Emended diagnosis and phylogenetic relationships of the Upper Cretaceous fossil snake Najash rionegrina Apesteguía and Zaher, 2006

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

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ABSTRACT—The fossil snake *Najash rionegrina*, from the Cenomanian–Turonian (Upper Cretaceous) of Argentina, is reinterpreted after examination of the type and referred material. The current diagnosis is emended in the light of important considerations that cast doubt on the attribution of type and referred specimens (a braincase, a quadrate, and two dentary/lower jaw fragments) used to systematize this taxon. Alternative interpretations of the anatomy of the sacrum and hind limbs are 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*, Madtsoiidae, and *Dinilysia*), and alternative outgroups. Regardless of the outgroup used to polarize the character-state transformations, our 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.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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 (2011).

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 exhibits a unique combination of primitive traits (e.g., retention of 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 provide 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

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Museum of Gannat, Gannat, France; **UAZM**, University of Alberta Zoology Museum, Edmonton, Alberta, Canada; **USNM**, 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 de Muñoz (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* (ZAHER ET AL., 2009)

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 problematic 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. 1). Moreover, the dentary of 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
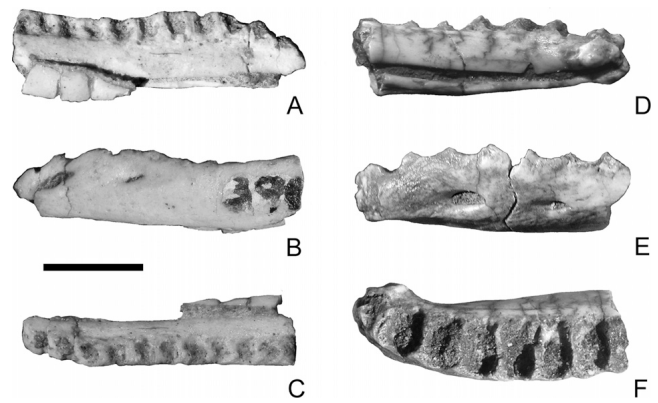

FIGURE 1. Comparison between the two partial dentaries MPCA 380 and MPCA 390. **A**, MPCA 390, medial view; note the fragment of the left splenial still attached to the posteroventral margin of the dentary; **B**, MPCA 390, lateral view; **C**, MPCA 390, dorsal view; **D**, MPCA 380, medial view; **E**,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

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 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

TABLE 1. Variability in the position of the mental foramen/foramina in a series of snake taxa.

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

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.

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* (UAZM 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. 2, 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. 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. 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.

As regards 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. 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.
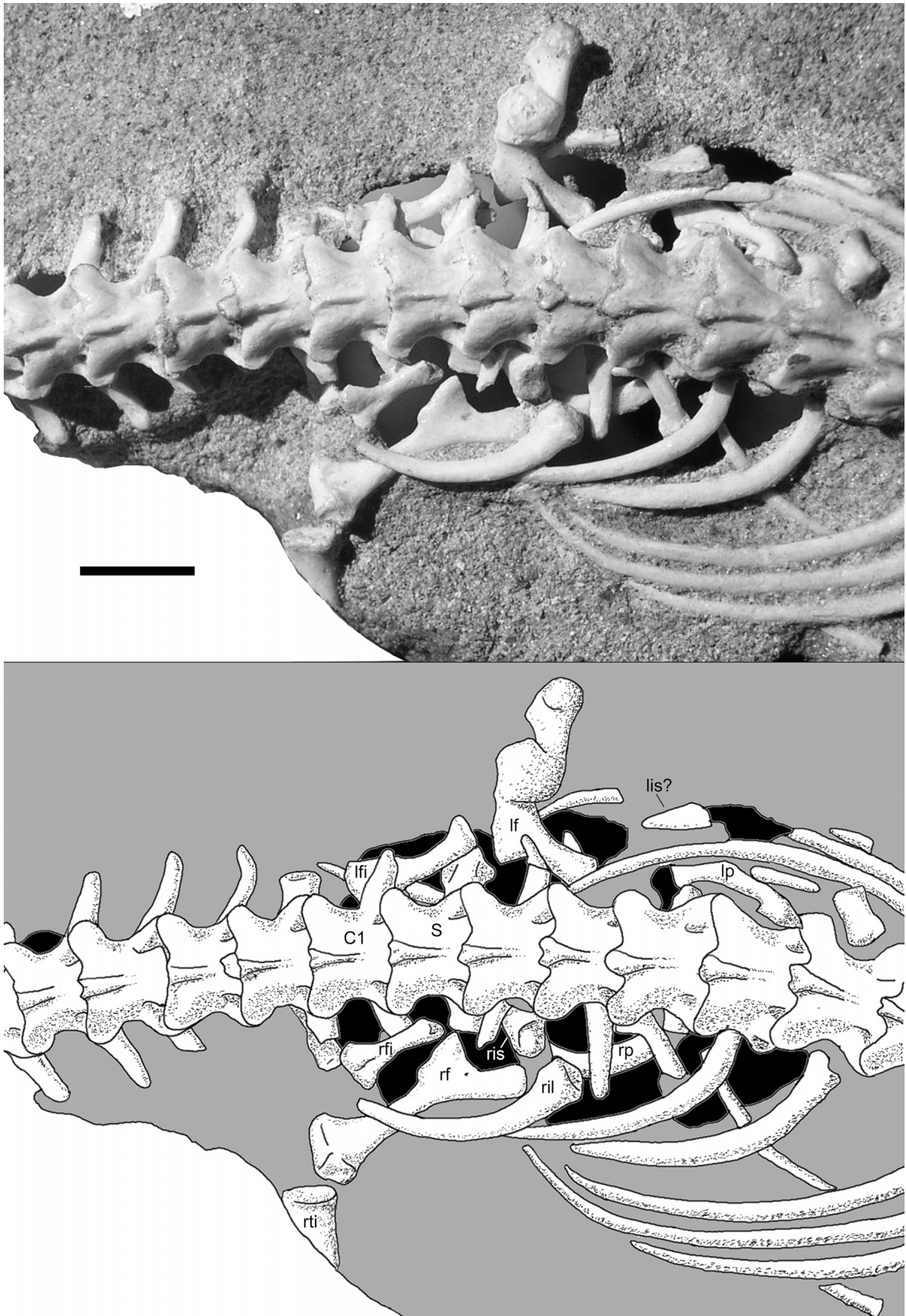
FIGURE 2. Photo and interpretative drawing of the sacral region and hind limbs of *Najash rionegrina* (MPCA 400) in dorsal view. **Abbreviations**: **C1**, first caudal vertebra; **lf**, left femur; **lfi**, left fibula; **lis?**, fragment of left ischium?; **lp**, left pubis; **rf**, right femur; **rfi**, right fibula; **ril**, right ilium; **ris**, right ischium; **rp**, right pubis; **rti**, right tibia; **S**, sacral vertebra. Scale bar equals 5 mm.
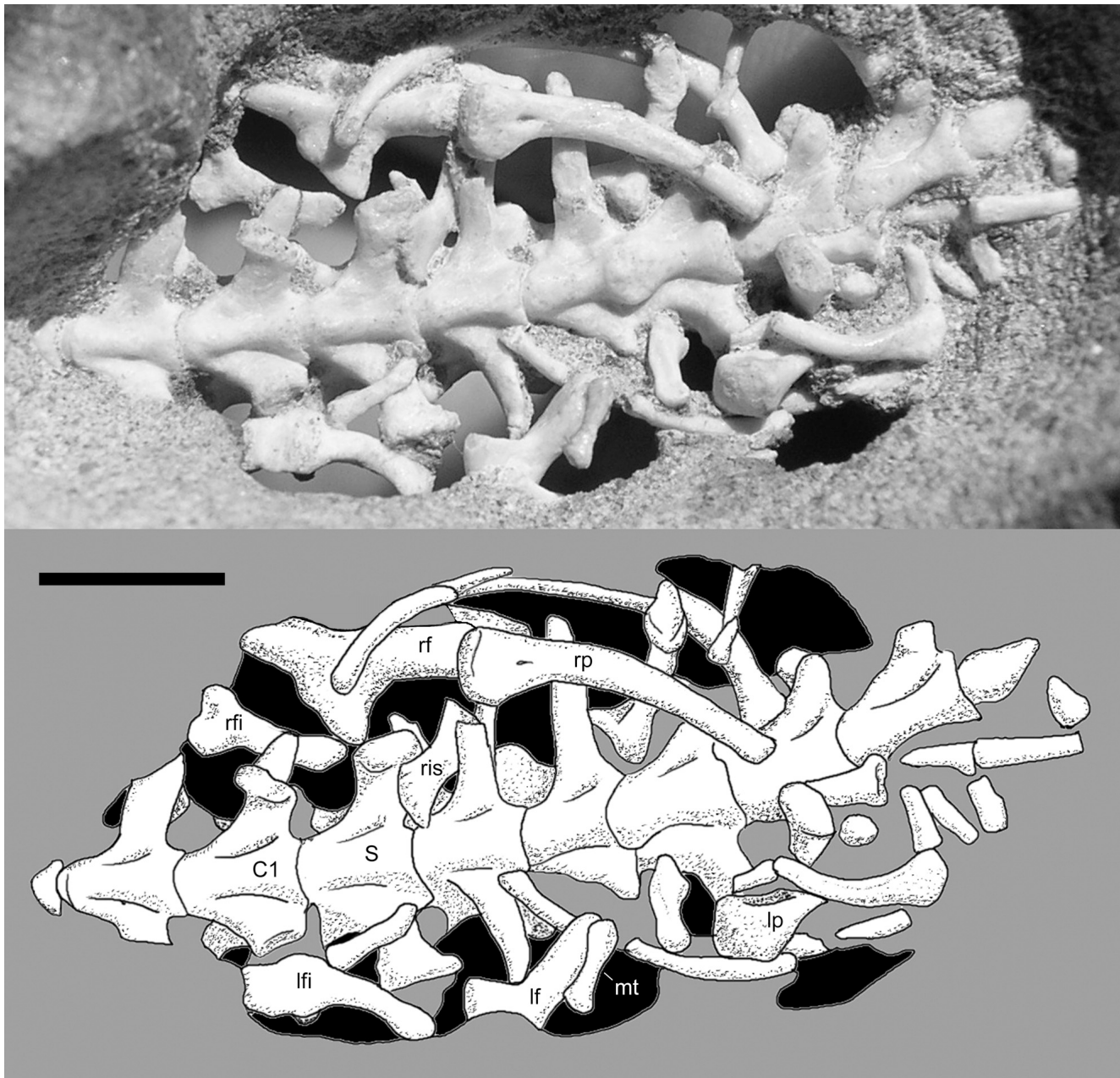
FIGURE 3. Photo and interpretative drawing of the sacral region and hind limbs of *Najash rionegrina* (MPCA 400) in ventral view. **Abbreviations**: **C1**, first caudal vertebra; **lf**, left femur; **lfi**, left fibula; **lp**, left pubis; **mt**, metatarsal; **rf**, right femur; **rfi**, right fibula; **ris**, right ischium; **rp**, right pubis; **S**, sacral vertebra. Scale bar equals 5 mm.

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 (2011). 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. As regards 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 online Supplementary Data 1–4). 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, and MCZ 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 online Supplementary Data S1.

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. 4A); the analysis that had Iguania as the outgroup yielded six most parsimonious trees of 590 steps, CI = 0.50, and RI = 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), so that these two clades do not even appear in the respective strict consensus tree. More 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 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). Interestingly, 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. 4B–C) or a paraphyletic assemblage (Fig. 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 (bootstrap <50%) and was retrieved in only 5 (only 2 for the clade inclusive of *Najash*) of our 17 trees. 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,
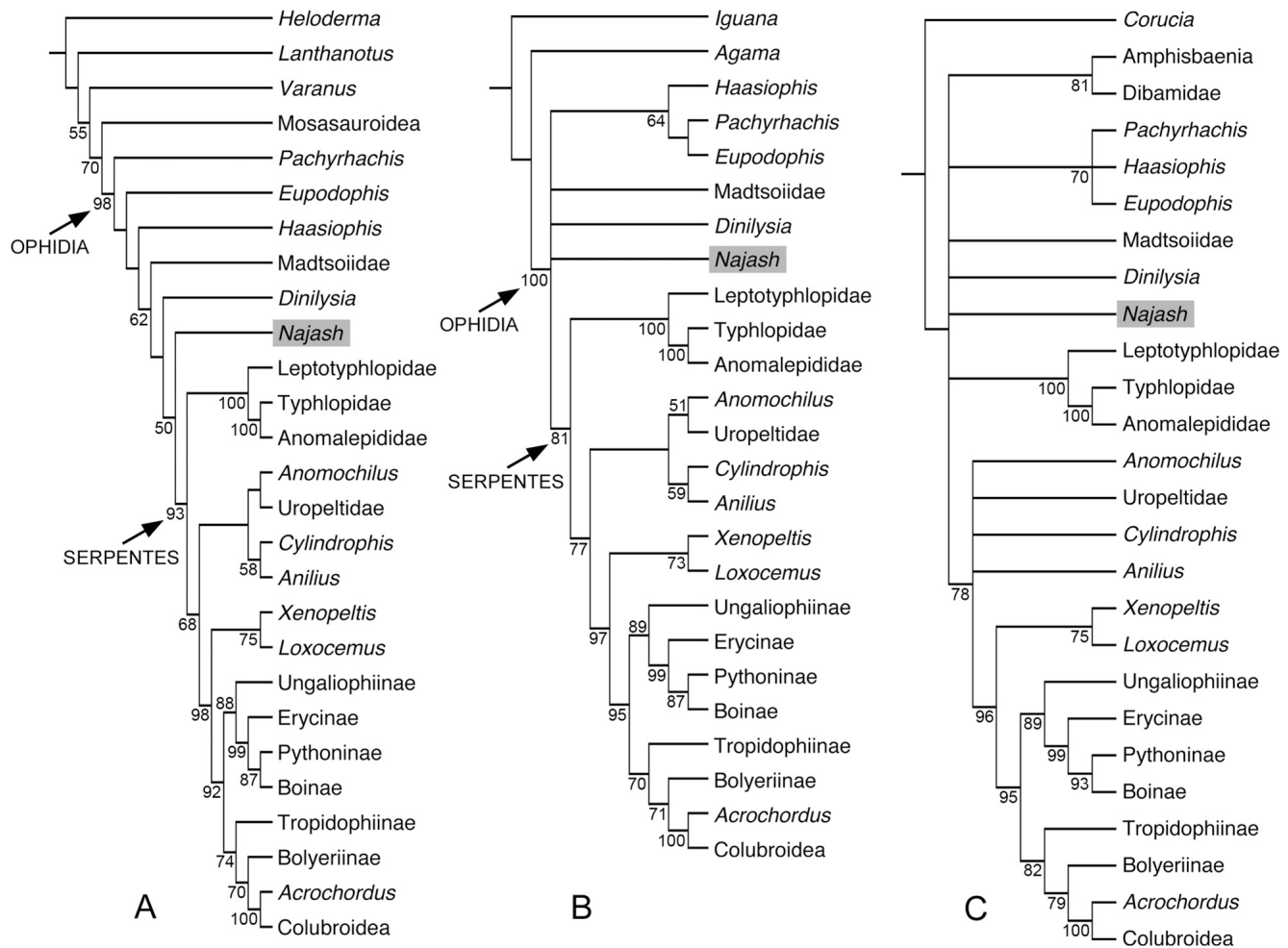
FIGURE 4. Most parsimonious trees retrieved in the three phylogenetic analyses of extinct and extant snakes. **A**, most parsimonious tree retrieved in the analysis that used varanoid lizards (*Heloderma*, *Lanthanotus*, *Varanus*, and Mosasauroidea) as outgroups; **B**, strict consensus of the six most 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.

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 method of the extant phylogenetic bracket (Witmer, 1995) to our cladogram in Figure 4A, 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, 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
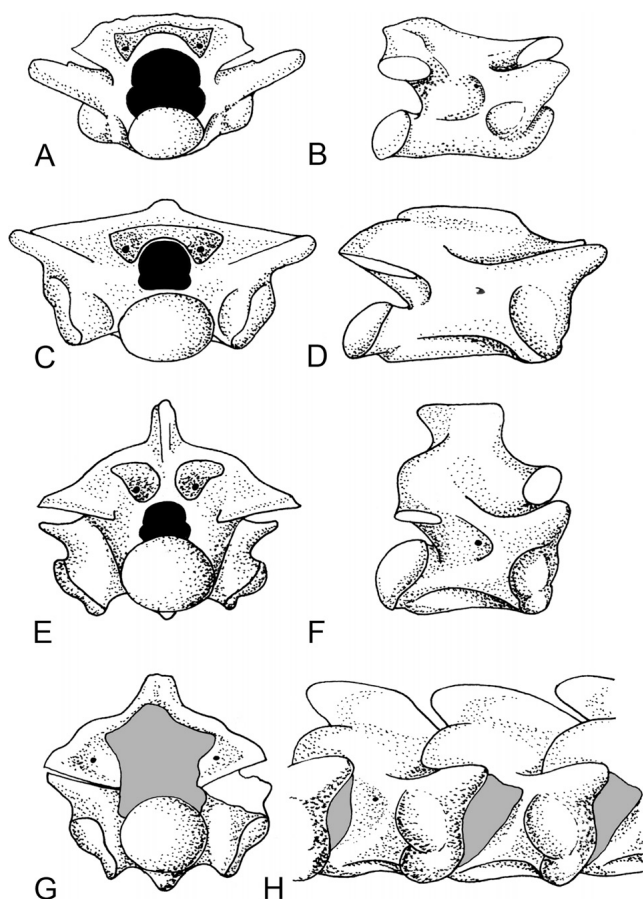
FIGURE 5. Comparison between the middle dorsal vertebrae of *Najash rionegrina* and those of some extant snakes. **A**, *Typhlops punctatus* USNM 320704, posterior view; **B**, *Typhlops punctatus* USNM 320704, right lateral view; **C**, *Anilius scytale* MCZ 19537, posterior view; **D**, *Anilius scytale* 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.

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. 5). Moreover, Zaher et al. (2009) estimated the total length of *Najash* to be about 2 m 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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