

The anatomy of the upper cretaceous snake *Najash rionegrina* Apesteguía & Zaher, 2006, and the evolution of limblessness in snakes

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Najash rionegrina Apesteguía & Zaher, 2006, a terrestrial fossil snake from the Upper Cretaceous of Argentina, represents the first known snake with a sacrum associated with robust, well-developed hind limbs. *Najash rionegrina* documents an important gap in the evolutionary development towards limblessness, because its phylogenetic affinities suggest that it is the sister group of all modern snakes, including the limbed Tethyan snakes *Pachyrhachis*, *Haasiophis*, and *Eupodophis*. The latter three limbed marine fossil snakes are shown to be more derived morphologically, because they lack a sacrum, but have articulated lymphapophyses, and their appendicular skeleton is enclosed by the rib cage, as in modern snakes.

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INTRODUCTION

An important event in the evolution of snakes was the loss of their limbs. Until recently, it was thought that snakes underwent a progressive loss of their limbs by the gradual diminution of their use (Underwood, 1977). A renewed interest in the origin and evolution of snakes has been triggered recently by the re-analysis and description of the Cretaceous limbed snakes *Pachyrhachis problematicus* Haas, 1979, *Haasiophis terrasanctus* Tchernov *et al.*, 2000, and *Eupodophis descouensi* Rage & Escuillié, 2000 (Caldwell & Lee, 1997; Zaher, 1998; Zaher & Rieppel, 1999a; Rage & Escuillié, 2000; Rieppel & Zaher, 2000a; Tchernov *et al.*, 2000; Zaher & Rieppel, 2000, 2002). These are all mid-Cretaceous marine forms with well-developed hindlimbs and several adaptations to macrophagy, which led some authors to inter-

pret them as the most basal snakes and transitional taxa linking snakes to an extinct group of marine lizards, the Mosasauroidea (Caldwell & Lee, 1997; Lee *et al.*, 1999; Lee & Scanlon, 2002). The hypothesis of a sister-group relationship between snakes and mosasauroids has been viewed as evidence for a scenario that supports a marine origin of snakes (Caldwell & Lee, 1997; Lee, 1997, 1998; Caldwell, 1999). However, a critical evaluation of the character evidence put forward in support of a basal position of the Cretaceous marine snakes with legs, as intermediates between snakes and mosasauroids, revealed that the hypothesis appears to have a weak morphological basis (Zaher, 1998; Zaher & Rieppel, 1999a,b, 2000, 2002; Rieppel & Zaher, 2000a,b). Indeed, the recognition of several advanced features of *Pachyrhachis*, *Haasiophis*, and *Eupodophis* supported a derived position for these taxa, as the sister group of the more advanced macrostomatan snakes (Zaher, 1998; Tchernov *et al.*, 2000), calling into question the scenario of

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a marine origin of snakes. Also critical for the outcome of such a result was the decision to increase the taxonomic resolution within snakes, by including the important Cretaceous terrestrial snake *Dinilysia patagonica* Smith-Woodward, 1901, and by breaking the alethinopidian terminal in the anilioids and macrostomatans in order to take into account the distribution of macrostomatan characters (Zaher, 1998).

Despite the profusion of papers that resulted, no consensus has emerged from the current debate on snake origins and relationships (e.g. Coates & Ruta, 2000), leaving us with two competing hypotheses: (1) that the Cretaceous marine snakes with legs were the most primitive (basal) snakes and transitional taxa linking extant snakes to an extinct group of marine lizards, the macrophagous Mosasauridae (Caldwell & Lee, 1997; Lee, 1997, 1998; Lee & Caldwell, 1998; Caldwell, 1999; Lee *et al.*, 1999, 2007); (2) that these fossils were advanced (macrostomatan) snakes with no special bearing on the origin and early evolution of extant snakes (Zaher, 1998; Zaher & Rieppel, 1999a,b, 2000, 2002; Rieppel & Zaher, 2000a,b, 2001; Tchernov *et al.*, 2000; Rieppel *et al.*, 2002). More recently, Lee & Caldwell (2000; see also Lee, 2005a,b; Caldwell, 2006) pushed further the hypothesis of a marine origin by nesting snakes within a paraphyletic assemblage of mosasaurids, aigialosaurids, and dolichosaurids, with the poorly preserved fossil *Adriosaurus suessi* Seeley, 1881 representing the sister group of snakes.

The position of *Haasiophis*, *Eupodophis*, and *Pachyrhachis* as derived macrostomatan snakes suggests that they might have re-developed complete hindlimbs or, more likely, that hindlimb reduction and loss have occurred repeatedly among extant snakes (Zaher & Rieppel, 1999a; Greene & Cundall, 2000). Alternatively, the presence of well-developed pelvis and legs in these snakes has been interpreted as evidence of their primitiveness, and of their 'almost ideal intermediate' position between mosasaurids and extant snakes, suggesting that their derived macrostomatan traits were convergent with extant snakes. However, all three marine fossil taxa lack differentiated sacral vertebrae, and their pelvises are not suspended from the axial skeleton, but rather lie within the ribcage (Zaher & Rieppel, 1999a; Tchernov *et al.*, 2000), suggesting a more derived condition of hindlimb reduction than has previously been assumed.

The recent finding of *Najash rionegrina* Apesteguía & Zaher, 2006, an early Late Cretaceous fully terrestrial snake, with a sacrum loosely supporting a pelvic girdle, and robust, functional legs outside of the ribcage, which is 10–15-Myr older than *Dinilysia*, and probably as old as *Pachyrhachis*, *Haasiophis*, and *Eupodophis* (see *stratum typicum*), provided

important new information on the controversy regarding the early evolution of snakes (Apesteguía & Zaher, 2006). The cladistic analysis of extinct and extant snakes presented by Apesteguía & Zaher (2006) showed that *Najash* is the most primitive snake known so far, and represents the sister group to the crown-clade Serpentes that include all living snakes, as well as the marine Cretaceous snakes *Haasiophis*, *Pachyrhachis*, and *Eupodophis*, as derived macrostomatan snakes, thereby corroborating the hypothesis advanced by Zaher, Rieppel, and their collaborators (Zaher, 1998; Zaher & Rieppel, 1999a,b, 2000, 2002; Rieppel & Zaher, 2000a,b, 2001; Tchernov *et al.*, 2000; Rieppel *et al.*, 2002). In this paper, we present a detailed morphological description of this important new legged snake from the early Late Cretaceous of Argentina.

THE FOSSIL-BEARING STRATA OF LA BUITRERA

The 'La Buitrera' (Vulture Roost) is a fossil locality in the Province of Río Negro, located close to the town of Cerro Policía in north-western Patagonia, approximately 100 km east from the Andes foothills, and close to the south shore of the Ezequiel Ramos-Mexía dam (Fig. 1). The outcrops of La Buitrera are mainly composed of almost horizontal sandstones of the early Upper Cretaceous Candeleros Formation (Neuquén Basin), exposed in an area of 4 km², and surrounded by tall, reddish cliffs of approximately 40 m in height. La Buitrera also encompasses a few isolated mudstone patches of lacustrine origin, suggesting

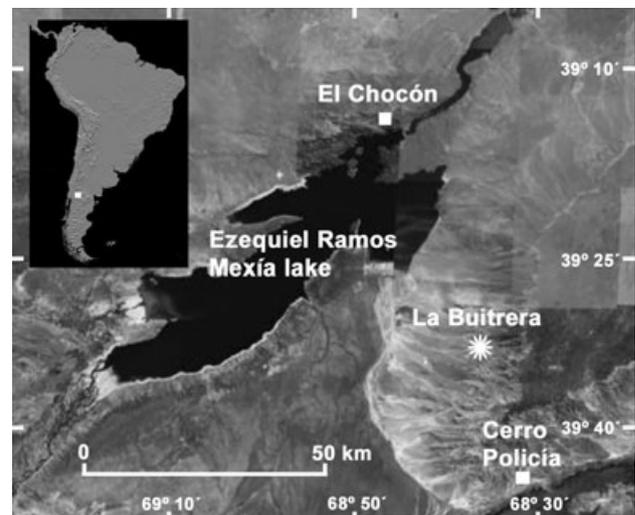


Figure 1. Geographic map of the fossil locality in north-western Patagonia (Río Negro Province). The asterisk indicates the position of La Buitrera, where specimens of *Najash rionegrina* Apesteguía & Zaher, 2006 were found.

that ephemeral lakes were formed during times of flooding. These La Buitrera sandstones represent the debris of the North Patagonian Massif, carried out by an ancient fluvial system that meandered towards the Pacific Ocean just a few million years before the uplifting of the Andes.

According to Leanza *et al.* (2004), the Neuquén Group began its deposition in the Early Cenomanian, at about 97.3 Mya (Leanza, 1999). The Candeleros Formation, its first unit, was deposited between 97.3 and 90 Mya. The upper section of the Candeleros Formation, to which the rocks of La Buitrera belong, could be dated to around 92–94 Mya. A fission track study made on a tuff from the base of the immediately overlying upper Huincul Formation, resulted in a date of 88 Mya (Corbella *et al.*, 2004), in agreement with its younger position.

The locality yields abundant and beautifully preserved 3D skeletons of small-sized tetrapods, including mammals, pterosaurs, theropods, turtles, crocodyliforms, rhynchocephalian lepidosaurs, and snakes. Although rare in comparison with the other tetrapods, dinosaurs are represented by the recently described deinonychosaur *Buitreraptor gonzalezorum* (Makovicky *et al.*, 2005), and by fragments of large saurischian species (Apesteguía *et al.*, 2001).

La Buitrera largely exceeds all other known Late Cretaceous Gondwanan localities in terms of abundance, concentration, and quality of the articulated 3D fossil terrestrial vertebrate remains. Moreover, the undeformed nature of the bones, preserving exquisite histological details and marks of scavenging, indicates a superb preservation of the articulated skeletons or complete skulls. It is possible that this aspect reflects rapid burial and preservation by major fluvial deposition in North Patagonian localities, as happened in the Djadokhta Formation, Gobi Desert (Dashzeveg *et al.*, 1995).

One of the limiting, but most interesting, aspects of La Buitrera is its oligotypicity. Unlike the contemporaneous and nearby deposits of El Chocón, where carcharodontosaurid theropods, rebbachisaurids, and basal titanosaurs are common, the La Buitrera fauna shows a strong bias towards a few species of articulated micro- and mesovertebrates that include predominantly the sphenodontid *Kaikaiifilusaurus calvoi* Simón & Kellner, 2003 (by far the most abundant taxon; Apesteguía & Novas, 2003; Apesteguía, 2008), the crocodyliform *Araripesuchus buitreiraensis* (Pol & Apesteguía, 2005), the limbed basal snake *N. rionegrina*, the deinonychosaur *B. gonzalezorum*, two undescribed mammalian species, and an unidentified species of the chelid genus *Prochelidella* (M.S. de la Fuente, pers. comm.). The oligotypicity of La Buitrera helps to assign the abundant, isolated material to these few species known to occur in the locality. This

is specifically true for *N. rionegrina*, the only known snake to occur in La Buitrera, to which all the isolated and partially articulated snake material discovered has been unequivocally assigned so far. The environmental and taphonomical conditions that resulted in the exceptional preservation at this locality were briefly described by Apesteguía (2008).

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 basiocranium 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. *Kaikaiifilusaurus*, *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).

SYSTEMATIC PALEONTOLOGY

LEPIDOSAURIA HAECKEL, 1866

SQUAMATA OPPEL, 1811

SERPENTES LINNAEUS, 1758

NAJASH APESTEGUÍA AND ZAHER, 2006

Emended diagnosis: A snake nearly 2 m long with robust hindlimbs and a sacrum, tip of dentaries with a medially projected facet that bears a straight anteroposteriorly directed margin, suggesting a tightly connected mandibular symphysis, lack of dentary shelf, prootic exposed dorsally between the otooccipital and parietal, lack of laterosphenoid, developed laterally projected basipterygoid process, lack of a crista circumfenestralis, robust stapedial footplate, single large parazygantral foramen on vertebrae, arqual ridges on middle and posterior presacral vertebrae, and blunt haemapophyses on caudal vertebrae. It exhibits the following autapomorphies: (1) a thick splenial; (2) strongly concave ventral surface of the parasphenoid rostrum, forming a deep and straight gutter; (3) strongly faceted condition of the neural arch laminae; (4) enlarged and blade-like femoral trochanter.

NAJASH RIONEGRINA APESTEGUÍA & ZAHER, 2006

Diagnosis: As for the genus, of which this is the only known species.

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 hindlimbs. The holotype is represented by the following articulated and associated postcranial elements: an articulated section bearing the axis, four anterior presacral vertebrae, and the broken anterior part of the fifth vertebra (MPCA 391); a section bearing a continuous string of 47 articulated presacral vertebrae, with associated ribs and two isolated vertebrae (MPCA 392), from which the proximal head of a middle presacral rib (MPCA 389) was prepared separately; three sections bearing no more than six, seven, and nine presacral vertebrae, respectively (MPCA 393); two sections bearing only associated ribs (MPCA 394); one section bearing five articulated mid-presacral vertebrae, and the broken anterior part of a sixth vertebra (MPCA 395); two articulated caudal vertebrae (MPCA 396); eight fragmentary sections bearing a total of 18 articulated presacral vertebrae (MPCA 397); five undetermined and fragmentary elements (MPCA 398); several fragmentary associated presacral vertebrae (MPCA 399); a section containing the pelvic girdle and hindlimb elements, articulated with eight posterior presacral, two sacral, and nine caudal vertebrae (MPCA 400).

Referred material: Five specimens: (1) a fragmentary skull comprising the posterior half of the braincase, and associated vertebrae of a small specimen (MPCA 385); (2) several associated cranial and vertebral elements of a larger individual, probably twice as large as the holotype, including an incomplete left dentary (MPCA 380), two undetermined cranial elements (possibly mandibular fragments) (MPCA 381 and 382), axis (MPCA 383), and associated presacral and caudal vertebrae (MPCA 384); (3) a right quadrate and five associated presacral vertebrae (MPCA 387); (4) four associated sections of articulated vertebrae, and one fragment totaling 16 middle presacral vertebrae (MPCA 386); (5) a posterior presacral vertebra of a large individual (MPCA 388).

Stratum typicum: Mid to upper layers of the Candeleros Formation, basal unit of the Neuquén Group, early Upper Cretaceous. The bearing strata, about 40 m under the boundary with the overlying Huincul Formation, are considered as having been deposited around 92–94 Mya, during the Cenomanian. The

fission track study on a tuff in the overlying Huincul Formation gave an age of 88 ± 3.9 Myr (Corbella *et al.*, 2004).

Locus typicus: La Buitrera, Rentería Mesa, 30 km north-west from the town of Cerro Policia.

DESCRIPTION

We based our description on the partly articulated holotype, and on five additional specimens represented by disarticulated, but associated, cranial and postcranial materials. In the following section, a detailed description of each element belonging to the holotype will be provided, followed by additional information from the referred specimens.

All five specimens can be referred to *N. rionegrina* because their elements include associated vertebrae identical with the holotype. We consider the significant size variation of these specimens as due to distinct ontogenetic stages. Given the difference in size between the dentary and vertebrae of the holotype (MPCA 389–400), and the dentary and vertebrae of referred specimens MPCA 380, 383, 384, and 388, we conclude that the holotype is a juvenile specimen, whereas the other referred specimens are large adult individuals. Similarly, referred specimens MPCA 385 (braincase and associated vertebrae) and MPCA 387 (quadrate and associated vertebrae) correspond to juvenile stages of the species.

CRANIAL ELEMENTS

Two elements from the skull have been found associated with the nearly complete and articulated postcranial skeleton of the holotype: a large fragment of the left dentary and the anterior portion of the corresponding splenial (Fig. 2A–D). The dentary and splenial are articulated, and were kept as such during preparation. Additional cranial material was provided by three referred specimens: MPCA 385 corresponds to a small individual, with the posterior half of the braincase and its right oticooccipital region preserved (Figs 3, 4); MPCA 380 and 383 correspond to a significantly larger specimen, from which an incomplete left dentary and axis were preserved, associated with each other and with several presacral vertebrae (Fig. 2E–H); MPCA 387 corresponds to the right quadrate of a small individual that was found associated with various presacral vertebrae (Fig. 5).

Braincase: The posterior half of the braincase of referred specimen MPCA 385 comprises the posterior portion of the rostrum and main body of the parabasisphenoid (fused parasphenoid and basisphenoid), parietal, left and right prootics, right stapedial

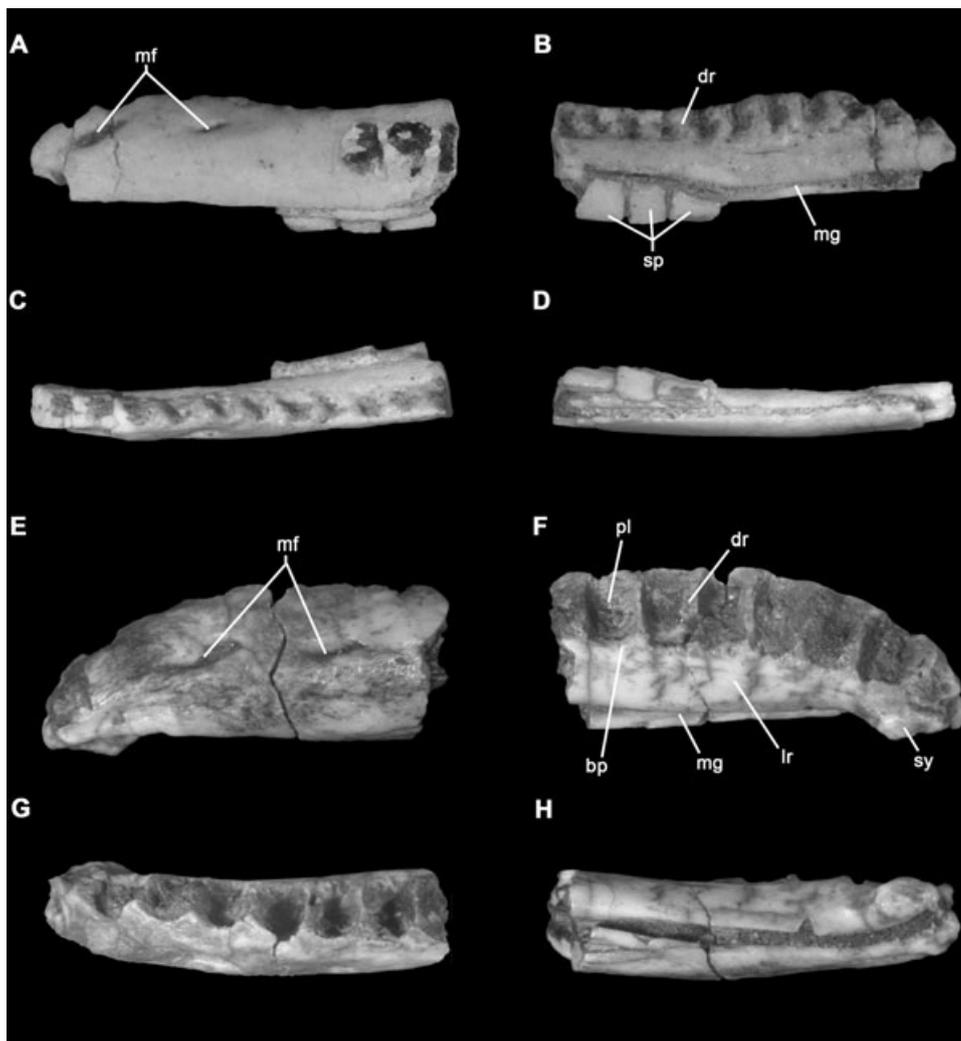


Figure 2. Dentary of *Najash rionegrina* Apesteguía & Zaher, 2006. Left incomplete dentary and splenial of the holotype (MPCA 391): A, lateral view; B, medial view; C, dorsal view; D, ventral view. Left incomplete dentary of the referred specimen (MPCA 380): E, lateral view; F, medial view; G, dorsal view; H, ventral view. Abbreviations: bp, basal plate; dr, dental ridge; lr, lingual ridge; mf, mental foramina; mg, Meckelian groove; pl, pleura; sp, splenial bone; sy, mandibular symphysis. The left-hand column presents the anterior portion directed to the left, whereas the right-hand column presents the anterior portion directed to the right.

footplate, right otooccipital, supraoccipital, and the posterior ramus of the left pterygoid (Figs 3, 4). The skull suffered some dorsoventral and lateral compression, which caused a slight crushing and displacement of the elements to the right. As in *Dinilysia*, *Anilius*, and *Cylindrophis*, the posterior half of the skull is laterally expanded across the otic region.

The parabasisphenoid is broken anteriorly, and only the posteriormost portion of the parasphenoid rostrum is preserved. The ventral surface of the parasphenoid rostrum is deeply concave, with a transversely U-shaped form in ventral view that is unique to *Najash* (Fig. 3B, C). However, anilioid snakes and *Dinilysia* also share a smooth anteriorly concave

parasphenoid rostrum, although the concavity of their rostrum is always shallow, contrasting with the deeply U-shaped parasphenoid rostrum of *Najash*. The posterior portion of the parasphenoid rostrum meets the descending flanges of the parietal in a straight sutural contact (Fig. 3B, C). The deep gutter formed by the U-shaped condition of the parasphenoid rostrum fades towards the level of the base of the parasphenoid rostrum, where the parabasisphenoid expands to form the sella turcica on its dorsomedial surface, disappearing between the bases of the two basiptyergoid processes. The basiptyergoid processes are massive, clearly laterally orientated, and slightly anteroventrally directed. Only the left basiptyergoid

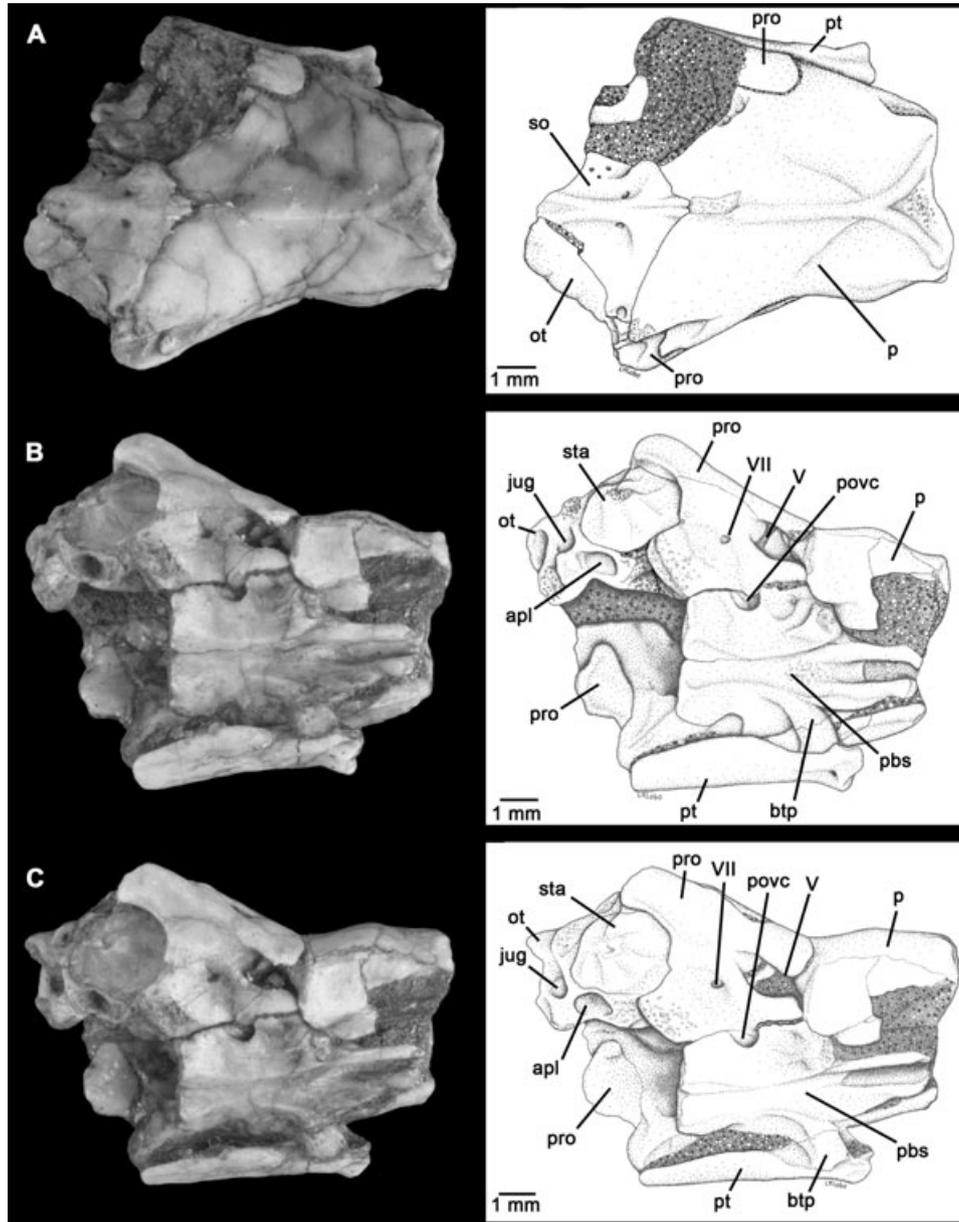


Figure 3. Brainscase of *Najash rionegrina* Apesteguía & Zaher, 2006 (referred specimen MPCA 385): A, dorsal view; B, ventral view; C, ventrolateral view; D, right (lateral) view; E, left (lateral) view; F, posterior view. Abbreviations: apl, apertura lateralis recessus scalae tympani; btp, basipterygoid process; jug, jugular foramen; ot, otooccipital bone; p, parietal bone; pbs, parabasisphenoid; povc, posterior opening of the Vidian canal; pro, prootic bone; pt, pterygoid bone; so, supraoccipital bone; sta, stapes; V, foramen for the maxillary and mandibular branches of the trigeminal nerve; VII, foramen for the hyomandibular branch of the facial nerve.

process is complete, and articulates with the dorso-medial surface of the pterygoid, where it is received in a somewhat oval and deep notch (Fig. 3C). The right basipterygoid process is broken at its base, and reveals a close sutural contact of the parabasisphenoid with the parietal, just anterior to the prootic-parietal contact. At that level, the posteromedial edge

of the parietal overlaps the anterolateral edge of the parabasisphenoid, laterally to the base of the basipterygoid process. Aside from the basipterygoid processes, which are well developed and lizard-like, the posteriorly expanded part of the parabasisphenoid of *Najash* is similar to that of anilioids, in having a smooth ventral surface, typical of fossorial or

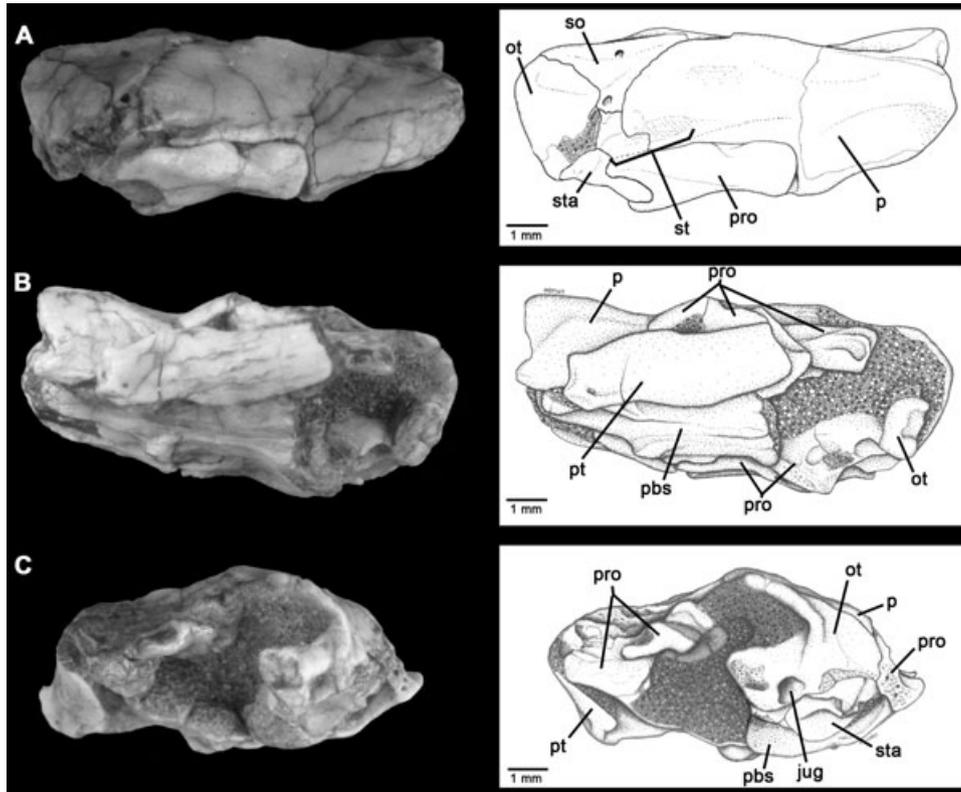


Figure 4. Braincase of *Najash rionegrina* Apesteguía & Zaher, 2006 (referred specimen MPCA 385): A, right (lateral) view; B, left (lateral) view; C, posterior view. Abbreviations: jug, jugular foramen; ot, otooccipital bone; p, parietal bone; pbs, parabasisphenoid; pro, prootic bone; pt, pterygoid bone; so, supraoccipital bone; st, deep and narrow recess that receives the anterior portion of the missing supratemporal bone; sta, stapes.

secretive snakes, and significantly different from that of *Dinilysia*, which shows strongly ventrolaterally projected posterolateral corners, from which arise laterally projected crests (a typical lizard-like condition). The posterior edge of the parabasisphenoid articulates with the anterior edge of the basioccipital in a straight, transversely directed contact, at the level of the rounded anterior edge of the fenestra ovalis, a position that is further back in the skull than that in scolecophidians and most alethinophidians. Exceptions are *Dinilysia* (Estes, Frazzetta & Williams, 1970), *Haasiophis* (Rieppel *et al.*, 2003), and *Anomochilus* (Cundall & Rossman, 1993), which also have a posterior position of the parabasisphenoid–basioccipital contact. The lateral borders of the parabasisphenoid expand anterolaterally in a straight, sutural contact with the medioventral edges of the prootics, to the level of the prootic–parietal contact. Laterally expanded lateral wings of the basisphenoid are lacking. The posterior opening of the Vidian canal lies ventromedial to the basisphenoid–prootic suture, at the level of the posterior border of the undivided trigeminal foramen, and is completely enclosed on the ventral surface of the basisphenoid (Fig. 3B, C). The

ventral surfaces of the basisphenoid and prootic, just lateral to the large foramen, are depressed and form a shallow groove that extends to the small foramen of the palatine branch on the prootic. The anterior opening of the Vidian canal could not be located on the preserved anterior part of the parabasisphenoid.

The azygous parietal is badly eroded and broken on a straight, transverse line anteriorly, having lost its anteriormost part that bears the sutural contact with the frontal and the recesses for the postorbital/postfrontal contact (Fig. 3A). Posteriorly, the parietal meets the supraoccipital in a broadly V-shaped suture, with the blunt apex pointing anteriorly. In dorsal view, the parietal is narrower anteriorly, and broader posteriorly, as in *Dinilysia* and anilioids. Dorsally and anteriorly, the parietal forms a flattened triangular parietal table, delimited by the lateromedially and anteroposteriorly directed adductor crests, from which the adductor externi muscles originate. Both crests converge posteriorly to form a low sagittal crest that extends to the posterior edge of the parietal, and meets the blunt anterior apex of the supraoccipital. The sagittal crest is broken on its posterior region. The laterally descending flanges of

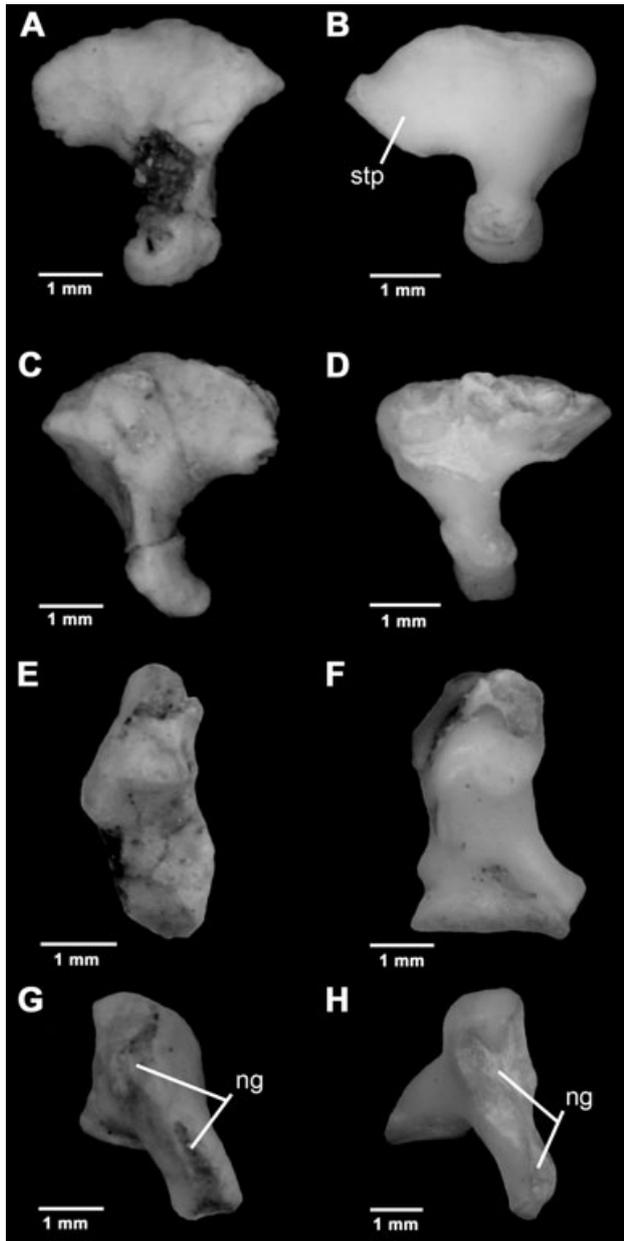


Figure 5. Quadrate bone of *Najash rionegrina* Apesteguí & Zaher, 2006 (MPCA 387; A, C, E, G) and *Cyllindrophis ruffus* Boulenger, 1893 (LSUMZ 14075; B, D, F, H): A, B, lateral view; C, D, medial view; E, F, posterior view; G, H, dorsal view. Abbreviations: ng, narrow gutter; stp, suprastapedial process.

the parietal are somewhat crushed and slightly displaced to the right, as a result of dorsoventral compression of the skull. Their relation to the optic foramen remains unknown as the anterior parts of the flanges are missing. However, the preserved part contacts the lateral margin of the parabasisphenoid in a closed suture (Fig. 3B, C). Posteriorly, the lateral

flange of the parietal meets the anterior and dorsal edges of the prootic in a broad, mostly L-shaped sutural contact (Fig. 4A). On its posterior dorsolateral corner, the parietal overlaps the prootic (Fig. 3A). At that level, both the posterolateral portion of the parietal and the posterodorsal portion of the prootic form a deep and narrow recess that receives the anterior portion of the missing supratemporal, which was incorporated into the cranial wall as in *Dinilyisia*, *Cyllindrophis*, *Anilius*, and *Anomochilus* (Figs 3A, 4A, C). As in the latter taxa, the recess is located laterally to the contact between the prootic and the supraoccipital, suggesting a dorsal exposure of the prootic between the supratemporal, otooccipital, and supraoccipital.

The supraoccipital is broadly exposed dorsally (Fig. 3A). The left side is missing, along with the left oticooccipital region. The supraoccipital is diamond-shaped, with both anterior and posterior edges meeting the parietal and otooccipitals in a broadly V-shaped suture, with their apexes pointing anteriorly and posteriorly, respectively. The weakly developed sagittal crest of the parietal continues on the supraoccipital. The sagittal crest of the supraoccipital terminates at the posterior margin in a distinct, knob-like expansion that contributes to the dorsal border of the foramen magnum (Fig. 3A). Laterally, the supraoccipital gradually tapers to a narrow process that is clasped between the posterior edge of the dorsal prong of the prootic and the anterolateral edge of the otooccipital. The shape of the supraoccipital is characteristic of an ontogenetic stage comparable with the young individuals in many extant species, and suggests that the holotype of *N. rionegrina* was a subadult. This is in accordance with the findings of other significantly larger individuals that were assigned to the species in the present paper.

The otooccipitals (fused exoccipital and opisthotic *sensu* Maisano, 2001; see also Conrad, 2004) form the posterior part of the otic region and occipital part of the skull, and are in contact with the supraoccipital and supratemporal dorsally, the prootic anteriorly, and the basioccipital ventrally. They also contribute to the formation of a crista circumfenestralis, by the development of both cristae interfenestralis and tuberalis. The otooccipitals are only represented in the referred specimen by the right element, which is broken dorsally and ventrally (Figs 3B, C, 4C). The dorsolateral 'paroccipital process' is lacking, being broken at the level of the mediodorsal limit of the prootic. Dorsomedially, the otooccipital forms an occipital tectum that bears a small atlantal crest. The atlantal border reaches the midline, where it contacts with the posteriorly projected knob-like expansion of the supraoccipital, suggesting that left and right otooccipitals did not contact posterior to the

supraoccipital. The ventrolateral expansions of both cristae interfenestralis and crista tuberalis are broken, but the posterior margin of the otooccipital remains intact, and shows that the juxtastapedial recess remains widely open posteriorly because of a poorly developed posterodorsal margin of the crista tuberalis, a plesiomorphic feature present in *Dinilyisia*, scolecophidians, anilioids, *Xenopeltis*, and *Loxocemus*, but which is absent in *Wonambi*, *Yurlunggur*, and derived macrostomatan snakes (Rieppel *et al.*, 2002; Scanlon, 2006). The jugular foramen is clearly visible in posterior view. The apertura lateralis of the recessus scalae tympani opens into the posteroventral corner of the juxtastapedial recess, behind the stapedial footplate, and just anteromedially to the jugular foramen. Most of the extension of the crista interfenestralis, which separates the lateral aperture of the recessus scalae tympani from the fenestra vestibuli, is missing. However, the orientation of the remaining basis of the crista interfenestralis and the contact scars present on the posteromedial wall of the prootic, just below the stapedial footplate, show that the crista interfenestralis formed the ventral rim of the crista circumfenestralis (Fig. 3B, C). The medial view of the otooccipital (and prootic) is obliterated by sediment, and could not be described.

Only the right prootic is mostly complete and visible (Figs 3B, C, 4A). As in scolecophidians, *Dinilyisia*, *Yurlunggur*, and possibly *Wonambi* (see Scanlon, 2006), the laterosphenoid is absent in *Najash*, and the prootic retains a single trigeminal foramen delimited by a longer and broader dorsal anterior process (alar process), and by a shorter and narrower ventral anterior process (Fig. 3C). The ventral surface of the dorsal anterior process is distinctly concave, as it delimits the dorsal margin of the trigeminal foramen. The anteroventral tip of the dorsal anterior process of the prootic is broken. However, the clearly marked area of contact on the surface of the parietal shows that the dorsal process contacted the parietal in a broad, dorsoventrally expanded suture that overlapped the descending flange of the parietal. The latter condition is typical of snakes, except for the basal macrostomatans *Wonambi* and *Yurlunggur* (Rieppel *et al.*, 2002; Scanlon, 2005, 2006), where the anterior process underlies the descending flange of the parietal, instead of overlapping it. The sutural marks on the parietal also suggest that the anteroventral tip of the dorsal anterior process met the dorsal tip of the ventral anterior process in a non-sutural, narrow contact, closing anteriorly the trigeminal foramen, as in *Dinilyisia*. The contact between the anterior edge of the dorsal process and the descending flange of the parietal is smoothly rounded, and turns dorsally to a straight horizontal contact with the parietal that extends to

the posterodorsal end of the prootic. The ventral anterior process of the prootic has a concave dorsal edge that delimits the ventral margin of the trigeminal foramen. It projects anteriorly to contact the descending flange of the parietal through a somewhat rounded anterior tip. The foramen for the facial nerve lies just posteroventral to the posterior border of the trigeminal foramen, in a shallow recess of the prootic that extends posteroventrally to the prootic-basioccipital suture, at the level of the opening of the posterior Vidian canal. The dorsolateral border of the prootic is deeply concave, as it forms the anterior border of the fenestra ovalis. Although present, the crista circumfenestralis of *Najash* is only represented by a weakly defined crista prootica, comparable with that present in *Dinilyisia*, and representing the least developed condition among snakes. In both *Najash* and *Dinilyisia*, the crista prootica projects weakly laterally to the stapedial footplate only on its anterodorsal portion (*contra* Caldwell & Albino, 2002), although without overlapping the stapedial footplate, as in all modern snakes. The posterodorsal extension of the prootic that borders the dorsal edge of the juxtastapedial recess is missing, preventing an exact definition of its relation with the otooccipital, dorsomedially. However, its lateral edge probably also projected laterally to the edge of the stapedial footplate, contributing to a continuous dorsally developed crista prootica.

The stapes is somewhat rounded, massive, and broad, as in *Dinilyisia* and alethinophidians such as anilioids and *Xenopeltis*. The stapedial shaft is broken at its base and missing, but the orientations of both the stapedial footplate and the base of the stapedial shaft suggest that the latter was posterodorsally directed, as in *Dinilyisia* and anilioids, and would have touched the posteromedial surface of the supra-stapedial process of the quadrate (Figs 3B, C, 4C).

Pterygoid: Only the left pterygoid is preserved, being represented by its quadrate ramus (Figs 3B, C, 4B, C). It is broken anteriorly, just in front of the articulation for the basiptyergoid process and behind the level of the lateral process, and posteriorly along the curved posterior part that meets the medial aspect of the quadrate. The remaining pterygoid section is preserved in place, and articulates with the parabasipterygoid through the basiptyergoid process. The cross section of the quadrate ramus of the pterygoid is somewhat blade-like and dorsomedially concave, rather than massive and round or triangular (Fig. 4B, C). Its dorsal surface faces dorsomedially the ventrolateral wall of the braincase (parietal and prootic), and lacks the distinct longitudinal groove for the insertion of the protractor pterygoidei muscle. Further anteriorly, the pterygoid constricts medially

to receive, on its dorsomedial surface, the basiptyergoid process that fits in a somewhat oval and deep notch. The presence of a pterygoid notch for the articulation of the basiptyergoid process is a plesiomorphic condition of *Najash* that is also present in *Dinilysia*, and which is lost in *Yurlunggur*, *Wonambi*, and all recent snakes.

Quadrate: Only the right quadrate of referred specimen MPCA 387 was preserved, in association with several presacral vertebrae (Fig. 5). It is broken ventrally and posterodorsally, having lost the mandibular condyle and the tip of the suprapedial process (Fig. 5A, C, E, G). Nevertheless, it is recognizable as such because of the very similar morphology with the quadrates of *Dinilysia*, *Anilius*, *Yurlunggur*, and *Cylindrophis* (Fig. 5B, D, F, H), with which it shares a broad cephalic condyle, with a developed suprapedial process and a robust, short, and laterally expanded shaft. The cephalic condyle has a smooth, bulged lateral surface, whereas the medial surface is rugose and depressed at its articulation with the braincase, being broader anteriorly and narrower posteriorly in a transverse section. The dorsal edge of the cephalic condyle is rounded in lateral and medial views, and is excavated on its posterodorsal surface by a characteristic narrow gutter that is also present in *Dinilysia*, *Yurlunggur*, *Anilius*, and *Cylindrophis* (Fig. 5G, H). Its anterior surface is broad and concave, with its lateral edge being more anteriorly positioned than the parallel medial edge.

Dentary: Only a small anterior portion of the dentary is preserved in the holotype (Fig. 2A–D). The curved anterior tip and the posterior part of the dentary, including the intramandibular septum, are missing. Whether the missing posterior end of the dentary has two distinct, dorsal and ventral processes, as in alethinophidians, or only a slightly concave posterior margin for the contact with post-dentary elements, as in scolecophidians, cannot be ascertained. The preserved portion of the dentary retains two mental foramina located on its lateral surface towards its anterior end (Fig. 2A). Meckel's groove is open throughout its length, and runs on the medioventral aspect of the dentary, where it deepens posteriorly, being concealed only in its posterior region by the splenial rostrum (Fig. 2B, D). None of the teeth are preserved in place, but there are 11 tooth positions left on the dentary. Tooth implantation in *Najash* seems to be of the modified alethinophidian type (*sensu* Zaher & Rieppel, 1999b), as the teeth appear to have been set in distinct sockets that are formed by prominently developed interdental ridges (Zaher & Rieppel, 1999b) (Fig. 2B, F). Similar to the condi-

tion found in alethinophidian snakes, the interdental ridges separate the tooth sockets (and probably their teeth) from one another, and form the lingual wall of the tooth socket that is received by a subdental shelf (*sensu* Conrad, 2004), which provides bony support for the ankylosis of the lingual base of the tooth. A basal plate is absent in *Najash*. A small notch is still preserved on the posterolingual wall of some sockets, and corresponds to the small alveolar foramen typical of snakes. Although the alethinophidian-type of tooth socket is clearly present in *Najash*, the orientation of the sockets in respect to the pleura retains a typical labial pleurodont condition (*sensu* Zaher & Rieppel, 1999b), comparable with that of non-alethinophidian squamates (including scolecophidians, and more specifically the genus *Typhlops*). The sockets sit in the lingual wall of a highly developed and obliquely sloping pleura, whereas the lingual dental ridge is vertically directed, instead of forming a medially expanded flange on the posterior half of the dentary, as in alethinophidians. The presence of a flange that expands medially from the lingual ridge of the dentary is typical of alethinophidian snakes, and is absent in non-ophidian squamates and scolecophidians (compare Fig. 6A–C with Fig. 6D). The formation of a horizontally directed medial flange of the lingual ridge of the dentary causes the impression that the teeth of snakes are sitting in shallow and obliquely orientated 'sockets' (Fig. 6D). This condition is clearly distinct from the one described in derived mosasauroids, in which the lingual ridge of the dentary forms a vertically directed medial flange that contributes to the formation of a deep 'alveolar groove' (Zaher & Rieppel, 1999b: fig. 1D). The latter condition is absent in basal mosasauroids, including aigialosaurids and dolichosaurids, which retain a typical pleurodont tooth implantation (see Haber & Polcyn, 2005).

The dentary of the larger referred specimen (MPCA 380) is represented by its anterior portion, broken posteriorly through the eighth alveolus (Fig. 2E–H). This element provides information on the structure of the symphysis in *Najash* (Fig. 6), which is not preserved in the holotype. The anteriormost alveolus is shallow and poorly formed, as is commonly the case in snakes where the first alveolus of dentaries tends to form only partially, and bears significantly smaller teeth. The anterior tip is curved medially, and bears a medially projected, massive, and convoluted facet (Figs 2, 6). The facet is somewhat kidney-shaped, being grooved on its ventromedial surface by Meckel's cartilage, which extends until the very tip of the dentary, anteriorly. In dorsal view, the facet has a straight anteroposteriorly directed margin (Fig. 6A), characteristic of non-ophidian squamates (Fig. 6B, C) and distinct from the rounded condition typical of the

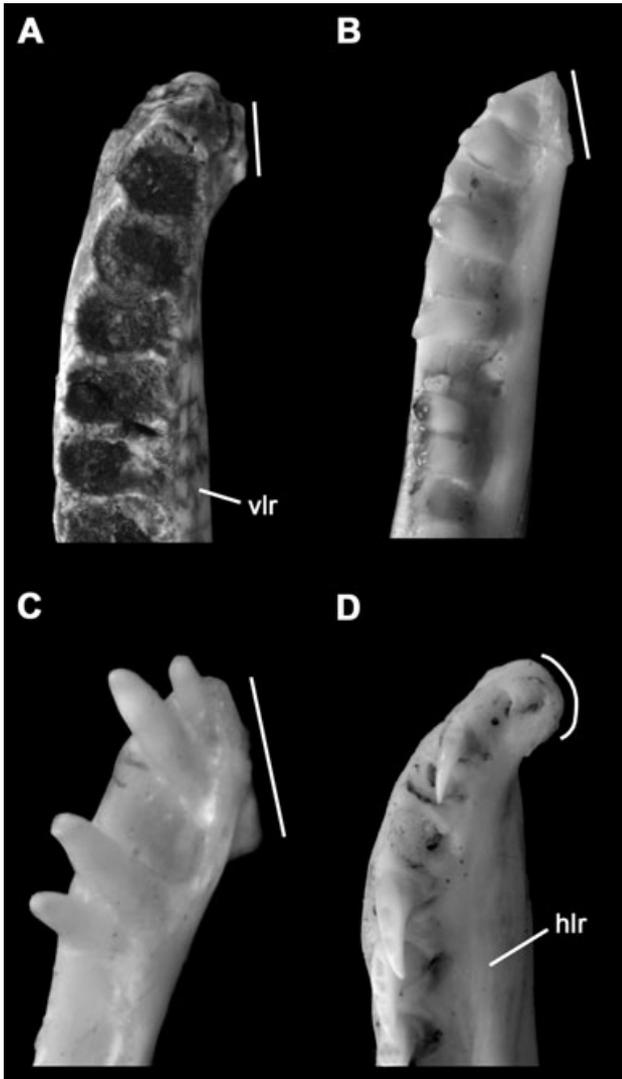


Figure 6. Anterior portion of the left dentary of several squamates in dorsal view. A, *Najash rionegrina* Apesteguía & Zaher, 2006 (MPCA 380); B, *Ophisaurus ventralis* Linnaeus, 1766 (MZUSP 40409); C, *Amphisbaena mertensi* Strauch, 1881 (MZUSP 6661); D, *Cylindrophis ruffus* Boulenger, 1893 (LSUMZ 14075). Abbreviations: hlr, horizontally directed lingual ridge; vlr, vertically directed lingual ridge. Not shown at the same scale.

dentary tip of extant snakes (Fig. 6D). Additionally, the straight facet is positioned medially with respect to the dentary tooth row (Fig. 6A), whereas the rounded facet is continuous with the tooth row and represents the distal tip of the dentary in extant snakes (Fig. 6D). It can be concluded that *Najash* had a tight contact, comparable with the one present in extant lizards with limited mobility between their dentaries as a result of strong ligaments being present instead of a bony symphysis [e.g. *Varanus*

griseus (Daudin, 1803) and *Xantusia vigilis* Baird, 1859; Young, 1942; Bellairs, 1984).

Meckel's groove is open throughout its length, and runs on the medioventral aspect of the dentary, where it deepens posteriorly. As in the holotype, the sockets for the teeth are formed by prominent interdental ridges that curve mediolingually to form shallow sockets on which the tooth sits. The dentary of the referred specimen also bears two mental foramina on its lateral surface, located at the level of the fourth and sixth tooth sockets, respectively (Fig. 2E). Dentaries of the holotype and referred specimen lack any trace of dentine infolding into the sockets, suggesting that *Najash* lacked plicidentine.

Splénial: The splénial is preserved in medial view, applied to the medioventral surface of the dentary of the holotype, where it encloses Meckel's groove (Fig. 2B–E). Only the anteriormost 'rostrum' of the splénial is preserved, and is broken in three pieces (Fig. 2B). The tip of the rostrum and the posterior body of the splénial that bears the anterior mylohyoid foramen are missing. The preserved part corresponds to a robust lamina of bone that seems to completely cover the Meckelian groove, and which is distinct from the slender lamina that forms the splénial rostrum of snakes, and only covers the medial aspect of Meckel's groove. However, the fragmentary nature of the preserved element does not allow a precise definition of the condition present in *Najash*.

POSTCRANIAL ELEMENTS

Among the six specimens available, the holotype has the better and most completely preserved postcranial material. The preserved postcranium of the holotype is composed of several small sections with articulated vertebral material, associated with other larger sections bearing articulated vertebrae and ribs. The largest section (MPCA 392) bears a continuous string of 47 articulated middle presacral vertebrae, with associated ribs, that are only exposed dorsally (Fig. 7). The same slab bears two other isolated vertebrae. Three smaller sections of articulated material were prepared to reveal the whole morphology of the elements preserved. The first articulated section (MPCA 391) contains the axis, four anterior presacral vertebrae, and the anterior half of the fifth presacral vertebra (Fig. 8). The second portion (MPCA 395) bears six articulated vertebrae from the anterior presacral region, the last one broken on its middle (Fig. 9). The third section (MPCA 400) contains the pelvic girdle and hindlimb elements associated with eight posterior presacral, two sacral, and nine caudal vertebrae (Figs 10, 11). Additionally, from the latter section we

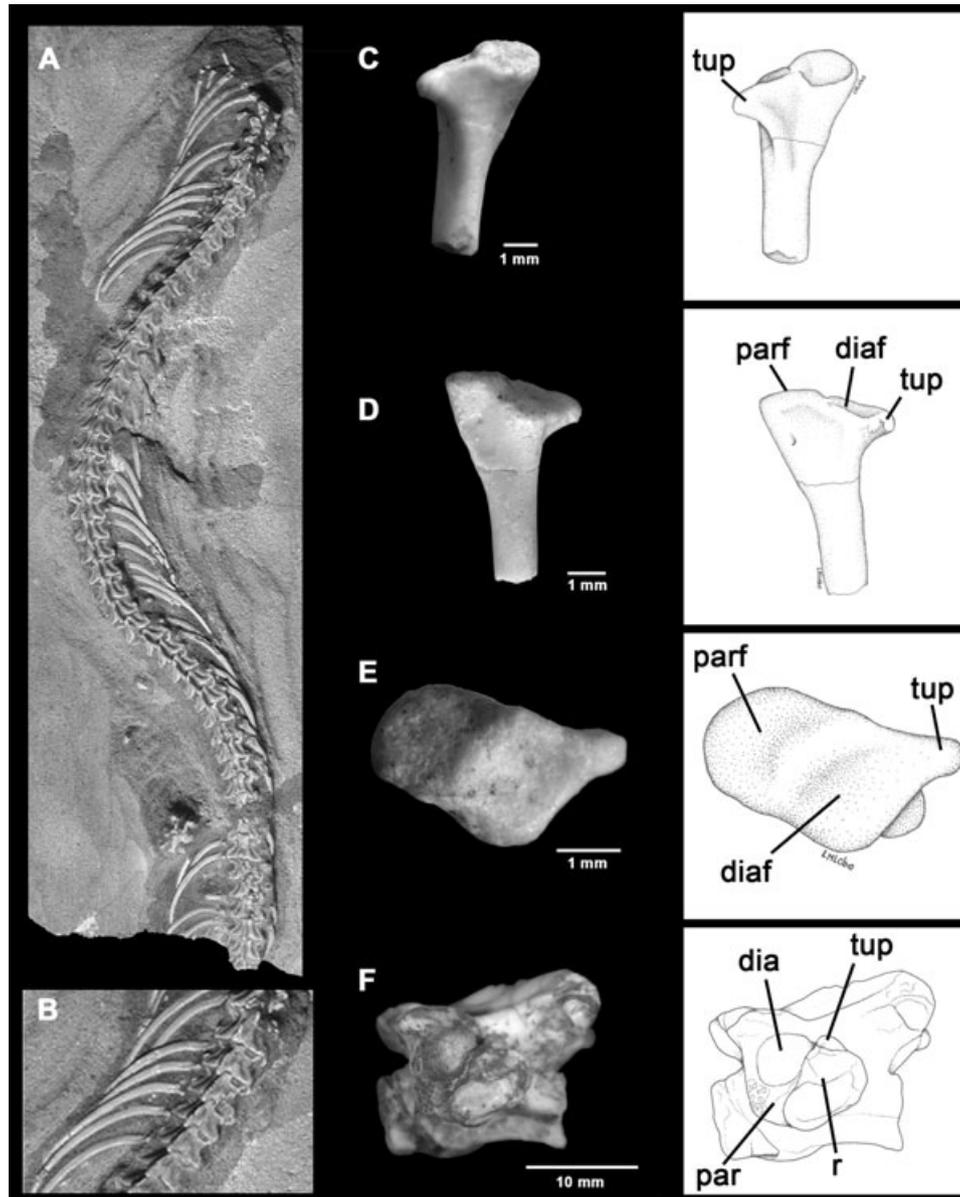


Figure 7. Articulated middle presacral vertebrae and ribs of *Najash rionegrina* Apesteguía & Zaher, 2006: A, string of articulated vertebrae and ribs of the holotype (MPCA 392); B, close-up of the anterior portion of the string. Broken proximal portion of an isolated rib of the holotype (MPCA 389): C, ventral view; D, dorsal view; E, proximal view. F, vertebra of referred specimen (MPCA 388) in lateral (left) view, in which the head of the left rib is preserved and articulated with the synapophyses. Abbreviations: dia, diapophysis; diaf, diapophysial facet; par, parapophysis; parf, parapophysial facet; r, rib head; tup, tuberculiform process.

removed and prepared separately (MPCA 396) the last two preserved and articulated caudal vertebrae (Fig. 12). Because the holotype is a young individual, the axis and the anterior and posterior presacral vertebrae of three other larger individuals (MPCA 383, 386, and 388) were prepared and used to describe differences between the juvenile and adult vertebral morphology of *Najash* (Figs 7F, 8F–H).

Presacral vertebrae: An important character is common to all of the vertebrae of *Najash*: the neural arch laminae broaden posteriorly on the lateral extremity of the zygantral roof, and have a larger surface that faces dorsally, and a smaller surface that faces laterally, conferring a strongly faceted condition to the neural arch laminae (Figs 8A, 9A, B, E, F). Additionally, a small anteroposteriorly directed ridge is present at the posterodorsal corner of the neural

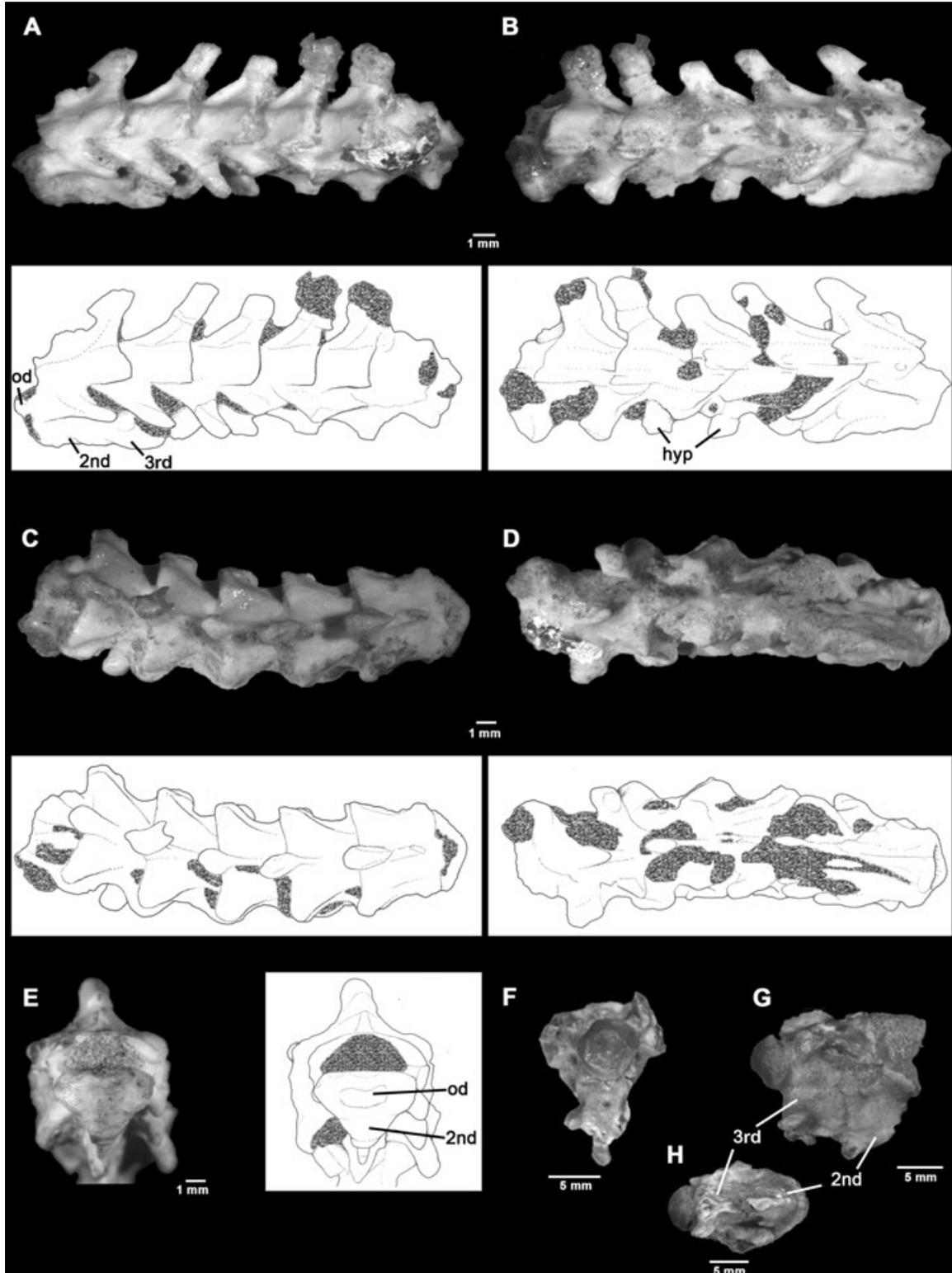


Figure 8. Axis and first anterior presacral vertebrae of the holotype of *Najash rionegrina* Apesteguía & Zaher, 2006 (MPCA 391): A, lateral (left) view; B, lateral (right) view; C, dorsal view; D, ventral view; E, anterior view of the axis. Broken portion of the axis of referred specimen (MPCA 383): F, anterior view; G, lateral view; H, ventral view. Abbreviations: 2nd, second intercentrum; 3rd, third intercentrum; hyp, hypapophysis; od, odontoid process (atlas centrum).

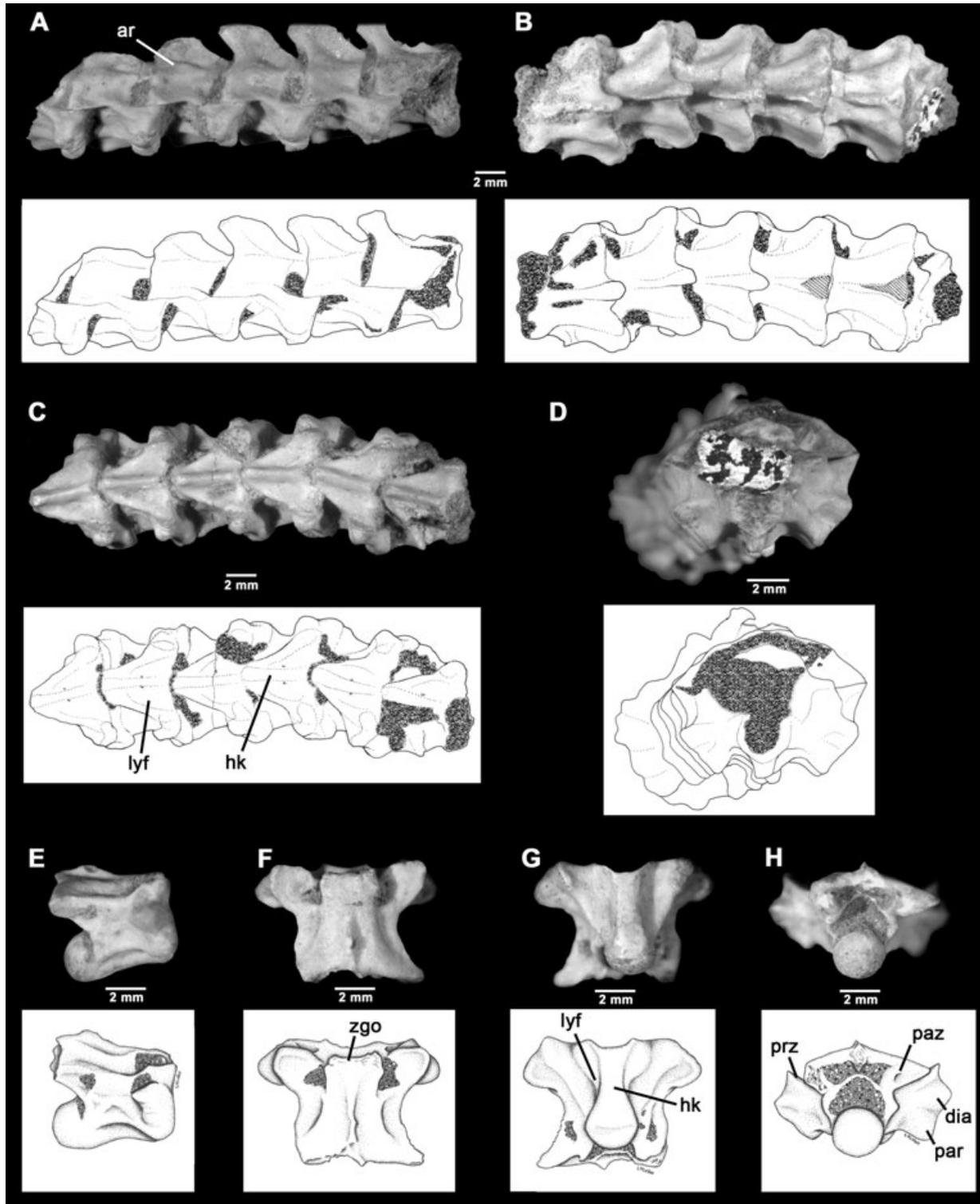


Figure 9. Middle posterior and posterior presacral vertebrae of the holotype of *Najash rionegrina* Apesteguía & Zaher, 2006. Articulated string of six middle presacral vertebrae (MPCA 395): A, lateral view; B, dorsal view; C, ventral view; D, anterior view. Isolated posterior presacral vertebra (MPCA 397): E, lateral view; F, dorsal view; G, ventral view; H, posterior view. Abbreviations: ar, arqual ridge; dia, diapophysis; hk, haemal keel; lyf, sublymphatic fossa; par, parapophysis; paz, parazygantral foramen; prz, prezygapophysis; zgo, zygosphene.

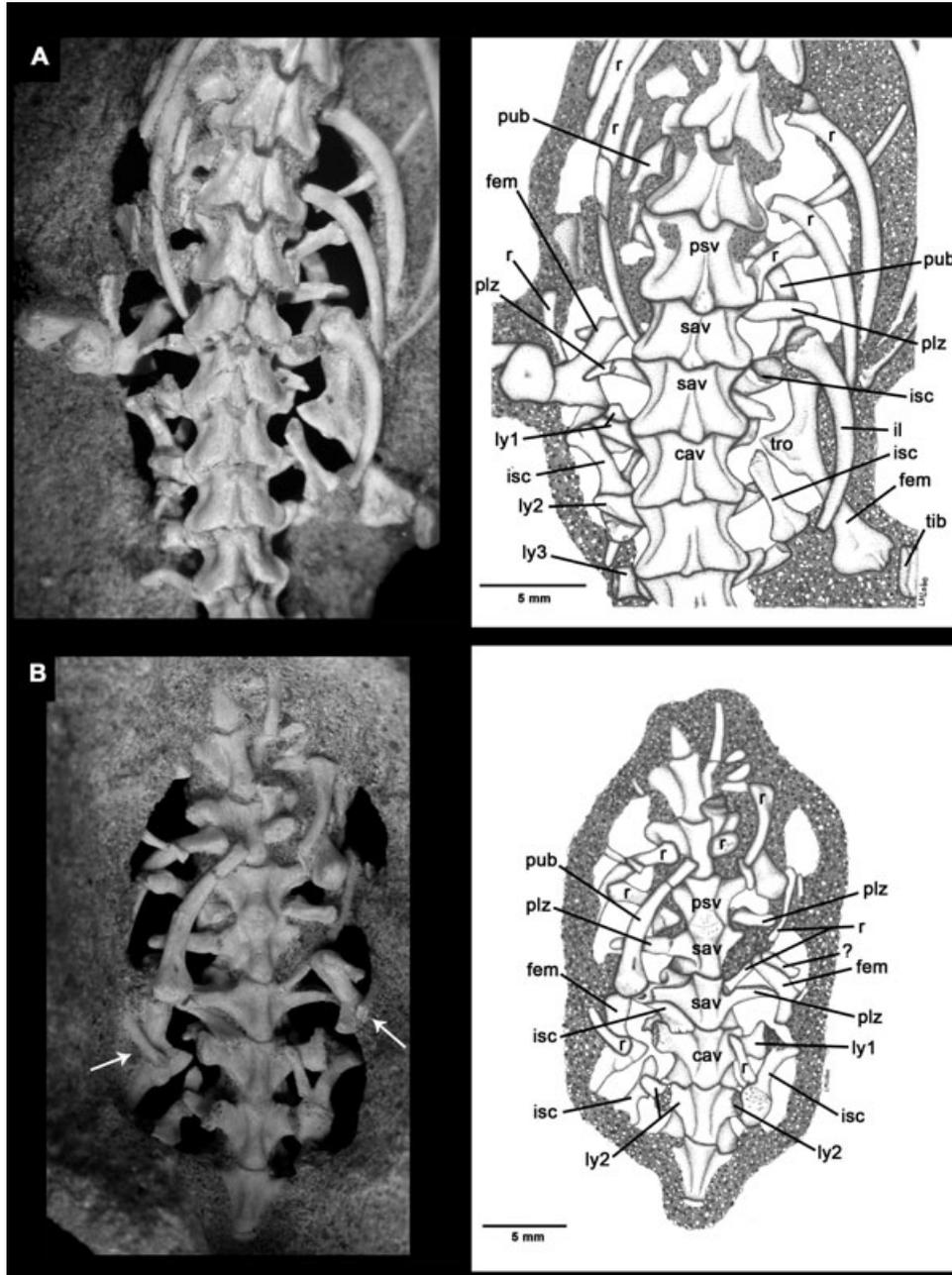


Figure 10. Sacral region of the holotype of *Najash rionegrina* Apesteguía & Zaher, 2006 (MPCA 400): A, dorsal view; B, ventral view. Abbreviations: cav, first caudal vertebra; fem, femur; il, ilium; isc, ischium; ly1–ly3, first, second, and third lymphapophyses; plz, sacral pleuroapophysis; psv, last presacral vertebra; pub, pubis; r, rib; sav, sacral vertebrae; tib, tibia; tro, trochanter. White arrows point to left and right ribs that pass ventral to the femora.

arch of all presacral vertebrae (Apesteguía & Zaher, 2006; ‘arqual ridge’ of Scanferla and Canale, 2007). The ‘arqual ridge’ is poorly developed in young specimens, and is more easily observed in larger individuals. This latter structure has also been documented in *D. patagonica* (Apesteguía & Zaher, 2006; Scanferla & Canale, 2007).

The vertebrae are always procoelous on the trunk and the tail (Figs 9, 10, 12). When observable, the cotyle forms a rounded or very slightly oval surface that receives a rounded condyle (Fig. 9). The prezygapophysial and zygantral articular facets are separated by a non-articular area (Fig. 12E). When visible in dorsal view, the zygosphenal tectum has a straight

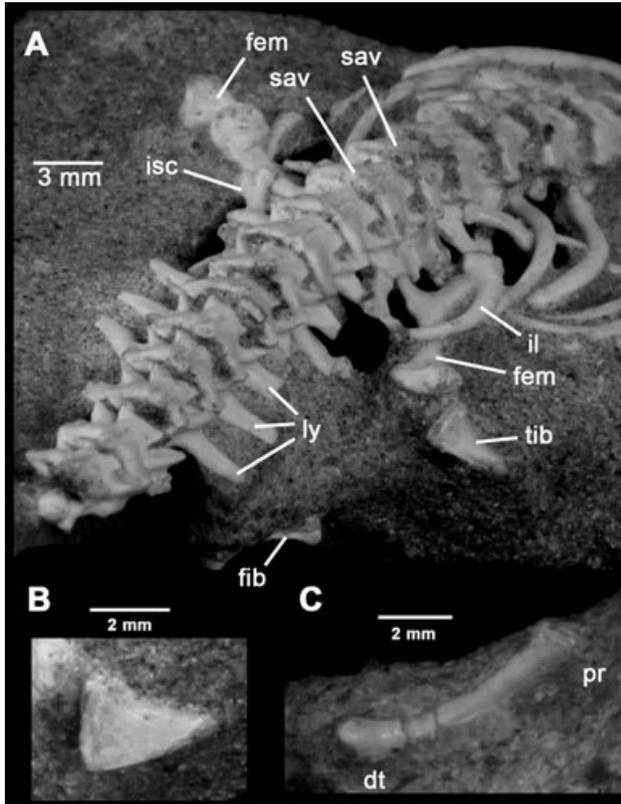


Figure 11. Sacral and caudal regions with limb elements of the holotype of *Najash rionegrina* Apesteguía & Zaher, 2006 (MPCA 400): A, posterodorsal view; B, tibia; C, fibula. Abbreviations: dt, distal head; fem, femur; fib, fibula; il, ilium; isc, ischium; ly, lymphapophyses; pr, proximal head; sav, sacral vertebra; tib, tibia.

or slightly convex anterior margin (Fig. 9E). In anterior view, the zygosphenes are somewhat thick and well-developed, as in macrostomatid snakes. The interzygapophysial constriction is shallow, and the posterior neural arch notch is absent. Parazyngantral foramina are recessed in modest fossae, and are present in all trunk vertebrae. Paracotylar foramina are lacking in all of the specimens examined. Where exposed, the zygapophysial facets are produced laterally, with their long axis being at least twice the length of the short axis. Prezygapophysial articulations are inclined at approximately 20–30° to the horizontal. As in madtsoiid snakes, the accessory (prezygapophysial) processes are lacking, which is in contrast with the poorly developed process present in *Dinilysia* and extant snakes. As expected, there is a degree of variation throughout the trunk region in the size and shape of the neural spines, hypapophyses, and synapophyses, as well as in the size of the vertebrae that are larger on the middle presacral region, and smaller in the anterior and posterior presacral regions.

The atlas is not preserved. In the articulated section containing the first cervical vertebrae (MPCA 391), the axis is somewhat elongated, with the neural arch being equal in length to the following anterior presacral vertebra (Fig. 8). The neural spines are high and anteroposteriorly short, and are restricted to the caudal portion of the neural arches. It bears developed pleurapophyses directed strongly posterovertrally. The posterior hypapophysis is long, projecting below the anterior half of the following vertebra. It bears a peculiar hook-like lateral projection on each side, proximally. Both hypapophyses (intercentra 2 and 3) seem to be fused to the axis. However, a disarticulated axis from a second specimen (MPCA 383) shows the typical snake-like condition, with the second intercentrum sutured, whereas the third is fused to the centrum (Fig. 8F–H). The axis bears an odontoid (atlas centrum) that retains an odontoid process, absent only in the uropeltines within snakes (Williams, 1959). There is no vestige of ribs associated with the axis and first two anterior trunk vertebrae of *Najash*. However, the apex of the paradiapophyses from the first two vertebrae shows a rugose surface, where ribs may have been articulated. Whether or not *Najash* possessed articulated ribs on the third and fourth anterior presacral vertebrae remains to be ascertained.

The third and fourth presacral vertebrae exhibit a well-developed ‘rod-like’ hypapophyses (Fig. 8A, B). However, there is no evidence of the large, posteriorly positioned hypapophyses, with unfused intercentra (peduncle), present in *Dinilysia* (Caldwell & Albino, 2002) and some anguimorph lizards (Hoffstetter & Gasc, 1968, 1969). The marked enlargement in size from the anteriormost vertebrae towards the more posterior ‘cervical’ vertebrae, typical of macrostomatid snakes, is much less marked in *Najash*, where the anterior vertebrae show only a slight gradual enlargement. Contrary to the condition found in macrostomatid snakes, the third anterior trunk vertebra is almost the same size as the following vertebrae.

The hypapophyses present on the anterior presacral vertebrae are replaced by a shallow and thin transverse haemal keel, which extends along the entire ventral surface of the centrum of the middle presacral vertebrae (Fig. 9C). These are narrow transversely in the mid-presacrals, and are wide and dorsoventrally low towards the posterior presacral region (Fig. 9G). The same condition is present in *Dinilysia*, anilioids, and *Xenopeltis*. Together with the subcentral ridges, the haemal keel defines two deep subequal concavities: the subcentral lymphatic fossae.

Synapophyses are well developed, and are somewhat divided into a dorsal, laterally convex diapophysial head, and a ventral parapophysial facet (Fig. 9A, D). However, such subdivision is no longer clearly

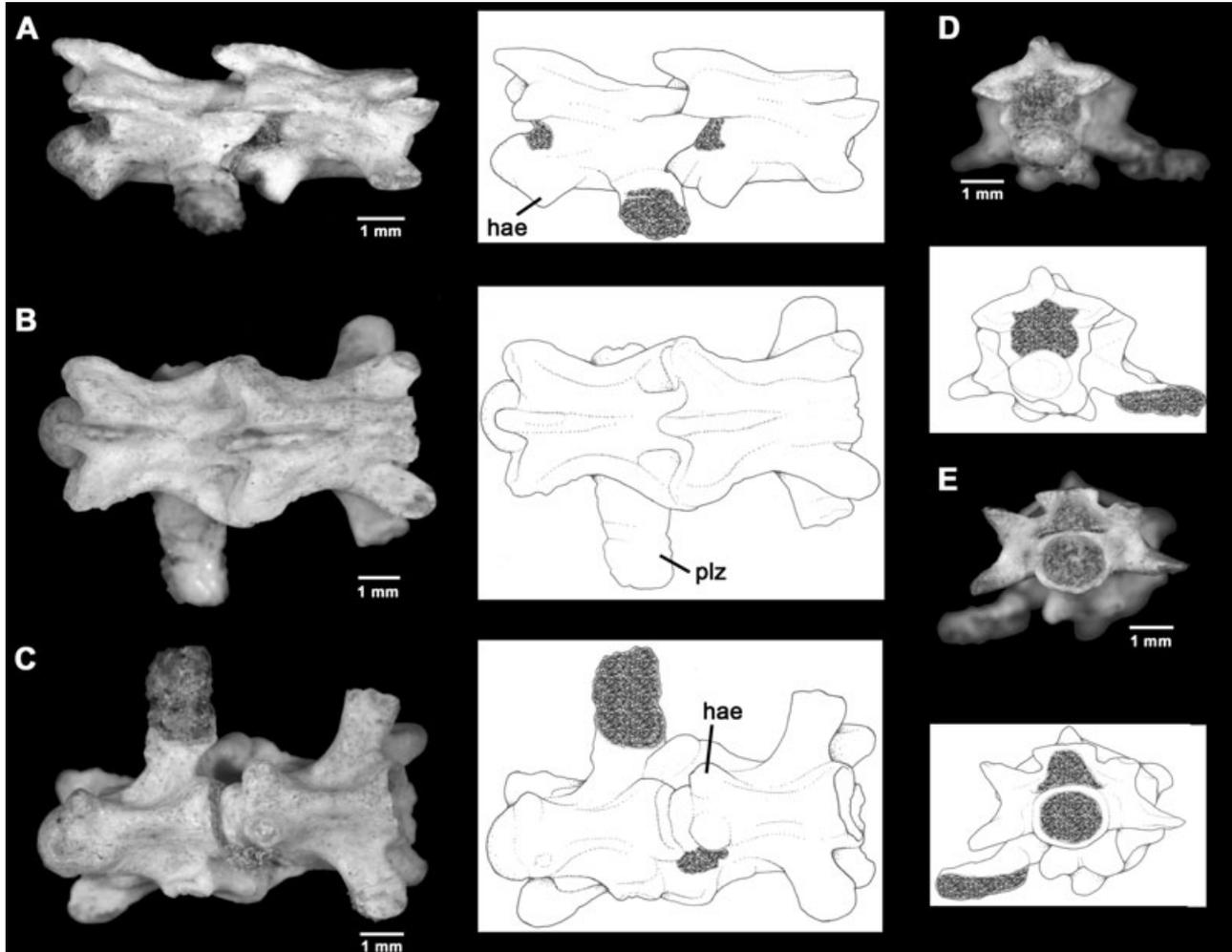


Figure 12. Caudal vertebrae of the holotype of *Najash rionegrina* Apesteguía & Zaher, 2006 (MPCA 396): A, lateral view; B, dorsal view; C, ventral view; D, posterior view; E, anterior view. Abbreviations: hae, haemapophysis; plz, pleuroapophysis.

visible on the more posterior presacral vertebrae (Fig. 9E, G). The disarticulated posterior presacral vertebra reveals strongly projected synapophyses, with the parapophysial part reaching the level of the prezygapophysial tip, whereas the diapophysial part projects laterally beyond this point (Fig. 9F, H). The paradiapophysial condition of *Najash* is unique among snakes, and approaches the general plesiomorphic condition found among lizards, where the diapophyses tend to project beyond the prezygapophysial tip. Among snakes, only the Madtsoiids (*Wonambi* and *Yurlunggur*) show diapophyses reaching the level of the prezygapophysial tip.

On the most posterior presacral vertebrae, the sub-central ridge is deeply marked. The neural arch bears a small 'arqual ridge' on each side and above the interzygantral ridge. These ridges are reduced or absent in the most posterior presacrals. The neural

spines are high and narrow on the first four anterior trunk vertebrae (Fig. 8), and decrease in length, but increase in width, proximally, to form a blade-like, posteroventrally directed spine with a subquadratic shape (Fig. 9). The anterior and dorsal edges of the neural spine are sharp, whereas the posterior edge is expanded, forming a robust, posterodorsally directed pillar, a condition also found in *Dinilysia* and madtsoiid snakes. The anterior edge of the neural spine originates near the anterior border of the zygosphenes (zygosphenal tectum) on most presacral vertebrae. However, the neural spines decrease significantly in size towards the posterior trunk region, being reduced to a low crest that is mostly restricted to the posterior half of the neural arch in the posteriormost presacral vertebrae (Fig. 9E, F, H). The zygapophysial articular surfaces are oval shaped, and decrease in size towards the posteriormost trunk vertebrae.

Sacral vertebrae: Two distinct sacral vertebrae are present and bear long pleurapophyses (Fig. 10). The first sacral vertebra bears slightly upturned pleurapophyses that are dorsoventrally broad, but anteroposteriorly narrow, at their base, and taper distally to a somewhat rounded tip, oriented laterally. The first left pleurapophysis is broken and displaced slightly anteriorly, as shown in ventral view (Fig. 10B). The first right pleurapophysis is preserved in place, as it extends laterally and slightly anteriorly, with its distal part lying dorsal to the displaced pubis. Although the neural arch and spine of the first sacral vertebra are essentially similar to the immediately anterior presacral vertebrae, it is significantly shorter than both the latter and the second sacral vertebra, a difference that is known to occur in the cloacal vertebrae of modern snakes (Hoffstetter & Gasc, 1969; Hoffstetter & Gayraud, 1965). Unfortunately, this difference cannot be confirmed with confidence on a ventral view, as the cotyle of the first sacral vertebra is fused with the condyle of the last presacral vertebra. This anomaly probably resulted from the injury that the snake suffered in the pelvic region, and that also caused the left femur to break, and eventually heal, as shown by the large callus formed just below the trochanter (Fig. 10A). Both pleurapophyses of the second sacral vertebra are preserved in place, with the tip of the left one being slightly crushed (Fig. 10B). These pleurapophyses are curved slightly posteriorly, have a broader base, and taper distally to a pointed tip that is oriented posterolaterally. The tip of the right pleurapophysis is clasped by the loosely articulated proximal heads of the pubis, ilium, and femur, which are probably only very slightly displaced from their original position. On the other hand, the tips of the right pleurapophyses from the first and second sacral vertebrae are separated from each other. Thus, the bone displacement and the trauma ossifications present in this region make it difficult to assess the exact relationship between the sacral vertebrae and the pelvis.

Caudal vertebrae: The holotype of *Najash* has nine preserved and articulated caudal vertebrae, following the second sacral vertebra (Fig. 11). Two more posterior caudal vertebrae, which were found slightly displaced from, but clearly associated with, the other caudal elements, were prepared separately (Fig. 12). The first three caudal vertebrae bear well-developed lymphapophyses that are fused to their centra, and are laterally and slightly anteroventrally directed (Figs 10, 11). The first lymphapophyses are robustly constructed, with a broad, undivided dorsoventrally expanded base that has a concave anterior surface. The right lymphapophysis of the first caudal vertebra is broken proximally. The left lymphapophysis also

lost the tips of the bifurcating branches. However, in dorsal view, the lymphapophysis clearly shows a posteriorly expanded posteroventral surface, which gives rise to the ventrally expanded branch, whereas the anterodorsal surface tapers distally to form a narrow dorsal branch. The length and shape of the undivided part of the first lymphapophysis, as compared with the second lymphapophysis, suggests that the distally bifurcating branches of the former were very short and ill-defined. The pair of lymphapophyses from the second caudal vertebra is better preserved than the first one, missing half of the ventral branch on the right side and the whole ventral branch on the left side. The second pair of lymphapophyses is more gracile than the first pair. The dorsal branch is slightly narrower than the ventral process. The branches are anteroventrally directed, and diverge from each other at the base of the lymphapophysis, forming a V-shaped (instead of a U-shaped) recess for the accommodation of the lymphatic heart. The dorsal branch tapers distally to a blunt tip, being in a slightly more anterior position than the ventral branch. As a result of postmortem displacement, the posterior tip of the left ischium came to lodge in the lymphatic recess of the second left lymphapophysis, whereas the broken posterior half of the right ischium is now lying on the dorsal surface of the dorsal process of the second right lymphapophysis. The third pair of lymphapophyses is better preserved than the former two, retaining a complete right ventral branch, whereas the other branches are preserved, but are distinctly broken at their distal ends. The third pair of lymphapophyses is very similar to the second pair, except for the size of the branches at the base of the bifurcation, where the ventral branch is significantly larger than the dorsal branch. Both branches taper to a blunt tip. The dorsal branch is slightly concave ventrally, whereas the ventral branch is slightly concave dorsally, with a tip pointing to an anterodorsal direction. The fourth to ninth preserved caudal vertebrae bear paired pleurapophyses that gradually decrease in size posteriorly (Fig. 11). The pleurapophyses are laterally and anteroventrally directed, and taper to a pointed tip that is slightly curved upwards. Pleurapophyses from the fourth and fifth vertebrae are more robustly built, with an anterodorsally expanded base and somewhat rounded distal half, whereas the more posterior pleurapophyses are progressively flattened dorsoventrally, to a flattened blade-like process.

The neural spines of the preserved caudal vertebrae are slightly higher than the sacral vertebrae. The first three caudal vertebrae bearing lymphapophyses are also ventrally identical to the sacral vertebrae, lacking any ventrally projecting haemapophyses, chevrons, or articulating surfaces for the sacral

chevrons (Fig. 10B). The sediment was not removed ventrally from the fourth vertebra, and thus it is not possible to define if this vertebra has any kind of structure projecting from the ventral surface of the centrum. However, the seven other more posterior caudal vertebrae bear weakly developed haemapophyses in the form of a pair of small button-like nodules (Figs 11, 12), resembling the condition found in *Anilius* and some macrostomatan snakes such as the basal *Xenopeltis*. These small haemapophyses are positioned in the posterior border of the ventral surface of the centra, suggesting that haemapophyses may start on the fourth or fifth caudal vertebrae. Haemapophyses are small, round, posterolaterally directed processes that are positioned on the ventral and ventrolateral aspects of the posterior border of the centra (Fig. 12). Their distal tips are blunt and slightly concave on caudal vertebrae 6 and 7, and are rounded on the other more posterior caudal vertebrae.

Ribs: The ribs are long, evenly curved, and have a blade-like shape (Fig. 7). The proximal head shows two distinct articular facets for the diapophyses and parapophyses (Fig. 7C–F). As in most extant terrestrial snakes, a well-developed tuberculiform process is present in all ribs (Fig. 7C–E), and contacts the posteromedial surface of the diapophysial surface, being directed somewhat vertically, as shown in MPCA 388 (Fig. 7F), where the head of the left rib is preserved articulated with the synapophyses (only slightly displaced from its original position). Free and distally bifurcated ribs ('sacral rib' of Lee & Caldwell, 1998) are absent in *Najash*, which retains only lymphapophyses fused to the centrum on the first three caudal vertebrae. Contrary to the condition found in *Haasiophis* and *Pachyrhachis*, and all recent snakes, the last ribs in *Najash* are ventral to both femora (Figs 10B, 11), reflecting the external position of the hindlimbs with respect to the ribcage. The most posterior rib on the left side can be seen in a somewhat dorsomedial position with respect to the femur (Fig. 10A). However, this position is clearly artifactual, as the rib in question is in a mediodorsal contact with the proximal head of the femur, which is clearly displaced from its more dorsal position.

Appendicular skeleton: Preserved elements of the appendicular skeleton include the pelvic girdle, both femora, the proximal articular head of the right tibia, and the right fibula (Figs 10, 11). The left pelvic and limb elements show signs of healed traumatism, with a large callus formation and displacement of the resulting parts on the fractured femur (Fig. 10). The left ilium is missing, whereas the left pubis is broken in the middle, and is displaced anteriorly, with the acetabular head and proximal body lying vertically

and laterally to the last two presacral vertebrae. The right pelvic elements are well preserved, and are mostly in place. The sacral pleurapophyses are long, slightly curved, and their pointed tips are separated, suggesting a loose suspension of the pelvis. The three elements of the pelvis – pubis, ilium, and ischium – are not sutured or fused together proximally, and the medioventral puboischial symphysis is also absent (Fig. 10B). The acetabular region of the right pelvic elements lies at the end of the second sacral pleurapophysis, suggesting a loose contact with that vertebra. However, this might also be the result of a slight anteroposterior postmortem displacement, as in most serpentiform squamates with a reduced pelvis and pointed pleurapophyses, the ilium is normally the one that approaches, or contacts loosely with, the tip of the pleurapophysis. The pubis retains a foramen obturator, which is not observed in the marine Cretaceous snakes (Fig. 10B). A pectineal tubercle is also not observed. The right pubis lies ventrally to the two sacral vertebrae and last trunk vertebra, in an anteroposterior and slightly mediolateral position. The right ilium is oriented anteroposteriorly, and lies dorsally to the other elements of the pelvic girdle and femur, and laterally to the two sacral and first caudal vertebrae. Medially, there is no evidence of marking or expansion for contact with the sacral pleurapophyses. The ilium and pubis are similar in size, and show a rounded, expanded proximal head, and a long curved rod-like body that tapers distally. The right ischium is broken distally. However, the proximal part retained its contact with the other two pelvic elements. As in *Pachyrhachis*, it is half the size of the latter two pelvic bones, exhibiting a somewhat concave surface that corresponds with its acetabular (proximal) tip. The broken distal half of the right ischium is posteriorly displaced, and lies on the laterodorsal tip of the broken right lymphapophysis of the second caudal vertebra. The distal tip of the ischium is unusual, as it is expanded in two rounded symmetrical lobes. The left ischium is displaced and upturned, with its posterior bilobed head directed anteriorly, whereas the anterior end is posteriorly directed and poorly preserved, bearing a large callus, probably produced by the same traumatism caused to the left hindlimb. The left ischium lies laterally to the first two caudal vertebrae, being anteriorly adpressed to the dorsal tip of the lymphapophysis, and posteriorly inserted between the two branches of the second lymphapophysis (Fig. 10A).

Both femora, as well as the right tibia and fibula, are preserved, whereas the left tibia, fibula, and both autopodia are missing in the holotype (MPCA 400). The left femur is badly deformed by a large callus formation caused by a healed traumatism. The right femur is a robust, curved element, with somewhat

cylindrical and expanded proximal and distal ends. The femoral head is rounded, and remains in a position of contact with the acetabular region of the pelvis (Fig. 10A, B). A conspicuous blade-like internal trochanter (*sensu* Romer, 1956) is present on the internal surface of the proximal part of the femoral diaphysis. The shape of the trochanter in *Najash* is clearly distinct from known saurian trochanters. Nonetheless, the presence of a conspicuous trochanter represents a plesiomorphic trait that is absent in Pachyophiid snakes with well-developed hindlimbs (Caldwell & Lee, 1997; Rage & Escuillié, 2000; Tchernov *et al.*, 2000), and in extant snakes, with the noticeable exception of Leptotyphlopids (List, 1966). The expanded distal head of the femur is distinctly bifaceted, with two, obliquely disposed, convex trochlea for the articulation of the tibia and fibula. Only the proximal head of the tibia is preserved (Figs 10A, 11B), being broken at the proximal end of the diaphysis close to the femoral distal epiphysis, and displaced from its natural position. The proximal section is expanded, with a slightly concave articular surface, and with no evidence of a cnemial crest. The right fibula was found disarticulated below the sixth and seventh caudal vertebrae (Fig. 11C). It is a long, gracile, curved bone, with weakly expanded similar proximal and distal heads. Proximally, the fibula might have articulated with the smaller oblique distolateral surface of the femoral trochlea, whereas the tibia articulated with the larger distoproximal surface of the trochlea.

DISCUSSION

Several well-preserved Cretaceous and Cenozoic snakes have been brought to light or redescribed in the last ten years. These are the Cenozoic terrestrial 'Madtsoiids' *Yurlunggur* sp. (Scanlon, 2006) and *Wonambi naracoortensis* Smith, 1976 (Scanlon & Lee, 2000; Rieppel *et al.*, 2002; Scanlon, 2005), the Cretaceous Tethyan marine snakes *Pr. problematicus* (Caldwell & Lee, 1997; Lee & Caldwell, 1998; Zaher, 1998; Zaher & Rieppel, 1999a, 2002; Rieppel & Zaher, 2000a), *H. terrasanctus* (Tchernov *et al.*, 2000; Rieppel *et al.*, 2003), *Pachyophis woodwardi* Nopcsa, 1923 (Lee *et al.*, 1999), and *E. descouensi* (Rage & Escuillié, 2000; Rieppel & Head, 2004), and the Cretaceous terrestrial snake *D. patagonica* (Caldwell & Albino, 2002). *Najash rionegrina* shares the following derived ophidian features with these fossil snakes and extant snakes: a completely enclosed braincase, fused parietals, large number of presacral vertebrae, and zygosphenal and zygapophysial facets separated by a non-articular area. Furthermore, it shares the following ophidian synapomorphies with extant snakes: axis with sutured anterior and fused

posterior hypapophyses, anterior margin of zygosphenal tectum straight or slightly convex, divided synapophyses, three distally forked lymphapophyses, and haemapophyses on posterior tail vertebrae (these features are either absent or unknown in *Haasiophis*, *Pachyrhachis*, *Pachyophis*, and *Eupodophis*).

Pachyrhachis problematicus, *H. terrasanctus*, and *E. descouensi* were, until now, the only known snakes with clearly preserved well-developed hindlimbs, although it is most probable that *Po. woodwardi*, *D. patagonica*, *W. naracoortensis*, and *Yurlunggur* sp. also retained hindlimbs. However, none of the articulated postcranial material of *Dinilyisia* has preserved the sacral and caudal regions, and the Australian 'Madtsoiids' are known only from disarticulated and incomplete specimens. On the other hand, *Po. woodwardi* has been considered to be closely related and very similar to *Pr. problematicus* (Lee *et al.*, 1999; Rieppel & Head, 2004), suggesting that it probably has well-developed hindlimbs and a pelvis, preserved but unprepared, under the mid-dorsal ribs and vertebrae (Lee *et al.*, 1999).

THE AXIAL AND APPENDICULAR SKELETONS OF *NAJASH*: A FRESH START FOR THE DEBATE ON THE EVOLUTION OF LIMBLESSNESS IN SNAKES

Forelimbs are completely absent in all extant snakes, and in the fossil snakes *Pachyrhachis*, *Haasiophis*, *Eupodophis*, *Dinilyisia*, and *Najash*. On the other hand, hindlimbs persist in several families of extant snakes as rudimentary elements, consisting of a pelvic girdle, a rudimentary femur, and an external claw-like vestige. These elements are completely lost in the derived Caenophidian snakes, and in a number of unrelated alethinophidian snake families (i.e. Xenopeltidae, most Uropeltinae, the genus *Tropidophis* within Tropidophiidae, Bolyeriidae, and Xenophidiidae).

The presence of fully formed hindlimbs in the Tethyan marine limbed snakes *Haasiophis*, *Pachyrhachis*, and *Eupodophis* enforced the idea that they were the most primitive snakes known, and that they were perfect transitional taxa linking extant snakes to the marine mosasauroids (Caldwell & Lee, 1997). However, as previously suggested by Zaher & Rieppel (2000), the appendicular skeleton of the Cenomanian marine limbed snakes corresponds more accurately to a derived ophidian morphology, with free lymphapophyses and a pelvis that is not suspended from the axial skeleton, but rather lies within the ribcage and lacks a differentiated sacral region (Fig. 13). On the other hand, *Najash* lacks free lymphapophyses, and retains two sacral vertebrae that anatomically separate the trunk region from the caudal region, with a pelvis that is functionally but

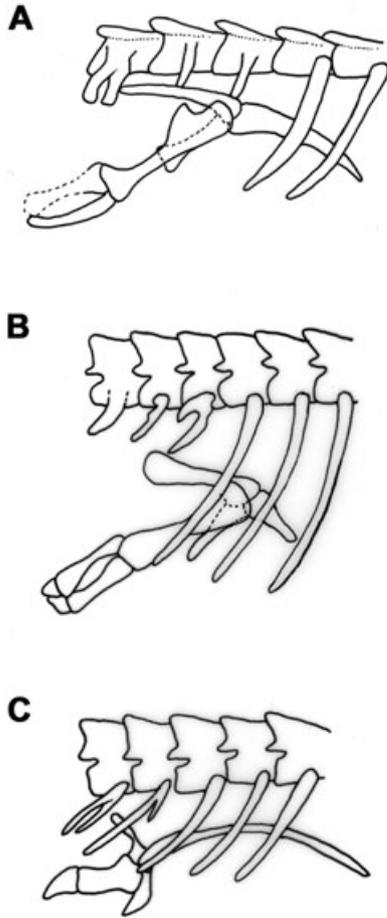


Figure 13. Reconstructions of pelvis and hindlimb elements: A, *Najash rionegrina* Apesteguía & Zaher, 2006; B, *Pachyrhachis problematicus* Haas, 1979; C, a boine snake.

loosely connected to the sacral region, and which lies outside of the ribcage: all being plesiomorphic non-ophidian conditions (Fig. 13).

The loss of a sacral region and consequent disconnection of the pelvis from the axial skeleton represents a synapomorphy of extant snakes, shared by *Pachyrhachis*, *Haasiophis*, and *Eupodophis*, whereas the presence of free lymphapophyses is a derived feature shared by extant snakes, *Pachyrhachis*, and probably *Haasiophis*, but not by *Eupodophis* (Rage & Escuillié, 2000; Rieppel & Head, 2004). The re-interpretation of the posterianal anatomy of *Pachyrhachis*, *Haasiophis*, and *Eupodophis* renders it more closely comparable with the rudimentary hindlimbs of extant snakes than to non-ophidian squamates, a result that is in accordance with a derived position of these fossil taxa within the extant snake clade (Zaher, 1998; Tchernov *et al.*, 2000; Rieppel *et al.*, 2002; Apesteguía & Zaher, 2006), rather than as the basalmost snakes (Caldwell & Lee, 1997; Rage & Escuillié, 2000).

Scanlon & Lee (2000) and Rage & Escuillié (2000) reported the presence of true chevron bones (Y-shaped elements that articulate or fuse with paired pedicels located at the posterior margin of the centrum of the caudal vertebrae) in *W. naracoortensis* and *E. descouensi*, respectively, another allegedly primitive feature of these snakes. However, Rieppel & Head (2004) argued convincingly that the structures called 'chevron bones' in *Eupodophis* are unique, and not homologous with the chevron bones of other squamates. The two arms of the Y-shaped element embrace an unpaired, blade-like pedicel that is located at the anterior end of the centrum, a morphology that is not comparable with any condition known in non-ophidian squamates (Rieppel & Head, 2004: 21). Similarly, the assignment of a single disarticulated caudal vertebra with a chevron bone to *W. naracoortensis* by Scanlon & Lee (2000) was questioned by Rieppel *et al.* (2002), as this vertebra might not belong to the specimen described by Barrie (1990; but see Scanlon, 2005: 143).

Scanlon (1993) recognized the presence of true haemapophyses (paired pedicels, laminae, or rod-like projections that do not fuse with each other distally, located at the posterior margin of the centrum of the caudal vertebrae) in the caudal vertebrae of an undetermined species of *Patagoniophis* from the Eocene of Tingamarra (Queensland), and Rage (1998) described haemapophyses in the posterior caudal vertebrae of *Madtsoia camposi* Rage, 1998 from the Paleocene of Itaboraí (Brazil). The presence of true haemapophyses in *Patagoniophis* and *Madtsoia* suggest that most 'Madtsoiids' did retain the derived condition known for all snakes, and that the chevron bone reported in *Wonambi* by Scanlon & Lee (2000) should be viewed with caution.

It can be concluded that there is no unquestionable record of true chevron bones in snakes, and the presence of well-preserved haemapophyses in the posterior caudal vertebrae of *N. rionegrina* seems to support the view that chevron bones are absent in snakes (Fig. 12).

The recent report by Cohn & Tickle (1999) on *Hox* gene expression patterns in *Python* represents an important piece of evidence from a distinct source, which helps in the better understanding of the evolution of limblessness in snakes. However, some of their conclusions regarding the steps that led to the acquisition of limblessness in snakes need to be re-evaluated, according to the new morphological and phylogenetic implications brought by the subsequent discovery of *N. rionegrina*.

Cohn & Tickle (1999) suggested that the progressive expansion of *Hox* gene expression domains along the body axis is the main factor responsible for the evolution of limblessness in snakes, and would account for the loss of forelimbs, hindlimbs, and

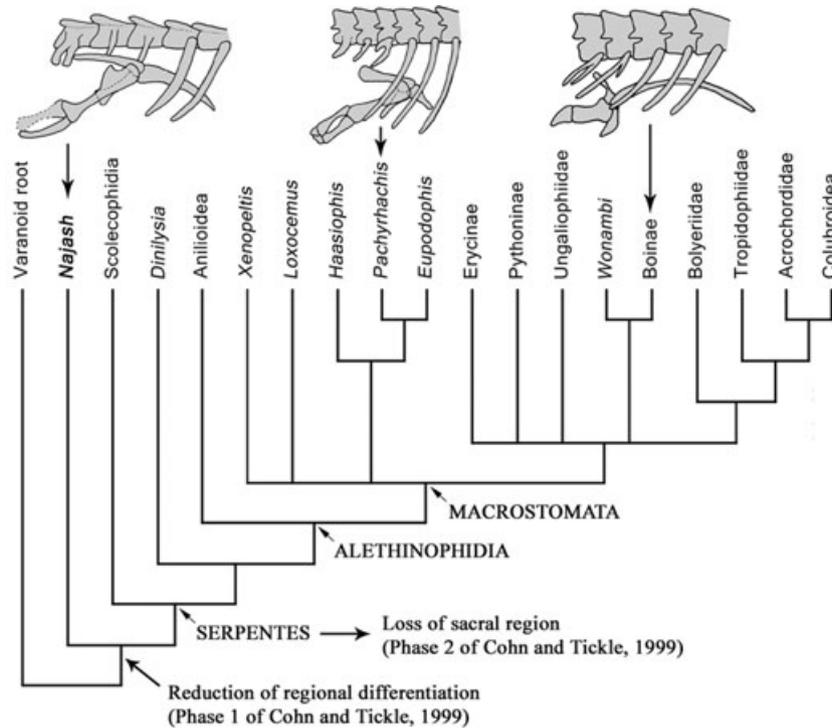


Figure 14. Alternative hypothesis for the appearance of the main developmental changes in the axial skeleton of snakes, optimized in a phylogenetic tree that includes the fossil taxa *Najash*, *Pachyrhachis*, *Haasiophis*, and *Eupodophis* (Apesteguía & Zaher, 2006).

regional identity along the axial skeleton in snakes (i.e. distinct cervical, thoracic, lumbar, and sacral regions). These authors used Caldwell & Lee's (1997) phylogenetic hypothesis, in which *Pr. problematicus* represents the most primitive snake, and an intermediate form between mosasaurs and extant snakes, as a backbone hypothesis for their developmental scenario of snake evolution (Cohn & Tickle, 1999: fig. 5). According to Cohn & Tickle's (1999) model, the expansion of *Hox* domains that led to the transformation of the entire axial skeleton towards thoracic identity, and to the reduction of hindlimb development by the elimination of the ectodermal competence, to form an apical ridge expansion, appeared only in the ancestor of extant snakes, excluding *Pachyrhachis* and, by extension, the remaining Tethyan marine legged snakes, *Haasiophis* and *Eupodophis*. Alternatively, if *Najash* represents the sister taxon to all known extant and extinct snakes, including *Pachyrhachis*, *Haasiophis*, and *Eupodophis*, and if the latter three are deeply nested within alethinophidian snakes as derived macrostomatans, then, according to the model advanced by Cohn and Tickle, the reduction of regional differentiation in the axial skeleton must have occurred in the ancestor of the clade formed by *Najash* and all other snakes, with the former retaining a sacral region posterior to a uniform presacral

region (i.e. there was a loss of a distinct cervical region; phase 1 of Cohn and Tickle; Fig. 14). The loss of the sacral region through the transformation of the entire axial skeleton towards thoracic identity (phase 2 of Cohn and Tickle) appeared only posteriorly, in the ancestor of the clade formed by extant snakes, including the Tethyan marine legged snakes (Fig. 14). The loss of the sacral region also caused the disconnection of the pelvis from the axial skeleton and the consequent anteroventral dislocation of the entire appendicular skeleton to a position internal to the ribcage. The loss of the apical ridge might also have occurred concomitantly in phase 2 described above (Fig. 14). However, the potential of the hindlimb bud mesenchyme to act as a polarizing region, and to coordinate limb bud outgrowth, as shown by Cohn & Tickle (1999) in *Python*, is retained not only in the latter genus, but also in most scolecophidians, anilioids, and macrostomatans. Such potential plasticity explains the strikingly distinct rudimentary patterns of the appendicular skeleton shown by scolecophidians, anilioids, and macrostomatans (Duerden & Essex, 1923; Bellairs, 1950; List, 1955, 1966; Mlynarski & Madej, 1961; Underwood, 1977). It also helps understand the presence of well-developed hindlimbs in the macrostomatans fossil snakes *Pachyrhachis*, *Haasiophis*, and *Eupodophis*.

A possible explanation for the presence of hindlimbs in the Tethyan marine snakes is that the reduction of hindlimb elements occurred independently in the major basal clades of extant snakes (i.e. in Scolecophidia, Anilioidea, and Macrostromata) (Zaher & Rieppel, 1999a; Greene & Cundall, 2000). Under such a scenario (our preferred hypothesis), basal representatives of most major modern snake lineages would have retained somewhat well-developed hindlimb morphologies during the Cretaceous. The process of independent reductions to vestigial posterior hindlimbs during the late Cretaceous, and possibly early Cenozoic, also resulted in independent losses within these lineages (e.g. in Xenopeltidae, most Uropeltinae, the genus *Tropidophis* within Tropidophiidae, Bolyeriidae, Xenophidiidae, and Caenophidia). The hypothesis of independent losses is directly open to testing by the fossil record, as it presupposes that basal fossil representatives of all major extinct and extant lineages of modern snakes are likely to have retained well-developed hindlimb morphologies during at least the Cretaceous period (Zaher & Rieppel, 1999a). Although the latter hypothesis is less parsimonious than the alternative re-development of complete hindlimbs in the Tethyan marine snakes, it fits more accurately with the new evolutionary scenario revealed by the intermediate morphology of *Najash*, which suggests that the loss of the sacral region occurred prior to the reduction of hindlimbs.

THE SKULL OF *NAJASH* AND ITS BEARING ON THE DEBATE ON THE ORIGIN OF FEEDING IN SNAKES

Although the skull of *Najash* is only known by some fragmentary parts, the known elements provide important new information that helps to fill the morphological gap between lizard and snake bauplans.

The skull of *Najash* retains several primitive features, such as (derived conditions are given in parenthesis): two mental foramina in the dentary (one mental foramen present); a well-developed symphyseal facet of the dentary, with a straight anteroposteriorly directed margin that suggests a tight interramal connection (distal tips of the dentaries round, with a loose interramal contact); pleurodont tooth implantation (alethinophidian-type of tooth implantation); laterosphenoid absent (laterosphenoid present); basipterygoid processes that are prominent, rounded, and longitudinally oriented, fitting in an articular facet of the pterygoid (poorly developed and only contacting the dorsal surface of the pterygoid); a weakly developed crista circumfenestralis (well developed); otooccipitals separated dorsally (meeting dorsally); juxtastapedial recess open widely posteriorly (enclosed by the crista tuberalis).

Recently, Lee *et al.* (1999) argued that mosasaurs (including aigialosaurids, dolichosaurids, and mosasaurids), as the nearest relatives of snakes, represent a crucial intermediate stage between the 'relatively inflexible lizard skull and the highly mobile snake skull'. According to these authors, mosasaurs and snakes share the derived conditions of flexible jaws and a more rigid braincase. Both groups acquired these two conditions by evolving interramal and intramandibular hinges in their mandibles, and by losing the meso- and metakinetic joints of the braincase, respectively (Lee *et al.*, 1999). Lee *et al.* (1999: fig. 1) illustrated their hypothesis with a simplified cladogram in which the distinct jaw systems of lizards, mosasaurs, and snakes are superimposed. According to this figure, 'lower jaw flexibility, enlarged pterygoid teeth, and reduced meso- and metakinesis' are novelties that arose in the ancestor of mosasaurs and snakes, whereas 'upper jaw flexibility, enlarged palatine teeth, loss of meso- and meta kinesis' appeared as evolutionary novelties in the ancestor of modern snakes.

Not surprisingly, Greene & Cundall (2000) questioned the oversimplified scenario advanced by Lee *et al.* (1999) for the evolution of the highly specialized feeding mechanism of snakes. Accordingly, Lee *et al.* (1999) failed to acknowledge the absence of pterygoid and palatine teeth in all three families of scolecophidian snakes, and their presence as tiny elements in *D. patagonica*. They also disregarded the fact that aigialosaurids retain the plesiomorphic varanoid condition of the supratemporal.

The combination of a large symphyseal facet of the dentary (corresponding to a tight interramal connection), a low anilioid-like quadrate, a prominent basipterygoid process fitting in an articular facet of the pterygoid, and a short supratemporal bone, suggest that *Najash* had only limited unilateral movements of the mandibles, and lacked the attributes of macrostomatan snakes to ingest large prey. The prominent symphyseal facet of the dentary of *Najash* further suggests that this snake had only limited intramandibular movements. The plesiomorphic skull morphology of *Najash* does not support the scenario suggested by Lee *et al.* (1999) for the evolution of snake feeding, as it suggests that the ancestral skull morphology for the root of extant snakes corresponds to the condition present in *Dinilysia* and anilioid snakes (with a low quadrate and large suprastapedial process, expanded posterior portion of the braincase, and short supratemporal incorporated into the braincase wall), instead of the highly flexible jaw condition of *Pachyrhachis*, *Haasiophis*, *Eupodophis*, and extant macrostomatan snakes.

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