A Snake Dentary from the Upper Cretaceous of Patagonia

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Abstract.—The first snake craniomandibular fossil specimen from the Campanian–Maastrichtian of South America is described herein. The specimen, from the Allen Formation in Río Negro Province, consists of an incomplete anterior portion of a left dentary. The general morphology of the bone resembles that of the basal legged snake *Najash* Apesteguía and Zaher and the small madtsoiids from the Eocene–Miocene of Australia. The dentary was found associated with several isolated snake vertebrae, most of which are referable to madtsoiids, thus it probably belongs to one of the already known madtsoiid taxa.

Resumen.—El primer resto craneomandibular de serpiente del Campaniano–Maastrichtiano de América del Sur es aquí descripto. El espécimen, de la Formación Allen en la provincia de Río Negro, consiste en la porción anterior incompleta de un dentario izquierdo. La morfología general del elemento es similar a la de la serpiente basal *Najash* Apesteguía y Zaher y a la de los pequeños madtsoiidos del Eoceno–Mioceno de Australia. El dentario fue hallado asociado a numerosas vértebras aisladas de serpiente, la mayoría de las cuales son referibles a madtsoiidos y por lo tanto, el mismo probablemente pertenezca a alguno de los taxones de madtsoiidos ya conocidos.

Craniomandibular remains of Cretaceous snakes are generally scarce. In South America, skull bones are known only for two taxa, *Dinilysia patagonica* (Woodward, 1901) and *Najash rionegrina* (Apesteguía and Zaher, 2006), both from the Upper Cretaceous of Patagonia. *Dinilysia* is represented by cranial and postcranial remains from the Bajo de la Carpa and Anacleto formations (Hugo and Leanza, 2001; Albino, 2007). Although this material has been studied extensively (Estes et al., 1970; Rage and Albino, 1989; Caldwell and Albino, 2002; Budney et al., 2006), the phylogenetic position of *Dinilysia* is not settled (see Caldwell and Calvo, 2008, for an updated revision). *Najash*, known by material from the Candeleros Formation, is the only terrestrial legged snake hitherto known and is possibly basal to all other snakes (Apesteguía and Zaher, 2006; Zaher et al., 2009).

All other known Cretaceous snakes from South America are represented by isolated vertebrae that belong mostly to small madtsoiids (Albino, 1986, 1994, 2000, 2007; Martinelli and Forasiepi, 2004), although the presence of anilioids (Gómez et al., 2008) and *Serpentes incertae sedis* (Albino, 2007) also has been noted. In contrast, cranial as well as postcranial material of madtsoiids is known from the Upper Cretaceous in Madagascar (LaDuke et al., 2010) and the Cenozoic in Patagonia (Hoffstetter, 1959), Brazil (Rage, 1998), and Australia (Scanlon, 1997, 2005a,b, 2006), but the evolutionary relationships of the small madtsoiids, such as *Nanowana* (Scanlon, 1997), and the large madtsoiids, such as *Madtsoia*, *Wonambi*, or *Yurlunggur*, have not yet been clarified (Scanlon, 2006; LaDuke et al., 2010).

We describe the first snake cranial specimen from the Campanian–Maastrichtian of South America. The specimen comes from the lower layers of the Allen Formation, exposed at Cerro Tortuga locality, in northern Patagonia, Argentina (Fig. 1). The fossil-bearing level yielded a diverse vertebrate assemblage, including fishes, turtles, snakes, dinosaurs, and mammals (Gómez et al., 2008; Rougier et al., 2009). It is approximately 48 m below the Cretaceous–Paleogene boundary.

The dentary from Cerro Tortuga is compared with those of other known Gondwanan fossil snakes as well as selected extant anguimorph and snake taxa and is considered under the current phylogenetic framework of snake interrelationships (Rieppel et al., 2002; Scanlon, 2006). In addition, disagreements about some character definitions and usage are discussed.

Materials and Methods

The specimen was found, together with several isolated vertebrae representing madtsoiids and one anilioid taxon, by screenwashing and further picking the resulting concentrate. The material was compared with dentaries of relevant fossil and extant taxa (listed below). Whenever possible, actual specimens were examined; otherwise photographs or figures and descriptions in the literature were used. The osteological terminology mainly follows Zaher and Rieppel (1999), Rieppel and Zaher (2000), and Rage and Augé (2010). Drawings were made with a Zeiss Stemi SV11 binocular microscope equipped with a camera lucida.

Institutional Abbreviations.—The following institutional abbreviations are used herein: FCEN, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; MML-Pv, Museo Municipal de Lamarque, colección Paleontología de Vertebrados, Lamarque, Argentina; and MPCA, Museo Paleontológico 'Carlos Ameghino,' Cipolletti, Argentina.

Comparative Material.—*Anilius scytale*, MACN 8817; *Bothrops alternatus*, FCEN 1394; *Boa constrictor*, FCEN uncataloged; *Dinilysia patagonica* †, MACN Pv RN 976; *Heloderma* sp., FCEN uncataloged; *Najash rionegrina* †, MPCA 380, 390–398; *Typhlops* sp., FCEN uncataloged; *Trimeresurus wagleri*, FCEN 1369; *Xenopeltis unicolor*, MACN 7568; *Varanus* sp., FCEN uncataloged.

Systematic Paleontology

Squamata Oppel, 1811
Ophidia Brongniart, 1800; sensu Lee, 1998
Genus and species indeterminate

Referred Material.—MML-Pv180, an incomplete left dentary lacking the symphyseal region, and preserving five alveoli, but no teeth (Fig. 2).

Locality and Horizon.—Cerro Tortuga locality (39°47′02″S, 66°42′17″W; Fig. 1), Bajo Trapalcó, Río Negro Province, Argentina (Fig. 1). Lower Member of the Allen Formation, Malargüe Group, upper Campanian–lower Maastrichtian (Hugo and Leanza, 2001).

Description.—Specimen MML-Pv180 (Fig. 2) is identified as the incomplete anterior portion of a left dentary, based on the incurving anterior tip in dorsal view when in natural position and the anteriorly tapering wall of the bone in lingual view (Fig. 2A,B). The anterior incurving tip shows a small bulbous bulge that is oriented medially with respect to the tooth row and slightly overhangs the Meckelian groove. The rough medial surface of this bulge might indicate a ligamentous attachment originally connecting both dentaries. Neither teeth nor ''bone of attachment'' (=alveolar bone in part of Caldwell et al., 2003) are preserved, although five alveoli, which presumably correspond to the positions 1–5 of the original series, are present. The alveoli increase their width posteriorly and their major axis becomes transversely oriented (i.e., they are wider labiolingually than anteroposteriorly). The alveoli are clearly defined labially by the pleura (labial margin), which is much higher than the lingual margin. Interdental ridges (=alveolar crests of Caldwell et al., 2003) that slope from the pleura fully delimit tooth positions, anteriorly and posteriorly (Fig. 2B). Nevertheless, these interdental ridges are poorly developed lingually. On the lingual side of the dentary, the Meckelian groove opens ventromedially (which in extant snakes enfolds Meckel's cartilage, and the mandibular branch of the trigeminal nerve; Rieppel and Zaher, 2000). Dorsally, this groove is delimited by the wide lingual wall of the dentary, which defines a slightly concave roof at the anteriormost preserved part of the dentary. The medioventral shelf is oriented ventrally rather than medially (Fig. 2A) and thus does not limit the Meckelian groove as it does in anguimorph lizards and some scolecophidians (Estes et al., 1988; Rieppel and Zaher, 2000). The Meckelian groove is moderately deep and slightly tapering anteriorly. It is not possible to ascertain whether it was open ventromedially up to the symphysis because, as mentioned above, the dentary tip is missing. The labial surface of the dentary is smooth, lacking any kind of ornamentation. Only a small mental foramen below the second preserved alveolar position, near the ventral margin of the dentary
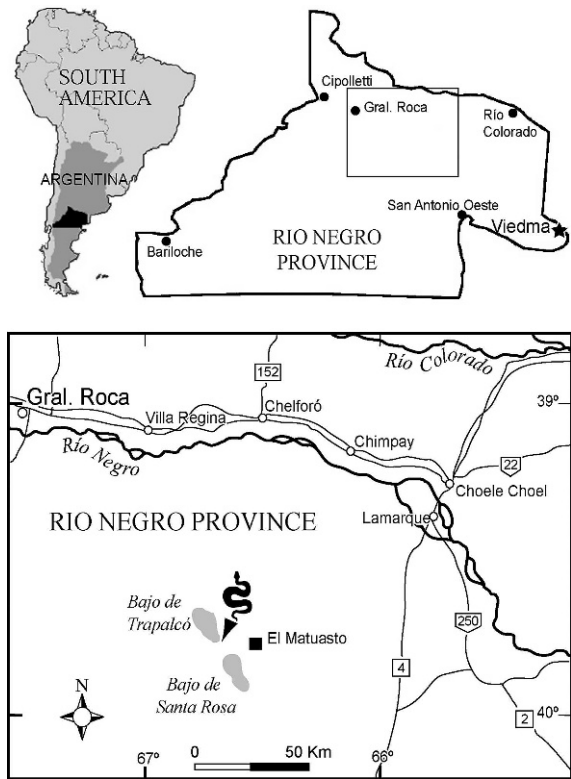
FIG. 1. Map showing the Cerro Tortuga locality of Argentina from which the dentary was discovered.

FIG. 2. Left dentary (MML-Pv180) in (A) occlusal, (B) labial, (C) lingual, and (D) posterior views. Scale bar = 2 mm.

pierces the labial wall (Fig. 2C). The cross section of the dentary, as revealed by the posterior broken surface, shows that the intramandibular septum is relatively thick and has a concave lingual surface at this point, separating at this point the Meckelian groove from the laterally positioned internal mental canal (canal for the alveolar ramus of the mandibular branch of the trigeminal nerve in extant snakes; Rieppel and Zaher, 2000), the latter leading up to the mental foramen (Fig. 2D). In addition, the cross section of a smaller canal is visible dorsal to the internal mental canal. This corresponds to the alveolar canal, which runs through the alveoli, piercing the interdental ridges. In this view, the great dentary width also becomes visible. The anterior cross section of the dentary exposes the wide-open Meckelian groove and the alveolar canal; the latter becomes broader than the nearby internal mental canal and extends further anteriorly than the mental foramen.

Measurements.—Total length of the fragment, 10.4 mm; maximum height, 5.8 mm; and maximum alveolar width, 2.3 mm.

DISCUSSION

Specimen MML-Pv180 is referred to Ophidia (sensu Lee, 1998) and not to Serpentes Linnaeus, 1758 (sensu Lee and Caldwell, 1998, crown clade definition of Serpentes = Alethinophidia + Scolecophidia), because recent hypotheses of snake interrelationships place the putative most basal fossil snakes outside the main radiation of modern snakes (Lee and Scanlon, 2002; Apesteguía and Zaher, 2006; Scanlon, 2006) and referral of the fossil dentary to Serpentes is not supported by synapomorphies owing to its fragmentary nature. Despite the fragmentary condition of the material described herein, some meaningful comparisons are possible. In this regard, it should be noted that the anterior portion of the dentary of *Dinilysia* remains unknown, precluding detailed comparisons with MML-Pv180.

In nearly all snakes, a tight contact between right and left dentaries is absent, leading to a more mobile mandibular symphysis (Rage, 1984). The only known exceptions might be a single dentary from the Cretaceous of India that has a broad bony symphyseal area and was referred to a ''cholophidian'' snake, representing a pre-Serpentes level of evolution according to Prasad and Rage (1995), and *Najash*, which has a massive straight facet at the tip of the dentary similar to the condition present in extant lizards with limited mobility between their jaws (Zaher et al., 2009). The bulbous bulge of MML-Pv180 recalls those of the Australian small madtsoiids *Nanowana*, *Patagoniophis*, and
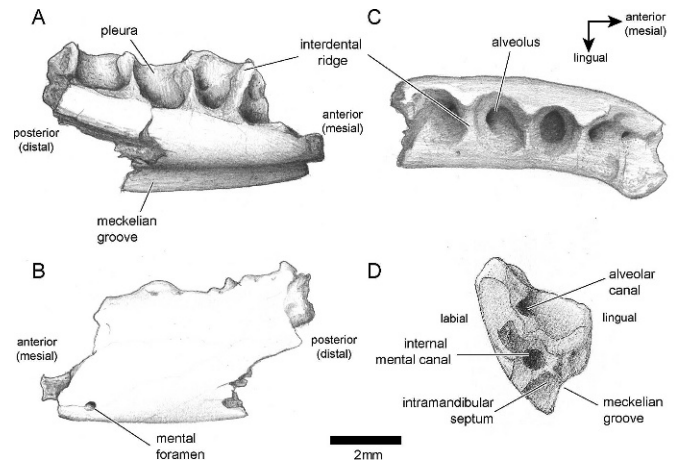
Alamitophis (Scanlon 1997, 2005a), although it seems to be less developed. The orientation of this bulge in the above-mentioned taxa and the orientation of the straight facet of *Najash* are similar and contrast with the condition in extant snakes, where a rounded facet at the tip of the dentary is continuous with the tooth row (Zaher et al., 2009). The Meckelian groove of MML-Pv180 opens ventromedially, thus resembling the condition present in anguimorph lizards and most snakes (Estes et al., 1988; Rieppel and Zaher, 2000). However, in anguimorph lizards the Meckelian groove is widely exposed ventrally from the level of the anterior inferior alveolar foramen to the tip of the bone (Estes et al., 1988), whereas in many snakes a ventromedial shelf covers the Meckelian groove ventrally to a variable degree (Lee and Scanlon, 2002; ROG, pers. obs.). In MML-Pv180, the ventromedial shelf is not developed medially so the Meckelian groove widely opens ventrally, at least in the anterior part of the dentary, which is the only portion preserved. The same condition is also present in a variety of alethinophidians (Lee and Scanlon, 2002; ROG, pers. obs.) and in Australian small madtsoiids (Scanlon, 2005a). Because MML-Pv180 is incomplete anteriorly, it is uncertain whether the Meckelian groove was open medially at the anterior tip of the bone. Comparisons with relevant taxa show that it might have been closed as in *Madtsoia* cf. *M. bai* (Hoffstetter, 1959), or open as in the dentary assigned to *Alamitophis tingamarra* (Scanlon, 2005a), and *Najash* (Zaher et al., 2009); the wide Meckelian groove of the fossil dentary, however, makes the latter condition more plausible.

The absence of attached teeth in MML-Pv180, which is probably a post-mortem artifact, reveals alveoli delimited by well-developed interdental ridges and a high pleura, many alveoli being pierced by a central foramen, a typical snake condition (Hoffstetter, 1959). In turn, the transverse orientation of the alveoli also occurs in nonmacrostomatan snakes (Lee and Scanlon, 2002; Apesteguía and Zaher, 2006), although basal macrostomatans as *Xenopeltis* share this feature (ROG, pers. obs.). This condition also has been reported in the fossil snakes *Najash* (Apesteguía and Zaher, 2006; Zaher et al., 2009), *Dinilysia patagonica* (Budney et al., 2006), and the small madtsoiid *Nanowana godthepi* from the Miocene of Australia (Scanlon, 1997). Within snakes, a distinctly high pleura occurs on the dentigerous dentaries of leptotyphlopids as well as on all tooth-bearing elements of other scolecophidians (Zaher and Rieppel, 1999). MML-Pv180 also has a relatively high pleura, but it is less developed than in scolecophidians and is similar to the structure present in *Najash* (Zaher et al., 2009) and Australian small madtsoiids (Scanlon, 1997, 2005a). A well-developed pleura is associated with a pleurodont tooth implantation, regarded as the primitive condition in snakes (Zaher and Rieppel, 1999). Interdental ridges sloping from the pleura are common in squamates with a labial pleurodonty (Zaher and Rieppel, 1999). However, prominent interdental ridges such as those of MML-Pv180 are typically present in snakes, although the degree of development of these structures varies within the group. In fact, the interdental ridges of MML-Pv180 more closely resemble those of scolecophidians, small madtsoiids, and *Najash*, than those of alethinophidians, the latter having further developed ridges that form the lingual walls of the alveoli (Zaher and Rieppel, 1999).

The small size and low position of the only visible mental foramen suggest that there might have been additional foramina more

posteriorly located. Nearly all extant snakes have a single, relatively large mental foramen (Rage, 1998) that is located more dorsally than in the fossil dentary. Two or three mental foramina have been recorded in the alethinophian *Acrochordus* (Hoffstetter and Gayrard, 1965) and in few scolecophidians (Lee and Scanlon, 2002) and colubroids (Cundall, 1981). More than one mental foramen also has been described in several fossil taxa such as *Najash* (Zaher et al., 2009); the madtsoiid genera *Madtsoia* (Hoffstetter, 1959; Rage, 1998), *Nanowana* (Scanlon, 1997), *Yurlunggur* (Scanlon, 2006), *Wonambi* (Scanlon, 2005b), *Alamitophis*, and *Patagoniophis* (Scanlon, 2005a); and the marine Cretaceous snake *Pachyrhachis* (Lee and Caldwell, 1998), although in the latter other authors have alternatively identified a single mental foramen (Rieppel and Zaher, 2000).

The intramandibular septum of MML-Pv180 is discernible in posterior view of the bone. A well-developed septum that extends far posteriorly, separating the internal mental canal from the Meckelian groove, was considered a synapomorphy of anguimorph lizards and was not observed among snakes by Estes et al. (1988); however, Lee and Scanlon (2001) demonstrated that this condition is also present in all snakes. Unfortunately, although a thick septum can be distinguished in MML-Pv180, it cannot be stated whether this structure is well developed posteriorly as in other snakes and anguimorph lizards.

Another feature of systematic interest is the subdental shelf, but a profuse and not always clear terminology surrounds it. Rage and Augé (2010) recently discussed this and other associated structures in squamates and proposed a terminology that is adopted herein. A subdental shelf has been considered to be present in all squamates except varanoid lizards, some iguanians, amphisbaenians, and snakes (Estes et al., 1988; Rieppel and Zaher, 2000). Following the terminology of Rage and Augé (2010), both MML-Pv180 and *Najash* have a subdental shelf (Zaher et al., 2009; contra Apesteguía and Zaher, 2006). Another topographically related structure that is usually confused with the subdental shelf is the basal plate (Zaher and Rieppel, 1999). The condition in MML-Pv180 cannot be confidently established, but it is noteworthy that although a ''discrete basal plate'' was formerly described in the dentary of *Najash* (Apesteguía and Zaher, 2006), this structure is apparently absent in this snake (Zaher et al., 2009).

In conclusion, the dentary described herein, despite its fragmentary nature, exhibits several features that are relevant for the discussion of early snake evolution. Specimen MML-Pv 180 is similar to dentaries of the madtsoiids *Nanowana*, *Patagoniophis australiensis*, and *A. tingamarra* (Scanlon, 1997, 2005a) in the configuration of the Meckelian groove, the transversely oriented alveoli, and the relatively high pleura. The fossil dentary from Cerro Tortuga also resembles scolecophidians in having some of these same features, but the overall aspect of the jaw is rather different, owing to the extreme modifications related to the fossorial habits of scolecophidians (Lee, 1998). Specimen MML-Pv 180 also resembles the dentary of the basal limbed snake *Najash* in many of the above-mentioned features.

Presumably, many of the characters that the fossil dentary shares with putative basal snakes represent symplesiomorphies, such as a distinctly high pleura, or transversely oriented alveoli. However, the phylogenetic position of these taxa within Ophidia and of snakes within Squamata remain highly controversial (Lee, 1998; Apesteguía and Zaher, 2006; Scanlon, 2006); hence, the polarities of some of these and other features are still unresolved.

In recent years, studies on Gondwanan fossil snakes have shown the existence of a group of extinct taxa that have common cranial (Scanlon, 2006; Caldwell and Calvo, 2008), as well as postcranial features (Apesteguía and Zaher, 2006; Scanferla and Canale, 2007; ROG, pers. obs.). The evidence presented here is consistent with the previously proposed hypothesis that all these Gondwanan fossil forms, including *Najash*, *Dinilysia*, and both the Patagonian and Australian madtsoiids, may form a clade of basal Gondwanan snakes (Caldwell and Calvo, 2008). As an alternative, however, it also has been proposed that these fossil forms may have constituted a basal stock that gave rise to alethinophidian snakes, implying a paraphyletic arrangement of this group with respect to alethinophidians (Apesteguía, 2007).

Finally, taking into account the similarities with Australian small madtsoiids, the size of the bone, and the presence of several small madtsoiid vertebrae in the same stratigraphic levels, it is likely that the dentary from Cerro Tortuga belongs to a madtsoiid taxon. However, this conclusion remains conjectural until articulated or closely associated material is found. Thus, further efforts aimed to collect associated skull remains of these intriguing fossil forms are needed to provide pivotal evidence on the comprehension of the early history of snakes and to help in resolving their phylogenetic relationships.

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