

EXCEPTIONALLY PRESERVED SKELETONS OF THE CRETACEOUS SNAKE
DINILYSIA PATAGONICA WOODWARD, 1901

MICHAEL W. CALDWELL¹ and ADRIANA ALBINO²

¹Department of Earth and Atmospheric Sciences and Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E3, Canada, mw.caldwell@ualberta.ca;

²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Departamento de Biología, Universidad Nacional de Mar del Plata, Funes 3250, 7600 Mar del Plata, Argentina

For over one hundred years the Upper Cretaceous snake *Dinilysia patagonica* has been known from only the holotype skull and associated vertebrae (Smith-Woodward, 1901; Estes et al., 1970; Frazetta, 1970; Hecht, 1982; Rage and Albino, 1989; Albino, 1996). Recent fieldwork near Neuquén, Argentina, has produced a large number of exceptionally well-preserved skulls and skeletons of *Dinilysia* that preserve osteological features missing in the holotype. This new information is timely as recent studies of snake phylogeny have relied upon incomplete descriptions of *Dinilysia* (Caldwell, 1999; Scanlon and Lee, 2000; Tchernov et al., 2000). Our study of the new fossils indicates that *Dinilysia* was a large-bodied snake with an aniliid/ xenopeltid-like middle-ear osteology, and an anguimorph-like hypapophyseal/intercentrum anatomy. These new data will certainly impact future studies of snake phylogeny. We provide the first diagnosis of *Dinilysia patagonica* Smith-Woodward, 1901, along with a preliminary description of the new material, followed by discussion of two important osteological features (i.e., postorbital vs. jugal, absence of a crista circumfenestralis).

The holotype and all new specimens of *Dinilysia* described here were found at three localities in or near Neuquén, Neuquén Province, Argentina. The fossil-producing units are red- to white-weathering, coarse-grained sandstones assigned to the Bajo de la Carpa Member, Rio Colorado Formation (?Coniacian, Upper Cretaceous; Caldwell and Albino, 2001). The holotype specimen (Smith-Woodward, 1901; Estes et al., 1970) and two fragmentary skulls were found at Boca del Sapo, just north of Neuquén. Another fragmentary skull, assigned here to *Dinilysia*, was collected in the 1980s from outcrops just north of the Universidad Nacional del Comahue in Neuquén. The most recent collection of excellent skulls and articulated postcranial skeletons is from outcrops of the Río Colorado Formation exposed at the “Tripailao Farm Locality.” These sections are located on the south side of the Río Negro approximately 8.5 km to the west of the bridge at Paso Córdoba, or approximately 23 km to the southeast of Neuquén on the south side of the river (Caldwell and Albino, 2001).

Institutional Abbreviations—MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MPCA-PV, Museo de la Ciudad de Cipoletti, Cipoletti, Río Negro Province, Argentina; MUCP, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

SQUAMATA Oppel, 1811

SERPENTES Linnaeus, 1758

DINILYSIIDAE McDowell, 1987

DINILYSIA Smith-Woodward, 1901

DINILYSIA PATAGONICA Smith-Woodward, 1901

(Figs. 1–4)

Holotype—MLP 26-410, a partial skull (Figs. 1A, 3B, C) and partial postcranium.

Locality and Horizon—Locality at Boca del Sapo, Neuquén, Argentina (Coniacian; Upper Cretaceous).

Diagnosis—Medium-sized snake uniquely possessing complex, interdigitating, frontal-parietal suture; maxilla with deep, anterolaterally directed trough on suborbital surface; palatine and prefrontal forming broad ventral facet for articulation with maxilla and also forming choanal groove; ventromedial process of coronoid contacting angular; triradiate postfrontal overlapping frontal-parietal suture; postorbital closing posterior orbital margin with distinct ‘foot’ articulating with maxillary trough; large ‘?’-shaped quadrate; stapes robust with extremely large and expanded stapedial footplate; extracolumella/intercalary element contacting quadrate suprastapedial process; unfused intercentra present on hypapophyses of third–fourth preloacals; fused hypapophyses/intercentra to at least 10th preloocal; anterior 1/3 of preloacals bearing prominent ventral hypapophyseal “keels.”

Referred Specimens—MACN-RN 1013 (isolated skull, Figs. 1B, 3A), MACN-RN 1014 (isolated skull; Figs. 1C, 3D–G), MACN-RN 976 (articulated partial skeleton, Fig. 2A, with very complete skull, Fig. 1D), MACN-RN 1015 (isolated skull; Fig. 1E), MACN-RN 1016 (29 vertebrae, possibly caudals), MACN-RN 1017 (45 dorsal vertebrae), MACN-RN 1018 (eight large, dorsal vertebrae), and MACN-RN 1021 (35 dorsal vertebrae), MPCA-PV 527 (single skull with associated partial postcranium; Figs. 1F, 4), from Tripailao Farm Locality, Paso Córdoba, Río Negro Province, Argentina (?Coniacian; Upper Cretaceous). MUCP v 38 (fragmentary skull, Fig. 1G), MACN-N 26 (isolated strings of vertebrae associated with MUCP v 38), MUCP v 39, 40, 98–102, 104–116, 119, 121 (isolated vertebrae and short, articulated strings), north of the Universidad Nacional del Comahue, Neuquén, Argentina (?Coniacian; Upper Cretaceous). MLP 79-II-27-1 (fragmentary skull; Fig. 1H), MLP 71-VII-29-1 (fragmentary skull; Fig. 1I), MLP 79-11-27-2 to 79-11-27-17 (articulated strings of vertebrae), from type locality at Boca del Sapo, Neuquén, Argentina (?Coniacian; Upper Cretaceous).

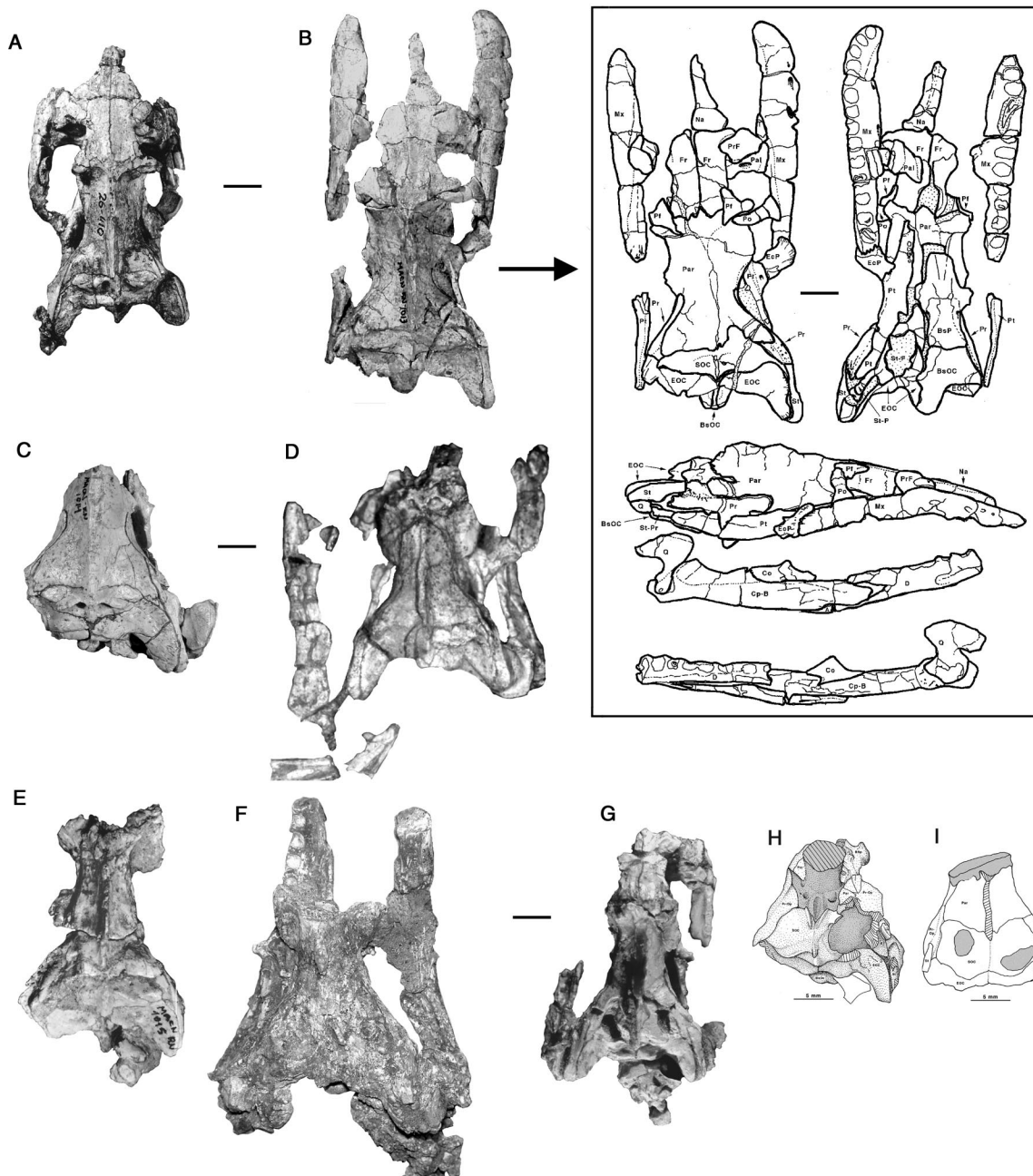


FIGURE 1. Skulls of *Dinilysia patagonica*. **A**, dorsal view of holotype skull, MLP 26-410. Scale equals 1 cm. **B**, dorsal view of skull of MACN-RN-1013; inset box with line drawings of MACN-RN-1013 in, dorsal, ventral and right lateral views, and lateral and medial views of right mandible. **C**, dorsal view of skull of MACN-RN-1014. **D**, dorsal view of skull of MACN-RN-976. **E**, dorsal view of skull of MACN-RN-1015. **F**, dorsal view of skull of MPCA-PV 527. **G**, dorsal view of skull of MUCP v 38. **H**, dorsal view of eroded skull of MLP 79-II-27-1. **I**, dorsal view of eroded skull of MLP 71-VII-29-1. **A–G**, Scale equals 1 cm; **H**, **I**, Scale equals 5 mm. **Abbreviations:** BsOC, basioccipital; cen, centrum; ns, neural spine; Co, coronoid; CpB, compound bone; D, dentary; EcP, ectopterygoid; ex-col, extracolumella; Fr, frontal; fld, foramen for the lachrymal duct; fPal-Mx, Palatine-Maxillary foramen; fRO, fenestra rotundum; Mx, maxilla; Na, nasal; Pal, palatine; Par, parietal; PrF, prefronta; Po, postorbital; Pf, postfrontal; Pr, prootic; Pt, pterygoid; Q, quadrate; SOC, supraoccipital; Bsp, basisphenoid; St, supratemporal; St-F, stapedial footplate; St-P, stapedial shaft/process; VI, 6th cranial nerve (abducens); X, 10th cranial nerve (vagus).

DESCRIPTION

Cranial—The new *Dinilysia* material includes osteological features that were either not preserved, or have since been lost, in the holotype specimen (Smith-Woodward, 1901; Estes et al., 1970), and we have chosen to focus our description on these new features. Some elements, such as the premaxilla, remain unknown (Fig. 1B).

The maxilla is long and low in lateral view, has at least fourteen tooth positions and three maxillary foramina, and is rounded on its anterior tip. At the midpoint of the maxilla there is a prominent medial process that articulates along a sloping facet with the prefrontal anteriorly and palatine posteriorly (Fig. 2A–C). Posterior to the palatine/prefrontal process the maxilla bears a broad groove for articulation with the foot of the postorbital. Posterior to the postorbital foot the maxilla expands and

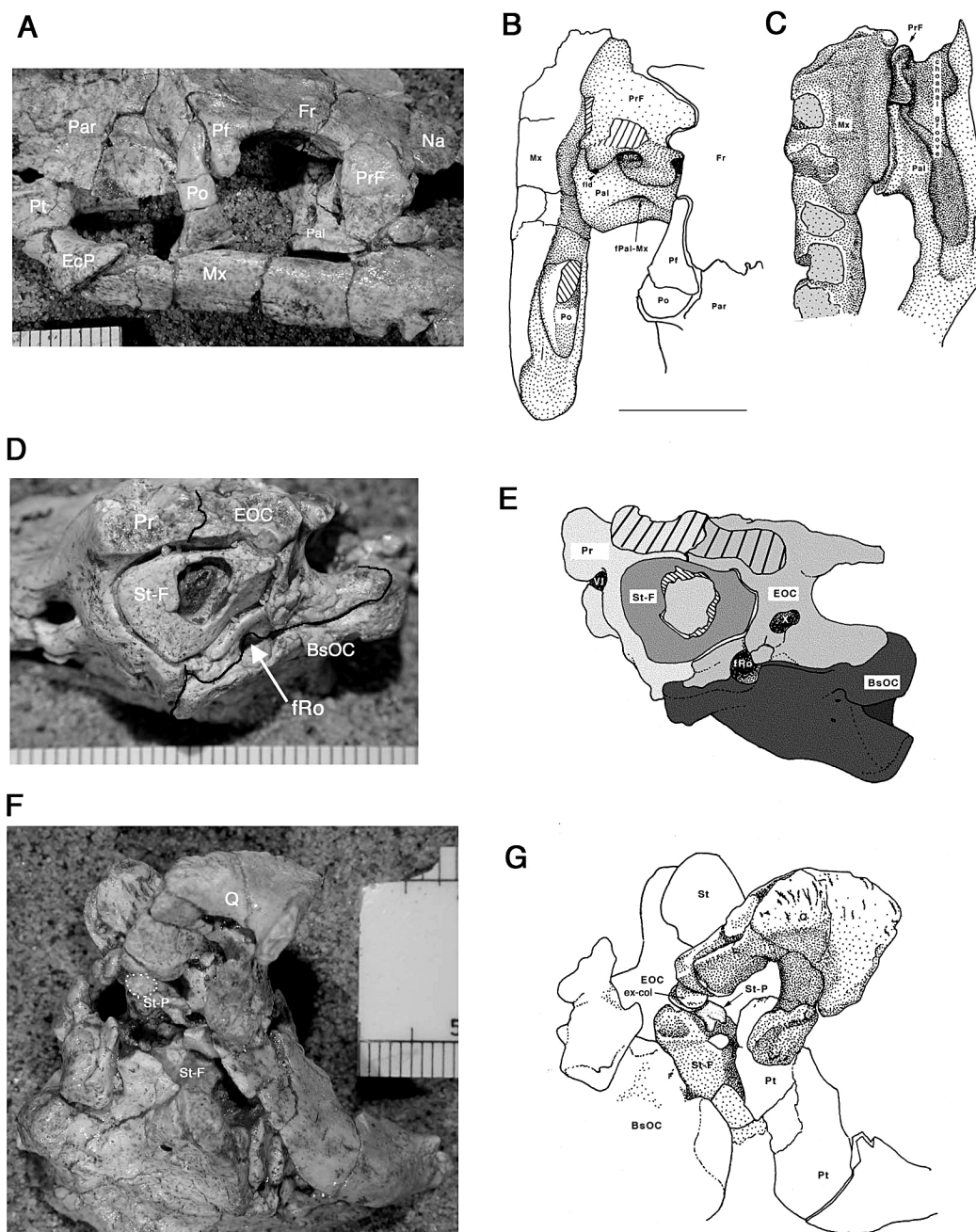


FIGURE 2. Details of skull features of *Dinilysia patagonica*. **A**, right lateral view of skull of MACN-RN 1013; note loose contact of maxilla with ectopterygoid, postorbital and palatine/prefrontal; **B**, line drawing in dorsal view of holotype (MLP 26–410) left maxilla, postorbital, and palatine/prefrontal; **C**, line drawing in ventral view of holotype (MLP 26–410) left maxilla, and palatine/prefrontal; **D**, left posteroventral view of skull (MACN-RN 1014) emphasizing size of stapedial footplate and absence of a crista circumfenestralis; **E**, shaded line drawing of braincase in left posteroventral view. Scale equals 1 cm; **F–G**, Right ventrolateral view and line drawing of skull of MACN-RN 1014. Note preservation and articulations of stapedial shaft/process (with suprastapedial process of enlarged quadrate). **Abbreviations**: see Figure 1.

flattens where it underlies the short, robust ectopterygoid in a broad non-sutural articulation; the ectopterygoid is broad and smooth at its contact with the maxilla.

The prefrontal is a small, pyramid-shaped element that is broadest along its contact with the maxilla, and narrowest at its articulation with the frontal where the apex inserts into a shallow v-shaped facet. There is no dorsal and anterior process of the prefrontal (Fig. 1B). Uniquely, the prefrontal contributes to the palate. Along its ventral surface, just anterior to the contact with the palatine, the prefrontal forms a channel that is contin-

uous with the choanal channel on the palatine (Fig. 2C) and appears to be unique within squamates.

The postfrontal is a small triangular bone that articulates with the frontal and parietal and clasps the tightly sutured frontoparietal articulation (Fig. 1A, B, D, G); the postfrontal enters the superior margin of the orbit but does not contact the prefrontal. The postorbital is dorsoventrally elongate and shaped like an inverted “T.” The dorsal tip loosely contacts the posterior margin of the postfrontal and sidewall of the parietal (Fig. 2A), while the ventral tip, broadened into a footplate-like struc-

ture, sits in the dorsal maxillary groove (Figs. 1B, 2A). The “jugal” that Estes et al. (1970) identified in *Dinilyisia* is the ventral tip of the postorbital. Neither a jugal nor a lachrymal can be identified in any of the known specimens of *Dinilyisia*.

The stapedia footplate is extremely large, completely obscures the fenestra ovalis (fenestra vestibularis), and is separated from the fenestra rotundum by a low ridge of bone derived from the exoccipital, the crista interfenestralis (Fig. 2D, E). The columellar shaft is at an acute angle relative to the footplate and is directed posteriorly towards the suprapedial process of the quadrate. It does not articulate directly with the suprapedial process but instead with a round, ossified element we identify as the extracolumella (Fig. 2F, G); this element has also been termed the intercalary or stylohyal (for recent use of these terms see Frazetta, 1999, or Rieppel, 1980a). The quadrate is a large ‘question mark’-shaped element with a broad cephalic condyle, robust shaft, and broad mandibular condyle. The suprapedial process is very large and expanded mediolaterally as well as ventrally. Articulation of the extracolumella-columella complex is with the extreme ventromedial tip of the suprapedial process.

Postcranial—Two of the new postcranial skeletons are particularly informative (Fig. 3A–E). The more complete and articulated specimen, MACN RN 976, preserves 123 vertebrae in a series of fractured but associated blocks (Fig. 3A). The longest complete string of 40 vertebrae consists of anteriormost preloacals that are still articulated with the skull (see Rage and Albino, 1989, for a description of the mid-preloacal vertebrae). All the vertebrae bear paracotylar foramina. Unsuspected vertebral features are found on the newest *Dinilyisia* specimen (MPCA–PV 527). The third and fourth most anterior preloacals bear large, posteriorly positioned hypapophyses with large, unfused intercentra (Fig. 3B). The intercentrum of the fourth preloacal has been lost, thus revealing the deeply concave surface of the hypapophysis (Fig. 3B). The anterior hypapophyses of *Dinilyisia* are remarkable as no known fossil or extant snake possesses hypapophyses with unfused intercentra. The posterior position of the hypapophyses and presence of unfused intercentra are also observed in mosasaurs (Russell, 1967), dolichosaurs (Caldwell, 2000), and varanoid lizards (Rieppel, 1980b). In contrast, the fifth most-anterior preloacal bears a large hypapophysis, likely with a fused intercentrum, that is typical of snakes (Fig. 3B).

DISCUSSION

Postfrontal and Postorbital—We identify a postfrontal and postorbital in *Dinilyisia*. While a postorbital is common to most modern snakes, a separate postfrontal is not. Estes et al. (1970) identified the latter bone in *Dinilyisia* as homologous to the postfrontal in lizards. We concur with this identification as the postfrontal of *Dinilyisia* passes the positional and relational criteria of the test of similarity (i.e., element clasping the fronto-parietal suture), and the test of composition (i.e., dermatocranial bone). Our identification of a postorbital in *Dinilyisia* follows the convention for snakes of identifying the element that descends ventrally from the area of the frontal-parietal suture, and framing the posterior margin of the orbit, as the postorbital. Though we follow this convention for *Dinilyisia*, we do find this identification problematic due to the presence of the postfrontal and the jugal-like articulations of the postorbital of *Dinilyisia*.

In non-snake squamates the postorbital contacts the postfrontal, sometimes fuses with it, extends a posterior ramus to contact the squamosal, and contacts the jugal where that element rises to meet the posterior margin of the postfrontal. In contrast, the jugal bone variably articulates with the postfrontal, postorbital, or postorbital frontal, articulates with the maxilla behind and beneath the orbit, and articulates with the lachrymal if pre-

sent. The jugal bone of the varanoid lizard *Lanthanotus* articulates with the postfrontal, maxilla-ectopterygoid, and lachrymal (the postorbital is absent in *Lanthanotus*). The remaining articulation, i.e., with the ectopterygoid, is variable among lizards and snakes (e.g., in *Python* the “postorbital” contacts the ectopterygoid). Comparisons to snakes such as scolecophidians are not possible as all superior and posterior orbital and temporal-arch bones are absent. The test of topological relation suggests a closer ‘fit’ with the jugal of non-snake squamates, not the postorbital. The possible presence of a jugal in *Dinilyisia* is relevant to recent arguments on the presence or absence of a jugal in *Pachyrhachis* (Caldwell and Lee, 1997; Zaher and Rieppel, 1999) and other legged snakes such as *Haasiophis* (Tchernov et al., 2000). Zaher and Rieppel (1999) have claimed that their studies have “revealed” the jugal of *Pachyrhachis* to be a broken ectopterygoid. Tchernov et al. (2001), using CT Scan reconstructions, argue that the bone is an enlarged postorbital that is symmetrically fractured on both sides of the holotype skull. While it seems unlikely that the element in question is an ectopterygoid (see the ectopterygoid of the paratype skull illustrated by Lee and Caldwell, 1998), it is intriguing that Tchernov et al. (2001) would identify an element with developed jugal-like topological connectivities as a postorbital, similar to the condition we note in *Dinilyisia*.

Stapes and Crista Circumfenestralis—As was noted by Estes et al. (1970), *Dinilyisia* does not possess an identifiable crista circumfenestralis, contra Rage (1984), Rieppel (1988), and Tchernov et al. (2000), nor is the crista prootica projecting laterally around the fenestra ovalis (contra Rieppel and Zaher, 2001). The enormous size of the stapedia footplate (Fig. 3D, E) may account for the absence of all cristae, i.e., the crista circumfenestralis, if ad hoc morphogenetic explanations are invoked (as has been argued for *Acrochordus* by Rieppel and Zaher, 2001). It may also be that *Dinilyisia* is plesiomorphically lacking the crista circumfenestralis as was argued by Estes et al. (1970) and McDowell (1974). However, at this point it can only be stated, prior to the test of congruence, that the test of similarity indicates that the crista circumfenestralis is absent in *Dinilyisia*.

Unlike the condition in snakes (see Wever, 1978), we also follow Estes et al. (1970) by identifying the opening ventral to the fenestra ovalis as the fenestra rotundum (Fig. 2). The fenestra rotundum is present in most lizards, but is considered absent in snakes and other squamates and turtles that possess a reentrant fluid circuit; the circuit cannot function if the round window membrane is present (Wever, 1978). A foramen, or niche (see Wever, 1978), is still present, as in almost all squamates, but in snakes it forms the channel of fluid movement from the recessus scala tympani to the pericapsular space. In the otic region of *Dinilyisia*, Estes et al. (1970) identified the fenestra ovalis, the fenestra rotundum, and the foramen for the 10th cranial nerve (Fig. 2D, E). The difficulty with identification of Estes et al.’s fenestra rotundum as the lateral aperture of the recessus scala tympani is that it is not within the crista circumfenestralis (the usual condition for extant snakes). In some basal snakes, where the crista circumfenestralis is incomplete posteriorly, the aperture is referred to as the fenestra pseudorotundum.

The osteology of the middle ear is also very intriguing. Comparison of the new specimens to the modern macrostomatan *Xenopeltis* (see Frazetta, 1999) indicates a number of shared characters. Both *Dinilyisia* and *Xenopeltis* possess a broad stapedia footplate with a posterodorsally angled stapedia shaft. That shaft contacts a small extracolumella/intercalary/stylohyal element that articulates with the suprapedial process of the quadrate. The head of the quadrate in both taxa is very broad and laterally flattened along the contact with the supratemporal. The topographic connectivities of the supratemporal are com-

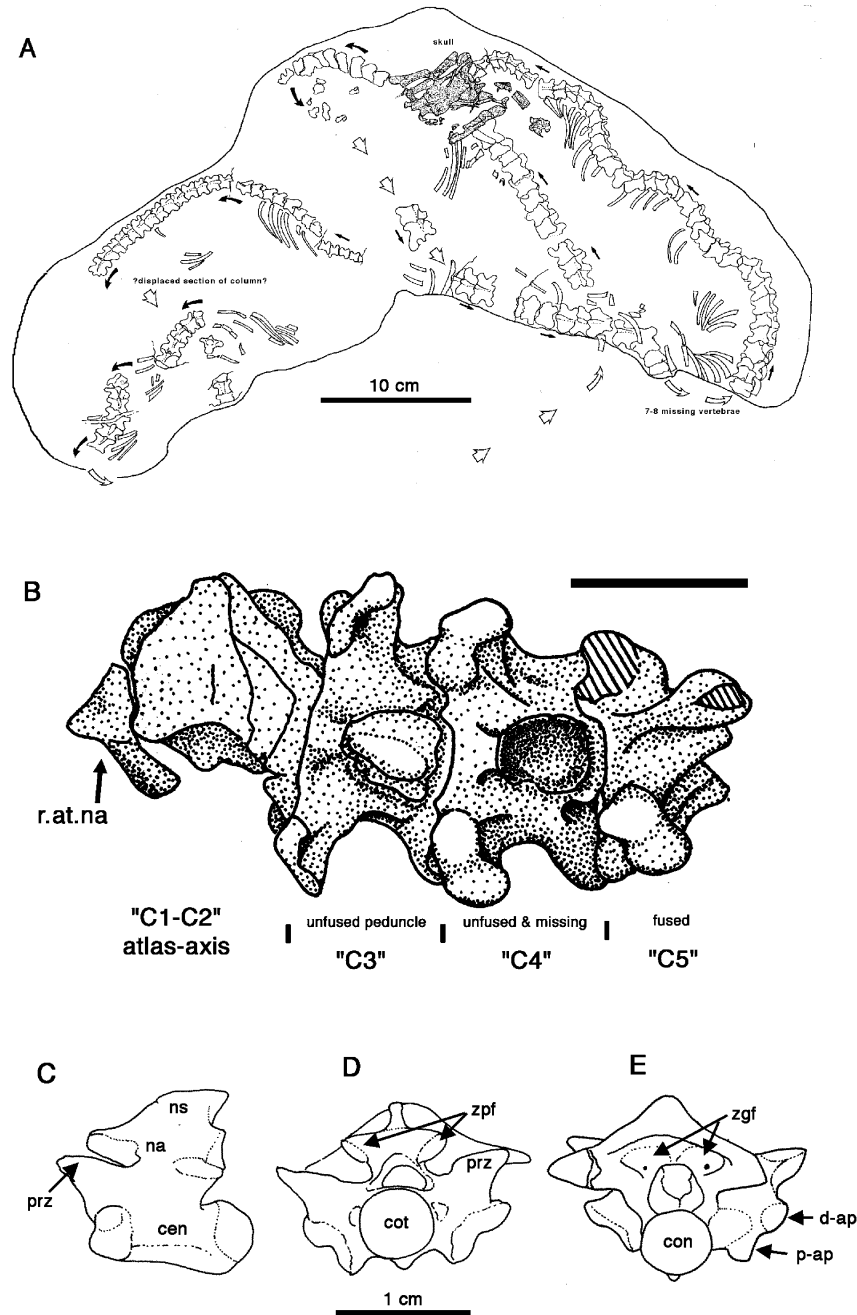


FIGURE 3. Postcranial skeletal elements of *Dinilyisia patagonica*. **A**, dorsal view of articulated specimen of *Dinilyisia patagonica* (MACN-RN-976); scale equals 10 cm. **B**, ventral view of the "cervical" series (anteriormost preloacals) of *Dinilyisia patagonica* (MPCA-PV 527); scale equals 1 cm. **C–E**, anterior dorsal vertebra from holotype in lateral, anterior, and posterior view (MLP 26–410); scale equals 1 cm. **Abbreviations:** **cen**, centrum; **con**, condyle; **cot**, cotyle; **d-ap**, diapophyses; **hk**, haemal keel; **na**, neural arch; **ns**, neural spine; **pactf**, paracotylar foramen; **p-ap**, parapophyses; **poz**, postzygaophyses; **prz**, prezygapophyses; **przap**, prezygapophyseal accessory process; **r.at.na.**, right atlas neural arch; **sf**, subcentral foramina; **sg**, subcentral groove; **zgf**, zygantral facets; **zpf**, zygosphenal facets.

mon in both snakes (i.e., articulating with the parietal, prootic, and exoccipital in a broad "L"-shaped groove). Modern aniliids also possess a similar osteology, though the ossified intercalary/extracolumellar element is absent in *Anilius* (Rieppel, 1980b).

Reference to the phylogenies present in the literature would suggest that the absence of a crista circumfenestralis in *Dinilyisia* is plesiomorphic. However, recent descriptions of the otic region of *Achrochordus* (Rieppel and Zaher, 2001) would suggest that absence of the feature in some snake taxa may be explained by pedomorphosis.

The many new features of *Dinilyisia*, such as the presence of a stylohyal element, the absence of a crista circumfenestralis, or the presence of unfused cervical intercentra, raise new questions about the phylogenetic relationships of snakes. Questions on primitive versus derived characters for snakes center on the phylogenetic position of scolecophidians, the Cretaceous marine snake taxa such as *Pachyrhachis* and *Haasiophis*, and early terrestrial Gondwanan snakes such as *Dinilyisia* and the Madtsoiidae (Caldwell and Lee, 1997; Rage and Escuillé, 2000; Scanlon and Lee, 2000; Tchernov et al., 2000).

ACKNOWLEDGMENTS

We thank P. Posse, L. Salgado, J. Calvo, and S. Heredia for assistance while working and living in Neuquén. We are indebted to J. Bonaparte for access to collections at the MACN and to R. Pascual for permission to study *Dinilysia* specimens in the MLP. We thank J. Rose and L. A. Lindoe for skilled preparation of the specimens. We thank G. Hanke, R. Holmes, H. Larsson, A. Nicholson, R. Nydam, and S. Pierce. We acknowledge financial support from a CMN RAC Grant to MC, NSERC Grant 238458-01 to MC, CONICET for support of AA, and a National Geographic CRE Grant for fieldwork support.

LITERATURE CITED

- Albino, A. 1996. The South American fossil Squamata (Reptilia: Lepidosauria); pp. 9–72 in G. Arratia (ed.), Contributions of Southern South America to Vertebrate Paleontology, Münchner Geowissenschaftlichen Abhandlungen (A) 30.
- Caldwell, M. W. 1999. Squamate phylogeny and the relationships of snakes and mosasauroids. *Zoological Journal of the Linnean Society* 125:115–147.
- . 2000. An aquatic squamate reptile from the English Chalk: *Dolichosaurus longicollis* Owen, 1850. *Journal of Vertebrate Paleontology* 20:720–735.
- , and A. Albino. 2001. Palaeoenvironment and palaeoecology of three Cretaceous snakes: *Pachyophis*, *Pachyrhachis*, and *Dinilysia*. *Acta Palaeontologica Polonica* 46:203–218.
- , and M. S. Y. Lee. 1997. A snake with legs from the marine Cretaceous of the Middle East. *Nature* 386:705–709.
- Estes, R., T. H. Frazzetta, and E. E. Williams. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward: Part I. Cranial morphology. *Bulletin of the Museum of Comparative Zoology* 140:25–74.
- Frazzetta, T. H. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward. Part II. Jaw machinery in the earliest snakes. *Forma et Functio* 3:205–221.
- . 1999. Adaptations and significance of the cranial feeding apparatus of the Sunbeam snake (*Xenopeltis unicolor*): Part I. Anatomy of the skull. *Journal of Morphology* 239:27–43.
- Hecht, M. 1982. The vertebral morphology of the Cretaceous snake, *Dinilysia patagonica* Woodward. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1982:523–532.
- Lee, M. S. Y., and M. W. Caldwell. 1998. Anatomy and relationships of *Pachyrhachis*, a primitive snake with hindlimbs. *Philosophical Transactions of the Royal Society, Series B* 353:1,521–1,552.
- McDowell, S. B. 1974. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop museum. Part 1. Scolecophidia. *Journal of Herpetology* 8: 1–57.
- . 1987. Systematics; pp. 3–50 in R. A. Siegel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York.
- Rage, J.-C. 1984. Serpentes. *Handbuch der Paläoherpetologie Teil 11*. Stuttgart, Gustav Fischer Verlag, 80 pp.
- , and A. Albino. 1989. *Dinilysia patagonica* (Reptilia, Serpentes); matériel vertébral additionnel du Crétacé supérieur d'Argentine. Etude complémentaire des vertébrés, variations intraspécifiques et intracolumnnaires. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1989:433–447.
- , and F. Escuillié. 2000. Un nouveau serpent bipède du Céno-manien (Crétacé). Implications phylétiques. *Comptes Rendus de l'Académie des Sciences, Paris, Serie Ia* 330:1–8.
- Rieppel, O. 1980a. The Phylogeny of Anguinomorph Lizards. Basel, Birkhauser Verlag, 86 pp.
- . 1980b. The sound-transmitting apparatus in primitive snakes and its phylogenetic significance. *Zoomorphology* 96:45–62.
- . 1988. A review of the origin of snakes. *Evolutionary Biology* 22:37–130.
- , and H. Zaher. 2001. The development of the skull in *Acrochordus granulatus* (Schneider) (Reptilia: Serpentes), with special consideration of the otico-occipital complex. *Journal of Morphology* 249:252–266.
- Russell, D. 1967. Systematics and morphology of American mosasaurs. Peabody Museum of Natural History, Yale University, Bulletin 23: 1–241.
- Scanlon, J. D., and M. S. Y. Lee. 2000. The Pleistocene serpent *Wombambis* and the early evolution of snakes. *Nature* 403:416–420.
- Smith-Woodward, A. 1901. On some extinct reptiles from Patagonia of the genera *Miolania*, *Dinilysia*, and *Genyodectes*. *Proceedings of the Zoological Society, London* 1901:169–184.
- Tchernov, E., M. J. Polcyn, and L. L. Jacobs. 2001. Application of computed tomography to *Pachyrhachis problematicus*, a snake with legs from the Cretaceous of Israel. *Journal of Vertebrate Paleontology* 21(3, suppl.):107A.
- , O. Rieppel, H. Zaher, M. J. Polcyn, and L. L. Jacobs. 2000. A fossil snake with limbs. *Science* 287:2,010–2,012.
- Wever, E. G. 1978. *The Reptile Ear, Its Structure and Function*. Princeton University Press, Princeton, 1,024 pp.
- Zaher, H., and O. Rieppel. 1999. The phylogenetic relationships of *Pachyrhachis problematicus*, and the evolution of limblessness in snakes (Lepidosauria, Squamata). *Comptes Rendus de l'Académie des Sciences, Paris* 329:831–837.

Received 21 March 2002; accepted 17 June 2002.