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An anilioid snake from the Upper Cretaceous of northern Patagonia

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Abstract

We report the first record of anilioids from southern South America, a region where they do not live today. The fossils come from the Allen Formation (Late Campanian–Early Maastrichtian) at Bajo Trapalcó and Bajo de Santa Rosa localities, Río Negro province, Argentina. The remains consist of several vertebrae, most of which belong to the mid–posterior precloacal region of the column. Comparisons to other extant and extinct anilioid taxa indicate that these remains represent a new taxon, *Australophis anilioides* gen. et sp. nov. *Australophis* is morphologically closer to Palaeocene *Hoffstetterella* from Brazil and extant South American *Anilius* than to any other snake. These taxa might be closely related, in which case they would represent a lineage distinct from that including *Cylindrophis* and uropeltids. The two lineages must have diverged by the Late Cretaceous.
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Keywords: Serpentes; Anilioidea; *Australophis*; Cretaceous; Patagonia

1. Introduction

Some of the most basal forms among living snakes have traditionally been considered to comprise a distinct lineage, Anilioidea (Rieppel, 1988). The extant South American *Anilius* Oken, 1816 and Asian *Anomochilus* Berg, 1901, *Cylindrophis* Wagler, 1828 and the uropeltids, as well as several extinct taxa, have been referred to this lineage (Rage, 1984). However, in recent morphology-based phylogenetic analyses of snakes, the taxa traditionally recognized as anilioids have been placed basal to all other alethinophidians, although they are not always recovered as a monophyletic taxon (Rieppel, 1988; Kluge, 1991; Cundall et al., 1993; Tchernov et al., 2000; Lee and Scanlon, 2002). Moreover, molecular evidence points to the paraphyletic or polyphyletic nature of 'anilioids' (Vidal and Hedges, 2002, 2004; Wilcox et al., 2002; Gower et al., 2005).

The earliest fossil remains referred to as anilioids are from the Albian–Cenomanian of North America (Gardner and Cifelli, 1999). In South America, the oldest records are from the lower Palaeocene of Bolivia (Muizon et al., 1983; Rage, 1991) and Peru (Rage, 1981), although the presence of anilioids from the Late Cretaceous Adamantina Formation of Brazil has been briefly reported but the material is still undescribed (Zaher et al., 2003). Herein we describe the first Late Cretaceous anilioid remains from southern South America, a location far to the south of their present range. The material consists of a few precloacal vertebrae recovered during the 2004 field season to outcrops of the Allen Formation in northern Patagonia. This expedition was carried out by one of us (GWR) in association with the Museo Municipal de Lamarque.

Institutional abbreviations. AC, Amherst College Museum of Natural History, Massachusetts, USA; DGM, Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Seção Paleontologia, Rio de Janeiro, Brazil; MML-PV, Museo Municipal de Lamarque, Río Negro, Argentina.

Anatomical abbreviations: PRW, prezygapophyseal width; CTW, cotyle width; ZW, zygosphene width; CL, centrum

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length; MVL, maximum length of vertebra; WIC, interzygapo-physeal constriction width.

2. Geological setting

The remains described herein were discovered at the Bajo Trapalcó (39°47′02″S, 66°42′17″W) and Bajo de Santa Rosa (39°54′28″S, 66°34′57″W) localities (hereafter both referred to as the Trapalcó area), which are located near the ranch post ''El Matuasto'' in the vicinity of the town of Lamarque, Río Negro province, Patagonia, Argentina (Fig. 1).

The snake-bearing rocks belong to the Allen Formation, a unit that is part of the infilling of the Neuquén Basin, one of a series of northwest-southeast trending basins formed by the widespread extension that affected Patagonia in the Early Jurassic (Franzese et al., 2003). Renewed tectonic activity and inversion during the earliest Late Cretaceous resulted in the accumulation of the continental deposits of the Neuquén Group and the lower part of the Malargüe Group (Vergani et al., 1995). The Allen Formation is the most basal unit of the latter group, which also comprises the Jagüel, Roca, and Carrizo formations (Barrio, 1990).

The Allen Formation, formerly known as ''Facies Lacustre Senoniana'' (Wichmann, 1927), is extensively exposed in the Trapalcó area. This sequence has been informally divided into lower and upper members, which represent a transgressive cycle that ended with the entrance of the Maastrichtian sea documented by the Jagüel deposits (Andreis et al., 1974; Uliana and Dellapé, 1981; Barrio, 1990). The Allen Formation has been interpreted as a nearshore-to-restricted-marine palaeoenvironment (Uliana and Dellapé, 1981). Barrio (1991), however, has drawn attention to differences in the facies associations that he ascribed to diverse tidal ranges related to basin architecture. Thus, while on the eastern part of the basin the facies association may be interpreted as representing

intertidal deposits, on the western part this unit exhibits features suggesting a tide-dominated estuary. At the Trapalcó area the lowermost levels, from which the fossils were collected, were deposited in a meandriform fluvial system with channel facies and floodplains (Artabe et al., 2004). These levels comprise an alternation of tabular layers of siltstones and fine-grained sandstones with intercalated conglomerates. The fossil-bearing bed consists of friable, yellowish, fine-grained clean sandstone enclosed between siltstone layers (Fig. 2).

At Bajo de Santa Rosa, one of the several fossiliferous levels of the Allen Formation has yielded abundant, taxonomically diverse vertebrate remains, in addition to the material
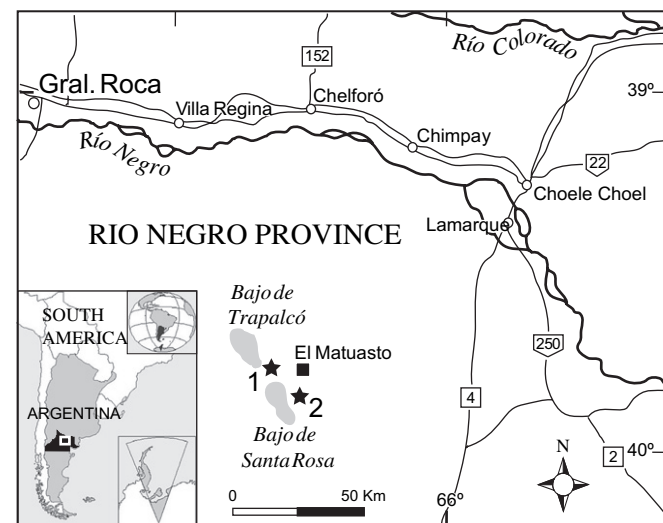

Fig. 1. Map showing the geographical location of the localities were the specimens of *Australophis anillioides* gen. et sp. nov. were discovered. 1, Bajo Trapalcó; 2, Bajo de Santa Rosa.
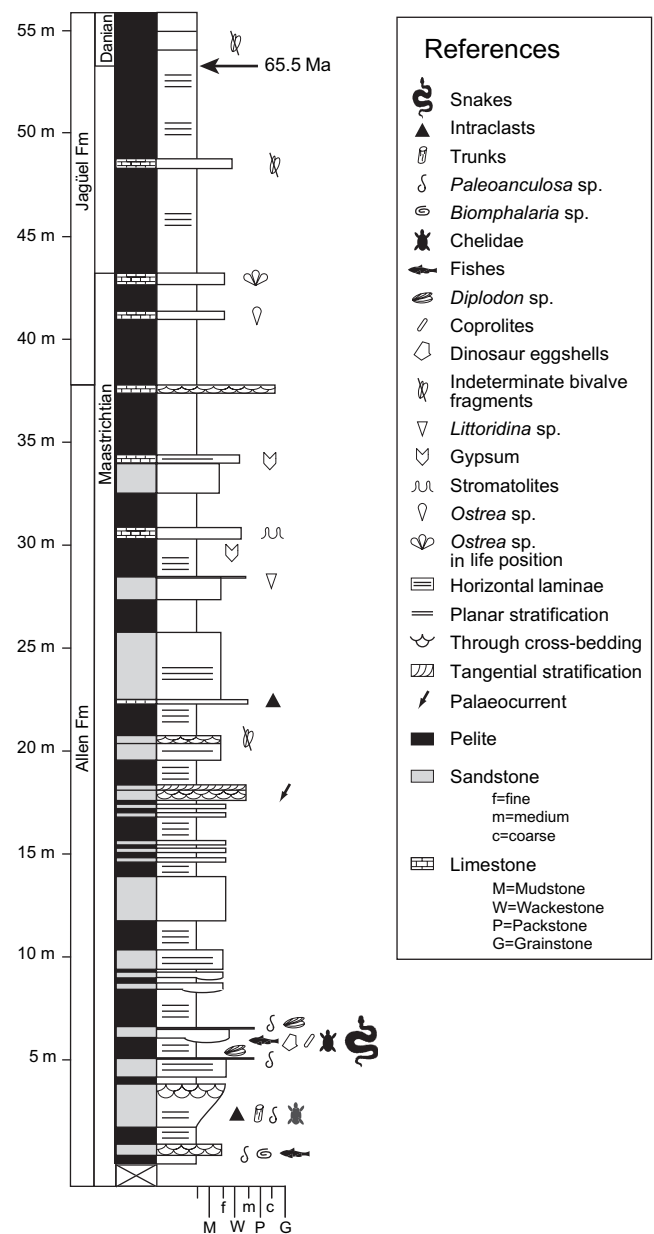

Fig. 2. Upper Cretaceous–Lower Palaeocene stratigraphy at Trapalcó area, showing the position of the snake-bearing bed (modified from Concheyro et al., 2002).

described here. These remains represent chondrichthyans, diplomystid siluriform, lepisosteid, cf. percichthyid, and dipnoid osteichthyans, pipid and neobatrachian anurans, chelid turtles, sphenodonts, elasmosaurid plesiosaurs, hadrosaurid, cf. carcharodontosaurid, and titanosaurid dinosaurs, and madtsoiid snakes (Martinelli and Forasiepi, 2004). At Bajo Trapalcó, the anilioid material was found in association with remains of many of these groups, all coming from a single bed and recovered by screenwashing and picking from sediments of a small area locally called ''Cerro Tortuga''. In addition to the vertebrates from Bajo de Santa Rosa listed above, the Bajo Trapalcó locality has provided a small assemblage of mammals. These mammals share many similarities with those from the putative Campanian−Maastrichtian Los Alamitos Formation (Papú and Sepúlveda, 1995) and belong to the same suprageneric taxa, although representing different species. The age of the Allen sequence is bracketed between the Early Campanian and Late Maastrichtian−Danian, according to the ages attributed to the underlying Anacleto Formation (Dingus et al., 2000; Hugo and Leanza, 2001; Leanza et al., 2004) and overlying Jagüel Formation (Uliana and Dellapé, 1981; Papú et al., 2000; Náñez and Concheyro, 1996), respectively. The Cretaceous/Paleogene boundary was identified in the latter unit on the basis of foraminiferal associations coming from a locality near the anilioid fossiliferous sites (Concheyro et al., 2002). This boundary has been placed about 48 m stratigraphically above the snake-bearing bed (Fig. 2). Additionally, Early Maastrichtian microfossils were described from the top of the Allen Formation (Ballent, 1980). All of this evidence points to a Late Campanian−Early Maastrichtian age for the fossils described here.

3. Systematic palaeontology

Serpentes Linnaeus, 1758
Alethinophidia Nopcsa, 1923
Anilioidea Fitzinger, 1826
Australophis gen. nov.

Type species. Australophis anilioides sp. nov.

Derivation of name. From the Latin *australis*, meaning ''southern'', and the Greek *ophidion, ophis*, meaning ''snake''.

Diagnosis. As for type and only known species.

Australophis anilioides sp. nov.

Fig. 3−4

Derivation of specific name. From *Anilius*, the genus of the only extant South American anilioid, and the Greek *-oeides*, suffix that means ''like'' or ''like that of''.

Holotype. MML-PV181. One mid−precloacal vertebra.

Type locality and horizon. Bajo Trapalcó (39°47′02″S, 66°42′17″W), 150 km south-west of Lamarque, Río Negro province, northern Patagonia, Argentina. Lower member of the Allen Formation (Malargüe Group, southern margin of the Neuquén Basin), Late Campanian−Early Maastrichtian.

Referred material. MML-PV182−190. 9 precloacal vertebrae.

Diagnosis. Medium-sized anilioid, the mid-precloacal vertebrae of which show a generally depressed aspect and have poorly-developed neural spines and low neural arches lacking a posterior median notch, as in all other anilioids. However, it differs from all known anilioid species in having a thick zygosphene and from all anilioids except *Hoffstetterella brasiliensis* Rage, 1998 by a more developed neural spine. It differs from the latter in having a shallower interzygapophyseal constriction, a less-marked posterior embayment of the neural arch, narrower neural canal, and subcentral ridges that are laterally convex in ventral view and which delimit a centrum that is slightly expanded anteriorly. Additionally, the cotyle and condyle are proportionally broad and the wide, shallow, and ventrally-flattened haemal keel is constricted at its mid-length and flanked posteriorly by small rounded depressions, in contrast to the condition in most anilioids.

4. Description

4.1. Holotype

Measurements: PRW 8.8 mm; CTW 2.9 mm; ZW 3.2 mm; CL 5.5 mm; MVL 7.4 mm; WIC 5.0 mm.

The holotype is the largest of the vertebrae referred to this species (Fig. 3). It is fairly complete, although the right anterolateral part (including prezygapophysis and paradiapophysis) and the left posterodorsal part (including postzygapophysis and zygantrum) are missing. It probably belongs to the mid-posterior precloacal transition area of the column based on the moderate development of the subcentral grooves and the laterally oriented paradiapophyseal facets. In anterior view, this vertebra exhibits a general depressed aspect with a proportionally broad and slightly dorsoventrally-depressed cotyle. The left anterior paracotylar notch, which is the only one preserved, is shallow and rounded. The zygosphene is thick for an anilioid, almost straight dorsally, and nearly as wide as the cotyle. The neural canal is relatively narrow, subtriangular to subtrifoliate in cross-section; along its length, a distinct subneural process projects dorsally from the slightly excavated floor. The preserved prezygapophyseal articular facet is prominently inclined, up to 20° above horizontal, and strongly surpasses the lateral end of the diapophysis. A small prezygapophyseal process barely projects laterally beyond the articular facet. The paradiapophyses are lateroventrally oriented with a significant lateral component. The diapophyseal portion is more strongly developed and more convex than the parapophyseal portion, which is rather flat and does not reach the cotylar margin ventrally. There are no traces of paracotylar foramina.

In dorsal view, the vertebra is a little shorter than it is wide. The prezygapophyseal facet is oval, with its main axis oblique, and inclined at about 40° relative to the sagittal plane. The
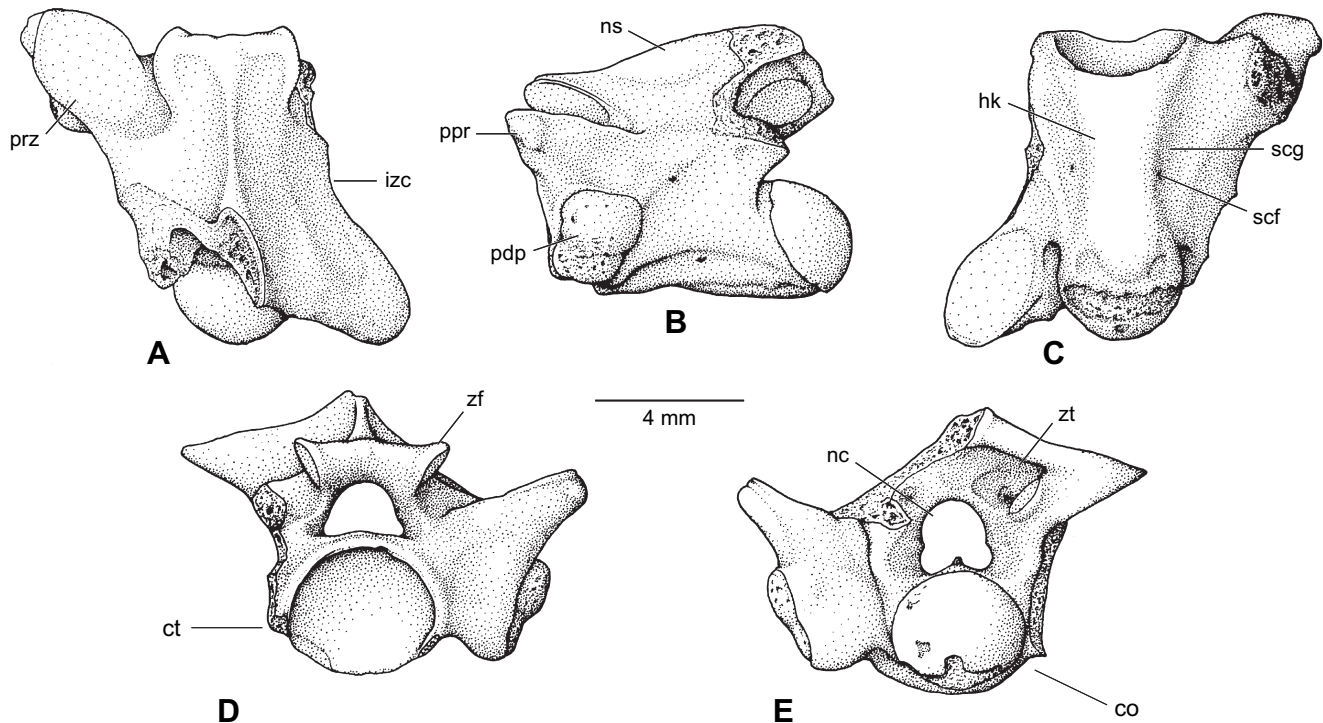
Fig. 3. *Australophis anilioides* gen. et sp. nov., mid–posterior precloacal vertebra (MML-PV181, holotype) in A, dorsal, B, left lateral, C, ventral, D, anterior, and E, posterior views. Abbreviations: co, condyle; ct, cotyle; hk, haemal keel; izc, interzygapophyseal constriction; nc, neural canal; ns, neural spine; pdp, paradiapophysis; ppr, prezygapophyseal process; prz, prezygapophysis; scf, subcentral foramen; scg, subcentral groove; zf, zygosphene; zt, zygantrum.

small prezygapophyseal process extends laterally beyond the articular facet. The interzygapophyseal constriction is shallow, but distinct. The anterior margin of the zygosphene is almost straight, with small lateral lobes. The neural spine does not extend up to the anterior margin of the zygosphene and gradually widens posteriorly. The posterior margin of the neural arch has a shallow embayment, instead of being indented by a median notch.

In posterior view, the neural arch appears depressed, whereas the condyle is almost circular. The zygantrum is deep, with a moderately thick roof that has a slightly convex ventral margin. There is a single foramen in each zygantral fossa. No foramen pierces the wide parazygantral area. The only preserved postzygapophysis is strongly inclined with respect to the horizontal plane.

In lateral view, the neural spine is almost as long as the total length of the neural arch. The neural spine is low, but higher than in other anilioids; its lamina becomes higher posteriorly, describing a shallow convexity all along its length, and ending in a tubercle. The condyle is slightly dorsally inclined and is not demarcated from the rest of the centrum by a precondylar constriction. The paradiapophysis is massively built and subrectangular, with a diapophyseal portion more posteriorly located than the parapophyseal portion. The lateral ridge is shallow and the subcentral ridge is barely arched dorsally. One lateral foramen is present on each pedicel of the neural arch.

In ventral view, the centrum is moderately long and wider anteriorly than posteriorly; the centrum has well-defined subcentral ridges that are concave laterally. The low, wide, and ventrally flattened haemal keel is slightly constricted at its middle portion and reaches the cotylar margin but not the condylar margin. The haemal keel is laterally delimited by shallow subcentral paralymphatic fossae, each of which bears a small subcentral foramen. Additionally, two small, rounded depressions flank the most posterior part of the haemal keel.

4.2. Intracolumnar variation

Only one vertebra (MML-PV182, Fig. 4) is referred to the anterior precloacal region of the column. This vertebra is smaller, shorter, and proportionally higher than the holotype, which is attributed to the mid-posterior precloacal region. Breakage of the prezygapophyses and the zygosphene precludes description of their features. The interzygapophyseal constriction is deeper than in the holotype. The neural arch is posteriorly vaulted and its posterior margin describes a wide angle when observed in dorsal view. The neural spine is incompletely preserved, but it appears to have been higher and shorter than in more posterior precloacal vertebrae. The neural canal is relatively wide with respect to that of the holotype. The condyle is almost posteriorly directed. The paradiapophyses, though eroded, show a kidney-shaped outline, with the parapophyses more posteroventrally located than in the holotype. The haemal keel is thin, but it appears bulky at its posterior end. A subcentral foramen occurs on both sides of the haemal keel.
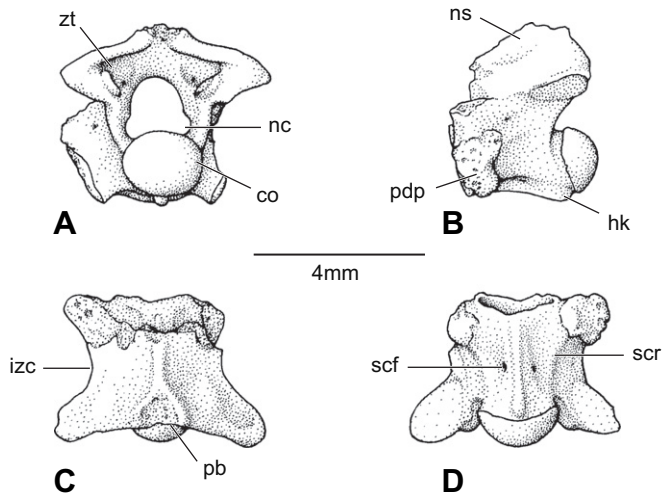
Fig. 4. *Australophis anilioides* gen. et sp. nov., anterior precloacal vertebra (MML-PV182) in A, posterior, B, lateral, C, dorsal, and D ventral views. Abbreviations: co, condyle; hk, haemal keel; izc, interzygapophyseal constriction; nc, neural canal; ns, neural spine; pb, posterior border of neural arch; pdp, paradiapophysis; scf, subcentral foramen; scr, subcentral ridge; zt, zygantrum.

5. Comparisons and taxonomic discussion

A phylogenetic analysis to assess the position of *Australophis* within Serpentes is not attempted here, owing to the limited material. Instead, the general framework of snake interrelationships provided by previous studies (Cundall et al., 1993; Lee and Scanlon, 2002) is used to discuss the relationships of *Australophis* to extant and extinct anilioid taxa.

As no unique vertebral features have been recognized for anilioids, *Australophis* is referred to Anilioidea (sensu Rieppel, 1979) on the basis of the following combination of character states of its mid−precloacal vertebrae: vertebrae depressed with low neural arches not rising much above the zygapophyseal plane, reduced neural spines, strongly-inclined zygapophyses, very short prezygapophyseal processes, and concave posterior border of neural arches lacking a median notch (Rage, 1998).

Australophis, as well as all other anilioids, clearly differs from the Late Cretaceous Patagonian snake *Dinilysia* Woodward, 1901 in having more depressed vertebrae with lower neural spines, centra that are only slightly broader anteriorly than posteriorly, and in lacking paracotylar foramina (Rage and Albino, 1989; Albino, 1990; Rage, 1998). It differs from the specialized uropeltids mainly in having a prominent neural spine on its mid-precloacal vertebrae, a distinct haemal keel, and comparatively well-marked subcentral ridges that are more divergent anteriorly. Comparison to *Anomochilus* cannot be made owing to the lack of knowledge of its vertebral morphology; however this taxon appears closer to uropeltids than to *Anilius* in phylogenies based on morphological (Cundall et al., 1993; Lee and Scanlon, 2002) as well as on molecular (Gower et al., 2005) data.

Among anilioids, the mid- and posterior precloacal vertebrae of *Australophis* bear neural spines comparable to those of *Anilius* and the extinct *Eoanilius* Rage, 1974 and *Hoffstetterella* Rage, 1998, although only in the latter are the neural spine laminae similarly developed. In *Australophis* the neural canals are proportionally narrower than in other anilioids excluding *Colombophis* Hoffstetter and Rage, 1977, and are similar in shape to those of *Anilius* (Fig. 5D$_1$). The prezygapophyseal facets of *Australophis* are steeply inclined above the horizontal plane, as they are in most other anilioids except *Eoanilius* and *Coniophis* Marsh, 1892; the prezygapophyses are also strongly projected laterally as in *Anilius*, *Cylindrophis*, and *Colombophis*, in contrast to the condition exemplified by *Eoanilius*. Additionally, *Australophis* differs from most anilioids, and resembles *Hoffstetterella*, in having shallower interzygapophyseal constrictions, slightly separated but distinct dia- and parapophyseal areas, and prezygapophyseal facets similar in orientation and outline. However, the vertebrae reported here are proportionally longer, lack anteriorly projecting
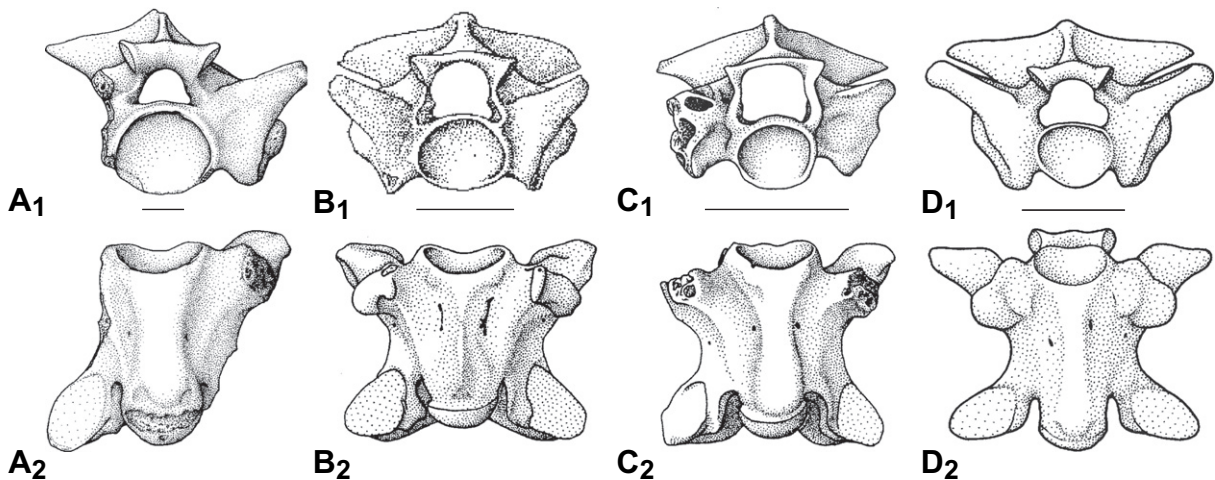

Fig. 5. Comparative morphology of anilioid precloacal vertebrae (top line, anterior views; bottom line, ventral views). A, *Australophis anilioides* gen. et sp. nov. (MML-PV182, holotype), B, *Hoffstetterella brasiliensis* (DGM 1323, holotype, from Rage, 1998), mid-precloacal, C, *Hoffstetterella brasiliensis* (DGM 1324b, from Rage, 1998), posterior precloacal, D, *Anilius scytale* (AC 1869-772, modified from Hoffstetter and Gasc, 1969), mid-precloacal. Scale bars equal 2 mm.

cotylar rims, and possess neural arches with less concave posterior margins, proportionally smaller neural canals, and wider haemal keels than those of *Hoffstetterella* (Fig. 5A–C). The haemal keel is reminiscent of those on the posterior precloacal vertebrae of *Hoffstetterella* (Fig. 5C$_2$), although the latter have much broader neural canals, a median notch on the posterior margin of the neural arches, cotylar rims that clearly project anteriorly, and condyles that are comparatively much smaller than those of the vertebrae from Patagonia. Finally, the anilioid mid-posterior precloacal vertebra illustrated here (MML-PV181, Fig. 3) is almost twice the size of the vertebrae of the same columnar region of *Hoffstetterella* (Fig. 5B), whereas it is threefold the size of the posterior precloacals of the latter taxon (Fig. 5C). Since these differences cannot be attributed to intracolumnar or to ontogenetic variation, we conclude that the vertebrae from Trapalcó represent a new taxon, *Australophis anilioides*. When compared with the extant anilioids, these vertebrae show a closer resemblance to *Anilius* than to any other genus.

6. *Australophis* and the anilioid fossil record

To date only five extinct genera, all based on isolated vertebrae, have been ascribed to Anilioidea (Fig. 6). *Coniophis* is known from many localities of the Upper Cretaceous, Palaeocene and Eocene of North America, South America, Europe and Africa (Marsh, 1892; Hecht, 1959; Estes et al., 1969; Fox, 1975; Armstrong-Ziegler, 1978; Holman, 1979, 2000; Gheerbrant et al., 1993; Rage, 1998; Gardner and Cifelli, 1999; Rage and Werner, 1999; Rage et al., 2004), *Hoffstetterella*, from the middle Palaeocene of São José de Itaboraí, Brazil (Rage, 1998), *Eoanilius*, from the upper Eocene to the lower Miocene of western Europe (Szyndlar, 1994), *Colombophis*, from the middle Miocene of Colombia (Hoffstetter and Rage, 1977), and *Michauxophis* Bailon, 1988, from the Pliocene of France (Bailon, 1988). These genera have generally been considered closer to the non-uropeltid anilioid taxa, although their position and interrelationships are far from being well-established (Rage, 1984; Szyndlar, 1994). *Eoanilius* and *Hoffstetterella* were related to the extant *Anilius* mainly based on overall morphology and the presence of neural spines throughout the column (McDowell, 1987; Rage, 1998; Szyndlar, 1994). *Michauxophis*, based on a single vertebra, was considered related to *Cylindrophis* rather than to *Anilius* (Bailon, 1988). However, the single known vertebra may belong to the anterior-mid-precloacal transition area of the column; as the morphology of the vertebrae of this region is similar in both *Cylindrophis* and *Anilius*, the relationships of *Michauxophis* are still uncertain (Szyndlar, 1994). In the case of *Colombophis*, originally described as morphologically close to *Cylindrophis*, it has been argued that it may have uropeltid affinities based on some similarities present in the vertebrae of the anterior-mid-precloacal transition area (McDowell, 1987; Szyndlar, 1994; Rage, 1998).
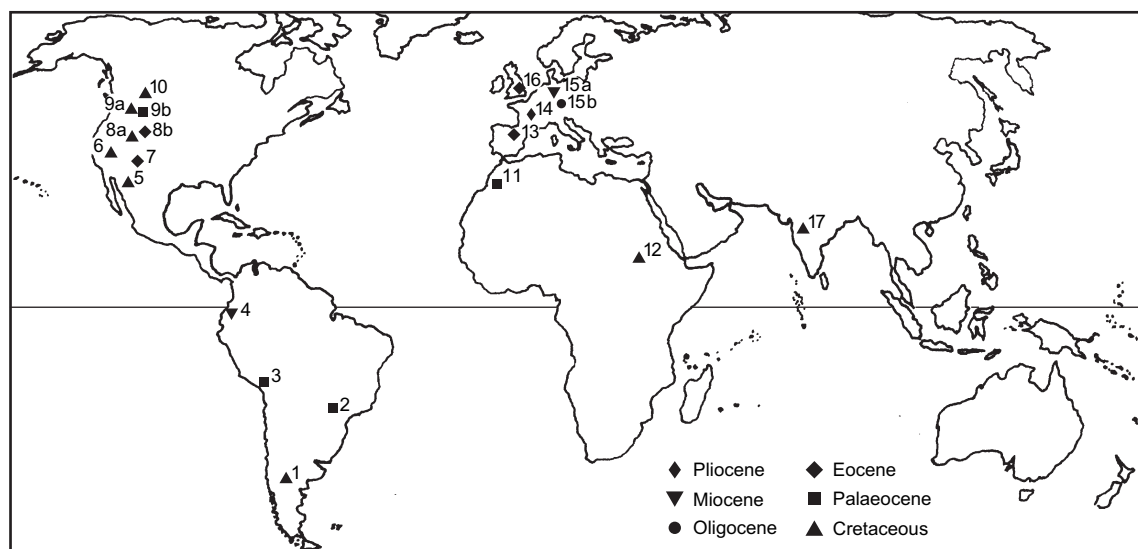

Fig. 6. Geographical distribution of fossil anilioids. 1, *Australophis anilioides* gen. et sp. nov.; Late Campanian–Early Maastrichtian; Bajo Trapalcó and Bajo de Santa Rosa, Argentina; 2, *Coniophis* cf. *C. precedens*, *Hoffstetterella brasiliensis*; Late Palaeocene; São José de Itaboraí, Brazil; Rage, 1998. 3, ?*Coniophis*; Early Palaeocene; Laguna Umayo, Peru; Rage, 1981. 4, *Colombophis portai*; Middle Miocene; La Venta, Colombia; Hoffstetter and Rage, 1977. 5, *Coniophis cosgriffi*; Campanian; New Mexico, USA; Armstrong-Ziegler, 1978. 6, *Coniophis* sp.; Late Albian–Early Cenomanian; Utah, USA; Gardner and Cifelli, 1999. 7, *Coniophis carinatus*; Middle Eocene; Colorado, USA; Hecht, 1959. 8a, *Coniophis precedens*; Maastrichtian; Wyoming, USA; Marsh, 1892. 8b, *Coniophis carinatus*, *Coniophis platycarinatus*, *Coniophis* sp.; Middle–Late Eocene; Wyoming, USA; Hecht, 1959; Holman, 1979. 9a, *Coniophis precedens*; Maastrichtian; Montana, USA; Estes et al., 1969. 9b, *Coniophis* sp.; Palaeocene; Montana, USA; Estes, 1976. 10, ?*Coniophis*; Campanian; Alberta, Canada; Fox, 1975; Rage, 1984. 11, *Coniophis* sp.; Late Palaeocene; Adrar Mgorn, Morocco; Gheerbrant et al., 1993; Augé and Rage, 2006. 12, *Coniophis dabiebus*, *Coniophis* cf. *C. dabiebus*; Cenomanian?; Wadi Abu Hashim, Sudan; Rage and Werner, 1999. 13, *Eoanilius europae*, *Coniophis* sp.; Late Eocene; Quercy, France; Rage, 1974, 1988. 14, *Michauxophis occitanus*; Pliocene; Herault, France; Bailon, 1988. 15a, *Eoanilius* sp.; Early Miocene; Bavaria, Germany; Szyndlar and Schleich, 1993. 15b, *Eoanilius oligocenicus*; Middle–Late Oligocene; Baden-Württemberg, Germany; Szyndlar, 1994; 16, *Eoanilius europae*; Late Eocene; Hampshire, England; Milner et al., 1982. 17, *Coniophis* sp.; Maastrichtian; Naskal, India; Rage et al., 2004. Records without generic allocation are not shown.

The Cretaceous anilioid record is restricted to *Coniophis*. This genus was first allocated to Anilioidea by Hecht (1959) and this taxonomic placement was later confirmed by Holman (1979) and Rage (1984). However, concern has been raised recently whether or not the snakes assigned to *Coniophis* correspond to the range of variation of a single genus (Rage et al., 2004), i.e., *Coniophis* may be a paraphyletic, or polyphyletic, grouping. The genus has even been regarded as representing a pre-anilioid grade basal to the scolecophidian/alethinophidian dichotomy (Rage, 1984, 1998).

Based on the similarity of the vertebrae of *Australophis* to those of *Anilius*, the former might represent one of the oldest records of the anilioid lineage, suggesting that by the Late Cretaceous it had already diverged from other alethinophidians.

7. Concluding remarks

Australophis anilioides, gen. et sp. nov. from northern Patagonia confirms the presence of anilioids in the Upper Cretaceous of South America, as hinted by the still undescribed material from Brazil (Zaher et al., 2003). The absence of anilioids in other contemporaneous fossiliferous units of Patagonia, which otherwise have yielded remains of the same vertebrate taxa including snakes (Albino, 2000; Leanza et al., 2004; Martinelli and Forasiepi, 2004), might be the result of collecting bias more than a real phenomenon.

Based on available data, *Australophis* is morphologically closer to *Anilius* and *Hoffstetterella* than to any other snake. Consistently, Rage (1998) found *Hoffstetterella* most similar to *Anilius* based mostly on its overall morphology. The great resemblance of *Australophis* to *Hoffstetterella* and *Anilius* suggests that these taxa might be closely related, indicating that this lineage represents an early divergent lineage of anilioids that, since the Latest Cretaceous, have been evolving independently from the lineage leading to the extant *Cylindrophis*, uropeltids, and their fossil relatives. In this regard, it is noteworthy that the latter two taxa appear more closely related to each other than to *Anilius* in snake phylogenies based on molecular data. Although alethinophidian interrelationships are still ambiguous, in these studies *Anilius* appears basal to most other alethinophidians whereas the remaining extant anilioid taxa have a more apical position in most recent phylogenetic trees (Vidal and Hedges, 2002, 2004; Gower et al., 2005).

The anilioid fossil record is still sparse and the interrelationships of many of these forms within Anilioidea, or even within snakes as a whole, remain unclear. However, the affinities of the taxa recorded to date show that South America might have been important in early alethinophidian evolution. Moreover, the oldest known anilioid records provide evidence of their already widespread distribution on the continent by the Late Cretaceous.

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