digimorph.org for both lizards and snakes.

RESULTS

Anatomy of the CCF

We recognize four principal anatomical organizations (Type 1-4) of the crest system leading to the CCF of higher snakes (Figs. 7-2 to 7-6). It is possible to consider these four types as an analog of the evolution of the CCF from a condition such as that in most lizards where the CCF is absent, to a fully developed condition as exemplified by colubroid snakes.

We strongly note however, that these types of organization reflect a simplified categorization of the great variability observed in the anatomy of the juxtastapedial region of squamates, and that the four forms we highlight here, are not a transformational series that can be considered a priori as an ordered suite of character states constraining evolutionary novelty through snake phylogeny. Rather, we treat these four conditions of form as typological variants displayed by snake and non-snake lizards, where more variants remain possible and likely occurred, particularly in fossil forms, and that only the recovery of synapomorphies via the Test of Congruence (Patterson, 1982; DePinna, 1991), can provide some sense of the evolution of the CCF from the condition observed in non-ophidian squamates to the condition typical of higher snakes.

Type 1 – CCF is Absent

At this level of anatomical organization, the crista tuberalis, crista interfenestralis and the crista prootica are present, but do not form a continuous rim around the space defined by the fenestra ovalis and the fenestra rotunda (juxtastapedial space), this anatomical organization corresponds to the absence of a CCF (Fig. 7-6).

The absence of a CCF can result from three distinct modes of anatomical organization: (Type 1-1) because the basioccipital tubera (or the adjacent ossified epiphyses) prevent contact between the crista tuberalis and the ventral portion of the crista interfenestralis. This stage is exemplified by lizards like *Varanus exanthematicus* (Fig. 7-2A), the fossil snake *Dinilysia patagonica* (Fig. 7-2B)*,* and most likely the fossil snake *Najash rionegrina* as well, though the crista tuberalis and part of the basioccipital are broken away in the only specimen referred to this taxon; (Type 1-2) the otooccipital forms the ventral border of the fenestra rotunda and contacts the prootic anteriorly, but the crista tuberalis, which is subvertical in these forms, is limited to an area between the paroccipital process and the basioccipital tuber, does not reach the crista interfenestralis, and therefore does not enclose the fenestrae ovalis and rotunda within a common recess (e.g., *Iguana*, *Dracaena*); (Type 1-3) the crista tuberalis extends anteriorly to make contact with the ventral margin of the crista interfenestralis, excluding the basioccipital from the ventral margin of the juxtastapedial space, but there is no juxtastapedial recess because of the lack of an anterior margin formed by the crista prootica, and also because the crista tuberalis projects laterally rather than dorsally, leaving the fenestra rotunda exposed in lateral view (e.g., *Varanus salvator*, and *Anomalepis flavapices*).

Type 2 – Partial CCF

In the second condition of anatomical organization, the basioccipital tubera are excluded from the lateral margin of the juxtastapedial space and the crista tuberalis contacts the prootic anteroventrally. Here the prootic and otooccipital form a continuous crest of bone that borders a juxtastapedial recess, partially hiding the lateral aperture of the recessus scalae tympani in lateral view. This stage is exemplified by snakes like *Cylindrophis* and *Anilius* (Fig. 7-3A), where an incipient CCF is recognized but weakly developed, i.e., the juxtastapedial recess is not completely enclosed by the crista tuberalis posteriorly, and a small notch persists between the crista tuberalis and the prootic. In most uropeltids the sutures between basioccipital, otooccipital, and prootic are not visible because of the extensive fusion of these bones; however, the sutures are visible ventral to the juxstastapedial recess in the genus *Melanophidium*, which suggests uropeltids belong to this second morphological category.

Type 3 – CCF of Basal Macrostomatans and Some Colubroids

The third condition of anatomical organization of the CCF can be observed in basal macrostomatan snakes like *Python* (Fig. 7-3B) and in some primitive colubroids (e.g., *Azemiops* and *Causus*). In these taxa the ventral portion of the crista interfenestralis contributes to the formation of the ventral margin of the CCF (i.e., the crista interfenestralis fills the notch between crista tuberalis and crista prootica), and the cristae prootica and tuberalis provide a more conspicuous contribution to the enclosure of the juxtastapedial recess.

Type 4 – CCF of Scolecophidia and Most Colubroids

The fourth and final major category of anatomical organization of the CCF is observed in the aberrant Scolecophidia (except *Anomalepis*) and in most colubroids (e.g., *Atractaspis, Bungarus*, *Bitis*, *Lampropeltis*, *Naja*, *Pareas*, *Pelamis*, *Heterodon*, *Vipera*) (Rieppel, 1979b) (Fig. 7-4A, B). In this stage the crista tuberalis is extremely expanded anterodorsally and has completely incorporated the crista interfenestralis, which is no longer visible in lateral view. At this stage the stapedial footplate is completely or almost completely concealed by the CCF and only the stapedial shaft emerges from the juxtastapedial recess. Some specialized colubroids may show further modification of this last pattern, for example in *Naja* the otooccipital sends both a dorsal and a ventral bony flange, the latter being the equivalent of the crista tuberalis, to divide the juxtastapedial recess into an anterior and a posterior portion, where the stapedial shaft emerges from the anterior opening.

DISCUSSION

An extensive review of the anatomy of the juxstastapedial region of squamates resulted in the recognition of a high degree of variation in the topological relationships of the elements that constitute this region of the skull. We identified four main categories, or types, of anatomical organization, three of which describe conditions that are typically lumped together under the morphological concept of “crista circumfenestralis” (e.g., Baird, 1960; Rieppel and Zaher, 2001; Zaher and Scanferla, 2012; Scanferla and Bhullar, 2014).

Type 2, 3, and 4

It is important to note that for categories 2, 3 and 4, where a CCF is considered present, that all three are characterized by the exclusion of the basioccipital from the ventrolateral margin of the juxtastapedial recess, which is bordered only by prootic (anteriorly) and otooccipital (posteriorly). Therefore, the contact between otooccipital and prootic along the ventral margin of the juxtastapedial space is clearly a prerequisite for the development of the CCF, which otherwise would not be a continuous crest, and by extension would not exist. The absence of such a contact in *Dinilysia* (Fig. 7-2B) clearly indicates the absence of a CCF in this ancient snake, while the incomplete preservation of the skull referred to *Najash* by Apesteguia and Zaher (2006) prevents any conclusive statement about whether or not a CCF was present in this taxon (contra Apesteguia and Zaher, 2006).

It is also important to point out that the CCF in snakes surrounds and supports the re-entrant fluid circuit in the middle ear of these animals, and as was noted by Wever (1973, 1978) and Rieppel (1988b), some lizards like *Anniella*, *Phrynosoma*, *Dibamus* and acontine skinks have a re-entrant fluid circuit despite the absence of a CCF. *Dibamus* and *Phrynosoma* retain the lacertilian condition of having the otooccipital not contacting the prootic along the ventral margin of the juxtastapedial space. *Anniella* is more problematic as the basioccipital is usually fused with the otooccipital. A suture line between the basioccipital and otooccipital could not be resolved in any of the examined specimens of *Anniella* (MCZ 21416, MCZ 14233, MCZ 21452); Baur (1894) mentioned a specimen where the sutures between basioccipital and otooccipitals (his “exoccipitals”) were visible, but he did not provide any illustrations nor specimen numbers. With regard to acontine skinks, and in particular the genus *Acontias*, this lizard not only has a re-entrant fluid circuit, as mentioned by Rieppel (1988b), but also a structure that is morphologically similar to the CCF of snakes, although not as well-developed. As a matter of fact the fenestra ovalis and the fenestra rotunda of *Acontias* are somewhat recessed within a space completely surrounded by a bony crest, and this crest is formed from exclusive contributions of the otooccipital and prootic. As in living snakes possessing a typical CCF (e.g., *Cylindrophis*), the basioccipital of *Acontias* is excluded from the margin of the juxtastapedial recess and the otooccipital contacts the prootic anteroventrally. However, as acontine skinks are not considered to be the sistergroup of alethinophidian snakes, we can only conclude that the anatomy of *Acontias* is convergent on that of higher snakes. Additional support for this conclusion is also provided by the unique path of the re-entrant fluid circuit in *Acontias*, which is very different from that of modern snakes (Rieppel, 1988b).

As shown by *Anniella*, *Phrynosoma* and *Dibamus*, even if the presence of a CCF implies the presence of a re-entrant fluid circuit, the reverse is not necessarily true, and perhaps the evolution of a re-entrant fluid circuit preceded the appearance of a CCF, which simply provides structural support for the fibrous membrane surrounding the juxtastapedial sinus; a notable consequence of this observation is that *Dinilysia* (Fig. 7-2B), despite not having a CCF, may still have had a re-entrant fluid circuit.

***Dinilysia patagonica* – CCF Absent**

Different authors have reached conflicting conclusions after observing the material available for the fossil snake *Dinilysia patagonica*. Estes et al. (1970), based on observations of only a single skull, the holotype MLP 26-410, concluded that *Dinilysia* had no CCF, because the prootic and the otooccipitals do not surround the stapedial footplate with a pericapsular chamber, and thus leave the whole footplate exposed in lateral view as in lizards. The same conclusion was reached by Caldwell and Albino (2002), and Caldwell and Calvo (2008), after examining the skulls of several specimens of *Dinilysia*.

Rage (1984), in his review of fossil snakes and snake evolution, reported the presence of a CCF in *Dinilysia*, but he did not provide any further details to support this statement. More recently, Zaher and Scanferla (2012) argued for the presence of a “weakly defined” crista prootica overhanging the stapedial footplate, a crista tuberalis that fails to enclose the juxtastapedial space, and a crista interfenestralis, which would participate in the formation of the ventral rim of a CCF. However, as noted by Zaher and Scanferla (2012), uniquely among snakes, the basioccipital forms most of the posteroventral margin of the lateral aperture of the recessus scalae tympani (“fenestra rotunda” of Estes et al., 1970), or put in other terms, the basioccipital forms most of the ventral margin of the juxtastapedial space. As noted above, in our Type 1 of anatomical organization (Fig. 7-2), this is a feature typical of lizards, i.e., of squamates that lack a CCF. We consider such a condition to be the pivot point upon which to reiterate that Estes et al. (1970), Caldwell and Albino (2002) and Caldwell and Calvo (2008) were correct in their interpretation: *Dinilysia patagonica* does not possess a CCF. To argue that *Dinilysia* has a CCF simply because it possesses a crista prootica, a crista tuberalis and a crista interfenestralis would lead to the paradoxical conclusion that all lizards possess a CCF, as they too possess the necessary cristae. As implied by the name itself, a “CCF” is a continuous crest that surrounds either partially or completely two fenestrae, the fenestra ovalis and the fenestra rotunda (i.e., lateral aperture of the recessus scalae tympani), and is formed, as discussed above, by exclusive contributions of the prootic and otooccipital. The fact that the basioccipital intervenes between the crista tuberalis and the crista interfenestralis of *Dinilysia* is clear evidence for the absence of a CCF in this fossil snake, because the CCF should, by definition, be a continuous crest of bone formed by the junction of the otooccipital and prootic.

However, even though the CCF is absent in *Dinilysia patagonica*, this does not mean that it also lacked a re-entrant fluid circuit. Unfortunately, this feature cannot be ascertained in the absence of a CCF, though the fluid circuit system is most certainly present in Type 2 and Type 3 categories of anatomical organization. The ongoing question in snake evolution is the presence of the fluid circuit, and not the presence of the derived colubroid condition in all snakes. We should not expect *Dinilysia* to possess a CCF simply because the latter is generally viewed as a necessary synapomorphy of the clade Ophidia. *Dinilysia* may have belonged to an early evolutionary grade within Ophidia where the CCF was not yet developed. Character state assignments in phylogenetic analyses should reflect robust hypotheses of primary homology, and not be artificially constrained to provide support to preconceived ideas of phylogenetic relationships (i.e., *Dinilysia* is a snake and therefore it must possess a CCF regardless of the absence of the structures necessary to identify a CCF).

***Xenopeltis*, *Acrochordus*, and *Anomalepis* – CCF Absent**

The derived alethinophidian snakes *Xenopeltis* and *Acrochordus* (Fig. 7-5) possess differing anatomical conditions of the otooccipital region where the juxtastapedial space is not surrounded by any projecting crests. In *Xenopeltis* the cristae tuberalis, prootica and interfenestralis are strongly reduced, leading to an absence condition for the CCF. In contrast, *Acrochordus* shows a unique condition of absence for the CCF, where the fissure metotica (which during embryonic development is typically divided by a crest of bone to form the jugular foramen and the lateral aperture of the recessus scalae tympani; Rieppel and Zaher, 2001) is undivided, and therefore a crista tuberalis and a crista interfenestralis cannot be recognized (McDowell, 1979).

In the most recent phylogenetic analyses of snakes (e.g., Gauthier et al., 2012, Wiens et al, 2012), both *Xenopeltis* and *Acrochordus* are nested within derived Alethinophidia. It is therefore reasonable to assume that the CCF was present in the most recent common ancestor of these taxa and other alethinophidians, and was independently lost in both *Xenopeltis* and *Acrochordus*. These snakes show an organization of the ventral margin of the juxtastapedial space typical of other snakes that have a CCF, i.e., where there is no contribution from the basioccipital and the entire margin of the juxtastapedial space is formed by the prootic and the otooccipital. Thus the only difference with snakes possessing a CCF, is that there is no projection of the margins of the prootic and the otooccipital to cover, even partially, the juxtastapedial space. This topology differs from that of a snake such as *Dinilysia* (Fig. 7-2B) (i.e., basioccipital present on the margin) and so further supports the hypothesis that the CCF of *Xenopeltis* and *Acrochordus* is secondarily reduced or lost.

An alternative scenario could be proposed in which *Xenopeltis* and *Acrochordus* represent the earliest stages of development of the juxtastapedial recess, where the cristae are undeveloped (i.e., an evolutionary grade in between that of *Dinilysia* and that of other more derived snakes that possess a typical CCF). However, considering that even lizards have well-developed cristae tuberalis, interfenestralis and prootica (even if separated), it is much more likely that *Acrochordus* and *Xenopeltis* represent a derived (autopomorphic) condition. Moreover, as already discussed, *Xenopeltis* and *Acrochordus* cannot represent a plesiomorphic condition for the development of the CCF because they are both placed in derived positions within the evolutionary radiation of snakes (Lee and Scanlon, 2002; Douglas and Gower, 2010; Gauthier et al., 2012; Wiens et al, 2012).

With regard to *Anomalepis*, its juxstastapedial space is recessed behind two crests that are best developed dorsally (formed by the prootic) and ventrally (formed by the otooccipital). However, the crista tuberalis does not extend dorsally to hide the lateral aperture of the recessus scalae tympani, which is still visible in lateral view along with most of the base of the stapes, and the crista interfenstralis does not contribute in any way to the partial enclosure of the juxtastapedial space. If we consider that all other scolecophidians have a well-developed CCF, a secondary reduction of the ossification of the otooccipital and prootic around the juxtastapedial space may have resulted in the condition observed in this taxon (a lack of ossification is also observed in Leptotyphlopidae and Typhlopidae, but it only affects the medial wall of the otic capsule).

As discussed above for *Acrochordus* and *Xenopeltis*, the fact that the basiocciptal is excluded from the ventral margin of the juxtastapedial space in *Anomalepis* may be indicative of its derived condition. The alternative would be that *Anomalepis* actually represents a primitive condition within Serpentes, and one of the first stages in the evolution of a CCF. However, this scenario would imply that *Anomalepis* is both the most primitive of all living snakes, and the most primitive scolecopidian; this scenario also implies that the CCF of the Leptotyphlopidae and Typhlopidae is independently derived from that of all other snakes. We consider these scenarios to be highly unlikely as several recent molecular studies have placed the Anomalepididae in a more derived position relative to Typhlopidae and Leptotyphlopidae (i.e., retrieved a paraphyletic Scolecophidia; e.g., Heise et al. 1995; Wiens et al, 2008, 2010, 2012).

Important implications of the hypothesis that sees *Anomalepis* as representative of the ancestral condition of the CCF would also be (1) that Anomalepididae must lie outside of the clade formed by all other living snakes (inclusive of Typhlopidae and Leptotyphlopidae, contrary to what has been suggested by all most recent molecular analysis) and (2) that the CCF evolved convergently at least twice, once within anomalepidids (i.e., *Liotyphlops* has a well-developed CCF) and a second time in the most recent common ancestor of Typlopidae, Leptotyphlopidae and all other living snakes. On the other hand, if recent molecular studies are accurate, and Typhlopidae and Leptotyphlopidae form a clade at the base of all other snakes, then the condition observed in *Anomalepis* is most parsimoniously interpreted as autapomorphic rather than primitive.

The CCF as a Character

The CCF is a system of multiple crests originating from different chondrocranial elements, and depends on the topological relationships of these elements and their crests in order to be recognized as present. The considerable degree of anatomical variation and the topological relations required to create a full CCF in snakes implies that the CCF does not exist as a single character. In other words, the CCF cannot be easily distilled into simplistic ‘0’ and ‘1’ states denoting absence and presence. The variation within snakes remains impressive, i.e., from *Dinilysia* to *Bungarus* or *Typhlops*, with every variation on the theme represented in between, including secondary loss of the crest in higher snakes such as *Xenopeltis* and *Acrochordus*.

It is important to reiterate here that characters are statements of primary homology (sensu DePinna, 1991), and since such statements may transcend form and function, then the relative size of an anatomical feature (in our case the size of the cristae prootica, interfenestralis and tuberalis) is useless in this respect, because size is independent from the topological criteria that must be at the base of any conjecture of homology (Rieppel and Kearney, 2002). For this very reason the degree to which the CCF (or any of its component crests) covers the stapedial footplate in lateral view cannot be used alone to construct a valid homology statement, and therefore a valid character for phylogenetic analyses. This point is clearly exemplified by *Xenopeltis* and *Acrochordus*, which lack distinct bony crests overhanging the stapedial footplate despite their retention of the topological relationships between prootic and otooccipital that are typical of all other living snakes.

In answering the questions posed in the introduction to this study: (1) a CCF can consist of only the crista tuberalis and crista prootica (the crista interfenestralis intervenes only in derived forms), as long as they meet each other and form a continuous crest around some part of the juxtastapedial space (e.g., *Anilius*; Rieppel and Zaher, 2001); (2) as regards the development of the crests, this is obviously a subjective matter, because different researchers may consider the same crest (e.g., the crista prootica of *Dinilysia*) as poorly or well developed (e.g., Estes et al., 1970; Rage, 1984; Caldwell and Albino, 2002; Caldwell and Calvo, 2008; Zaher and Scanferla, 2012; Scanferla and Bhullar, 2014). Moreover, as pointed out above and by Rieppel and Kearney (2002), the size of a crest makes for a poor conjecture of primary homology, because size depends on function and homologues are ideally independent from the latter. The size of the crests surrounding the juxtastapedial recess of snakes can be deceiving, and this was illustrated with the extreme examples of *Xenopeltis* and *Acrochordus* where the crests are absent, but the derived condition of these taxa is supported by the exclusion of the basioccipital from the ventral margin of the juxtastapedial recess; (3) last but not least, in order to consider the CCF present in a given taxon a prerequisite is that the otooccipital (crista tuberalis with possible involvement of the crista interfenestralis) must form a continuous ventral margin to the juxtastapedial space, otherwise the “CCF” would fall short of its own definition, and we would have two or three isolated crests (i.e., the condition typical of lizards) rather than a single distinct crista.

CONCLUSIONS

In conclusion, all conjectures of primary homology (sensu DePinna, 1991) must pass both the test of similarity and the test of topology in order to be valid. As noted by Rieppel and Kearney (2002), a character that simply codes for presence of a “bony crest”, especially when this crest has several constituent parts, refers only to similarity of shape and does not take into consideration topological correspondence. The conflicting interpretations regarding the presence or absence of a CCF in snakes stem from the fact that a rigorous test of topology was not always applied, and the test of similarity alone has lead some authors to the erroneous conclusion that the fossil snake *Dinilysia patagonica* possesses a CCF (e.g., Zaher and Scanferla, 2012; Scanferla and Bhullar, 2014). To score for the presence or absence of a CCF simply based on the size of the crests surrounding the juxtastapedial space of a given taxon, with no attention to which bones are contributing to those crests, would be analogous to scoring for the presence or absence of a “long snout” regardless of which bones are contributing to the snout itself. Such an approach would clearly be erroneous, and in a phylogenetic analysis would cause the artificial grouping of distantly related taxa that convergently evolved a superficially similar feature.

An interesting consequence to our findings is that the CCF may have evolved convergently in different groups of snakes, and that the CCF, and the re-entrant fluid circuit it supports, is not a synapomorphy of the Ophidia. This alternative scenario is supported by the fact that the scolecophidian snake *Anomalepis* as well as the undoubtedly primitive snake *Dinilyisa* lack a CCF.

Further support for this alternative includes the complete absence of the CCF in some derived groups of snakes (i.e., *Acrochordus*, *Xenopeltis*), and that ad hoc arguments for “loss”, such as paedomorphosis for *Acrochordus* (Rieppel and Zaher, 2001), have been invoked to explain their absence. We also note, as further thought-provoking support, that the categories of anatomical conditions outlined in this study for the CCF in snakes are extremely variable, and do not describe a single condition of morphology. The possibility that the CCF may have evolved convergently is also suggested by its presence in the scincid lizard *Acontias*, whose stapes is recessed medial to a bony crest that is morphologically equivalent to the ophidian CCF. It is highly unlikely that the CCF of *Acontias* can be homologous to that of snakes (primitive snakes like *Dinilysia* lack a CCF, and acontine skinks have never been retrieved in a sister group relationship to snakes), and this implies that the CCF likely evolved convergently at least twice within Squamata, once within acontine skinks and once within Serpentes (at least twice within Serpentes if the CCF evolved independently within Scolecophidia and Alethinophidia).

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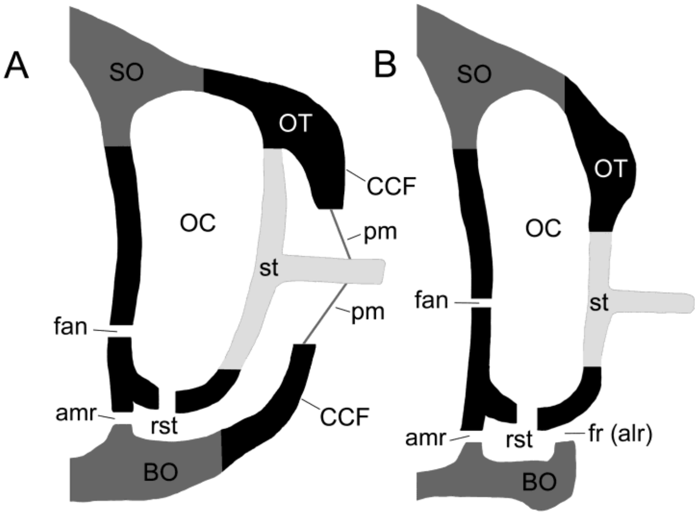
FIGURES

FIGURE 7-1. Comparison between the otic region of a lizard and a snake. **A**, schematic cross section of the otic region of a snake (medial is to the left); **B**, schematic cross section of the otic region of a lizard (medial is to the left). **Abbreviations**: **alr**, apertura lateralis recessus scalae tympani; **BO**, basioccipital; **amr**, aperture medialis recessus scalae tympani; **CCF**, crista circumfenestralis; **fan**, foramen for auditory nerve; **fr**, fenestra rotunda; **OC**, otic capsule; **OT**, otooccipital; **pm**, pericapsular membrane; **rst**, recessus scalae tympani; **SO**, supraoccipital; **st**, stapes.


A
SO
OT
CCF
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OT
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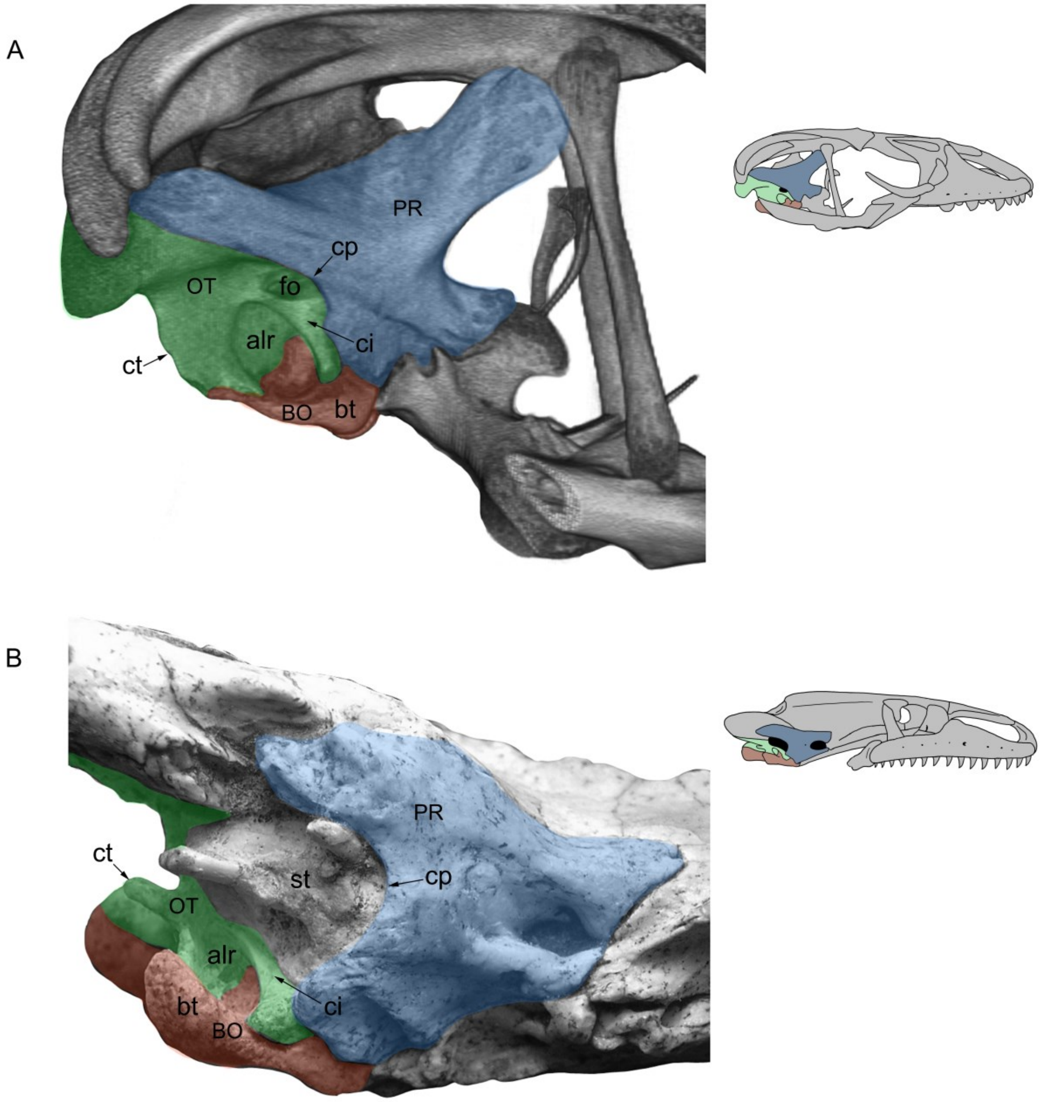
st
amr
rst
fr (alr)
BO

FIGURE 7-2. Lateral views of the otic regions (Type 1 variants) of a lizard and a fossil snake. **A**, *Varanus exanthematicus* (TMP 1990.7.33) (skull diagram has quadrate and stapes omitted to better illustrate the otic region); **B**, *Dinilysia patagonica* (MACN 1014), note that, because of a matrix infilling inside the lateral aperture of the recessus scalae tympani, the path of the suture between otooccipital and basioccipital inside this area is hypothetical (skull diagram has quadrate, stapes and pterygoid omitted to better illustrate the otic region). Images are not to scale. **Abbreviations**: **alr**, apertura lateralis recessus scalae tympani; **BO**, basioccipital (highlighted in red); **bt**, basioccipital tuber; **ci**, crista interfenestralis; **cp**, crista prootica; **ct**, crista tuberalis; **fo**, fenestra ovalis; **OT**, otooccipital (highlighted in green); **PR**, prootic (highlighted in blue); **st**, stapes.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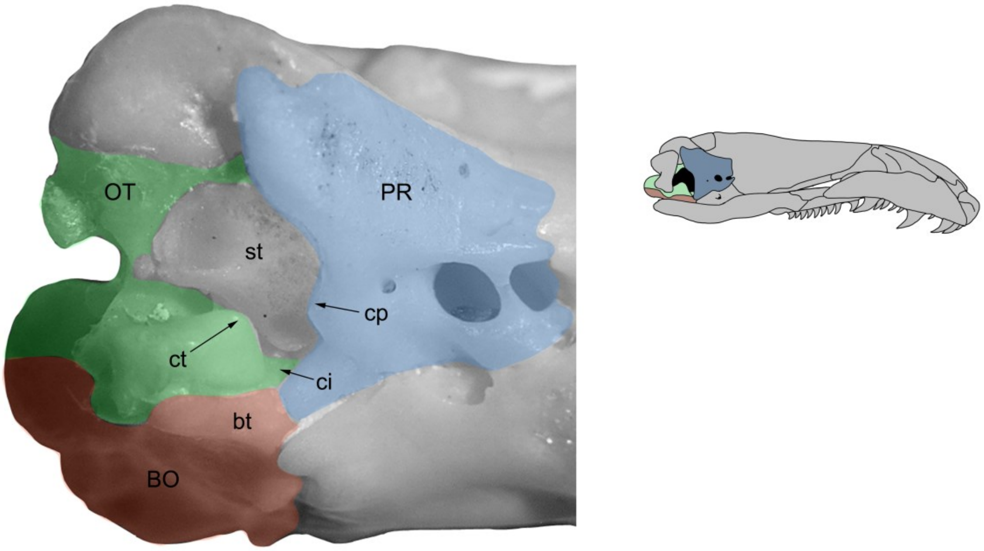
BO

FIGURE 7-3. Lateral views of the otic regions (Type 2 and Type 3 variants) of a basal alethinophidian and a basal macrostomatan snake. **A**, *Anilius scytale* (MCZ 17645) (skull diagram has stapes omitted to better illustrate the otic region); **B**, *Python molurus* (ZFMK 5161) (skull diagram has stapes omitted to better illustrate the otic region). Images are not to scale. **Abbreviations**: **alr**, apertura lateralis recessus scalae tympani; **BO**, basioccipital (highlighted in red); **bt**, basioccipital tuber; **ci**, crista interfenestralis; **cp**, crista prootica; **ct**, crista tuberalis; **OT**, otooccipital (highlighted in green); **PR**, prootic (highlighted in blue); **st**, stapes.

A



B

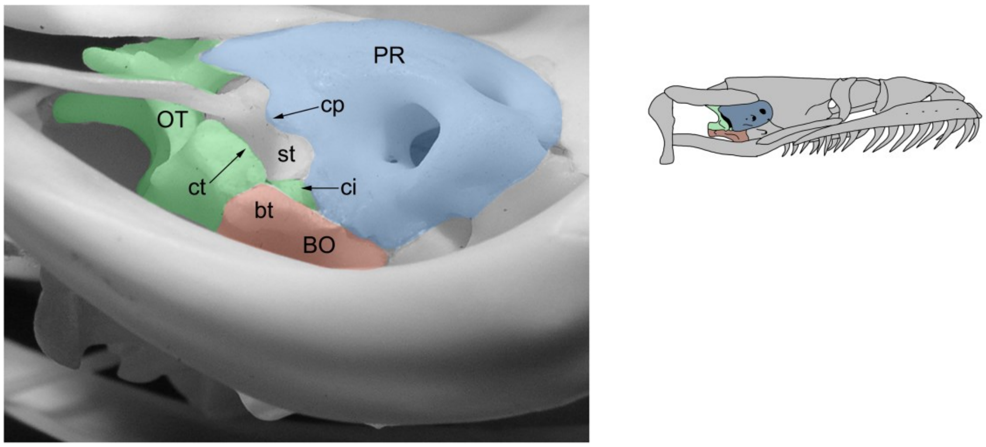
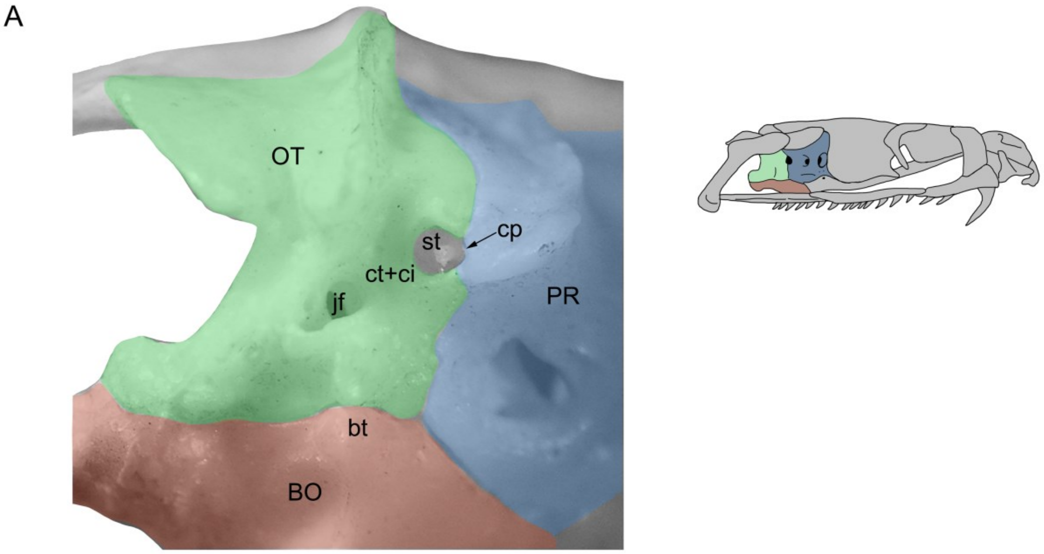


FIGURE 7-4. Lateral views of the otic regions (Type 4 variants) of an elapid and a scolecophidian snake. **A**, *Bungarus fasciatus* (AMNH 56198) (skull diagram has stapes omitted to better illustrate the otic region); **B**, *Rhinotyphlops schlegelii* (MCZ 38551) (skull diagram has quadrate, stapes and pterygoid omitted to better illustrate the otic region). Images are not to scale. **Abbreviations**: **alr**, apertura lateralis recessus scalae tympani; **BO**, basioccipital (highlighted in red); **bt**, basioccipital tuber; **ci**, crista interfenestralis; **cp**, crista prootica; **ct**, crista tuberalis; **jf**, jugular foramen; **OT**, otooccipital (highlighted in green); **PR**, prootic (highlighted in blue); **st**, stapes.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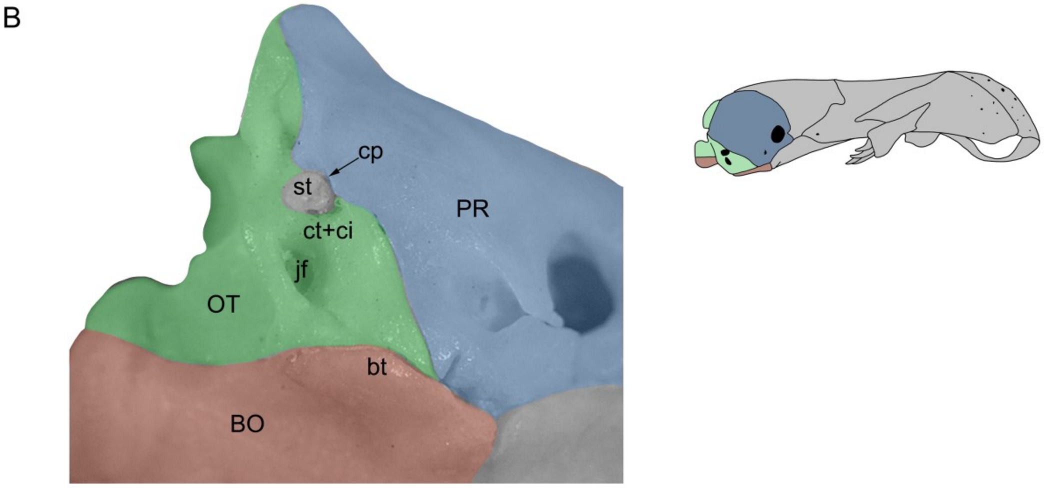
B
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PR
jf
OT
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BO

FIGURE 7-5. Lateral views of the otic regions of *Xenopeltis* and *Acrochordus*. **A**, *Xenopeltis unicolor* (USNM 122782) (skull diagram has quadrate, stapes and pterygoid omitted to better illustrate the otic region); **B**, *Acrochordus javanicus* (AMNH R-89839) (skull diagram has quadrate, stapes, pterygoid and ectopterygoid omitted to better illustrate the otic region). Images are not to scale. **Abbreviations**: **alr**, apertura lateralis recessus scalae tympani; **BO**, basioccipital (highlighted in red); **bt**, basioccipital tuber; **ci**, crista interfenestralis; **cp**, crista prootica; **ct**, crista tuberalis; **fm**, fissura metotica; **fo**, fenestra ovalis; **jf**, jugular foramen; **OT**, otooccipital (highlighted in green); **PR**, prootic (highlighted in blue); **st**, stapes.

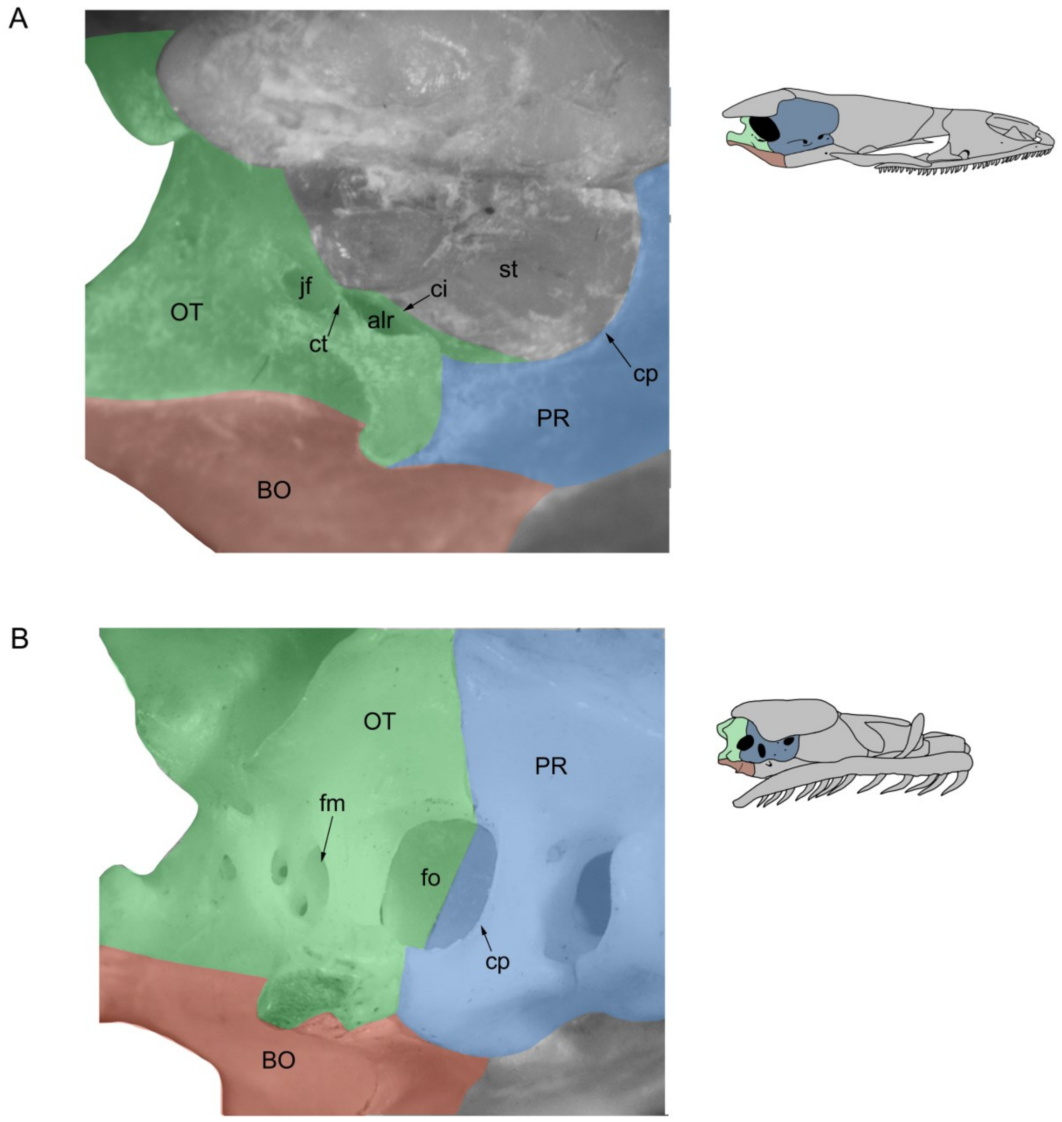
A
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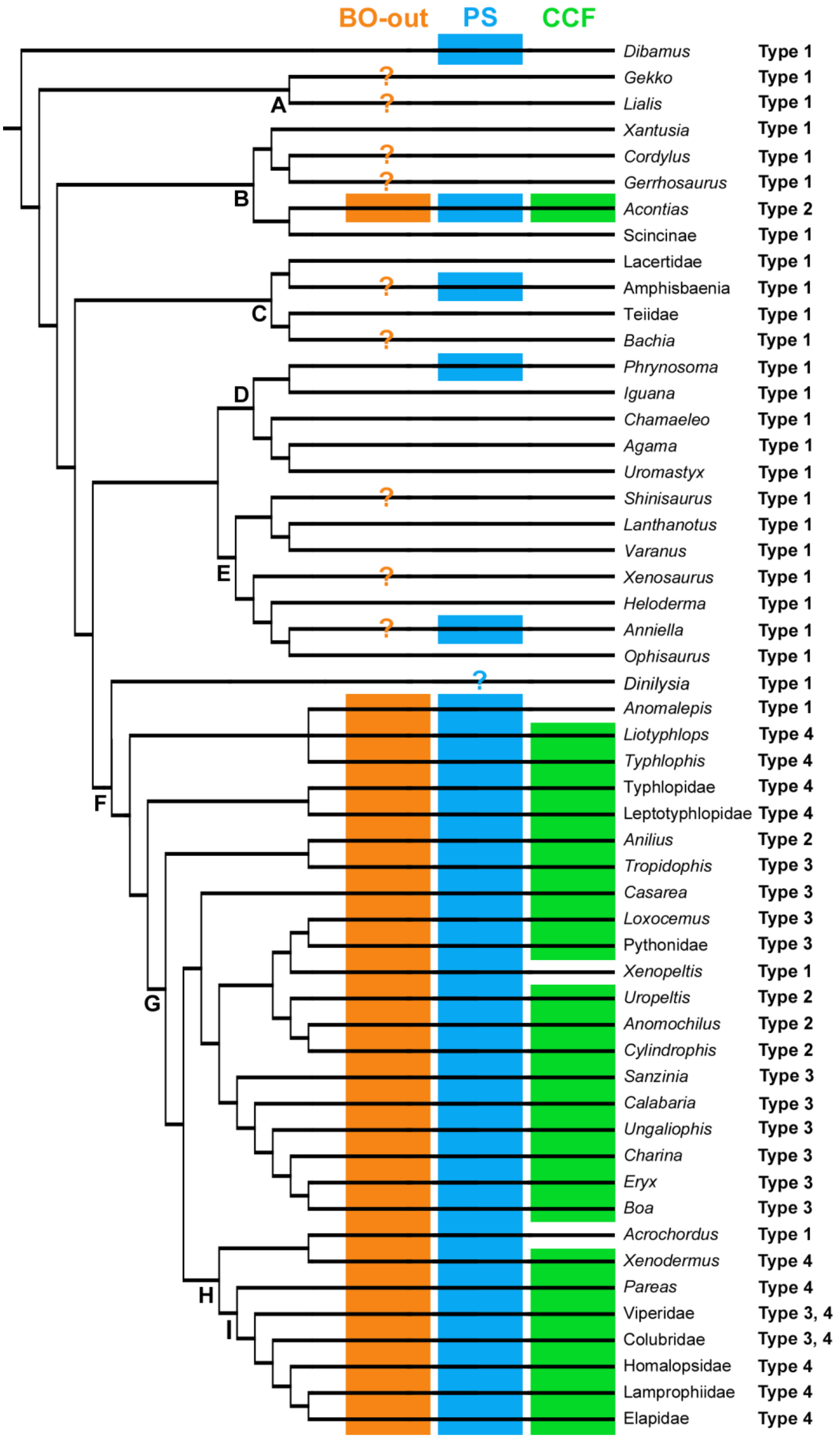
FIGURE 7-6. Distribution of the “crista circumfenestralis” (CCF), periotic sac (PS), and exclusion of the basioccipital from the juxstastapedial space (BO-out), within a phylogeny of Squamata (phylogenetic relationships from Pyron et al. 2013; position of *Dinilysia* according to Gauthier et al., 2012). Note correlation between CCF and BO-out. Taxa where the basioccipital is fused to the otooccipital are marked with a ‘?’ under BO-out. A: Gekkota; B, Scincoidea; C, Lacertoidea; D, Iguania; E, Anguimorpha; F, Ophidia; G, Alethinophidia; H, Caenophidia; I, Colubroidea.


BO-out
PS
CCF
A
B
C
D
E
F
G
H
I
Dibamus Type 1
Gekko Type 1
Lialis Type 1
Xantusia Type 1
Cordylus Type 1
Gerrhosaurus Type 1
Acontias Type 2
Scincinae Type 1
Lacertidae Type 1
Amphisbaenia Type 1
Teiidae Type 1
Bachia Type 1
Phrynosoma Type 1
Iguana Type 1
Chamaeleo Type 1
Agama Type 1
Uromastyx Type 1
Shinisaurus Type 1
Lanthanotus Type 1
Varanus Type 1
Xenosaurus Type 1
Heloderma Type 1
Anniella Type 1
Ophisaurus Type 1
Dinilysia Type 1
Anomalepis Type 1
Liotyphlops Type 4
Typhlophis Type 4
Typhlopidae Type 4
Leptotyphlopidae Type 4
Anilius Type 2
Tropidophis Type 3
Casarea Type 3
Loxocemus Type 3
Pythonidae Type 3
Xenopeltis Type 1
Uropeltis Type 2
Anomochilus Type 2
Cylindrophis Type 2
Sanzinia Type 3
Calabaria Type 3
Ungaliophis Type 3
Charina Type 3
Eryx Type 3
Boa Type 3
Acrochordus Type 1
Xenodermus Type 4
Pareas Type 4
Viperidae Type 3, 4
Colubridae Type 3, 4
Homalopsidae Type 4
Lamprophiidae Type 4
Elapidae Type 4

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CHAPTER EIGHT

PHYLOGENETIC ANALYSIS OF SNAKES BASED ON MORPHOLOGICAL AND MOLECULAR DATA

INTRODUCTION

Snakes are a very successful group of squamate reptiles, which count well over 3,000 living species (Uetz and Hošek, 2014). Snakes (Order Ophidia) are divided into two major groups: Scolecophidia (small, worm-like blind snakes) and Alethinophidia (medium to large snakes capable of swallowing large prey items) (Green, 1997). All members of the Ophidia are characterized by a combination of features, which include an elongate body, complete loss of forelimbs and pectoral girdle, hind limbs and pelvic girdle that are either vestigial or absent, eye covered by a spectacle, lack of external ear openings, a brain completely enclosed within the braincase, some degree of kinesis of the skull and lower jaw (i.e., intramandibular joint and free mandibular symphisis), supplementary articulations in the vertebrae (zygosphenes and zygantra) (Rieppel, 1988; Lee and Scanlon, 2002; Gauthier et al., 2012). Interestingly, none of these features taken alone is unique to snakes. Several groups of lizards independently evolved axially elongated bodies, limb loss, spectacles, and so on, but none of these groups show all of the ophidian features combined together (Rieppel, 1988; Gauthier et al., 2012).

The convergent nature of the diagnostic characteristics of snakes, has made it particularly arduous to identify their closest relatives within Squamata. Several studies have tried using either morphological (e.g., Estes et al., 1988; Wu et al., 1996; Lee, 1998, 2005a; Evans et al., 2005; Evans and Wang, 2005; Conrad, 2008; Gauthier et al., 2012) or molecular data (e.g., Townsend et al., 2004; Vidal and Hedges, 2004, 2005; Albert et al., 2009; Wiens et al., 2012; Pyron et al., 2013a).

The results have been most varied, and no universal consensus has been reached yet. For example, with regard to the morphological analyses, Estes et al., (1988), Wu et al. (1996), Evans et al. (2005) and Gauthier et al. (2012) found snakes to be closely related to amphisbaenians and dibamids; Lee (1998) found snakes to be the sister group of the Mosasauroidea (an extinct clade of marine lizards); Evans and Wang (2005) found that snakes may be the sister group of Amphisbaenia and both would form a clade that is the sister group of the Mosasauroidea; Lee (2005) found snakes to be closely related to dolichosaurs and mosasauroids.

With regard to the molecular analyses, Townsend et al. (2004) and Albert et al. (2009) found snakes to be in a sister group relationship with Acrodonta; Vidal and Hedges (2004) found snakes to be closely related to Iguania; Vidal and Hedges (2005), Wiens et al. (2012), and Pyron et al. (2013a) found support for a sister group relationship between snakes and a clade inclusive of both Iguania and Anguimorpha.

Very few studies included both morphological and molecular data in their analysis of squamate relationships (Lee, 2005b, 2009; Wiens et al., 2010). Lee (2005b, 2009) showed that inclusion of morphological data, as well as fossil taxa, provides support for the hypothesis that snakes would be the closest relatives of dolichosaurs and mosasauroids, while Wiens et al. (2010) found that snakes are either the sister group of Anguimorpha (parsimony analysis) or of Anguimorpha plus Iguania (Bayesian analysis).

The ingroup relationships of snakes do not fare much better, many taxa are shuffled around the tree in the published studies based on either morphological (e.g., Cundall, et al., 1993; Lee and Scanlon, 2002; Zaher and Scanferla, 2012; Longrich et al., 2012; Palci et al., 2013a, b) or molecular data (e.g., Heise et al., 1995; Slowinski and Lawson, 2002; Vidal and Hedges, 2002; Wilcox et al., 2002; Douglas and Gower, 2010; Pyron et al., 2013b). The most problematic taxa within these studies seem to be represented by the Scolecophidia (either monophyletic or paraphyletic), *Anomochilus*, uropeltids (e.g., *Uropeltis*, *Rhinophis*), *Cylindrophis* and *Tropidophis* (retrieved either as basal or derived alethinophidians), *Loxocemus*, and *Xenopeltis*. Similarly to phylogenetic studies of squamates as a whole, also in the case of ingroup analyses of snakes, morphological and molecular data have been combined very rarely (e.g., Lee et al., 2007).

A limitation of the above-mentioned studies is represented by the fact that molecular and morphological data were rarely combined together. Some notable exceptions are represented by Lee (2005b, 2009) and Wiens et al. (2010) for the phylogeny of Squamata. However, in these cases either the sampling of snake taxa or the sampling of genes was very limited. Lee (2005, 2009) only used 2 nuclear genes, while Wiens et al. (2010) used an extensive number of nuclear genes (22), but most of these genes provided incomplete coverage of the selected taxa; i.e., only four genes (out of 22) in their analysis were sequenced for all 45 taxa, with some genes not covering up to 9 taxa. Moreover, only 6 extant species of snakes were included in Wiens et al.'s (2010) analysis (*Typhlops jamaicensis*, *Leptotyphlops* sp., *Liotyphlops albirostris*, *Anilius scytale*, *Boa constrictor*, and *Xenopeltis unicolor*).

This study will try to address the problem of the phylogenetic position of snakes within Squamata, as well as the ingroup relationships of the Ophidia, with a special focus on resolving which snake taxa are located at the base of the evolutionary radiation. This will be accomplished by combining morphological and molecular data, using extensive taxon sampling (70 taxa), 10 nuclear genes that provide coverage of almost all the selected taxa (only the taxa *Bachia heteropus*, *Anomochilus leonardi* and *Vipera russelli* are excluded from the molecular data set because they had not been sequenced for any of the selected genes) and inclusion of representatives of both extant and fossil squamates.

Moreover, a series of tests will be performed in order to see the effect of taxon sampling on the final tree topology and if the phenomenon of long branch-attraction may be affecting the analysis (the possibility that long-branch attraction may affect analyses based on morphological data is still poorly understood and certainly worth further exploration; Bergsten, 2005). Partitioning of the molecular data set will be used to test the internal consistency of this type of data (i.e., are the partitions providing the same phylogenetic signal?). Finally, a series of non-parametric Templeton's tests (Templeton, 1983) will be performed using a series of constrained tree topologies, this in order to see if the constrained trees may represent valid alternatives to (i.e., show no statistically significant difference from) the result obtained from the parsimony analysis of the morphological and molecular data combined.

MATERIALS AND METHODS

Morphological Data

A total of 70 taxa were selected for the phylogenetic analyses. These taxa include 1 non-squamate lepidosaur (*Sphenodon punctatus*), 29 squamates (5 of which are fossil taxa), and 40 snakes (7 of which are fossil taxa). Although the main focus of the analyses is on the relationships of snakes, a large number of squamate representative was included because of the lack of a consensus about which group of squamates would represent the sister group of snakes, i.e., the best candidate for the outgroup.

Whenever possible only specimens that belong to the same species were used to score for characters; however, the rarity of dry specimens (i.e., skeletons) or the poor quality of the skeletons often required that specimens belonging to other species within the same genus had to be used. Whenever a genus was scored based on more than one species, the respective taxon name in the phylogeny and data matrices was limited to the generic level.

The morphological data consists mostly of characters from the osteology of the taxa under consideration, and in minor part from their soft-anatomy. Most of the 227 morphological characters used in this study are from Estes et al.

(1988) and Gauthier et al. (2012). Some characters were also taken from Gauthier et al. (1988), Lee (1997), Lee and Caldwell (1998), Lee and Scanlon (2002), and Kearney (2003). Most of the characters adopted to sort out the relationships of snakes are from Lee and Scanlon (2002). Some of these characters were partly modified from their original description in order to better define the observed morphological variation. Fifty new characters were added. The morphological characters used in this study are listed in Supplementary Data 8-1.

The scoring of the anatomical characters was mostly based on first-hand observations of dry specimens (i.e., skeletons) (see list below), and in small part on the literature (e.g., details of the soft anatomy; details of vestigial pelvic and pectoral girdles of limbless squamates, which are rarely preserved in skeletal collections; rare taxa). The literary sources adopted for this purpose were (list in alphabetical order): Bellairs, 1949; Bogert, 1968; Böhme, 1989; Colli et al, 1998; Conrad, 2006; Cundall et al., 1993; Cundall and Irish, 2008; Dunn and Tihen, 1944; Essex, 1927; Evans, 1955; Gans, 1975; Greer, 1985; Haas, 1964, 1973; Jerez and Tarazona, 2009; Kearney, 2003; Klein et al., 2005; Kley, 2006; Lee and Scanlon, 2002; Miller, 1944; Pierce and Caldwell, 2004; Rage and Escuillié, 2000; Rieppel and Zaher, 2000; Russell, 1967; Scanlon, 2005; Shea, 1993; Smith and Mackay, 1990; Stephenson, 1962; Stokely, 1947; Tarazona and Ramírez-Pinilla, 2008; Tarazona et al., 2008; Underwood, 1967, 1993; Vitt and Caldwell, 2008; Wallach, 1998; Wever, 1968; Wever, 1974; Zaher and Scanferla, 2012; Zangerl, 1945. Information on the skull anatomy of

Scolecophidia was also obtained from List (1966), Cundall and Irish (2008), and Rieppel et al. (2009). Information on the anatomy of the rare snakes *Anomochilus leonardi* and *Casarea dussumieri* was obtained from Rieppel and Maisano (2007) and Maisano and Rieppel (2007), respectively. Observations on uropeltid snakes were complemented with the work of Olori and Bell (2012). The animations available on DigiMorph.org for both lizards and snakes also provided a useful source of data.

The specimens examined belong to the following institutions: **AMNH**, American Museum of Natural History, New York, NY; **ANSP**, Academy of Natural Sciences of Philadelphia, Philadelphia, PA, USA; **CMNH**, Carnegie Museum of Natural History, Pittsburgh, PA, USA; **FMNH**, Field Museum of Natural History, Chicago, IL; **GBA**, Austrian Geological Survey, Wien, Austria; **HUI-Pal** Hebrew University of Jerusalem, Paleontology Collections; **LACM**, Los Angeles County Museum, Los Angeles, CA, USA; **MACN**, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; **MCSNT**, Museo Civico di Storia Naturale di Trieste, Trieste, Italy; **MCZ**, Museum of Comparative Zoology, Cambridge, MA; **MLP**, Museo de La Plata, La Plata, Argentina; **MSNM**, Museo di Storia Naturale di Milano, Milano, Italy; **NHML**, Natural History Museum, London, England; **QM**, Queensland Museum, Brisbane, Australia; **Rh-E.F.**, Natural History Museum of Gannat, Gannat, France; **FHSM**, Fort Hays Sternberg Museum, Fort Hays, Kansas, USA; **SMF**, Senkemberg Museum, Frankfurt, Germany; **TMP**, Royal Tyrrell Museum of Paleontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta

Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; **UAMZ**, University of Alberta Museum of Zoology, Edmonton, Alberta, Canada; **UF**, University of Florida, Gainesville, FL; **USNM**, United States National Museum of Natural History, Washington, DC; **ZFMK**, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Here follows a list (in alphabetical order) of the non-ophidian lepidosaurs that have been examined for this study: *Acontias meleagris* FMNH 187063, MCZ 21416, NHML 63-2-21-21; *Acontias plumbeus* MCZ 14233, MCZ 21452, NHML 94-6-29-38; *Amphisbaena alba* MCZ 32256, MCZ 32257, MCZ 165208, NHML unn., UAMZ R399, ZFMK 85471 (radiographs); *Anniella pulchra* FMNH 213666, MCZ 8855, MCZ 8858, MCZ 11798; *Agama agama* MCZ 173366, MCZ 173367; *Bachia heteropus* MCZ 9006, MCZ 79737; *Bachia trinasale* ZFMK 81766 (radiographs); *Bipes biporus* MCZ 31523, MCZ 83227, MCZ 145823, NHML 1454; *Clidastes propython* ANSP 10193, NHML R-4547; *Clidastes liodontus* AMNH 192, NHML R-2946, SM VP-2071; *Chamaeleo gracilis* MCZ 22559, MCZ 41654; *Chamaeleo* sp. UAMZ 404, UAMZ 375; *Cordylus cordylus* MCZ 21568, MCZ 21570; *Cordylus giganteus* MCZ 173607; *Cordylus breyeri* UALVP unn.; *Dibamus novaguineae* USNM 305916 (CT scanned), USNM 305914 (CT scanned); *Gekko gekko* UAMZ 377, UALVP unn., MCZ 43738, MCZ 131538, MCZ 173377; *Heloderma horridum* MCZ 5008, MCZ 5009, MCZ 5010; *Heloderma suspectum* TMP 90.7.357; *Lacerta lepida* FMNH 22098, MCZ 15733, MCZ 15736, MCZ 29977; *Lanthanotus borneensis* FMNH 134711, MCZ 8305, NHMF 66188; *Lialis burtonis* MCZ 59105, MCZ 59106, ZFMK 26427 (radiographs); *Ophisaurus apodus* MCZ 2094, MCZ 32249; *Ophisaurus ventralis* ZFMK 27411 (radiographs); *Phrynosoma solare* FMNH 22415, FMNH 98395, FMNH 98396; *Platecarpus tympaniticus* AMNH 1820, AMNH 1821, AMNH 1488, AMNH 1566, LACM 128319, UALVP 55497, YPM 4003; *Plesioplatecarpus planifrons* FHSM 2116, UALPV 24240, UALVP 40402; *Pontosaurus kornhuberi* MSNM V3662; *Pontosaurus lesinensis* GBA 1873/4/2; *Rhineura floridana* MCZ 4337, MCZ 55614, MCZ 55615; *Shinisaurus crocodylurus* UF 71623; *Sphenodon punctatus* UAMZ unn., MCZ 4702, MCZ unn.; *Trogonophis wiegmanni* NHML 1920-9-20-653, NHML 94-3-22-4; *Tupinambis teguixin* FMNH 140193, MCSNT unn.; *Tylosaurus proriger* MCZ 1031, FHSM VP-3; *Tylosaurus kansasensis* FHSM VP-2295; *Tylosaurus nepaeolicus* FHSM VP-2209, FHSM VP-3366; *Tylosaurus* sp. AMNH 130, FHSM VP-13742, FHSM VP-15631, FHSM VP-15632, FHSM VP-2209, FHSM VP-2495, FHSM VP-7262, FHSM VP-9350; *Uromastyx acanthinurus* MCZ 27377, MCZ 27381, MCZ 27382*; Varanus bengalensis* MCZ 33453, MCZ 43073, MCZ 43739; *Varanus albigularis* UAMZ 947; *Varanus salvator* TMP 1990.7.36; *Varanus Dumérilli* TMP 1990.7.71; *Varanus brevicauda* ZFMK 84241 (radiographs); *Varanus similis* ZFMK 64430 (radiographs); *Xantusia riversiana* CMNH 56451, CMNH 56457, MCZ 9177; *Xenosaurus grandis* MCZ 54311, MCZ 54313, MCZ 54315.

Here follows a list (in alphabetical order) of the snakes that have been used in this study: *Acrochordus granulatus* ZFMK 33613 (radiographs); *Acrochordus javanicus* AMNH R-46251, AMNH R-89839, AMNH R-140814;

Acrochordus sp. AMNH R-155254; *Agkistrodon piscivorous* AMNH R-57801, AMNH R-81544, AMNH R-155432, ZFMK 21724, ZFMK 21725; *Anilius scytale* MCZ 19537, MCZ 2984, MCZ 17645, NHML 1972.405 (dissected), NHML 58-8-23-48, ZFMK 47668 (radiographs); *Atractaspis aterrima* NHML 95-5-3-58, AMNH 12352 (CT scanned), ZFMK 17571 (radiographs); *Atractaspis bibroni* AMNH R-82071; *Atractaspis corpulenta* FMNH 58069, MCZ 4826, AMNH R142431 (radiographs); *Atractaspis irregularis* AMNH R-12355, FMNH 142994, MCZ 53534, ZFMK 56106 (radiographs), ZFMK 56107 (radiographs); *Atractaspis microlepidota* FMNH 58397; *Azemiops feae* FMNH 218628; *Boa constrictor* ZFMK 21661, ZFMK 21662, ZFMK 54844, ZFMK 49854 (radiographs); *Calabaria reinhardtii* AMNH R-10092, AMNH R-11714, AMNH R-11911 (cleared & stained), MCZ 49014, NHML 96-3-9-3, NHML 1911-10-28-17, ZFMK 89190; *Casarea dussumieri* AMNH 137771 (CT-scanned), MCZ 49135, NHML 1992-995, NHML 1992-996; *Causus rhombeatus* FMNH 2268, FMNH 51692, FMNH 51693, FMNH 164744; *Cylindrophis maculatus* NHML 1930-5-8-50, ZFMK 33609 (radiographs); *Cylindrophis ruffus* AMNH R-85647; NHML 1969.324 (dissected), NHML 1930-5-8-47, USNM 297456, ZFMK 16549; *Dinilysia patagonica* MLP 26-410, MACN PV 116, MACN RN 976, MACN RN 1013, MACN RN 1014, MACN RN 1015, MACN RN 1016, *Epicrates cenchria* ZFMK 5168, ZFMK 21665, ZFMK 21666, ZFMK 86470; *Eryx colubrinus* FMNH 223196, ZFMK 50246, ZFMK 46058 (radiographs); *Eryx conicus* NHML 1930-5-8-14, NHML 1930-5-8-15, NHML 1930-5-8-16; *Eryx jaculus* NHML 1930-5-8-21,NHML 1930-5-8-19, NHML 1930-5-8-30, FMNH 19624; *Eryx johni* NHML

1930-5-8-32, NHML 1930-5-8-33, NHML 1930-5-8-34, NHML 1964-1240, ZFMK 21660; *Eupodophis descouensi* Rh-E.F. 9001-9002- 9003, MSNM V 3660, MSNM V 3661, MSNM V 4014; *Haasiophis terrasanctus* HUJ-Pal EJ 695; *Heterodon platyrhinos* AMNH R-63590, AMNH R-69647, AMNH R-155313; *Homalopsis buccata* NHML 111-18-1-e, NHML 1930-5-8-630, NHML 1930-5-8-631, NHML 1930-5-8-632, NHML 1930-5-8-634, NHML 1964-10-25, NHML 1964-11-25; *Lampropeltis getulus* AMNH R-70097, AMNH R-75539, AMNH R-128202, ZFMK 5205; *Laticauda colubrina* FMNH 234147, FMNH 234149, FMNH 236242, FMNH 236243, ZFMK 73922 (radiographs); *Leptotyphlops dulcis* AMNH R160152, UAMZ 343 (CT scanned), NHML 1962.716 (dissected); *Leptotyphlops humilis* AMNH R-73716, USNM 222795; *Leptotyphlops melanotermus* ZFMK 53237 (radiographs); *Leptotyphlops scutifrons* (cleared & stained) MCZ 54515, MCZ 68781, ZFMK 87307 (radiographs); *Leptotyphlops septemstriatus* ZFMK 75033 (radiographs); *Lichanura trivirgata* UAMZ 3819*; Lichanura roseofusca* NHML 94-3-24-2; *Liotyphlops albirostris* MCZ 31541 (cleared & stained); *Loxocemus bicolor* AMNH R-19393, AMNH R-44902, AMNH R-110151, NHML 82-8-17-16, ZFMK 43849 (radiographs); *Micrurus fulvius* FMNH 34282, FMNH 229600; *Micrurus nigrocintus* FMNH 210092; *Naja naja* AMNH R-57807, AMNH R-74833, ZFMK 21704, ZFMK 21705, ZFMK 21706, ZFMK 14246 (radiographs), ZFMK 74286 (radiographs); *Najash rionegrina* MPCA 389, MPCA 391–397, MPCA 400; *Pachyrhachis problematicus* HUJ-Pal EJ 3659, HUJ-Pal EJ 3775; *Pareas carinatus* NHML 1964-1092, NHML 1964-1094; *Python curtus* ZFMK 76303 (radiographs); *Python molurus NHML*

1972-21-78, ZFMK 5161, ZFMK 21673, ZFMK 83431; *Python regius* UAMZ 3818, ZFMK 61718; *Python reticulatus* FMNH 15678, FMNH 51631, NHML 1972-2169, ZFMK 5175, ZFMK 21671, ZFMK 70207; *Python sebae* ZFMK 5200, ZFMK 21678, ZFMK 35527 (radiographs); *Rhamphotyphlops bituberculatus* ZFMK 49337; *Ramphotyphlops braminus* USNM 509423, UAMZ 363 (CT scanned), UAMZ 553 (CT scanned), ZFMK 35704 (radiographs), ZFMK 35705 (radiographs); *Ramphotyphlops subocularis* MCZ 65993, MCZ 65997, MCZ 72084; *Thamnophis sirtalis* AMNH R-74849, AMNH R-148084; *Thamnophis validus* AMNH R-62287; *Tropidophis canus* AMNH R-45839, AMNH R-73066, MCZ 6969; *Tropidophis haetianus* FMNH 31341; *Tropidophis pardalis* FMNH 233; *Tropidophis semicinctus* ZFMK 82869 (radiographs); *Typhlops angolensis* AMNH R-11633; *Typhlops diardi* NHML 1930-5-8-3; *Typhlops jamaicensis* ZFMK 70500 (radiographs), ZFMK 70501 (radiographs); *Typhlops lineolatus* MCZ 48063; *Typhlops punctatus* MCZ 7293, MCZ 22493, NHML 1975.568 (dissected), NHML 1911-6-9-2, SNHM 320704; *Typhlops pusillus* ZFMK 51831 (radiographs); *Typhlops reticulatus* AMNH R-3001; *Typhlops vermicularis* ZFMK 52242 (radiographs), ZFMK 60556 (radiographs); *Ungaliophis panamensis* AMNH R-58845, AMNH R-62639, MCZ 56051; *Ungaliophis maculatus* ZFMK 35494 (radiographs); *Uropeltis ocellatus* MCZ 3873; *Uropeltis pulneyensis* MCZ 3870, ZFMK 33590 (radiographs); *Uropeltis rubrolineatus* MCZ 47101; *Vipera russelli* AMNH R-74818, AMNH R-75739, ZFMK 5187, ZFMK 86077, ZFMK 65050 (radiographs); *Xenopeltis unicolor* AMNH R-29969, AMNH R-71531, NHML 1947-1-1-10, NHML 1947-1-1-12, USNM 287277, ZFMK 33601 (radiographs); *Xenodermus javanicus* FMNH 67427; *Yurlunggur sp.* QM 45073, QM 45111, QM43388, QM 45390, QM 45391, QM 45398, QM 45411, QM 45412, QM unn.; *Wonambi naracoortensis* SAM P30178, SAM P30178a, SAM 16172, SAM 16170c, SAM 16168.

Philosophy Behind Character Selection

In recent morphology-based phylogenetic studies there is a tendency to believe that the larger the data set, the more informative it will be on phylogenetic relationships, and that the relationships inferred from it will be the most stable and reliable. This philosophy has produced studies with hundreds of morphological characters is (e.g., 363 characters in Conrad [2008]; 601 characters in Gauthier et al. [2012]). However, including large numbers of characters in order to appear as the most extensive and up-to-date study on a given taxon may lead to the inclusion in the data set of a considerable number of ‘phylogenetically trivial’ anatomical features. Obviously, what is ‘phylogenetically trivial’ in a given study depends on the question being asked. For example, if a researcher is working on the phylogenetic relationships of a number of species within a certain genus of lizards (or even some genera within a family), then major osteological differences between the species examined can hardly be observed. In this situation, minor anatomical differences (e.g., scalation, number of digits, relative length of a process, details of the shape of a particular bone or organ, colour pattern) may prove significant in suggesting closely related species assemblages (e.g., Crother et al., 1986; Good, 1988; Arnold 1989, 1991; Campbell and Frost, 1993; Griffith et al., 2000). However, when the question being asked is about the phylogenetic relationships of taxa that are separated at a supra-generic level, then minor anatomical differences will likely be deceptive, and in many cases not even applicable to all the taxa under consideration (e.g., colour, scale morphology, and scalation patterns can vary greatly within different families of lizards; Greene, 1997).

Character selection is the first and most fundamental step in any phylogenetic analysis, as it constitutes the formulation of primary homologies, some of which will eventually be recovered after the test of congruence, as synapomorphies (secondary homologies) characterizing a clade (DePinna, 1991). In the current literature there are seven main categories of morphological characters that are used to define primary homologs and thus characters: (1) size-related, e.g., element ‘X’ is longer/shorter than element ‘Y’, often expressed as a relative percentage; (2) shape descriptors, e.g., element ‘X’ is square, round or triangular; (3) characters that try to describe the differing extent of development of a feature, e.g., crest ‘X’ well developed, poorly developed, or absent; (4) meristic characters that are based on the count of individual elements (e.g., teeth, vertebrae, scleral ossicles); (5) characters that refer to the presence or absence of an individual element (e.g., a particular bone, a foramen); (6) topological characters that describe the contacts between individual elements, e.g., element ‘X’ does or does not contact element ‘Y’; (7) contact-descriptors, characters that describe the type of contact between two elements (i.e., abutting, sutural, fusion).

Besides complying with the criteria of similarity and topological relations, ideal morphological characters should also be clear, unequivocal, and objectively defined (different researchers should all score a given character the same way for the same taxon). Based on these criteria, characters belonging to the first and second categories are potentially unreliable, and unwanted, phenetic concepts reliant on overall similarity and not on a well-defined concept of a homolog. Characters from the third category are potentially valuable, but sometimes problematic, as a continuous morphological series can easily occur between opposite states; meristic characters, the fourth category, require subjective subdivisions (state boundaries) of continuous variables, and therefore should be avoided; characters belonging to the last three categories comply with all the basic criteria defining ideal morphological characters, therefore should be considered the most reliable, as the homolog concepts are clear (e.g., topological relations of developmental units that pass the test of similarity). Only characters of this nature should be used in high-level cladistic analyses (i.e., at and above the generic level), because characters belonging to the remaining categories are bound to introduce a large source of error (noise) in the data matrix, which may obscure the phylogenetic signal provided by more valuable anatomical features.

Examples of problematic characters are provided below:

Size Related (Category 1): *"Frontal interorbital width/frontoparietal suture width I: (0) 14-19%; (1) 20-22%; (2) 24-26%; (3) 28-34%; (4) 36-40%. Scores determined with straight line measurements at the narrowest part of the frontal* *between the orbits, and between the lateral contactbetween the forntal and parietal, even if the suture is not straight"* (char. # 48 in Gauthier et al., 2012). This type of character is problematic because it provides subjective state divisions and no valid argument for considering a taxon with score 20% dissimilar from another taxon that has score 19%, but similar to a taxon of score 22%. For example, according to this character, *Varanus salvator* would not be grouped with *V. acanthurus* (a member of the same genus), but with *Lacerta viridis* (a member of a different family).

Shape Descriptor (Category 2): *"Dentary ventral margin: (0) straight to slightly bowed; (1) distinctly bowed"* (a similar character was used by Conrad [2008] [char. # 178], and by Gauthier et al. [2012] [char. # 357]).
Gauthier et al. (2012) noted that the shape of the lower margin of the dentary varies continuously across taxa, and that this character can be impossible to score where the shape of the element is markedly transformed (e.g., Typhlopidae, *Xenopeltis*, *Atractaspis*). Moreover, it is not clear what the state boundary is between "slightly bowed" and "distinctly bowed."

Extent of Development of a Feature (Category 3): *"Premaxilla internasal process length: (0) less than half nasal length; (1) more than half way to frontal between nasals; (2) nearly to, or articulates with, frontal"* (char. # 10 in Gauthier et al., 2012).

This type of character provides subjective state divisions of a feature that varies continuously. Such characters are prone to be scored differently by independent observers, e.g., when the length of the process is close to half that of the nasal. This category of characters may be useful for phylogenetic analysis at or below the generic level (if no ambiguity is present between states), but in higher-level phylogenies the large variance in the sample is bound to be problematic. When this character is applied to Gauthier et al.'s (2012) global phylogeny of squamates, the same states are chaotically distributed among well-supported clades. For example, *Varanus acanthurus* does not share the same state (2) with *V. salvator*, but it does with the amphisbaenian *Bipes biporus*.

Meristic Character (Category 4): *"Presacral vertebrae number increase: (0) 32 presacrals or fewer; (1) 33–39; (2) 50–55; (3) 61–84; (4) 89 or more"* (char. # 456 in Gauthier et al., 2012).

Similarly to characters in the third category, this type of character provides subjective state divisions of a feature that varies continuously. A taxon with 84 vertebrae is considered similar to (i.e., sharing a primary homology with) another taxon with 61, but different from a taxon with 89. The same states are chaotically distributed among well-supported clades (e.g., the mosasaur *Plotosaurus* and the pygopodid *Lialis* share state (2), the anguimorph *Anniella* and the scincomorph *Acontias* share state (3)).

Molecular Data

The molecular data consists of 10 nuclear gene sequences (BDNF, C-Mos, FSHR, NGFB, RAG1, GPR149, SLC8A1, SLC30A1, TRAF6, ZEB2) that were retrieved from GenBank (http://www.ncbi.nlm.nih.gov/genbank) (Supplementary Data 8-2, Table 8-1S). The genes were selected for their good coverage of the selected taxa, in order to minimize missing data that could negatively affect the results of the phylogenetic analyses (only the taxa *Anomochilus leonardi*, *Bachia heteropus*, and *Vipera russelli* were not sequenced for any of the selected genes, so they could not be included in the molecular analyses). Mitochondrial genes were not taken into consideration for several reasons: (1) because of their relatively high evolutionary rates, which tend to erase the phylogenetic signal required to reconstruct the deep nodes in a phylogeny (Lee, 2009); (2) because their alignment is typically problematic (i.e., dependant on structural models) and can result in more than one plausible solution (Hickson et al.,1996; Kjer et al., 2007); and (3) because mtDNA is subject to phenomena of hybridization that can hamper the accurate reconstruction of the phylogeny (e.g., Miller et al., 2012). As in the morphological analysis, when possible, only gene sequences from the same species (possibly the same species used in the morphological dataset) were used; however, the rarity of species sequenced for any given gene often required that gene sequences belonging to other species within the same genus had to be used. This is indicated in the phylogeny and data matrices by taxa that only appear with the name of their genus (further details on sequences and species are available in Supplementary Data 8-2).

The data was retrieved from GenBank as DNA (base) sequences (for a total of 7,155 base pairs), and these sequences were aligned using MAFFT version 7 (mafft.cbrc.jp/alignment/server) under default settings, with the exception of the strategy, which was set to G-INS-I (recommended for less than 200 nuclear gene sequences lacking long gaps).

After the alignment was complete, the sequences were also translated into protein (amino acid) sequences. This was done in order to avoid the problem of long-branch attraction caused by the third base positions in parsimony analyses (Bergsten, 2005), and also to test the congruence of the data in the two different formats (DNA vs. protein). The indels that resulted from the alignment were scored for presence or absence and the resulting characters were added to the data matrix. After the indels had been identified and noted, the alignments were trimmed using Gblocks (http://molevol.cmima.csic.es/castresana/Gblocks_server.html).

The morphological data, the indels and the protein sequences were analyzed using maximum parsimony and Bayesian analyses. The DNA sequences were analyzed using maximum likelihood and Bayesian inference.

In order to test the consistency of the signal within the molecular data, two partitions consisting of 5 genes each (Partition 1 = BDNF, C-MOS, FSHR, GPR149, NGFB; Partition 2 = RAG1, SLC8A1, SLC30A1, TRAF6, ZEB2) were analyzed separately using parsimony (protein sequences), maximum likelihood (DNA sequences), and Bayesian inference (DNA sequences).

Search Criteria

The parsimony analyses were run in PAUP∗ 4.0b10 (Swofford, 2002), the search criterion was set to heuristic with 1,000 random addition replicates, and the branch-swapping algorithm was set to tree-bisection-reconnection (TBR). The characters were left unordered and with equal weights (Fitch, 1971). The trees were rooted using the lepidosaur *Sphenodon punctatus*. Consistency index (excluding uninformative characters) (CI), retention index (RI), and rescaled consistency index (RC) were used ad indicators of the amount of homoplasy in the data set. Statistical measures of support for the branches retrieved in the phylogenetic analyses were obtained using 1000 non-parametric bootstrap replicates (Felsenstein, 1983, 1985). Bootstrap analyses were run using the software TNT (Goloboff, 2008). Bootstrap values higher than 70% were considered to provide strong branch support (Hillis and Bull, 1993).

The maximum likelihood analyses were run in Seaview version 4 (Gouy et al, 2010). The model selected was GTR+I+Γ (Rodriguez et al., 1990), and more in particular, the search criteria were set to empirical nucleotide equilibrium frequencies, optimized invariable sites, and optimized across site rate variation. Tree searching was performed under the “Best of NNI and SPR” option, and the starting tree topology was optimized adding 5 random starts. One hundred bootstrap replicates were performed in order to obtain some measure of statistical support for the branches in the tree topology.

The Bayesian analyses were run in MrBayes version 3.2 (Ronquist et al., 2012). The models selected were GTR+Γ+I for base sequences (DNA)

(Rodriguez et al., 1990), and Mk1 for aminoacid (protein) and morphological data (Lewis, 2005). All searches but one (morphological dataset) were set to last 1 million generations, with sampling every 1,000 generations. Due to lack of convergence between runs after 1 million generations, the analysis of the morphological data set was set to last 10 million generations. All searches employed 2 runs with 4 chains each, and no priors were specified (default). In order to make sure that convergence had been reached at the end of the search, the average standard deviation of split frequencies (ASDSF) and the convergence diagnostics Estimated Sample Size (EES) and Potential Scale Reduction Factor (PSRF) were examined (ASDSF should approach zero; EES should be above 100; PSRF should approach 1). The burnin interval (samples that precede convergence and that are to be discarded) was estimated based on the plot of the log probability over the generations (only the trees and parameters that correspond to the plateau in the graph were retained). A burnin of 10% of the samples was discarded for all analyses. Clades with posterior probabilities (PP) equal to or above 95% were considered strongly supported (Huelsenbeck and Rannala, 2004).

All datasets, morphological, molecular (partitioned and combined, DNA and protein sequences) and their combination, are available in nexus format in Supplementary Data 8-3.

Taxon Sampling and Templeton's Tests

The effect of taxon sampling was tested on the complete dataset (morphology, indels, protein) using parsimony. Three tests were performed: (1) all fossil taxa were removed from the analysis; (2) amphisbaenians were removed from the analysis; (3) scolecophidians were removed from the analysis. Removal of these groups of taxa was meant to see if their presence has any effect on the position of snakes within squamata and/or on the internal relationships of snakes (i.e., to test possible long-branch attraction phenomena; Bergsten, 2005).

A series of Templeton's tests (Templeton, 1983) were performed in order to see whether the topology retrieved from the parsimony analysis of the complete dataset (morphology, indels, protein) is statistically compatible with that of certain constrained topologies. The null hypothesis of the Templeton's test states that there is no difference between the compared tree topologies (null hypothesis is rejected if $p<0.05$). The search for the constrained topologies was performed under the same settings used for the original search (i.e., heuristic, 1,000 random addition replicates, TBR). The constraints used were as follows: (1) Ophidia was constrained to be the sister group of other squamates, this was done to test the possibility that snakes may be derived from a pre-lacertilian ancestor. Such a possibility was raised in the literature by Rieppel (1980, 1988). This argument is based on features like the course of the ramus communicans externus, which is anterior to the stapes in *Sphenodon* and snakes, but posterior to the stapes in all lizards, or on the presence of both rods and cones in some snakes, while all lizards lack the former type of visual cells; (2) Anguimorpha was constrained to be the sister group of the Ophidia. This constraint was enforced because the Anguimorpha are considered by many as the closest living relatives of snakes (e.g., Estes et al., 1988; Lee and Caldwell, 2000; Lee, 2005), but this relationship was not supported by the results of the parsimony analysis of the complete data set used in this study; (3) the clade inclusive of the extinct *Pontosaurus* and mosasauroids was constrained to be the sister group of the Ophidia. This constraint was enforced to test whether or not such a hypothesis, which has been previously presented in the literature on multiple occasions (e.g., Pierce and Caldwell, 2004; Caldwell and Palci, 2009; Palci and Caldwell, 2007, 2009), would constitute a possible alternative to the results obtained herein; (4) Scolecophidia were constrained as forming a clade with *Uropeltis* and *Anomochilus*. This was done in order to test the possibility that scolecophidians may actually represent an aberrant lineage of basal alethinophidian snakes. Such a possibility has been previously raised by List (1966) and Dowling and Duellman (1978); (5) Scolecophidia were constrained as forming a clade nested within Colubroidea. This was done in order to test the possibility that scolecophidians may actually represent an aberrant lineage of colubroid snakes. This is a novel hypothesis, but the possibility is hinted at by a series of morphological similarities between certain scolecophidians (Typhlopidae and Anomalepididae) and some colubroids (e.g., Viperidae, *Atractaspis*). These features include, but are not limited to: hinged erectable maxillae, strongly developed prezygapophyseal processes on the vertebrae, well-developed crista circumfenestralis, lack of teeth on the premaxillae, presence of a tracheal lung (only occasionally present outside of the Colubroidea).

RESULTS

Morphological Dataset: Parsimony

The strict consensus of 135 most parsimonious trees (1052 steps, CI=0.27, RI=0.75, RC=0.21) (Fig. 8-1) obtained from the parsimony analysis of the morphological dataset retrieved the Iguania as the most basal clade of squamates, followed by *Pontosaurus* plus Mosasauroidea. The next clade consists of taxa that have been traditionally placed within Scincomorpha, Gekkota and Anguimorpha, and this clade is followed by the legless taxa *Bachia*, *Anniella*, a paraphyletic "Amphisbaenia" and *Dibamus*. Ophidia was retrieved in a sister group relationship to *Dibamus*. Scolecophidia (*Leptotyphlops*, *Typhlops* and *Liotyphlops*) was found to be a monophyletic clade at the base of all other snakes. The scolecophidia are followed by *Uropeltis*, *Anomochilus*, and a clade consisting of *Cylindrophis*, *Anilius* and all the fossil snakes included in this analysis (*Wonambi*, *Yurlunggur*, *Najash*, *Dinilysia*, *Haasiophis*, *Eupodophis*, and *Pachyrhachis*). All remaining non-caenophidian snakes, with the exception of *Casarea*, form a clade that is sister group to *Casarea* plus Caenophidia. Interestingly, *Python* was retrieved as the sister taxon to *Calabaria*, and within Colubroidea, Viperidae are nested inside a paraphyletic Elapidae.

This analysis was also run a second time after excluding all the postcranial osteological characters (characters 174-208) (the fossil snake *Najash rionegrina* was also excluded from the analysis, because as rediagnosed by Palci et al. [2013a] the type and referred specimens only consists of postcranial material). This analysis retrieved 5345 most parsimonious trees (892 steps, CI=0.27, RI=0.75, RC=0.21), and the strict consensus (Supplementary Data 8-4, Fig. 8-1S) shows a considerable decrease in resolution for the relationships of non-ophidian squamates, while the relationships of taxa within the clade Ophidia remain almost unchanged; one major exception is represented by the position of the fossil snakes *Pachyrhachis*, *Eupodophis* and *Haasiophis*, that are moved crownward in the tree and placed in a clade that is sister group to *Calabaria*. Interestingly, despite the removal of postcranial characters, *Dibamus* and amphisbaenians (either mono or paraphyletic) are still recovered as the closest relatives of snakes.

Morphological Dataset: Bayesian

The clade credibility tree obtained from the Bayesian analysis of the morphological dataset (run 1: ln[L]=-4541.36; run 2: ln[L]=-4544.26) (Supplementary Data 8-4, Fig. 8-2S) is mostly in agreement with the tree obtained from the parsimony analysis of the same dataset. The main differences are as follows: (1) Bayesian analysis retrieved a paraphyletic Iguania, where *Phrynosoma* lies in a more derived position relative to other iguanians; (2) the clade consisting of lacertiformes, scincoids, gekkotans and anguimorphs is collapsed to a polytomy where most members of each group are more or less separated into the respective traditional groupings (i.e., gekkotans, scincoids and anguimorphs; with exceptions provided by *Cordylus* and *Xantusia*); (3) *Dibamus* is shifted to a more basal position, basal to the paraphyletic "Amphisbaenia"; (4) Scolecophidia is not monophyletic, i.e., *Leptotyphlops* lies in a more derived position than other "scolecophidians"; (5) *Dinilysia* is moved to a position at the base of all other fossil snakes; (6) *Xenopeltis* and *Loxocemus* are moved at the base of the large clade consisting of the common ancestor of *Tropidophis* and *Vipera*, and all of its descendants.

Molecular Dataset: Maximum Likelihood (ML)

The tree (ln[L]=-81486.35) obtained from the Maximum Likelihood analysis of the molecular dataset (DNA) is very different from the trees obtained from the analyses of the morphological data (both Bayesian and parsimony) (Fig. 8-2). In this tree *Dibamus* is retrieved as the most basal squamate, followed by gekkotans (i.e, *Gekko* and *Lialis*). The next clade consists of ((*Eumeces*, *Acontias*) (*Xantusia*, *Cordylus*)), and is followed by a clade inclusive of *Tupinambis* and a paraphyletic Amphisbaenia (*Lacerta* is retrieved between *Rhineura* and *Bipes*). In a yet more derived position is a large clade consisting of anguimorphans and iguanians in a sister group relationship, and this whole clade is the sister group to the Ophidia. Within the Ophidia, the Scolecophidia are found to be paraphyletic, with *Liotyphlops* in a more derived position than (*Typhlops*, *Leptotyphlops*). The clade (*Anilius*, *Tropidophis*) is at the base of the

Alethinophidia, which are divided into two (poorly supported) large clades. One clade consists of *Casarea* plus all Caenophidians, and the other clade includes all remaining alethinophidians. Within Colubroidea, *Xenodermus* and *Pareas* are the two most basal representatives of the group, followed by viperids. *Atractaspis* is retrieved as the sister taxon to elapids.

Molecular Dataset: Parsimony

The strict consensus of 159 most parsimonious trees (4269 steps, CI=0.48, RI=0.64, RC=0.35) (Supplementary Data 8-4, Fig. 8-3S) obtained from the analysis of the molecular (protein and indels) dataset is mostly in agreement with the ML tree obtained from the equivalent data set (DNA). Minor inconsistencies are as follows: (1) *Chamaeleo* and *Agama* are inverted in position; (2) *Xenosaurus* and *Heloderma* are retrieved as sister taxa in the parsimony analysis; (3) *Acrochordus* and *Casare*a are inverted in position; (4) *Pareas* forms a clade with Viperidae in the parsimony analysis. It must also be noted that compatibility between this strict consensus and the ML tree obtained from the same data set is mostly due to lack of resolution in the former (i.e., several polytomies).

Molecular Dataset: Bayesian

The Bayesian analysis of the molecular data set translated into amino acid sequences (Protein) retrieved a tree (run 1 ln[L]=-36847.85; run 2 ln[L]=-

36852.23) that is totally compatible with the strict consensus obtained from the parsimony analysis of the equivalent data set (Protein and Indels) (Supplementary Data 8-4, Fig. 8-4S). The Bayesian analysis of the DNA sequences resulted in a tree (run 1 ln[L]=-81133.63; run 2 ln[L]=-81136.29) that is almost identical to the ML tree from the same dataset (DNA), the only difference consisting of the inverted positions of *Chamaeleo* and *Agama* within iguanians.

Several minor differences can be observed between the tree obtained from the Bayesian analysis of the protein data and the Bayesian tree obtained from the DNA data (Supplementary Data 8-4, Fig. 8-5S). These differences are as follows: (1) *Gekko* and *Lialis* form a sister group to *Dibamus* in the tree based on protein sequences; (1) *Xenosaurs* and *Heloderma* are sister taxa in the tree based on protein sequences (*Heloderma* is basal to *Xenosaurus* in the tree based on DNA); (2) *Liotyphlops* and *Leptotyphlops* are inverted in position, with the latter in a more derived position in the tree based on protein sequences; (3) the clade (*Xenopeltis* (*Loxocemus*, *Python*)) is placed just above (*Anilius*, *Tropidophis*) in the tree based on DNA sequences (while it is located in a much more derived position in the tree based on protein data); (4) *Acrochordus* and *Casarea* are inverted in position; (5) *Pareas* does not form a clade with Viperidae in the tree based on DNA data; (6) *Micrurus* and *Laticauda* are inverted in position.

Combined Morphological and Molecular Data: Parsimony

When morphological and molecular data (indels and protein data) were combined together the parsimony analysis retrieved 53 most parsimonious trees (5414 steps, CI=0.43, RI=0.67, RC=0.32). The strict consensus of these trees (Fig. 8-3) shows *Dibamus* in the most basal position, followed by (*Gekko*, *Lialis*) and ((*Acontias*, *Eumeces*) (*Cordylus*, *Xantusia*)). The next clade is represented by (*Lacerta* (*Tupinambis*, *Bachia*)) at the base of Iguania and Anguimorpha in a sister group relationship to each other. Moving further up the tree is a clade consisting of *Pontosaurus* and mosasauroids, and even further up is a monophyletic Amphisbaenia. The Amphisbaenia is in a sister group relationship to the Ophidia. Within the Ophidia, the Scolecophidia are a monophyletic group at the base of all other snakes, followed by a paraphyletic “Anilioidea” (i.e., *Uropeltis*, *Anomochilus*, *Cylindrophis*, and *Anilius*). All fossil snakes are grouped together in a clade that is in a polytomy with *Anilius* and all remaining alethinphidians. Above this clade is a polytomy with (*Xenopeltis* (*Loxocemus*, *Python*)), ((*Charina*, *Ungaliophis*) (*Calabaria* (*Eryx* (*Epicrates*, *Boa*)))), and a large clade inclusive of *Tropidophis*, *Casarea* and the Caenophidia. Within the Colubroidea, *Xenodermus* and *Pareas* are the two most basal representatives, followed by Viperidae. *Atractaspis* is the sister group of a monophyletic Elapidae.

Snake Synapomorphies

Below is the list of synapomorphies for the clades Ophidia, Scolecophidia, Alethinophidia, and Colubroidea, as retrieved in the pasimony analysis of the combined data set. Synapomorphies that have been found only with the Acctran (A) or Deltran (D) optimization criteria are indicated by an ‘A’ or a ‘D’, respectively (bold arrow indicates unambiguous transformation):

OPHIDIA

1) Premaxillary teeth: absent (6:0**→**1). Note: this synapomorphy is possibly an artifact of having the Scolecophidia placed at the base of the clade (all scolecophidians lack premaxillary teeth). The premaxillary teeth are present in many lineages of snakes, and their presence is plesiomorphic within Squamata. So, it is unlikely that the most recent common ancestor of all snakes lacked premaxillary teeth and that they re-evolved in more derived ophidians. It is more likely that lack of teeth is a synapomorphy of the Scolecophidia.
2) Premaxillary processes of maxilla (anteromedial lobe-shaped or triangular flange visible in palatal view): absent (12:1→0; A).
3) Palatine shelf/process of maxilla: a distinct triangular, square or lobe-shaped process is present on the medial margin of the maxilla. The base of this process is typically 1/3 or less of the length of the maxilla (14:1→2; A).
4) Posterior dentigerous ramus of maxilla: extends posteriorly well beyond posterior margin of the orbit (16:0→1; A).
5) Nasal-maxilla sutural contact: absent. (27:0→1; D).
6) Septomaxilla free lateral flange or process: present (29:0**→**1).

7) Septomaxilla: contacts nasal dorsomedially (31:0→1; D).

8) Septomaxilla: not in sutural contact with maxilla, if contact is present there is no suture between the two elements (abutting contact) (32:0→1).

9) Septomaxilla: septomaxilla contributes to the margin of the external naris (33:0→1; A). Note: this character is restricted to scolecophidian snakes and reversed in all other snakes except uropeltids.

10) Septomaxilla dorsolateral contacts: abuts laterally with prefrontal and nasal (35:0→1; A). Note: This condition is further modified in derived snakes.

11) Medial vertical septum of vomer: septum present but lacks fenestration (37:0→1). Note: this character is modified in derived snakes.

12) Posterior border of vomeronasal opening (opening for Jacobson's organ): (0) vomer not sutured to maxilla (39:1→0; A).

13) Anterior border of vomeronasal opening (opening for Jacobson's organ): vomer not in sutural contact with maxilla anterolaterally (40:0→1; D).

14) Vomeronasal nerve: pierces vomeronasal capsule with one large foramen (sometimes with one or two additional small foramina) at posterior end of vomer (41:0→1). Note: this character is further modified in the Caenophidia, which show state 2.

15) Palatine-maxilla contact: palatine meets maxilla in a loose overlapping joint between maxillary process of the former (if present) and palatine process of the latter (43:0→1).

16) Ectopterygoid: anterior end of ectopterygoid with two anterior processes

projecting dorsally along maxilla (60:0→2).

17) Contact between maxilla and ectopterygoid: mobile articulation (64:0→1).

18) Ventrolateral ectopterygoid flange: absent (65:0→1; D).

19) Prefrontal-nasal contact: prefrontal contacts nasal (67:0→1). Note: this condition is modified in derived snakes.

20) Prefrontal-maxilla contact: maxilla loosely articulated to prefrontal, long contact between prefrontal and maxilla (70:0→1; A). Note: This condition is further modified in derived snakes.

21) Frontal subolfactory process: sutured to parasphenoid (77:1→0; D).

22) Optic foramen: located within frontal (80:4→2; D). Note: This condition is further modified in derived snakes.

23) Jugal: absent (87:0→1; D). Note: this synapomorphy is clearly due to having the Scolecophidia (most of which lack a jugal) placed at the base of the tree. This synapomorphy was not recovered in the analyses constrained after the Bayesian trees (see below).

24) Jugal contact with maxilla and ectopterygoid: jugal does not contact either maxilla or ectopterygoid (91:3→2). Note: this is a condition observed in *Liotyphlops*, the only scolecophidian included in this analysis that retains a jugal; however, several more derived snakes show a jugal that contacts the maxilla (e.g., *Dinilysia*, *Yurlunggur*, some specimens of *Python*).

25) Parietal: has firm sutural contact with prootic anterolaterally and extends

ventrally to contact parabasisphenoid (99:1→2).

26) Basipterygoid process: absent or weak, consisting of a small crest or mound that usually does not contact pterygoid (118:0→1).

27) Juxtastapedial space (depressed area immediately surrounding fenestrae ovalis and rotunda): crista tuberalis contacts crista interfenestralis (i.e., ventral margin of crista interfenestralis sandwiched between crista tuberalis and prootica) (130:0→1; A). Note: this feature is further modified in derived snakes.

28) Paroccipital process (= joined posterolateral rami of prootic and exoccipital-opisthotic): indistinct or absent (132:0→1).

29) Processus ascendens tecti synotici of supraoccipital: absent (136:1→0).

30) Exoccipitals: in contact above foramen magnum (137:0→1).

31) Orbitosphenoid: absent (140:1→0; D).

32) Mental foramina on lateral surface of dentary: one (142:0→1; A).

33) Mandibular symphysis: absent, ligamentous connection between anterior tips of dentaries (145:0→1; D).

34) Anterior end of coronoid: lacks lateral and medial processes (156:0→2; D).

35) Marginal tooth replacement: replacement tooth develops posterolingually, resorption pit absent (169:0→2).

36) Prezygapophyseal process: present, process extends laterally from prezygapophyseal facet (185:0→1).

37) Caudal vertebrae: no processes project from ventral surface of caudal

centra (189:1→3). Note: this is a character observed in scolecophidians and other burrowing snakes (e.g., *Anilius*, *Cylindrophis*); other snakes show a different condition, typically paired processes projecting posteroventrally (haemapophyses) (189:2).

38) Sternum; absent (194:0→1; D).

39) Trabeculae cranii: platybasic (209:0→1).

40) Tongue: foretongue is retractible within hindtongue (210:1→0).

41) Lungs: left lung visibly reduced (>20%) to absent (213:0→1; D).

42) Type of retina: duplex, i.e., both rods and cones present (214:2→0; A). Note: this feature is modified in derived snakes, with many forms lacking rods (e.g., Colubridae) and other forms retaining only rods (e.g., Scolecophidia).

SCOLECOPHIDIA

1) Anterior surface of premaxilla: pierced by multiple foramina (3:0→2). D
2) Nasals: fused (21:0→1; A).
3) Nasals: pierced by several foramina (22:0→1).
4) Septomaxilla: contributes to the margin of the external naris (33:0→1; D).
5) Pterygoid quadrate ramus: rod-like (53:0→1).
6) Ectopterygoid: absent (59:0→1; A). Note: this synapomorphy implies that the ectopterygoid in anomalepidids like *Liotyphlops* is a secondary aquisition.

7) Posterior transverse wall of prefrontal: neither pierced nor notched (73:0→3; D).
8) Dorsoposterior (suprastapedial) process of quadrate; small or absent (108:0→1).
9) Prootic, alar process (i.e., portion of prootic extending above trigeminal notch, foramen, or foramina: small or absent (113:1→0).
10) Juxtastapedial space (depressed area immediately surrounding fenestrae ovalis and rotunda): crista tuberalis contacts prootic and the ventral margin of the crista interfenestralis is hidden in lateral view (130:0→2, D) (130:1→2, A).
11) Supraoccipital; paired (133:0→1; A). Note: although the supraoccipital is often paired within the Scolecophidia, there are numerous exceptions (List, 1966).
12) Foramen within splenial (= inferior alveolar foramen or posterior mylohyoid foramen): absent (151:1→0).
13) Type of retina: only rods present (214:2→1, D) (214:0→1, A).

ALETHINOPHIDIA

1) Anterior surface of premaxilla: not pierced by foramina (3:2→0; A).
2) Vomerine processes of premaxilla (i.e., paired V-shaped posterior processes): present (9:1→0).
3) Palatine shelf/process of maxilla: a distinct triangular, square, or lobe-shaped process is present on the medial margin of the maxilla. The base

of this process is typically 1/3 or less of the length of the maxilla (14:0→2; D).

4) Nasal-frontal contact: not sutural, bones articulate in a prokinetic joint or may even be separated by a gap (23:0→1).
5) Vertical lamina of nasal: contacts frontal ventrally (where the descending flanges meet, if these are present) (26:1→0).
6) Trigeminal nerve maxillary branch: nerve goes through foramen in the palatine (46:2→1).
7) Posterior transverse wall of prefrontal: notched ventrally by lacrimal duct (73:0→1, D) (73:3→1, A).
8) Medial descending processes of frontal: present and complete, i.e., they divide olfactory tracts completely (78:0→1).
9) Jugal: contacts parietal (92:1→0; A).
10) Quadrate shaft: subvertical (109:0→1).
11) Medial aperture of the recessus scalae tympani (MARST): between basioccipital and opisthotic (116:1→0; A).
12) Posterior auditory foramen: bordered by opisthotic (otooccipital) posteromedially (117:1→0; A).
13) Trabecular facets visible in ventral view of enlarged parabasisphenoid rostrum (125:1→0; A).
14) Laterosphenoid bridge in prootic (“ophidiosphenoid” of Gauthier et al. [2012]): present, forming vertical bar between exits of V2 and V3. (128:0→1).

15) Mental foramina on lateral surface of dentary: one (142:0→1; D).

16) Splenial and coronoid: contact very limited (point contact) or absent (153:0→1; D).

17) Surangular lateral foramina: single foramen (anterior surangular foramen) (165:0→1).

18) Marginal tooth implantation: teeth set in alveoli located along the dorsal margin of the dentigerous element (168:0→2).

19) Vertebral centrum annular constriction: constricted anterior to condyle, presence of a distinct neck (178:0→1; A).

20) Ovipary vs. ovovivipary/vivipary: ovovivipary to vivipary (220:0→1; A). Note: this synapomorphy is reversed in several groups of alethinophidian snakes.

COLUBROIDEA

1) Posterior dentigerous ramus of maxilla: does not extend posteriorly past the posterior margin of the orbit (16:1→0).
2) Ectopterygoid flange of maxilla: maxilla with distinct posteromedial (ectopterygoid) process (20:1→2).
3) Vomerine (choanal) process of palatine: does not meet parasphenoid (45:0→1; A).
4) Teeth on quadrate ramus of pterygoid (i.e., posterior to ectopterygoid process): present, dentition extends posteriorly well past the posterior end of ectopterygoid (55:0→1).

5) Medial aperture of the recessus scalae tympani (MARST): entirely within opisthotic (116: 0→1; D).
6) Posterior ventral surface of parabasisphenoid: smooth posteriorly, lacking midsagittal keel or crest (122:2→0; D).
7) Juxtastapedial space (depressed area immediately surrounding fenestrae ovalis and rotunda): crista tuberalis contacts prootic and the ventral margin of the crista interfenestralis is hidden in lateral view (130:1→2). Note: reversed in some colubroids.
8) Sagittal eminence on parietal: absent, dorsal surface of parietal flat (134:1→0; D).
9) Medial wall of adductor fossa: expanded dorsally beyond lateral wall of adductor fossa (163:0→1; A). Note: this synapomorphy is reversed in some colubroids.
10) Parapophyseal processes (distinct processes projecting from ventral margin of synapophyses, these processes are not an extension of the rib articular surface): present (180:0→1).
11) Ovipary vs. ovovivipary/vivipary: ovipary (220:1→0; D). Note: this synapomorphy is reversed in several colubroids.
12) M. retractor vomeris: present (224:0→1; D).

The synapomorphies retrieved for the clade inclusive of all fossil snakes (*Yurlunggur*, *Wonambi*, *Najash*, *Dinilysia*, *Pachyrhachis*, *Haasiophis*, and *Eupodphis*) are listed below:

1) Nasal-frontal contact: sutural (23:1→0; A).
2) Vertical lamina of nasal: does not contact frontal (26:0→1).
3) Palatine-vomer contact: palatine has extensive contact with vomer (sutured or fused) (42:2→0; A).
4) Prefrontal-nasal contact: prefrontal fully separated form nasal by fissure or gap (67:2→3).
5) Medial descending process of frontal: absent (78:1→0; A).
6) Optic foramen: located between parietal, frontal and parabasisphenoid (80:0→3).
7) Postorbitofrontal ossification: one discrete ossification, either in front of frontoparietal suture or clasping the frontoparietal suture, lacking a posterior process: postfrontal (81:4→1).
8) Jugal contact with maxilla and ectopterygoid: jugal contacts maxilla, but not ectopterygoid (91:2→0).
9) Large, laterally expanded crest for m. levator pterygoidei on parietal: present (96:0→1).
10) Basipterygoid process: prominent, i.e., a pedicel or flange (118:1→0; D).
11) Posterior ventral surface of parabasisphenoid: smooth posteriorly, lacking midsagittal keel or crest (122:2→0; A).
12) Laterosphenoid bridge in prootic: absent, V2 and V3 exits of trigeminal foramen confluent (128:1→0).
13) Small, square, posterodorsal flange of splenial bordering the inferior alveolar foramen posteriorly: absent (152:0→1; A).

14) Surangular, lateral foramina: two foramina, anterior and posterior (165:1→0; A).

15) Paracotylar foramina (foramen on anterior surface between cotyle and transverse process): present (183:1→0).

16) Caudal/postcloacal vertebrae: with articulated “chevron bones” (i.e., elements consisting of neural arch and neural spine) (189:3→0; A).

17) Pelvis: present and connected to the axial skeleton (sacrum) (196:1→0; A).

18) Hindlimb: hindlimb present, with distinct femur, tibia and fibula (197:1→0; A).

Combined Morphological and Molecular Data: Bayesian

The tree obtained from the Bayesian analysis of the morphological and molecular data set (indels and protein) (run 1: ln[L]=-41638.55; run 2: ln[L]=-41640.29) (Fig. 8-4) differs in several details from the consensus tree obtained from the same data set through parsimony analysis. These differences include: (1) *Lacerta* is now moved away from (*Tupinambis*, *Bachia*) and placed at the base of Amphisbaenia; (2) Amphisbaenia and *Lacerta* are forming a clade that is the sister group of (*Tupinambis*, *Bachia*); (3) *Pontosaurus* and the mosasauroids are placed in a polytomy with Iguania and Anguimorpha; (4) Scolecophidia are not monophyletic, *Leptotyphlops* is in a more derived position than (*Typhlops*, *Liotyphlops*); (5) *Cylindrophis*, *Anomochilus*, and *Uropeltis* form a clade in a polytomy with *Anilius*, *Tropidophis*, a clade consisting of all fossil snakes, and another clade that contains all remaining alethinophidians; (6) *Wonambi* and *Yurlunggur* form a clade; (7) *Calabaria* is placed at the base of booids (not nested within); (8) *Loxocemus*, *Python* and *Xenopeltis* no longer form a clade (i.e., *Xenopeltis* is more derived); (9) *Acrochordus* and *Casarea* are inverted in position; (10) *Homalopsis* is no longer the sister taxon to *Atractaspis* and elapids, but occupies a position at the base of *Atractaspis*, elapids and (*Heterodon* (*Lampropeltis*, *Thamnophis*)).

The tree obtained from the Bayesian analysis of the morphological and molecular data set (indels and DNA) (run 1: ln[L]=-86242.94; run 2: ln[L]=-86246.25) (Supplementary Data 8-4, Fig. 8-6S) is very similar to the previous tree. The differences are as follows: (1) the branch connecting Iguania and Anguimorpha is very close to being collapsed into a polytomy (PP=55); (2) *Heloderma* and *Xenosaurus* are not sister taxa (*Heloderma* is more basal); (3) *Leptotyphlops* and *Liotyphlops* are inverted in position; (4) the clade inclusive of all fossil snakes is the most basal group of snakes above the paraphyletic "Scolecophidia"; (5) *Xenopeltis* forms a clade with *Loxocemus* and *Python* (instead of being more derived than both); (6) *Casarea* and *Acrochordus* are inverted in position; (7) *Pareas* does not form a clade with Viperidae; (8) *Micrurus* and *Laticauda* are inverted in position.

The compatibility analysis (Templeton's test; Templeton, 1983) between the trees obtained through parsimony and Bayesian analyses shows no statistically significant difference ($p>0.05$) between the parsimony trees and the Bayesian tree based on morphology and protein sequences; a statistically significant difference (p<0.05) was found between the parsimony tree and the Bayesian tree based on morphology and DNA sequences. When the parsimony analysis was constrained after the Bayesian tree obtained from morphological data and protein sequences, the search yielded 9 trees (5437 steps, CI=0.42, RI=0.67, RC=0.32). The only uncertainty in these trees revolved around the ingroup relationships of the clade constituted by all fossil snakes. Interestingly, this constrained search resulted in a more extensive list of synapomorphies for the clade Ophidia, compared to the unconstrained analysis (68 synapomorphies). Of the 68 synapomorphies, many were shared with the unconstrained analysis, but many were new or different states of the same character (marked with *) ('A' indicates synapomorphies retrieved only with Acctran optimization, 'D' indicates synapomorphies only retrieved with Deltran optimization; bold arrow indicates an unambiguous transformation):

1) Premaxillary palatal foramina: paired (8:3→0; A).
2) Contact between premaxilla and vomers: contact limited (point contact) (10:0→1; A).
3) Palatine shelf/process of maxilla: a distinct triangular, square or lobe-shaped process is present on the medial margin of the maxilla. The base of this process is typically 1/3 or less of the length of the maxilla (14:0→2; A).*
4) Nasals: pierced by several foramina (22:0→1; A). Note: this is a feature typical of Scolecophidians (retrieved as paraphyletic in this analysis) and is modified in more derived forms.

5) Vertical medial lamina of nasal: present (24:0→1).
6) Pterygoid quadrate ramus: rod-like (53:0→1; A). Note: this is a feature typical of Scolecophidians (retrieved as paraphyletic in this analysis) and is modified in more derived forms.
7) Epipterygoid: absent (56:0→1).
8) Ectopterygoid: anterior end of ectopterygoid with single anterior process projecting dorsally along maxilla (60:0→1; A).*
9) Posterior transverse wall of prefrontal: neither pierced nor notched (73:0→3; D). Note: this state is typical of scolecophidians, but not of other snakes.
10) Lateral descending processes of frontals: in contact below olfactory tracts (76:0→1).
11) Postorbitofrontal ossification(s) in adults: no discrete ossifications (81:0→4).
12) Jugal anteroventral ramus extending dorsal to maxilla: absent (88:0→1).
13) Parietal has firm sutural contact with prootic anterolaterally, and extends ventrally to contact parabasisphenoid (99:0→2).*
14) Posterolateral (supratemporal or suspensorial) processes of parietal: posterolateral margin of parietal with a distinct flat triangular flange forming the roof of the skull (102:0→1).
15) Squamosal: absent (103:0→1).

16) Dorsoposterior (suprastapedial) process of quadrate: small or absent (108:0→1; A).

17) Prootic alar process (i.e., portion of prootic extending above trigeminal notch, foramen, or foramina): small or absent (113:1→0; A). Note: this state is typical of scolecophidians, but not of other snakes.

18) Crista sellaris: absent or poorly differentiated (121:0→1).

19) Trigeminal foramen, lateral anterior margin: closed by parietal (129:2→0).

20) Juxtastapedial space (depressed area immediately surrounding fenestrae ovalis and rotunda): crista tuberalis contacts prootic and the ventral margin of the crista interfenestralis is hidden in lateral view (130:0→2; A).* Note: this is a feature typical of Scolecophidians (retrieved as paraphyletic in this analysis) and is modified in more derived forms (reversal in some colubroids).

21) Paroccipital process (= joined posterolateral rami of prootic and exoccipital-opisthotic): indistinct or absent (132:0→1).

22) Supraoccipital-parietal suture: supraoccipital sutured to parietal along entire anterodorsal margin (135:0→1; D).

23) Foramen within splenial (= inferior alveolar foramen or posterior mylohyoid foramen): absent (151:1→0; A).

24) Coronoid-angular contact: coronoid contacts angular (155:0→1; A).

25) Anterior end of coronoid: contacts dentary at anterior end, no lateral process present (156:0→1).*

26) Surangular and articular + prearticular: fused together, no suture visible (compound bone) (166:0→1; D).

27) Number of precloacal vertebrae: about 120 or more (174:0→1).

28) Neural spine on mid-trunk vertebrae: low ridge or absent (182:0→1; A).

29) Lymphapophyses (forked cloacal ribs): present (187:0→1).

30) Caudal/postcloacal vertebrae: no processes project from ventral surface of caudal centra (189:0→3).*

31) Ribs: posterodorsal tuber costae well developed (191:0→1).

32) Clavicle: absent (192:0→1).

33) Pelvis: present, but not connected to the axial skeleton (no sacrum) (196:0→1).

34) Hindlimb: hindlimb vestigial, with one bone (femur) only, sometimes with a single distal spur (197:0→1; A).

35) Type of retina: only rods present (214:2→1).* Note: this is a feature typical of Scolecophidians (retrieved as paraphyletic in this analysis) and is modified in more derived forms.

36) Spectacle: eye covered by a head scale (215:0→2). Note: this is a feature typical of Scolecophidians (retrieved as paraphyletic in this analysis) and is modified in more derived forms.

37) M. retractor pterygoidei: present (225:0→1).

38) External auditory meatus (ear opening): absent (226:0→1).

Some synapomorphies from the unconstrained analysis were not produced by the constrained analysis: 27(0→1); 35(0→1); 39(0→1); 67(0→1); 87(0→1); 136(1→0); 142(0→1).

Molecular Partitions 1&2, a Test for Consistency: Maximum Likelihood

The phylogenetic trees obtained from the Maximum Likelihood analyses of the two molecular partitions provide relationships that are somewhat similar in the broad strokes, but differ in several details (Supplementary Data 8-4, Figs. 8-7S, 8-8S). More in particular, the tree obtained from Partition 2 (RAG1, SLC8A1, SLC30A1, TRAF6, ZEB2) (ln[L]=-39666.93) (Supplementary Data 8-4, Fig. 8-8S) differs from that obtained from Partition 1 (BDNF, C-Mos, FSHR, GPR149, NGFB) (ln[L]=- 41627.66) (Supplementary Data 8-4, Fig. 8-7S) in the following points: (1) In the tree based on Partition 2 *Gekko* and *Lialis* do not form the sister group of *Dibamus*, but are placed in a more derived position; (2) In the tree based on Partition 2 Iguania is basal to Anguimorpha, rather than its sister group; (3) within Iguania, *Agama* and *Chamaeleo* are swapped in position; (4) within Anguimorpha, *Heloderma* and *Xenosaurus* are swapped in position; (5) within Ophidia, *Liotyphlops* and *Typhlops* are swapped in position; (6) In the tree based on Partition 2, within Ophidia, *Loxocemus* and *Python* do not form a sister group to *Xenopeltis*; (7) In the tree based on Partition 2 *Cylindrophis* and *Uropeltis* do not form the sister group of (*Calabaria* (*Charina*, *Ungaliophis*) (*Eryx* (*Epicrates*, *Boa*)))), they form the sister group of (*Loxocemus*, *Python*) instead; (8) *Calabaria* and *Eryx* are swapped in position; (9) *Xenopeltis* and *Casarea* are swapped in position; (10) *Causus* and *Azemiops* are swapped in position; (11) *Micrurus* and *Naja* are swapped in position.

Molecular Partitions 1&2, a Test for Consistency: Parsimony

The strict consensus of the 187 most parsimonious trees (2507 steps, CI=0.52, RI=0.68, RC=0.38) (Supplementary Data 8-4, Fig. 8-9S) retrieved from the analysis of Partition 1 is in general agreement with the ML tree obtained from the analysis of the same partition. The only points of disagreement are: (1) *Lacerta* is sister taxon to *Tupinambis*, so that Amphisbaenia are monophyletic; (2) the anguimorphans *Heloderma* and *Xenosaurus* are swapped in position; (3) *Typhlops* is the most basal snake.

The strict consensus of the 42 most parsimonious trees (1754 steps, CI=0.44, RI=0.60, RC=0.31) (Supplementary Data 8-4, Fig. 8-10S) retrieved from the analysis of Partition 2 retains some general points of agreement with the strict consensus from Partition 1, however, there are several inconsistencies both with this tree and the tree obtained from the same partition through ML. For example, this consensus shows *Lacerta* as sister taxon to *Rhineura*, but *Lacerta* is the sister taxon of *Tupinambis* in the consensus from Partition 1, and is placed between *Rhineura* and *Bipes* in the ML tree obtained from the same partition. Many of the relationships within the Ophidia could not be resolved using this data set.

Molecular Partitions 1&2, a Test for Consistency: Bayesian

The phylogenetic trees obtained from Bayesian analysis of the two molecular partitions (DNA) (Partition 1: run 1 ln[L]=-39488.47 and run 2 ln[L]=-39489.88; Supplementary Data 8-4, Fig. 8-11S) (Partition 2: run 1 ln[L]=-41559.13 and run 2 ln[L]=-41559.35; Supplementary Data 8-4, Fig. 8-12S) are mostly identical to the trees retrieved from the ML analyses. The only difference can be observed for Partition 2, where the Bayesian tree retrieved *Xenopeltis* in a position just above (*Anilius*, *Tropidophis*) rather than at the base of *Casarea* plus all Caenophidia. However, the branch length supporting this difference is very short in both trees.

Testing the Effect of Taxon Sampling: Fossils Removed

Removal of all fossil taxa from the analysis of the morphological and molecular data (indels and protein) resulted in 2 most parsimonious trees (5321 steps, CI=0.43, RI=0.67, RC=0.33) (Supplementary Data 8-4, Fig. 8-13S) that show no change in the relationships of extant squamates. The Amphisbaenia is still the sister group of the Ophidia. The only difference between this analysis and that inclusive of all taxa, is some uncertainty regarding the placement of the clade (*Lacerta* (*Tupinambis*, *Bachia*), which is either placed as the sister group of the clade inclusive of Iguania and Anguimorpha, or at the base of this clade and its sister group which include Amphisbaenia and Ophidia.

Testing the Effect of Taxon Sampling: Amphisbaenia Removed

When amphisbaenians are removed from the analysis (102 most parsimonious trees; 5026 steps, CI=0.44, RI=0.67, RC=0.33) (Supplementary Data 8-4, Fig. 8-14S) the next closest clade becomes the new sister group to the Ophidia. In half of the trees (51) this clade consists of the Mosasauroidea plus *Pontosaurus*, and in the other half it consists of the Mosasauroidea only (*Pontosaurus* is the next more basal taxon).

Testing the Effect of Taxon Sampling: Scolecophidia Removed

When scolecophidians are removed from the analysis the effect on the tree topology is quite unexpected. The analysis retrieved 406 trees (5038 steps, CI=0.44, RI=0.68, RC=0.34) (Supplementary Data 8-4, Fig. 8-15S), and the differences are as follows: (1) Amphisbaenia is moved away from its sister group position with the Ophidia and is placed in a polytomy with *Lacerta*, *Tupinambis* and *Bachia*; (2) Iguania and Anguimorpha are no longer sister groups (Anguimorpha occupies a more derived position); (3) The fossil snakes *Dinilysia*, *Pachyrhachis*, *Eupodophis* and *Haasiophis* form a polytomy at the base of the clade Ophidia, followed by an unresolved clade which includes *Wonambi*, *Yurlunggur* and *Najash*; (4) *Anomochilus* and *Uropeltis* are sister taxa and are placed in a polytomy with *Cylindrophis* and the clade inclusive of all other extant snakes.

Constrained Analysis and Templeton’s Test: Ophidia as Sister Group of Other Squamates

When Ophidia was constrained as the sister group of all other squamates, the parsimony analysis retrieved 204 most parsimonious trees (5452 steps). The Templeton’s test between these trees and those retrieved in the analysis of the unconstrained dataset (5414 steps) found a statistically significant difference between the two pools of trees (null hypothesis was rejected, $p<<0.05$).

Constrained Analysis and Templeton’s Test: (Anguimorpha, Ophidia)

When Anguimorpha and Ophidia were constrained as sister groups, the parsimony analysis retrieved 459 most parsimonious trees (5424 steps). The Templeton’s test between these trees and those retrieved in the analysis of the unconstrained dataset (5414 steps) retrieved no statistically significant difference between the two pools of trees (null hypothesis was not rejected, $p>>0.05$).

Constrained Analysis and Templeton’s Test: (*Pontosaurus*, Mosasauroidea) Ophidia))

When the clade (*Pontosaurus*, Mosasauroidea) was constrained to be the sister group of the Ophidia, the parsimony analysis retrieved 153 most parsimonious trees (5417 steps). The Templeton’s test between these trees and those retrieved in the analysis of the unconstrained dataset (5414 steps) retrieved no statistically significant difference between the two pools of trees (null hypothesis was not rejected, $p>>0.05$).

Constrained Analysis and Templeton's Test: (*Anomochilus*, *Uropeltis*, Scolecophidia)

When Scolecophidia was constrained to be in the same clade as *Anomochilus* and *Uropeltis* (two very scolecophidian-like alethinophidians), the parsimony analysis retrieved 231 most parsimonious trees (5440 steps). The Templeton's test between these trees and those retrieved in the analysis of the unconstrained dataset (5414 steps) retrieved 66 trees that show no statistically significant difference with the trees from the unconstrained analysis (null hypothesis was not rejected, $p>0.05$). The strict consensus of these 66 trees is shown in Figure 8-5. It is interesting to note that the strict consensus of these 66 trees is very similar to the strict consensus obtained when the Scolecophidia were removed from the analysis (Supplementary Data 8-4, Fig. 8-15S): (1) Amphisbaenia is moved away from its sister group relationship with the Ophidia and is placed in a clade with *Lacerta*, *Tupinambis* and *Bachia*; (2) Iguania and Anguimorpha are no longer sister groups (Anguimorpha occupies a more derived position); (3) The fossil snakes *Dinilysia*, *Pachyrhachis*, *Eupodophis* and *Haasiophis* form a polytomy at the base of the clade Ophidia, followed by an unresolved clade which includes *Wonambi*, *Yurlunggur* and *Najash*. In a position more derived that that occupied by (*Wonambi*, *Yurlunggur*, *Najash*) is the clade (*Anomochilus* (*Uropeltis* (*Leptotyphlops* (*Typhlops*, *Liotyphlops*)))).

Constrained Analysis and Templeton's Test: Scolecophidia within Colubroidea

When the Scolecophidia was constrained to be placed within Colubroidea (to test whether or not these forms may represent aberrant viperids or atractaspidids) the parsimony analysis retrieved 1260 most parsimonious trees (5474 steps), where scolecophidians form a clade at the base of Colubroidea. The Templeton's test between these trees and those retrieved in the analysis of the unconstrained dataset (5414 steps) retrieved a statistically significant difference between the two pools of trees (null hypothesis was rejected, $p<<0.05$).

Considering the possibility that scolecophidians may not be monophyletic, a second analysis was run enforcing a constraint where only *Liotyphlops* and *Typhlops* were forced to be within colubroids (*Liotyphlops* and *Typhlops* are the two scolecophidians that are more viper-like, due to features like the hinged maxillae and presence of a tracheal lung). This second constrained analysis retrieved 12 trees (5478 steps) where *Typhlops* and *Liotyphlops* are placed at the base of Colubroidea. These trees show a statistically significant difference from the trees obtained from the unconstrained analysis ($p<<0.05$).

DISCUSSION

Morphological Data

The results of the parsimony and Bayesian analyses of the morphological dataset share some similarities with those presented by Conrad (2008) and Gauthier et al. (2012). Like in Conrad (2008) and Gauthier et al. (2012) dibamids and amphisbaenians are found to be the closest relatives of snakes; however, in the present study amphisbaenians do not form a monophyletic group, but a paraphyletic series at the base of the Ophidia in the parsimony analysis and an unsolved polytomy with the Ophidia in the Baysian analysis. Moreover, *Dibamus* rather than amphisbaenians is the sister taxon to the Ophidia in the parsimony analysis (but not in the Baysian tree).

Similar to Gauthier et al. (2012), the parsimony analysis found support for a monophyletic Scolecophidia, but the Bayesian analyses in both studies found this group to be possibly paraphyletic. Possible paraphyly of the Scolecophidia is also suggested by Conrad (2008).

The position of the fossil snakes *Dinilysia* and *Najash* differ from both studies; Gauthier et al. (2012) found these snakes at the base of the Ophidia (i.e., more basal than the Scolecophidia) in their parsimony tree, but in a more derived position (as the sister group of macrostomatans) in the Bayesian tree; Conrad (2008) found *Dinilysia* in a polytomy with *Pachyophis*, *Wonambi* and all other snakes (i.e., above the Scolecophidia; *Najash* was not included in that study).

The fossil snakes *Eupodophis*, *Haasiophis*, and *Pachyrhachis* form a clade that is the sister group to macrostomatan snakes in Conrad (2008), nested within macrostomatan snakes in the parsimony tree of Gauthier et al. (2012), and between (*Najash*, *Dinilysia*) an all other snakes in the Bayesian tree of Gauthier et al. (2012).

In the present study these fossil snakes are nested within a clade inclusive of all fossil forms. *Dinilysia* shifts from a position as the sister group of *Eupodophis*, *Haasiophis*, and *Pachyrhachis* in the parsimony analysis, to a position as the most basal fossil snake within the clade in the Bayesian tree. Regardless of the positioning of the most basal taxa within this clade of fossil snakes, the derived position of *Eupodophis*, *Haasiophis*, and *Pachyrhachis* within it suggests that the macrostomatan condition observed in these snakes evolved convergently with that of extant macrostmatan snakes. This scenario would explain why *Eupodophis*, *Haasiophis*, and *Pachyrhachis* still retain primitive features like the presence of well-developed hind limbs and chevron bones in the tail, features that are lost not only in all extant macrostomatans, but also in all other extant snakes.

With regard to the ingroup relationships of extant snakes, not much can be compared with Conrad (2008), who assumed the monophyly of anilioids and macrostomatans and combined them into two terminal taxa in his analysis. Gauthier et al. (2012), on the other hand, included several representatives of extant groups of snakes, so their results can be compared with those of the present study. Apart from the already discussed different position of the fossil snakes, the main differences between this and their study are as follows: (1) this study found the clade (*Tropidophis* (*Ungaliophis* (*Lichanura* (*Eryx* (*Python*, *Calabaria*) (*Epicrates, Boa*))))) as the sister group of (*Loxocemus*, *Xenopeltis*). Interestingly, with the only exception of *Tropidophis*, those taxa still form a clade also in the Bayesian tree of Gauthier et al. (2012), but they are arranged differently and the whole clade is placed in a position just above (*Loxocemus*, *Xenopeltis*) rather than as its sister group. In the parsimony tree of Gauthier et al. (2012) those taxa are divided into four successive clades leading towards the Caenophidia; (2) *Casarea* has a much more derived position in this study (sister group of the Caenophidia) compared to the parsimony tree of Gauthier et al. (2012); however, their Bayesian tree agrees with this study; (3) *Acrochordus* and *Xenodermus* are inverted in position (*Xenodermus* is more derived in the present study); (4) *Atractaspis* is not closely related to elapids in Gauthier et al. (2012), instead is placed in a clade at the base of the colubroid radiation. Interestingly, both studies found Viperidae to be nested within a paraphyletic Elapidae at least in some of the trees retrieved from the parsimony analysis (also in the Bayesian analysis in this study).

Overall, although the results of Gauthier et al. (2012) differ in some details from those presented here (especially the relationships of basal macrostomatans), most of the major relationships are consistent: amphisbaenians (paraphyletic or not) and/or dibamids are the closest relatives of snakes; Scolecophidia are a group of basal snakes, and are possibly paraphyletic; the position of *Najash* and *Dinilysia* as more derived than

Anomochilus, *Uropeltis*, *Anilius* and *Cylindrophis* is consistent with the Bayesian tree of Gauthier et al. (2012); the Caenophidia and most of its broad internal relationships (only exception of *Atractaspis*) are consistent between the two studies.

Postcranial characters were excluded from the analysis, in order to see if axial elongation and limb-loss could be responsible for the grouping of snakes and other axially elongated and limbless forms. However, the strict consensus of the 5345 trees retrieved in this analysis shows that this is not the case. Clearly, cranial characters are also responsible for placing *Dibamus* and amphisbaenians as the closest realtives of snakes. The internal relationships of the clade Ophidia were minimally affected by the exclusion of the postcranial characters, and the major change observed was in the positioning of the clade (*Haasiophis*, *Pachyrhachis*, *Eupodophis*), which was placed as the sister group of *Calabaria*, i.e., within extant macrostomatan snakes. This was somewhat expected, considering that removal of postcranial characters implies ignoring primitive features of these snakes like the presence of well-developed hind limbs and chevron bones in the tail. When those characters are removed, the modified macrostomatan structure of the skull places these fossil snakes within extant macrostomatans.

Gauthier et al. (2012) suggested that the close phylogenetic relationship of snakes, amphisbaenians, dibamids and other limbless forms may well be the result of convergent evolution due to similar lifestyles (i.e., burrowing or cryptic). If we consider the low consistency index and rescaled consistency index of the morphological analyses (with and without postcranial characters; CI=0.27, RC=0.21) we can infer that homoplastic morphological traits are widespread within Squamata. For this reason it is valuable to explore other sources of data that can complement the morphological characters and provide a phylogenetic signal that is independent from the ecological habits of the taxa under consideration. These data comes in the form of DNA sequences and their potential to approach the “true” phylogeny will be discussed in the next section.

Molecular Data

The most recent and comprehensive (44 nuclear genes) molecular study is that of Wiens et al. (2012). Pyron et al., (2013a) also presented an extensive study of squamate relationships, but despite the enormous number of species considered (4161), they only used 12 genes, five of which were mitochondrial, to sort out phylogenetic relationships. However, the results of Pyron et al. (2013a) only differ from those of Wiens et al. (2012) in minor details (e.g., in Pyron et al. [2013a] Anomalepididae are the most basal snakes, the Booidea are organized differently, Acrochordidae is the sister group of Xenodermatidae), so, for sake of conciseness, only Wiens et al. (2012) will be compared here with the results of the present study. The results of the ML analysis of the molecular data presented here agree very well with those of Wiens et al. (2012). The only noticeable difference between the two studies resides in the position of *Casarea*, which according to Wiens et al. (2012) should be placed at the base of the clade (*Calabaria* (*Eryx* (*Boa*, *Epicrates*) (*Lichanura* (*Exiliboa*, *Ungaliophis*)))), while in this study is placed either as the sister taxon to *Acrochordus* plus colubroids (ML tree and Bayesian tree based on DNA), or swapped in position with *Acrochordus* as the sister taxon to colubroids (Bayesian and parsimony trees based on protein data). However, *Casarea* is a problematic taxon, whose position fluctuates in the phylogeny depending on the dataset (e.g., Pyron et al. [2013a] place *Casarea* in yet a different position).

Such general agreement is partly to be expected, because this dataset is a subset of that of Wiens et al. (2012) both in terms of taxa and sequences; however, it is interesting to see that even with far fewer genes (10 vs 44) the phylogenetic signal remains strong enough to provide a consistent result. Internal consistency of the molecular data was also tested by partitioning the molecular data in this study. The two partitions (5 genes each) showed that regardless of the methodology used to reconstruct the phylogeny (parsimony, maximum likelihood, or Bayesian) and of the format of the data (either base or protein sequences), the results are quite consistent between partitions and agree with the phylogeny obtained from the analysis of the whole data set. If genes were evolving randomly (i.e., independently from the phylogeny) then a great inconsistency between partitions should be observed. Instead, the inconsistencies observed were mostly limited to the placement of a few taxa between the clade (*Anilius*, *Tropidophis*) and the Caenophidia, where branch lengths are very short (i.e., evolutionary relationships cannot be resolved because of the limited number of changes in the sequences).

Moreover, it is to be noted that the combination of the molecular data into a single data set produced trees that were always better supported. The ML tree from the combined molecular data shows an overall increase in bootstrap support (44 nodes show BS>75 [30 nodes have BS=100] in the tree from the combined data, against 39 nodes with BS>75 in each partition [19 nodes have BS=100 in Partition 1; 13 nodes have BS=100 in Partition 2]); the Bayesian analysis produced trees that are very similar to the maximum likelihood trees and also here the tree from the combined data set shows the strongest support in the form of posterior probabilities (only 8 nodes show PP<95 in the tree from the combined data, against 13 and 11 nodes in the trees from Partition 1 and Partition 2, respectively); finally, the parsimony analysis also produced a better supported tree when the data were combined (24 nodes show BS>75 [8 nodes have BS=100] in the tree from the combined data, against 18 nodes with BS>75 in Partition 1 [4 nodes have BS=100] and 8 nodes with BS>75 in Partition 2 [2 nodes have BS=100]). This is a clear indication of the fact that adding more molecular data strengthens the phylogenetic signal, and implies that different nuclear genes, regardless of their position in the genome, tend to reconstruct the same evolutionary history. A series of questions that should be raised at this point are: can the molecular data provide a robust framework into which morphological data can be incorporated? Can this molecular signal overcome the disrupting noise generated by morphological homoplasy and enhance the phylogenetic signal of morphological data? These questions will be addressed in the next section.

Combined Data

After combining morphological and molecular data, and including fossil taxa in the analysis, different authors came to conflicting results (e.g., Lee, 2005, 2009; Wiens et al., 2010).

Lee (2005b, 2009), in the combined analysis of morphological and molecular data, found snakes to be nested within Anguimorpha, and in particular in a position closely related to *Adriosaurus*, Dolichosauridae and Mosasauroids. With regard to the ingroup relationship of snakes, Lee (2005) found *Pachyrhachis* and *Haasiophis* to be in a polytomy at the base of the Ophidia, followed by a monophyletic Scolecophidia. The relationships of basal alethinophidians are poorly resolved, and several clades are joined into a polytomy. The clade Caenophidia (i.e., *Acrochordus* plus *Colubroidea*) is well resolved and shows the typical relationships retrieved in most of the recent molecular studies, with the Xenodermatidae and Viperidae at the base and Elapidae at the crown.

Wiens et al. (2010) found snakes to be either the sister group of Anguimorpha (inclusive of Mosasauria) plus Iguania (Bayesian analysis) or a clade between Iguania (at the base) and Anguimorpha (i.e., Ophidia was the sister group of the Anguimorpha) (parsimony analysis). Scolecophidia were found to be a paraphyletic assemblage of snakes located at the base of the ophidian radiation, followed by the fossil snake *Dinilysia*. The fossil snakes *Pachyrhachis*, *Haasiophis* and *Eupodophis* were found to form the sister group to the extant macrostomatan *Boa*. The position of the fossil snake *Wonambi* was dependant on the search method: it was found just above *Dinilysia* in the parsimony analysis and at the base of the clade (*Eupodophis* (*Haasiophis*, *Pachyrhachis*)) in the Bayesian analysis.

In this study, the parsimony analysis of the combined data produced a consensus tree (53 trees) that is in partial disagreement with Lee (2005b, 2009) and Wiens et al. (2009). Despite the inclusion of molecular data snakes are still placed as the sister group to a monophyletic Amphisbaenia, and the next closest relatives to Ophidia and Amphisbaenia are *Pontosaurus* plus the Mosasauroidea. However, in the Bayesian analysis based on morphological data and protein sequences, Ophidia is the sister group of a large clade inclusive of Iguania, Anguimorpha and (*Pontosaurus*, Mosasauroidea), and these three clades are joined in a polytomy. Except for the position of *Pontosaurus* and mosasauroids, this result is most in agreement with the Bayesian tree of Wiens et al. (2010). In the Bayesian analysis based on morphological and DNA sequences, the result is similar, but the branch joining Iguania and Anguimorpha is extremely short; the Ophidia are in a polytomy with the clades (Iguania, Anguimorpha) and (*Pontosaurus*, Mosasauroidea).

In order to test whether the differences observed between these hypotheses are statistically significant, a series of constrained parsimony analyses was performed (Templeton's test; Templeton, 1983). When the search was constrained to find the Ophidia as the sister group of the Anguimorpha (rather that of both Iguania and Anguimorpha) the parsimony search retrieved a set of trees (459) that show no statistically significant difference with the original topology that had snakes as the sister group of the Amphisbaenia. This means that the data collected in this study is not in disagreement with the results of Lee (2005b, 2009) and Wiens et al. (2010). To go even further in testing the compatibility between the results presented here and those of Lee (2005b, 2009), a second constrained search was performed with the Ophidia forced in a sister group relationship with the clade (*Pontosaurus*, Mosasauroidea). Once again, no statistically significant difference was found, and the two tree topologies (constrained and unconstrained) were found to be compatible.

Another set of constrained analyses (Templeton's tests) was performed in order to test the possibility that scolecophidian snakes may be an aberrant lineage of alethinophidian snakes, a possibility suggested by List (1966) and Dowling and Duellman (1978). Despite some superficial resemblance between typhlopids and burrowing asps (*Atractaspis*), the possibility that scolecophidians may represent an aberrant, perhaps neotenic, lineage of colubroid snakes had to be rejected. Trees constrained to have Scolecophidia (not necessarily monophyletic; i.e, a very loose constraint) nested within colubroids were found to be incompatible with the trees obtained from the unconstrained analysis. However, when the Scolecophidia were constrained to form a clade with *Anomochilus* and *Uropeltis* (two scolecophidian-like basal alethinophidians) the parsimony analysis produced 231 shortest trees, 66 of which were found to be statistically compatible with the tree from the unconstrained analysis. Furthermore, the placing of the Scolecophidia in a slightly more derived position within the Ophidia, away from the base of the clade, broke the link, probably due to long-branch attraction, between scolecophidians and Amphisbaenia, which were moved away from snakes and placed in a clade with *Bachia*, *Tupinambis* and *Lacerta* (i.e., towards the base of the tree). The new closest relatives of snakes became *Pontosaurus* and the Mosasauroidea (collapsed in a polytomy), and basal to them a clade inclusive of all extant anguimorphans (a phylogeny very similar to that of Lee [2005b, 2009]). At the base of the ophidian radiation, the most basal snakes were the fossil taxa *Dinilysia*, *Haasiophis*, *Eupodophis* and *Pachyrhachis*, all collapsed into a polytomy. This is an intriguing result, which apart from the position of the Scolecophidia is very similar to what Lee (2005, 2009) found in his analysis. It is important to note that such drastic change in the tree topology was triggered by a different placement of the Scolecophidia. The possibility that the Scolecophidia may be attracted towards the base of the Ophidia due to convergent traits with the Amphisbaenia (long-branch attraction) is definitely worth further investigation (note: as noted by Bergsten [2005], although molecular data is more prone to long-branch attraction, morphological data can also be affected).

To additionally explore the phenomenon of long-branch attraction, a series of experiments with taxon-sampling were also performed. Exclusion of fossil taxa or of the Amphisbaenia from the analysis did not affect the results in any major way, but exclusion of the Scolecophidia deeply affected the tree topology, and produced a consensus tree that is almost identical to that obtained when the Scolecophidia were constrained in a clade with *Uropeltis* and

Anomochilus. Once again, the Scolecophidia seem to play a major role in anchoring the Ophidia within Squamata in a position that is close to burrowing forms (i.e., amphisbaenians). If the Scolecophidia are excluded from the analysis, or constrained in a more derived position, both the ingroup and outgroup relationships of snakes are dramatically affected. Interestingly, this change in topology reflects a shift from an ancestral burrowing ecology for the most basal snakes to an aquatic ecology (i.e., the sister group of snakes is represented by marine reptiles and the most basal snakes are aquatic forms).

CONCLUSIONS

Despite a few doubts in the literature (e.g., Rieppel 1980, 1988), currently there seems to be a common consensus that snakes are nested within Squamata, and this result found further support in this study, where the constrained analysis with snakes as the sister group of all other squamates was found to be statistically incompatible with the topology obtained from the analysis of the unconstrained complete dataset (Templeton's test; Templeton, 1983). However, the position of snakes within Squamata and some of the ingroup relationships within the clade Ophidia itself remain elusive.

Molecular data definitely shows some promising features, as the inclusion of more and more nuclear genes results in an amplification of the phylogenetic signal and in a general increase in resolution. It is hard to believe that genes from completely different and unrelated parts of the genome could provide a consistent signal that is not due to common ancestry. Moreover, different methodologies (parsimony, maximum likelihood, and Bayesian) and different data formats (protein or DNA) all produce broadly consistent results. Minor differences are observed, but these are mostly due to uncertainties in the placement of certain taxa for which the molecular data still doesn’t provide enough information. Molecular data is not immune to homoplastic changes (parsimony analysis of the molecular dataset retrieved 159 trees with CI=0.48, RI=0.64, and RI=0.35), and some lineages are more affected than others (e.g., basal alethinophidians, whose relationships could not be completely and/or consistently resolved). However, there is hope that with the future addition of more molecular data (perhaps in the order of one hundred nuclear genes or more) also the smallest inconsistencies will eventually be resolved. Does this mean that molecular data alone will provide the final answer to all phylogeny-related questions? The answer is no. Several publications have shown the importance of including fossil taxa in phylogenies, and how these taxa can radically change the resulting tree topologies (e.g., Lee, 2005, 2009; Quental and Marshall, 2010; Wiens et al. 2010; Slater et al., 2012). Fossil taxa can only be included in phylogenetic analysis through the use of morphological characters, therefore morphological data remains vital for the reconstruction of the so-called “tree of life”. Moreover, molecular phylogenies provide a pattern of relationships, but tell us nothing about the order of morphological changes through time, so they don’t provide any insights on character transformations and evolutionary pathways. Systematists should still be able to categorize taxa based on shared morphological features, and a polymerase chain reaction should not be necessary every time a naturalist needs to identify a given species (see also Wiens [2004] for a detailed discussion of this topic).

One of the most interesting results of this study is that the sister group relationship between Amphisbaenia and Ophidia, commonly retrieved in morphological studies, is likely due to phenotypic convergence between the burrowing scolecophidians and amphisbaenians, and perhaps also a phenomenon of long-branch attraction (Bergsten, 2005). If the Scolecophidia are removed or constrained in a more derived position, or if Bayesian analysis is performed instead of parsimony (Bayeisan analysis is known to be less prone to long-branch attraction; Bergsten, 2005), amphisbaenians are no longer retrieved as the sister group of snakes.

Another intriguing result involves the fact that a clade inclusive of all fossil snakes was found in the analyses that included morphological data (i.e., with or without the addition of molecular data, and both under parsimony and Bayesian search criteria). What is interesting about this clade is that it opens up the possibility that the macrostomatan skull typical of advanced alethinophidian snakes may have evolved convergently within an extinct clade of fossil forms. This evolutionary scenario would explain why fossil taxa like *Haasiophis*, *Eupodophis*, and *Pachyrhachis* show adaptations for a larger gape (macrostomatan condition) together with plesiomorphic features like the retention of well-developed hindlimbs and chevron bones in the tail, features that are lost in all extant snakes.

One last interesting possibility raised by this study is that the Scolecophidia may be a branch of aberrant alethinophidians. No statistically significant difference was found when the parsimony analysis of the combined dataset was constrained to have scolecophidians in a clade with *Anomochilus* and *Uropeltis*. A hypothesis according to which the scolecophidians are an aberrant lineage of burrowing basal alethinophidians is in agreement with what was suggested by List (1966) and Dowling and Duellman (1978). Scolecophidians are too specialized to represent the ancestral body plan of snakes, and the fossil record does not support the presence of scolecophidian-like snakes among the oldest representatives of the clade. The oldest fossil ophidians known up to date all look more like typical alethinophidians than like any of the Scolecophidia (e.g., *Dinilysia*, *Najash*, *Coniophis*, *Haasiophis*, *Pachyrhachis*, *Eupodophis*). The position of the Scolecophidia at the very base of the tree in morphological studies is likely due to the above-mentioned phenomenon of long-branch attraction with other burrowing squamates (e.g., amphisbaenians). Molecular data seem to be less prone to the artifact of long-branch attraction, and still place scolecophidians at the base; however, similar to what happened in previous molecular studies (Heise et al., 1995; He et al., 2010; Wiens et al., 2010, 2012), all the analyses based on molecular data, and the Bayesian analyses based on morphology and molecules, retrieved a paraphyletic “Scolecophidia.” When the scolecophidians were found to form a monophyletic group (i.e., when morphological data was included and the search method was parsimony), the statistical support for the clade was invariably very low (BS<60). This is yet another result that casts doubts on our perceived knowledge of the phylogenetic position of these snakes, and may indicate that the group, or at least some of its members, may be placed elsewhere in the phylogeny. More data is certainly needed, both from the genome and the fossil record, to untangle this problem and obtain a better understanding of the series of anatomical transformations that lead to the origin of snakes.

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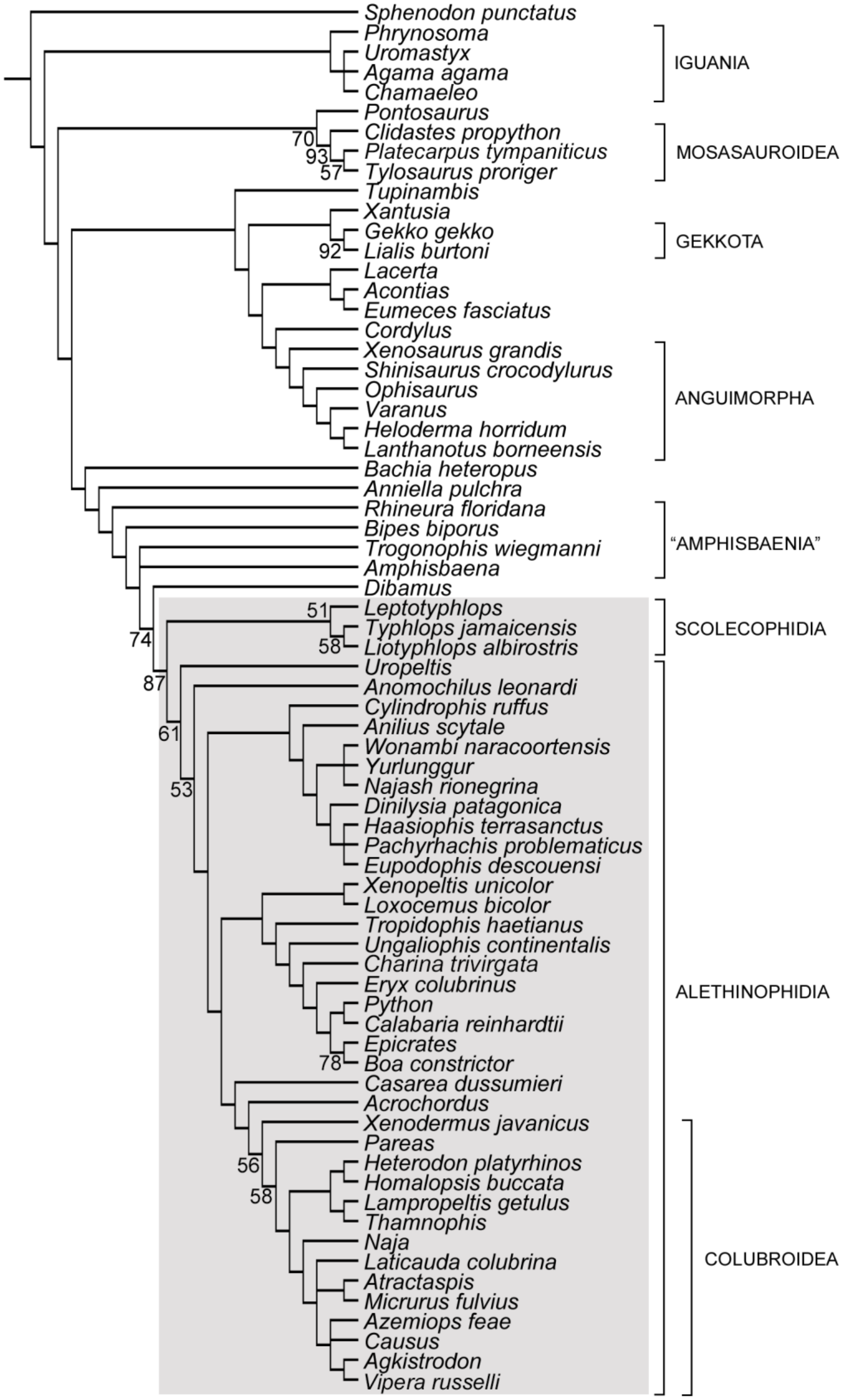
FIGURES

FIGURE 8-1. Strict consensus of 135 most parsimonious trees (1052 steps, CI=0.27, RI=0.75, RC=0.21) recovered from the parsimony analysis of the morphological data set (70 taxa, 227 characters [210 informative]). Numbers next to nodes are values of bootstrap support (1000 replicates; values below 50 are not shown). The gray box highlights the clade Ophidia.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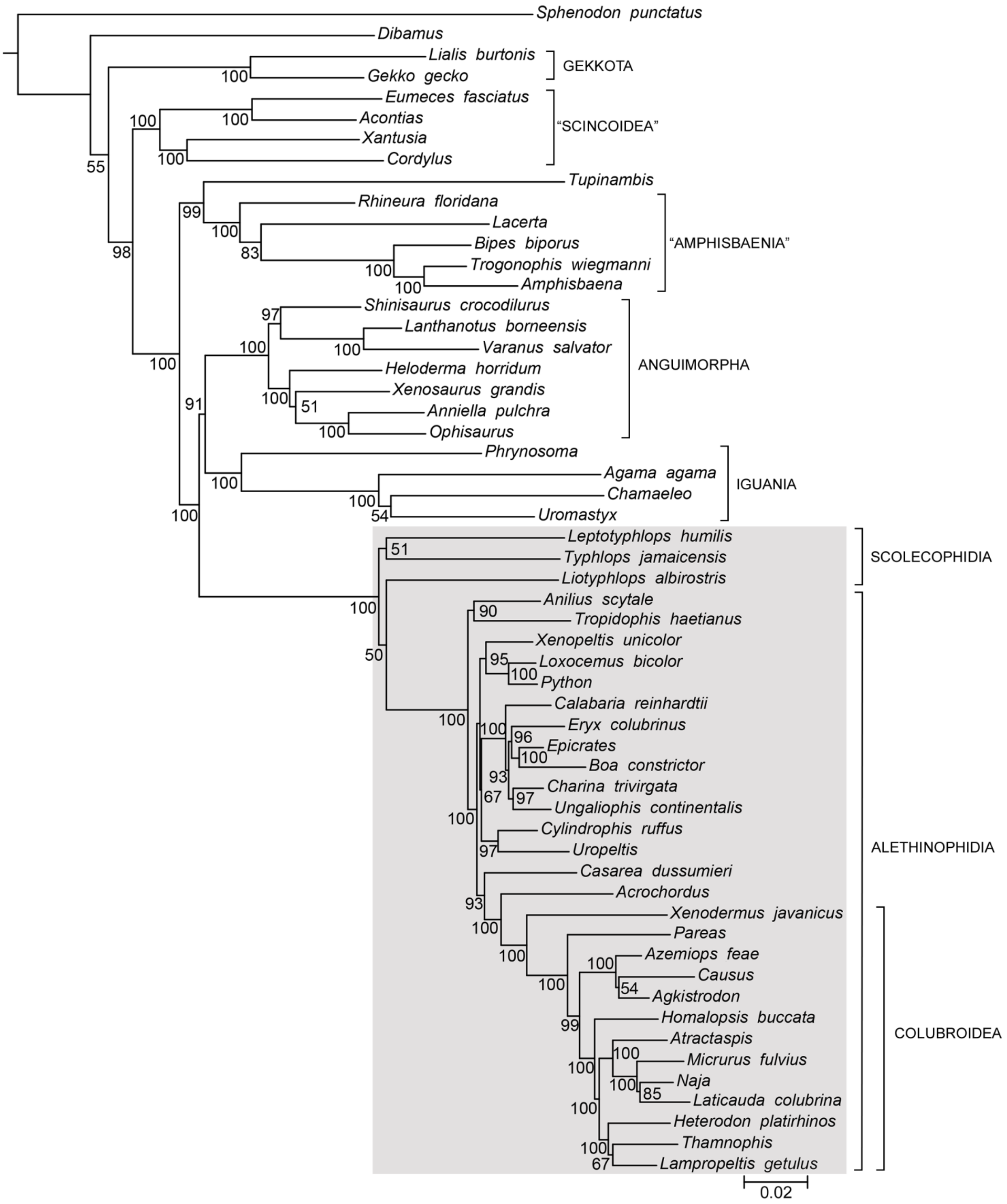
Phrynosoma
Uromastyx
Agama agama
Chamaeleo
IGUANIA
Pontosaurus
70
Clidastes propython
93
Platecarpus tympaniticus
57
Tylosaurus proriger
MOSASAUROIDEA
Tupinambis
Xantusia
Gekko gekko
92
Lialis burtoni
GEKKOTA
Lacerta
Acontias
Eumeces fasciatus
Cordylus
Xenosaurus grandis
Shinisaurus crocodylurus
Ophisaurus
Varanus
Heloderma horridum
Lanthanotus borneensis
ANGUIMORPHA
Bachia heteropus
Anniella pulchra
Rhineura floridana
Bipes biporus
Trogonophis wiegmanni
Amphisbaena
"AMPHISBAENIA"
Dibamus
51
Leptotyphlops
Typhlops jamaicensis
58
Liotyphlops albirostris
SCOLECOPHIDIA
74
87
Uropeltis
Anomochilus leonardi
61
Cylindrophis ruffus
Anilius scytale
Wonambi naracoortensis
Yurlunggur
53
Najash rionegrina
Dinilysia patagonica
Haasiophis terrasanctus
Pachyrhachis problematicus
Eupodophis descouensi
Xenopeltis unicolor
Loxocemus bicolor
Tropidophis haetianus
Ungaliophis continentalis
Charina trivirgata
Eryx colubrinus
Python
Calabaria reinhardtii
Epicrates
78
Boa constrictor
ALETHINOPHIDIA
Casarea dussumieri
Acrochordus
Xenodermus javanicus
Pareas
56
Heterodon platyrhinos
Homalopsis buccata
58
Lampropeltis getulus
Thamnophis
Naja
Laticauda colubrina
Atractaspis
Micrurus fulvius
Azemiops feae
Causus
Agkistrodon
Vipera russelli
COLUBROIDEA

FIGURE 8-2. Maximum Likelihood tree (ln[L]= -81486.4) based on the analysis of the complete molecular data set (DNA sequences of ten nuclear protein-coding genes, 56 taxa, 7155 sites). Numbers next to nodes are values of bootstrap support (values below 50 not shown). The gray box highlights the clade Ophidia.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Dibamus
Lialis burtonis
Gekko gecko
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GEKKOTA
Eumeces fasciatus
Acontias
100
100
Xantusia
Cordylus
100
"SCINCOIDEA"
55
Tupinambis
99
Rhineura floridana
100
Lacerta
83
Bipes biporus
100
Trogonophis wiegmanni
Amphisbaena
100
"AMPHISBAENIA"
98
Shinisaurus crocodilurus
97
Lanthanotus borneensis
100
Varanus salvator
100
100
Heloderma horridum
Xenosaurus grandis
100
51
Anniella pulchra
100
Ophisaurus
ANGUIMORPHA
91
Phrynosoma
100
Agama agama
100
Chamaeleo
54
Uromastyx
IGUANIA
100
Leptotyphlops humilis
51
Typhlops jamaicensis
Liotyphlops albirostris
SCOLECOPHIDIA
100
50
Anilius scytale
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Tropidophis haetianus
Xenopeltis unicolor
95
Loxocemus bicolor
100
Python
Calabaria reinhardtii
100
Eryx colubrinus
96
Epicrates
100
Boa constrictor
93
67
Charina trivirgata
97
Ungaliophis continentalis
100
Cylindrophis ruffus
97
Uropeltis
Casarea dussumieri
93
Acrochordus
100
Xenodermus javanicus
100
Pareas
100
Azemiops feae
Causus
54
Agkistrodon
99
Homalopsis buccata
Atractaspis
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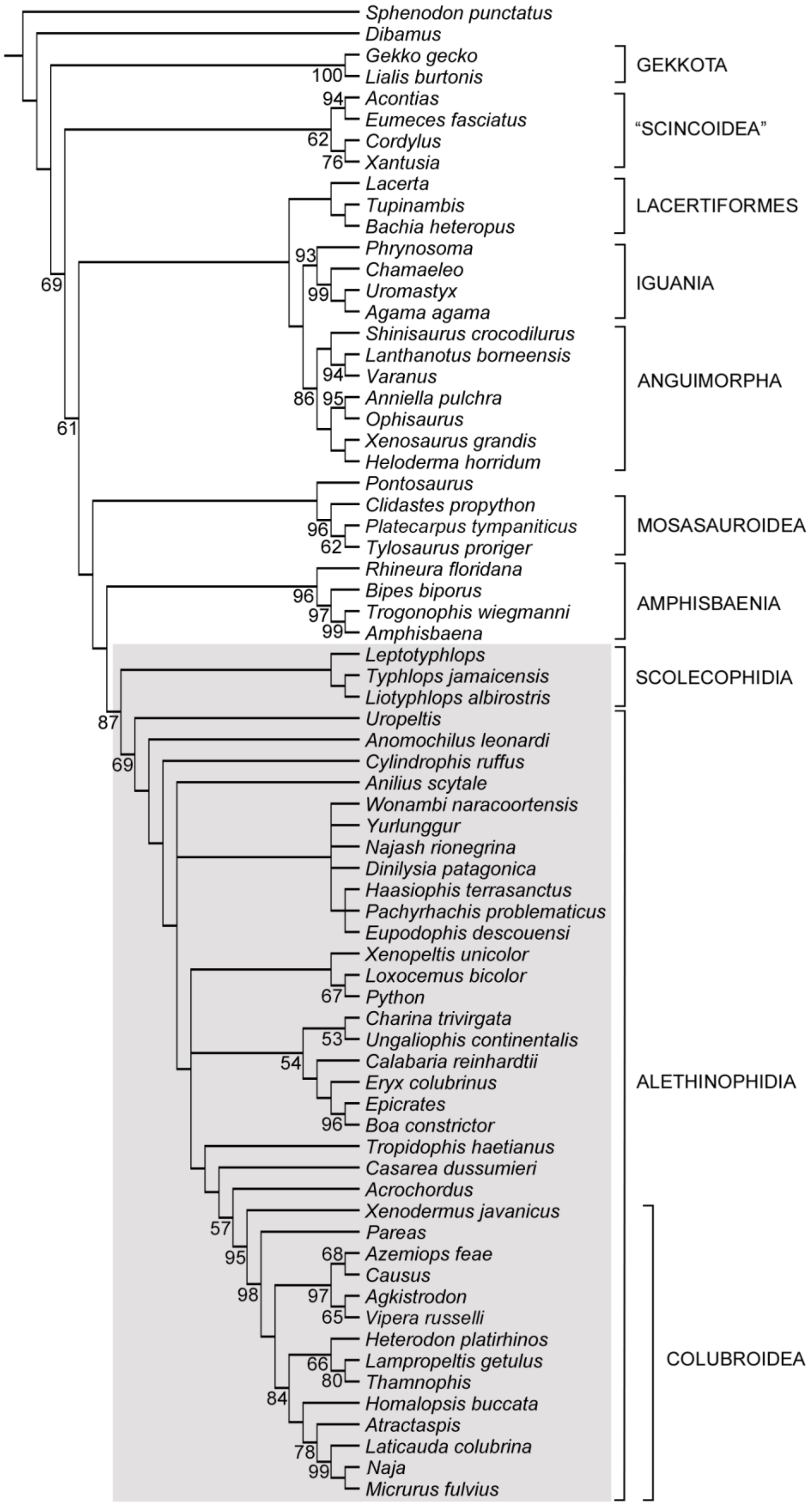
Micrurus fulvius
100
Naja
85
Laticauda colubrina
100
100
Heterodon platirhinos
100
Thamnophis
67
Lampropeltis getulus
ALETHINOPHIDIA
COLUBROIDEA
0.02

FIGURE 8-3. Strict consensus of 53 most parsimonious trees (5414 steps, CI=0.43, RI=0.67, RC=0.32) recovered from the parsimony analysis of the morphological and molecular (protein and indels) data set (70 taxa, 2630 characters [898 informative]). Numbers next to nodes are values of bootstrap support (1000 replicates; values below 50 are not shown). The gray box highlights the clade Ophidia.


Sphenodon punctatus
Dibamus
Gekko gecko
100
Lialis burtonis
GEKKOTA
94
Acontias
Eumeces fasciatus
62
Cordylus
76
Xantusia
"SCINCOIDEA"
Lacerta
Tupinambis
Bachia heteropus
LACERTIFORMES
69
93
Phrynosoma
Chamaeleo
99
Uromastyx
Agama agama
IGUANIA
Shinisaurus crocodilurus
Lanthanotus borneensis
94
Varanus
86
95
Anniella pulchra
Ophisaurus
Xenosaurus grandis
Heloderma horridum
ANGUIMORPHA
61
Pontosaurus
Clidastes propython
96
Platecarpus tympaniticus
62
Tylosaurus proriger
MOSASAUROIDEA
Rhineura floridana
96
Bipes biporus
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Trogonophis wiegmanni
99
Amphisbaena
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Leptotyphlops
Typhlops jamaicensis
Liotyphlops albirostris
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Cylindrophis ruffus
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Dinilysia patagonica
Haasiophis terrasanctus
Pachyrhachis problematicus
Eupodophis descouensi
Xenopeltis unicolor
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Python
Charina trivirgata
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Ungaliophis continentalis
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Calabaria reinhardtii
Eryx colubrinus
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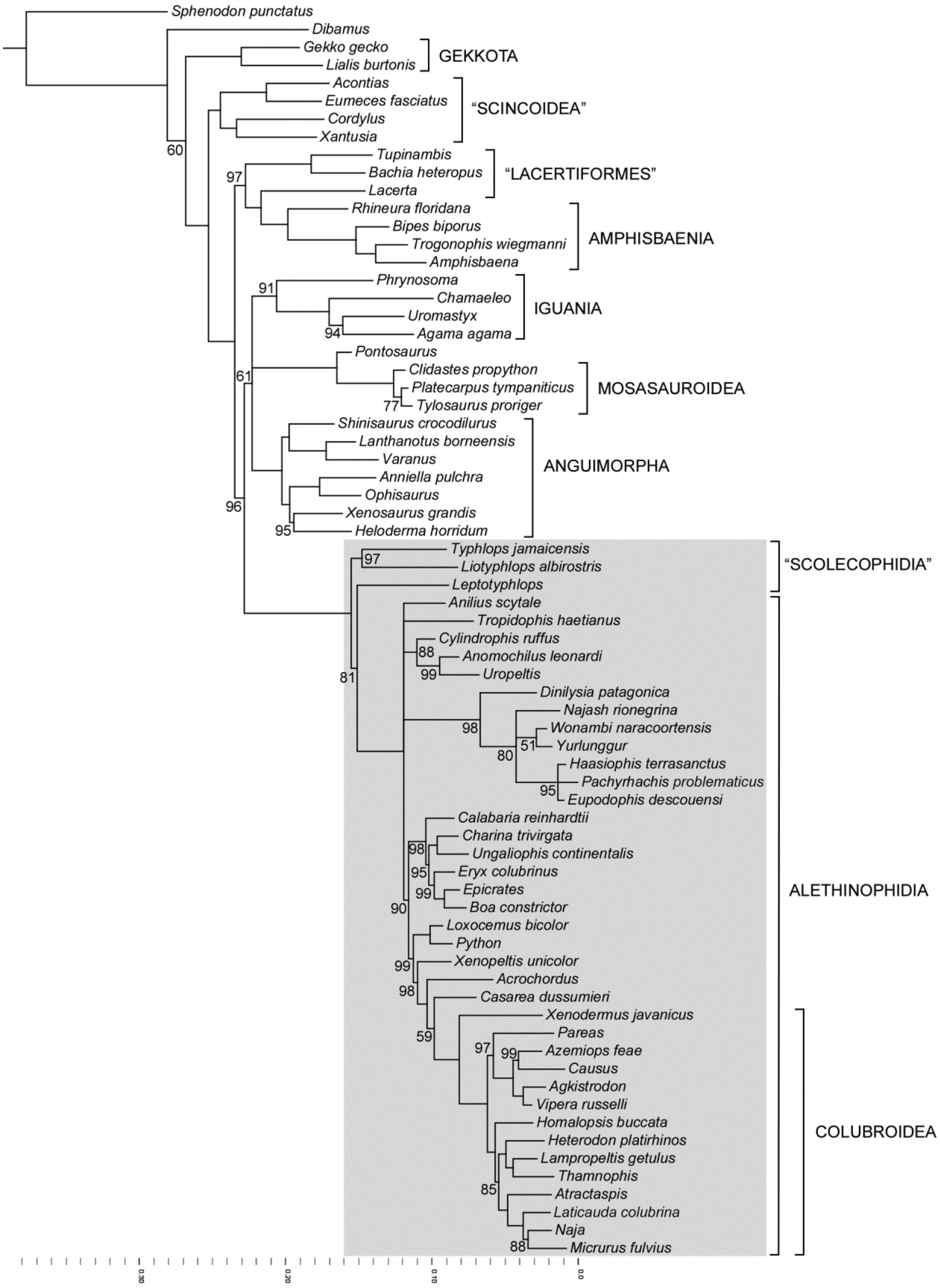
Boa constrictor
ALETHINOPHIDIA
Tropidophis haetianus
Casarea dussumieri
Acrochordus
57
Xenodermus javanicus
95
Pareas
68
Azemiops feae
Causus
98
97
Agkistrodon
65
Vipera russelli
Heterodon platirhinos
66
Lampropeltis getulus
80
Thamnophis
84
Homalopsis buccata
Atractaspis
78
Laticauda colubrina
99
Naja
Micrurus fulvius
COLUBROIDEA

FIGURE 8-4. Tree obtained from the Bayesian analysis of the morphological and molecular (protein and indels) dataset (70 taxa, 2630 characters) (run 1: ln[L]=-41638.55; run 2: ln[L]=-41640.29). Numbers next to nodes are Posterior Probabilities (PP), only PP<100 are shown. The gray box highlights the clade Serpentes.


Sphenodon punctatus
Dibamus
Gekko gecko
Lialis burtonis
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Eumeces fasciatus
Cordylus
Xantusia
"SCINCOIDEA"
60
Tupinambis
Bachia heteropus
Lacerta
"LACERTIFORMES"
97
Rhineura floridana
Bipes biporus
Trogonophis wiegmanni
Amphisbaena
AMPHISBAENIA
Phrynosoma
91
Chamaeleo
Uromastyx
Agama agama
94
IGUANIA
Pontosaurus
Clidastes propython
Platecarpus tympaniticus
Tylosaurus proriger
77
MOSASAUROIDEA
61
Shinisaurus crocodilurus
Lanthanotus borneensis
Varanus
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Ophisaurus
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Eupodophis descouensi
Calabaria reinhardtii
Charina trivirgata
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Ungaliophis continentalis
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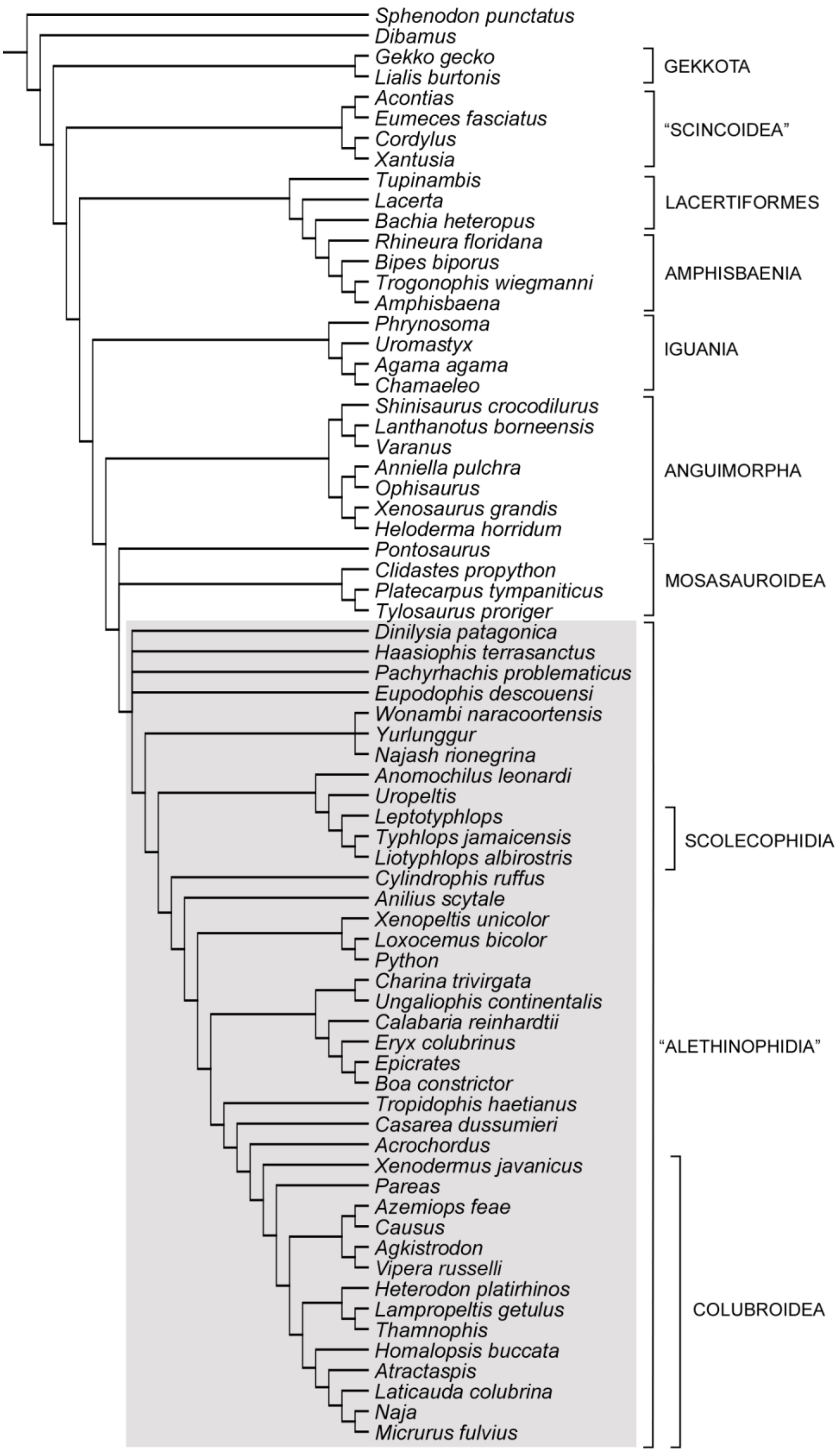
Epicrates
Boa constrictor
90
Loxocemus bicolor
Python
Xenopeltis unicolor
99
Acrochordus
98
Casarea dussumieri
Xenodermus javanicus
59
Pareas
97
99
Azemiops feae
Causus
Agkistrodon
Vipera russelli
Homalopsis buccata
Heterodon platirhinos
Lampropeltis getulus
Thamnophis
85
Atractaspis
Laticauda colubrina
Naja
88
Micrurus fulvius
ALETHINOPHIDIA
COLUBROIDEA
0.30
0.20
0.10
0.0

FIGURE 8-5. Strict consensus of 66 of the 231 most parsimonious trees (5440 steps, CI=0.42, RI=0.67, RC=0.32) recovered from the parsimony analysis of the morphological and molecular (protein and indels) data set after constraining the analysis to have scolecophidians*, Uropeltis*, and *Anomochilus* in the same clade. The 66 trees used to obtain this strict consensus were found to show no statistically significant difference with the trees recovered in the unconstrained analysis (Templeton's test, p>0.05). The gray box highlights the clade Ophidia.


Sphenodon punctatus
Dibamus
Gekko gecko
Lialis burtonis
GEKKOTA
Acontias
Eumeces fasciatus
Cordylus
Xantusia
"SCINCOIDEA"
Tupinambis
Lacerta
Bachia heteropus
LACERTIFORMES
Rhineura floridana
Bipes biporus
Trogonophis wiegmanni
Amphisbaena
AMPHISBAENIA
Phrynosoma
Uromastyx
Agama agama
Chamaeleo
IGUANIA
Shinisaurus crocodilurus
Lanthanotus borneensis
Varanus
Anniella pulchra
Ophisaurus
Xenosaurus grandis
Heloderma horridum
ANGUIMORPHA
Pontosaurus
Clidastes propython
Platecarpus tympaniticus
Tylosaurus proriger
MOSASAUROIDEA
Dinilysia patagonica
Haasiophis terrasanctus
Pachyrhachis problematicus
Eupodophis descouensi
Wonambi naracoortensis
Yurlunggur
Najash rionegrina
Anomochilus leonardi
Uropeltis
Leptotyphlops
Typhlops jamaicensis
Liotyphlops albirostris
SCOLECOPHIDIA
Cylindrophis ruffus
Anilius scytale
Xenopeltis unicolor
Loxocemus bicolor
Python
Charina trivirgata
Ungaliophis continentalis
Calabaria reinhardtii
Eryx colubrinus
Epicrates
Boa constrictor
"ALETHINOPHIDIA"
Tropidophis haetianus
Casarea dussumieri
Acrochordus
Xenodermus javanicus
Pareas
Azemiops feae
Causus
Agkistrodon
Vipera russelli
Heterodon platirhinos
Lampropeltis getulus
Thamnophis
Homalopsis buccata
Atractaspis
Laticauda colubrina
Naja
Micrurus fulvius
COLUBROIDEA

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CHAPTER NINE

GENERAL CONCLUSIONS

Hundreds of specimens of squamates (lizards, amphisbaenians and snakes), including both extant and fossil species, have been examined in the course of this Ph.D. project. The main results and conclusions coming from these observations will be briefly summarized below.

Observations on the fossil snakes *Pachyrhachis problematicus*, *Eupodophis descouensi*, and *Haasiophis terrasanctus* lead to reinterpretations of previously identified structures and new taxonomic diagnoses for these important fossil hind-limbed marine snakes. The anatomical reinterpretations and new observations include: (1) *Haasiophis* and *Eupodophis* show no evidence of possessing a laterosphenoid; (2) *Pachyrhachis* and *Eupodophis* do retain a jugal; (3) *Haasiophis*, like *Eupodophis*, has chevron bones in the caudal region; (4) *Haasiophis* has a large number of unfused intercentra along the anterior portion of the precloacal column; (5) the dentary of *Pachyrhachis* has numerous mental foramina (at least four), a primitive condition for Squamata; (6) *Pachyrhachis* has at least one sacral vertebra with unfused sacral ribs. To test the effect of these observations on the phylogenetic relationships of snakes, three phylogenetic analyses were performed using alternative outgroups to polarize the character transformations. The ingroup consisted of all well-preserved fossil snakes from the Cretaceous, the madtsoiids, and taxa that are representative of all major groups of extant snakes. The analyses produced a series of most parsimonious trees that placed *Pachyrhachis*, *Eupodophis*, and *Haasiophis* either as stem taxa at the base of the radiation of snakes (two analysis), or as members of a clade of fossil snakes that are the sister group of all living alethinopidians (one analysis).

The fossil snake *Najash rionegrina* from the Cenomanian–Turonian (Upper Cretaceous) of Argentina, was reinterpreted after examination of the type and referred material. The diagnosis was emended in the light of important considerations that cast doubt on the attribution of type and referred specimens (a braincase, a quadrate, and two fragments from the lower jaw) used to systematize this taxon (Apesteguía and Zaher, 2006; Zaher et al., 2009). Alternative interpretations of the anatomy of the sacrum and hind limbs have been proposed. Following the reevaluation of the anatomy of the type specimen and the removal from this taxon of the above-mentioned referred material, the phylogenetic position of *N. rionegrina* was tested in a series of maximum parsimony analyses that included all groups of extant snakes, all best-known fossil snakes (i.e., *Pachyrhachis*, *Haasiophis*, *Eupodophis*, Madstoiidae, and *Dinilysia*), and alternative outgroups. Regardless of the outgroup used to polarize the character-state transformations, the phylogenetic analyses found no support for the hypothesis that *Najash rionegrina* occupies a position as the most basal snake. Depending on the outgroup, *Najash* is placed (1) in a position basal to all living snakes, but more derived than other fossil forms (most notably *Pachyrhachis*, *Eupodophis*, and *Haasiophis*); or (2) as the most basal representative of a clade of fossil snakes that is the sister group of living snakes; or (3) as the most basal representative of a clade of fossil snakes that is located between the Scolecophidia and the Alethinophidia.

Examination of the material available for the fossil snake *Wonambi naracoortensis*, in the paleontological collections of the South Australian Museum in Adelaide (Australia), lead to the discovery of a new skeletal element previously unreported for this important fossil taxon: a pelvic girdle. Presence of a pelvic girdle in *Wonambi* could be predicted from its relatively basal position within the phylogeny of snakes (with the only exceptions of uropeltids and anomalepidids, all basal groups of snakes possess at least a vestigial pelvis; Dowling, 1959). No clear indication about the presence or absence of hind limbs could be inferred from the morphology of the pelvis of *Wonambi*; the lack of an acetabulum would suggest that hind limbs were absent, but distinct crests for limb muscle attachment seem to suggest that perhaps hind limbs were at least present as a sexually dimorphic character, and possibly used during mating and courtship, as in extant booids (Bellairs, 1950).

Some snakes have two circumorbital ossifications that in the current literature are usually referred to as the postorbital and supraorbital. The arguments proposed to justify this interpretation have been reviewed and counter-arguments that reject those conjectures of primary homology have been presented. Topological and structural arguments were proposed for reinterpretation of the primary homologies of the dorsal and posterior orbital ossifications of snakes (Rieppel, 1977). Upon application of the test of similarity (Patterson, 1982; De Pinna, 1991), it was concluded that the posterior orbital ossification of snakes is topologically consistent as the homolog of the lacertilian jugal, and that the dorsal orbital ossification present in some snakes (e.g., pythons, *Loxocemus*, and *Calabaria*) is the homolog of the lacertilian postfrontal. Therefore, it was proposed that the terms postorbital and supraorbital should be abandoned as reference language for the circumorbital bones of snakes, and should be replaced with the terms jugal and postfrontal, respectively. The primary homology claim for the snake "postorbital" fails the test of similarity, while the term "supraorbital" is an unnecessary and inaccurate application of the concept of a neomorphic ossification, for an element that passes the test of similarity as a postfrontal. This reinterpretation of the circumorbital bones of snakes is bound to have important repercussions for future phylogenetic analyses and consequently for our understanding of the origin and evolution of snakes.

Studies on the phylogenetic relationships of squamates are limited by problematic interpretations of morphological features that are then used to define characters and states (e.g., Conrad, 2008; Gauthier, 2012). State assignments and character descriptions must be clear characterizations of observable anatomy and topological relationships if homologies are to be hypothesized and tested. A supposed homology of snakes, not observed in lizards, is represented by the crista circumfenestralis (CCF), a system of bony crests surrounding the fenestra ovalis and lateral aperture of the recessus scalae tympani (equivalent of the fenestra rotunda of lizards). However, there are some fossil and extant snakes that lack a CCF, and some extant lizards that possess a morphological equivalent. The Upper Cretaceous fossil snake *Dinilysia patagonica* has been interpreted by different authors as either having or lacking a CCF (Estes et al., 1970; Rage, 1984; Rieppel, 1988; Caldwell and Albino, 2002; Caldwell and Calvo, 2008; Zaher and Scanferla, 2012; Scanferla and Bhullar, 2014). These conflicting results for *Dinilysia* were tested by reexamining the morphology of the otic region in a large sample of squamates. An unambiguous criterion arising from the test of topology was used to define the presence of a CCF: the enclosure of the ventral margin of the juxtastapedial recess by flanges of the otooccipital (crista tuberalis and crista interfenestralis) that extend forward to contact the posterior margin of the prootic; a necessary condition for the formation of a continuous crest (i.e., the crista circumfenestralis). According to this topological criterion *Dinilysia patagonica* does not possess a CCF.

In order to elucidate the phylogenetic relationships of snakes, a large sample of squamate taxa, both extant and fossil, was examined (over 300 specimens of snakes, and over 100 specimens of lizards). This data set was combined with molecular data from 10 nuclear genes available for the same taxa (at least at the genus level) on GenBank (www.ncbi.nlm.nih.gov/genbank). This data set was analyzed using different methods and approaches. The morphological data was analyzed using both parsimony and Bayesian inference; the molecular data was analyzed using parsimony (protein sequences), Bayesian inference (DNA sequences) and maximum likelihood (DNA sequences). The morphological and molecular data were then combined and analyzed using parsimony and Bayesian inference.

The analysis of the morphological data produced results that were in stark contrast with those obtained from the molecular data. According to morphology the closest relatives of snakes would be represented by *Dibamus*, amphisbaenians and other limbless squamates (*Anniella* and *Bachia*), a result quite similar to that of previous morphological studies (e.g., Conrad, 2008; Gauthier et al., 2012). However, according to the molecular data set, the sister group of snakes would consist of a clade inclusive of Anguimorpha and Iguania, a result consistent with previous molecular studies (e.g., Vidal and Hedges, 2005; Wiens et al, 2012). The results of the combined data (morphology and molecules) depend on the analytical method. When the data set was analyzed under parsimony, Amphisbaenia were recovered as the sister group of snakes, followed by mosasauroids; however, when the data set was analyzed using Bayesian inference, the closest sister group of snakes was a clade consisting of Anguimorpha, Mosasauroidea and Iguania. In all analyses, scolecophidians (either mono- or paraphyletic) were always recovered as the most basal snakes (but see below).

Several statistical tests (Templeton test; Templeton, 1989) were performed in order to test the statistical significance of the difference observed between the results obtained here and alternative phylogenetic hypotheses. These tests showed that the results obtained from the analysis of the whole data set are statistically compatible with some alternative hypothesis: 1) snakes may be the sister group of anguimorphan lizards (rather than a clade inclusive of both anguimorphans and iguanians); 2) snakes may be the sister group of the clade

(*Pontosaurus*, Mosasauroidea); 3) Scolecophidia may be an aberrant lineage of basal alethinophidians (closely related to *Anomochilus* and uropeltids). The last hypothesis is perhaps the most intriguing possibility, as it would make the Alethinophidia paraphyletic and also suggest that the anatomy of the scolecophidians is not representative of that of the most primitive snakes.

Removal of certain taxa was also used to test the effect of taxon sampling and the possibility of long-branch attraction (Bergsten, 2005). The most interesting result was obtained after removal of the Solecophidia, because that caused the amphisbaenians to move away from snakes (i.e., to a position close to lacertiformes) and the fossil snakes *Dinilysia*, *Pachyrhachis*, *Eupodophis* and *Haasiophis* were moved into a polytomy at the base of the clade Ophidia.

Another interesting result was the recovery of a clade of fossil snakes that suggests the possibility that the macrostomatan condition (i.e., a series of modifications of the skull to increase the gape of the mouth) could have evolved convergently in extant alethinophidians and a group of fossil forms. This hypothesis would explain the odd combination of primitive (i.e., well-developed hind limbs and chevron bones) and advanced (the macrostomatan skull) anatomical features in the fossil snakes *Eupodophis*, *Haasiophis*, and *Pachyrhachis*.

Overall, the results showed that despite a general tendency of the molecular data to place snakes as the sister group of anguimorphans and iguanians, other possibilities remain open, as the statistical difference between some of the alternative scenarios was found to be insignificant.

Finally, it is important to point out that the selected molecular data showed to be very self-consistent, and regardless of the data partition and analytical method (parsimony, Bayesian or maximum likelihood) the results were always very similar. This would suggest that the addition of more molecular data, in combination with data from new fossil specimens, might eventually help reach a stable consensus regarding the closest relatives of snakes.

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SUPPLEMENTARY DATA

All supplementary data from this dissertation are available in electronic format at: http://dx.doi.org/10.7910/DVN/27016