A NEW SPECIES OF *NOTOBATRACHUS* (AMPHIBIA, SALIENTIA) FROM THE MIDDLE JURASSIC OF NORTHWESTERN PATAGONIA

ANA MARIA BÁEZ[1] AND LAURA NICOLI[2]

Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. Pabellón II Ciudad Universitaria, C1428EHA, Buenos Aires, Argentina, [1]<baez@gl.fcen.uba.ar>; [2] <lnicoli@gl.fcen.uba.ar>

ABSTRACT—*Notobatrachus degiustoi* is the most completely known Jurassic frog and has been recorded in many outcrops of the La Matilde Formation of the Deseado Massif area in southern Patagonia. Herein, we erect a new species of the genus based on partially articulated remains collected from the Callovian Las Chacritas Member of the Cañadón Asfalto Formation, about 500 km northwest of the northern limit of the known geographical distribution of *N. degiustoi*. The new species differs from the latter in having a maxilla with a distinct pterygoid process and lacking teeth at least along the posterior two-thirds of its length, and a complete maxillary arch. We also provide an expanded diagnosis of *Notobatrachus*. This finding adds to our understanding of the early diversification of frogs.

INTRODUCTION

RECENT STUDIES based on molecular data have placed the origin of crown-group anurans (the last common ancestor of living frogs and all of its descendants) in the Triassic (Roelants and Bossuyt, 2005), or even earlier (San Mauro et al., 2005). However, the fossil record has not contributed significantly to our understanding of the basal divergence of the crown-group owing to the fragmentary condition of the available remains and their uncertain taxonomic position. Whereas the oldest record of crown frogs is of Late Bathonian age (Evans et al., 1990), few other remains, either ascribed to the crown-group or considered as salientians (amphibians more closely related to Anura than to Caudata) outside the anuran node, have been described from Jurassic rocks (Reig, 1961; Stipanicic and Reig, 1957; Evans and Milner, 1993; Henrici, 1998; Jenkins and Shubin, 1998). Most of these fossils have been recovered as disarticulated bones and lack sets of traits usually considered diagnostic of extant family-level groupings. By contrast, the few known Jurassic records from South America consist of impressions of articulated skeletons, which in the case of the Callovian-Oxfordian *Notobatrachus degiustoi* Reig, 1956 are not only superbly preserved, but also numerous and belonging to different ontogenetic stages (Estes and Reig, 1973; Báez and Nicoli, 2004). Even though the taxonomic placement of these fossils is still unresolved (Báez and Basso, 1996; Sanchiz, 1998; Roček, 2000; Gao and Wang, 2001, Gao and Chen, 2004), the fact that many specimens are articulated allowed us to gather valuable information about the structure and relative proportions of skeletal parts that usually are not preserved and are unknown in other Jurassic frogs. To date, all known specimens of *Notobatrachus degiustoi* have been recovered from various exposures of the fluvio-lacustrine La Matilde Formation of the Deseado Massif region, in southern Patagonia (Fig. 1.1).

Recent fieldwork carried out by the Museo Paleontólogico Egidio Feruglio of Trelew, Argentina, in continental deposits of Jurassic age of the Cañadón Asfalto Basin, in northwestern Patagonia, led to the discovery of the frog remains described herein. The frog-bearing beds are part of the Cañadón Asfalto Formation, a continental unit that is exposed extensively in the middle section of the Río Chubut Valley in northern Chubut Province. This formation is well known for its abundant fossiliferous content, which includes plants (Stipanicic et al., 1968; Stipanicic and Bonetti, 1970), invertebrates (Tasch and Volkheimer, 1970), and vertebrates (Bonaparte, 1986; Rauhut et al., 2002; Rauhut, 2005). The Cañadón Asfalto Formation consists of a thick volcano-sedimentary sequence that overlies the Aalenian-Callovian volcanic and pyroclastic rocks of the Lonco Trapial Formation. It has been divided into two sections: a lower section, Las Chacritas Member, and an upper section, Puesto Almada Member (Silva Nieto et al., 2002; Silva Nieto et al., 2003). The Las Chacritas Member is 250 m thick at the type locality of the Cañadón Asfalto Formation

and is composed mainly of limestones, shales, pyroclastic deposits, and basalts that represent a lacustrine depositional system (Figari and Courtade, 1993; Silva Nieto et al., 2003; Cabaleri et al., 2005). Gray siltstones overlying basaltic levels of this member at the Cañadón Bagual, in the Cerro Cóndor area (Fig. 1.2), yielded the frog remains in association with plants. Stratigraphically, these beds are slightly lower in the sequence than the layer from which the mammal *Asfaltomylos* (Rauhut et al., 2002) was collected in the middle part of the Las Chacritas Member at a nearby locality. Although the age of the Cañadón Asfalto Formation has been the subject of much discussion, a general Callovian-Oxfordian age generally has been accepted based on the stratigraphic position of the formation and its fossils (Page et al., 1999; Silva Nieto et al., 2002). Recent palynological data from the vicinity of the Cerro Cóndor locality suggest the Callovian age of the Las Chacritas Member (Martin and Rauhut, 2005). This evidence is in agreement with the Callovian-Oxfordian age attributed to a non-marine microfossiliferous association collected in the upper member of the Cañadón Asfalto Formation (Musacchio et al., 1990; Musacchio, 1995), which disconformably underlies the Cretaceous Chubut Group.

Institutional abbreviations.—CMN, Canadian Museum of Nature, Ottawa, Canada; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; MPM-PV, Museo Padre Molina, Paleontología Vertebrados, Río Gallegos, Santa Cruz, Argentina.

SYSTEMATIC PALEONTOLOGY

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Class AMPHIBIA Linnaeus, 1758
Superorder SALIENTIA Laurenti, 1768
Genus NOTOBATRACHUS Reig, 1956 "1955"

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Type species.—*Notobatrachus degiustoi* Reig, 1956 "1955" in Stipanicic and Reig, 1955.

Emended diagnosis.—(after Reig, 1957 in Stipanicic and Reig, 1957; Estes and Reig, 1973; Báez and Basso, 1996; Báez and Nicoli, 2004) Large-sized salientian that differs from all other known salientians in having a parasphenoid with a trifid cultriform process and is distinguished from *Triadobatrachus* also in possessing nine presacral vertebrae and a urostyle. *Notobatrachus* differs further from crown anurans by having an independent intermedium in the carpus, a dorsoventrally curved clavicle, and an earlike acetabular fossa of the ilium. It can be also differentiated from other saliention taxa by the following combination of characters: sculptured dermal skull bones; long maxilla with a dorsally directed pars palatina; extensive nasal articulating with frontoparietal and bearing distinct rostral process; cartilaginous septum nasi; T-shaped squamosal with free-ending, plate-like zygomatic ramus; columella; vomer bearing well-developed postchoanal process that forms a wide angle with the corpus of the bone; discrete
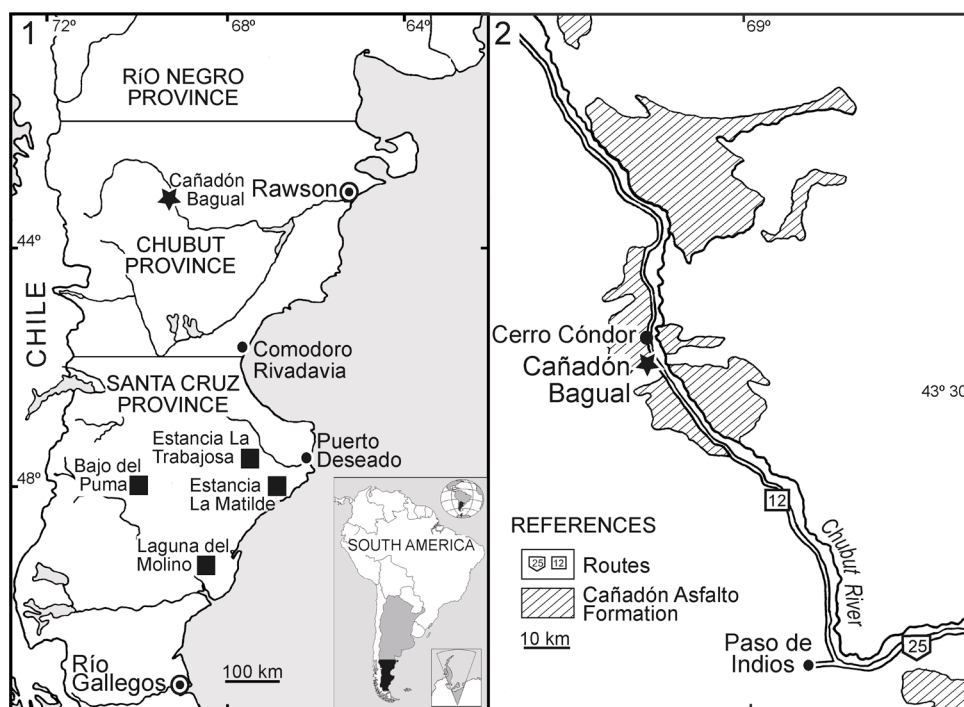
FIGURE 1—Maps of Patagonia. 1, Map of Patagonia showing the location of the Jurassic *Notobatrachus*-bearing sites. The star indicates the locality where the new material was collected. 2, Map of the Cerro Cóndor area showing the Cañadón Asfalto Formation outcrops and the locality for the new record of *Notobatrachus*.

palatine absent; paired sphenethmoid; crescent-shaped parahyoid bone; notochordal presacral vertebrae; four pairs of free ribs associated with V2–V5, occasionally also with V6; transverse processes of posterior presacral vertebrae as long as sacral diapophysis; imbricated neural arches; cartilaginous sacro-urostylar articulation; one postsacral vertebra either discrete or partially incorporated into urostyle bearing transverse processes; short scapula with medial notch; clavicle with blunt, slightly expanded medial end; sternal end of coracoid widely expanded; robust humerus with unossified humeral ball; radioulna lacking well-developed olecranon process; carpus with nine to eleven discrete elements; ilia without distinct tubercles for muscular attachment; unfused tibiale and fibulare; cartilaginous distal tarsals.

NOTOBATRACHUS REIGI new species
Figures 2.1, 2.2, 2.4, 3.1, 3.2

Diagnosis.—Species of *Notobatrachus* that differs from *N. degiustoi* in having a complete maxillary arch by the presence of an ossified quadratojugal and lacking teeth at least on at least the posterior two-thirds of the maxilla.

Etymology.—The specific noun honors the late Dr. Osvaldo Reig for his contribution to evolutionary biology and his unwavering commitment to excellence in science.

Type.—Holotype, MPEF 3006, impressions of several bones of different skeletal regions of one individual, most of them exposed in ventral aspect, not preserved in natural position.

Occurrence.—Zitarrosa Site, Cañadón Bagual, 3 km SW Cerro Cóndor, Departamento de Paso de Indios, Provincia de Chubut, Argentina; Cañadón Asfalto Formation, Las Chacritas Member. Middle Jurassic (Callovian).

Description.—The impressions occur on three slabs that were collected in a small area. Because the bones are not duplicated and belong to specimens of the same size, we assume that they are remains of one individual. Some of the cranial impressions are preserved as part and counterpart. Study of this material was based on the original specimens, as well as on high fidelity latex molds. The snout-vent length of the specimen represented by these remains is estimated to be 12 cm, based on the proportions of *Notobatrachus degiustoi*. The holotype of the latter species and that of *N. reigi* are similar in size.

Cranial elements.—Skull represented by bones of maxillary arch, suspensorial region, and lower jaw of left side (Fig. 2.1).

Anterior one-sixth of the maxilla missing, but preserved portion suggests a long element, posterior terminus of which lay near quadrate articular facet for lower jaw. Lingual side of maxilla well exposed. Ventral margin of pars dentalis appears sectioned along anterior one fourth of preserved portion of bone and bears shallow depressions; however, it is not possible to ascertain whether teeth were present. In contrast, unaltered ventral margin of remaining part of maxilla indicates that teeth were absent, at least along posterior two thirds of complete bone (Fig. 2.1, 2.4). Well-developed pars palatina forms wide laminar shelf, its width nearly uniform along most of preserved part of maxilla, gradually decreasing in width near posterior end of bone. Angle formed between pars palatina and pars dentalis varies along maxilla; angle obtuse in middle portion of preserved fragment, distinctly narrower at anterior and posterior ends. Short laminar bone broken into two pieces clearly visible medially to posterior portion of maxilla (Fig. 2.1); we identify this bone as the quadratojugal. Posterior end of latter element attached to quadrangular ossification corresponding to pars quadrata of palatoquadrate. Anteriorly to latter element and medially to quadratojugal, rodlike bone bearing a distinct groove is partially obscured by lower jaw, corresponds to distal portion of entral ramus of squamosal. Pterygoid triradiate; shapes of anterior and posterior rami difficult to estimate, being overlapped by mandible; medial ramus poorly preserved. Dorsal surface of anterior ramus bears a channel for pterygoid process of palatoquadrate. Impression of nearly complete lower jaw preserved medially adjacent to maxillary arch. Angulosplenial relatively long; anterior end terminates near inferred location of premaxilla-maxilla articulation, wide, open Meckelian canal evident on dorsal surface. Laminar dentary fused to well-developed mentomeckelian bone. Elongated bone lies almost perpendicular to left maxillary arch and lower jaw (Fig. 2.1, 2.2). Narrow flange, its width diminishing at both ends, occurs along one side of bone, forms right angle with bottom, whereas opposite side disappears into the sediment; rough surface of this bone suggests it is a dermal element. All this evidence suggests that it might be the right frontoparietal preserved in ventrolateral view.
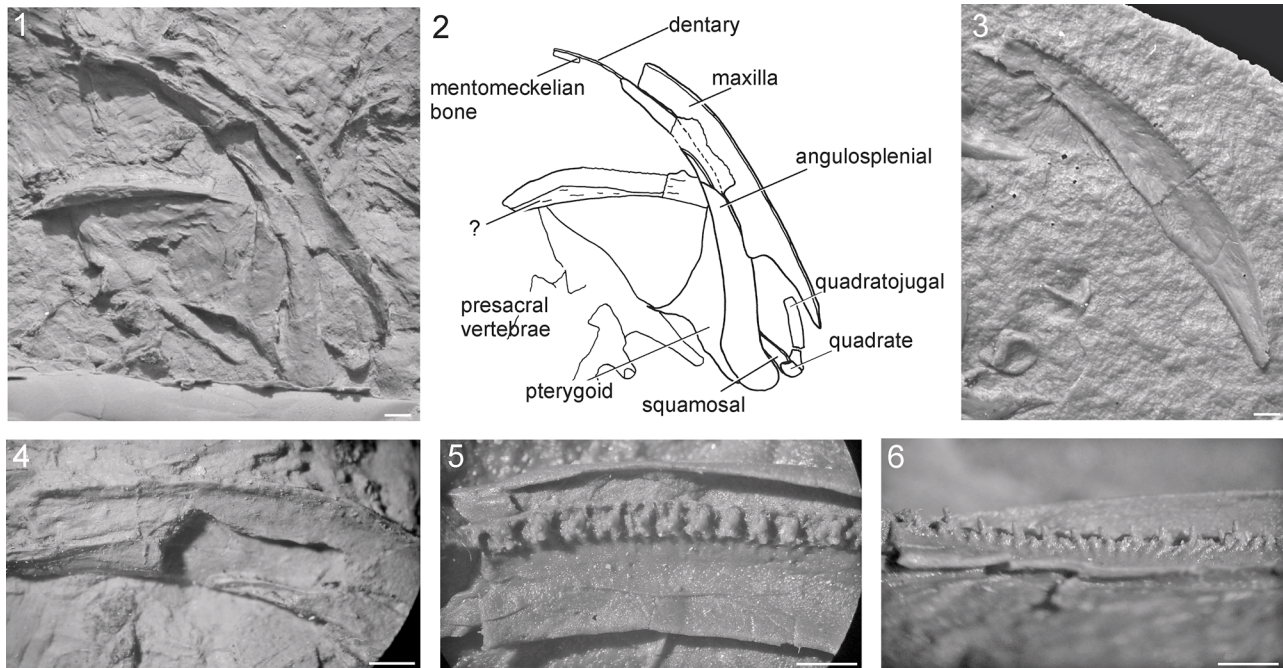
FIGURE 2—*Notobatrachus reigi* n. sp. *1*, Photograph of the silicon-rubber mold of *Notobatrachus reigi* n. sp. (Holotype, (MPEF 3006) from the Cañadón Asfalto Formation showing skull remains in ventral aspect. *2*, Schematic interpretive drawing of 1. *3*, Photograph of the silicon-rubber mold of the left maxilla of *Notobatrachus degiustoi* Reig (MACN 17723) from the La Matilde Formation, in ventral aspect. *4*, Left maxilla of *Notobatrachus reigi* n. sp. (Holotype, MPEF 3006) in ventral view. *5*, Left maxilla of *N. degiustoi* (MPM-PV-3948) in occlusal view. *6*, Left maxilla of *N. degiustoi* (MPM-PV-3948) in lingual view. Scale bar: 2 mm.

Postcranial elements.—A few partially articulated vertebrae poorly preserved; these belong to anterior presacral region as evidenced by robust transverse processes articulating with free ribs. Right forelimb represented by radioulna and articulated partial autopodium (Fig. 3.1, 3.2). Proximal end of radioulna with shallow articular facet for humerus, lacking a well-ossified olecranon. Shaft of radioulna stout, distal end distinctly expanded. Carpus of several independent elements arranged in three rows. Although the ontogenetic history of these bones is unknown to us, we used the nomenclature by Fabrezi and Alberch (1996) to identify these elements based on their sizes, morphologies, relative positions, and spatial relationships. Basal row of elements consists of three bones, two of which are relatively large, in contact with radial and ulnar portions of radioulna, respectively; thus, we identify them as radiale and ulnare. Distal part of latter bone bears distinct process on postaxial side (Fig. 3.1, 3.2). Third element of smaller size present between radiale and ulnare. We tentatively identify this bone as the intermedium. Second row contains two large elements, one distal to ulnare, other distal to radiale. Former transversely elongate, its medial part in contact with both radiale and bone distal to it. Thus, the bones of the second row are identified as Distal Carpal 5 and Element Y (sensu Shubin and Alberch, 1986). Distally to these two bones, three smaller elements visible at bases of three inner metacarpals. Larger of these elements occurs at base of Metacarpal 4, flanked proximally by Distal Carpal 5 and Element Y; this bone is considered Distal Carpal 4. We identify a small, rounded bone at base of Metacarpal 3 as Distal Carpal 3; element between Element Y and base of Metacarpal 2 corresponds to Distal Carpal 2. Two additional bones visible next to Element Y on preaxial side we consider as components of prepollex. Metacarpals relatively short; their lengths representing nearly half the length of radioulna. Distal to metacarpals, proximal phalanges of all four digits are preserved (Fig. 3.1, 3.2). Impressions of long bones of both right and left hind limbs also exist. Femur slightly sigmoid, nearly as long as tibiofibula, lacking well-developed, ossified head. Proximal and distal ends of tibiofibula somewhat expanded, bearing sulci that reveal the dual origins of the bone. Tibiale and fibulare separate, about one-third length of femur.

DISCUSSION

In their morphology and general proportions, most of the preserved elements described herein resemble the distinctive corresponding bones of *Notobatrachus degiustoi*. As in the latter species, the maxilla is a long bone that bears a laminar pars palatine, which is dorsally directed and extends far from the base of the area of tooth attachment, even if teeth were absent in the new species (Fig. 2.1, 2.3). This morphology differs from that of other Jurassic anurans for which the lingual side of the maxilla is known, such as *Vieraella herbstii* Reig, 1961 (Báez and Basso, 1996), *Rhadinosteus parvus* Henrici, 1998, and *Eodiscoglossus oxoniensis* Evans et al., 1990, wherein which, as in most living frogs, the pars palatina extends horizontally from near the base of the tooth row. The few, poorly-preserved anterior presacral vertebrae resemble those of *N. degiustoi* in having amphicoelous centra (although lacking evident notochordal canals), and robust transverse processes that are round in cross-section and articulate with free ribs. The structure of the carpus from Cañadón Asfalto is within the variation recorded among the numerous specimens of *N. degiustoi* (Fig. 3.5). In this species, the number of discrete carpal bones ranges between eleven and nine (Estes and Reig, 1973), more than is known in extant frogs (Fabrezi, 1992), including the most basal taxa (Fig. 3.6, 3.7). This variation reflects the fusion or independence of adjacent elements of doubtful homology in the basal and central carpal rows. As in most specimens of *N. degiustoi* for which the carpus is known (Fig. 3.3, 3.4), there are three bones distal to the radioulna; instead, only a single bone is in contact with distal carpals 5, 4, 3, and 2, and the proximal element of the prepollex.

Despite these similarities, the remains from the Cañadón Asfalto Formation differ from *Notobatrachus degiustoi* in a few features. The maxilla lacks teeth along the posterior two-thirds of
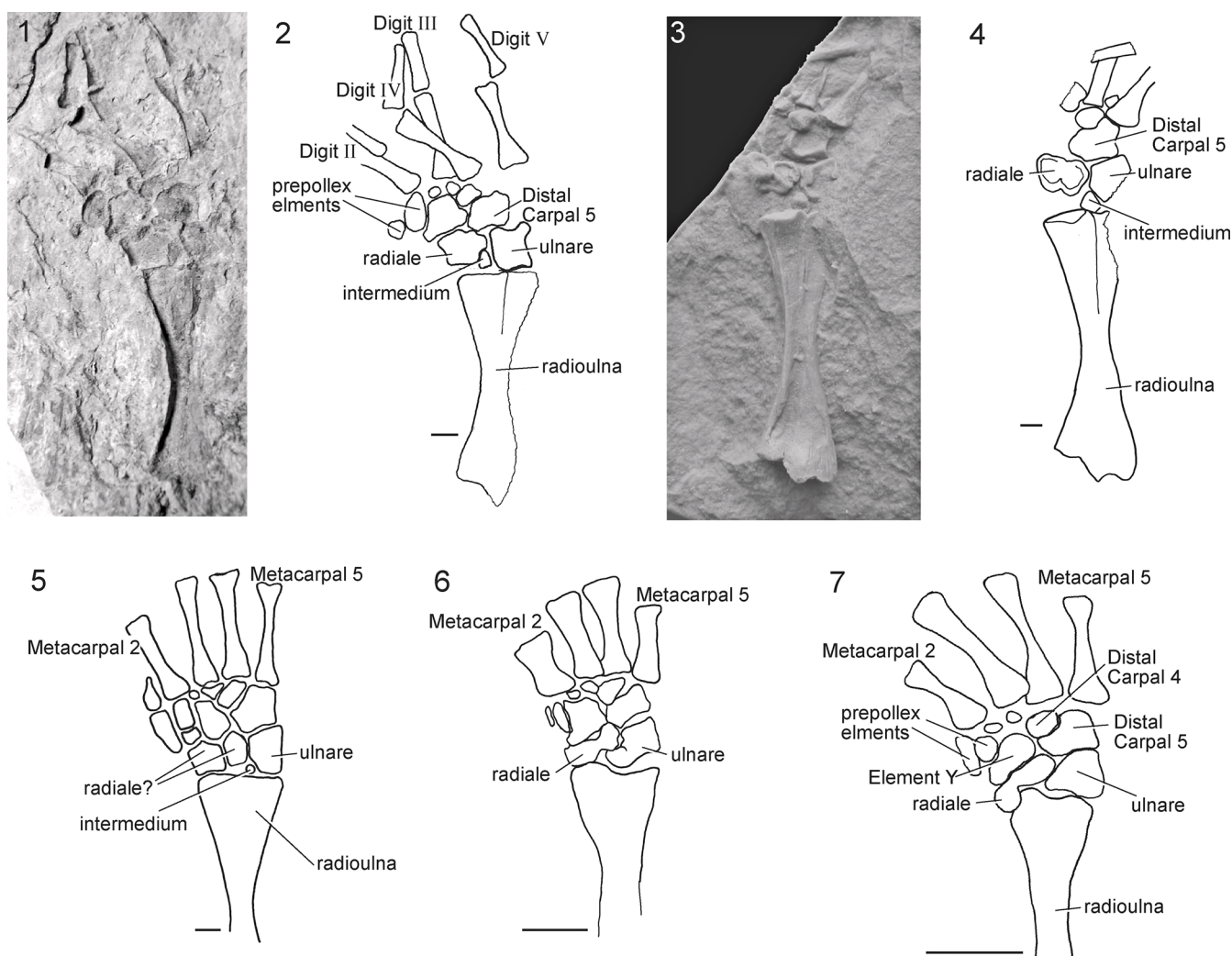
FIGURE 3—1, Photograph of the right carpus of *Notobatrachus reigi* n. sp. (Holotype, MPEF 3006) from the Cañadón Asfalto Formation. 2, Interpretive drawing of 1. 3, Left carpus (reversed) of *N. degiustoi* (MPM-PV-3949) from the La Matilde Formation. 4, Schematic drawing of 3. 5, Schematic drawing of the right carpus of *N. degiustoi* showing the maximum number of carpal elements recorded in this species (modified from Báez and Nicoli, 2004). 6, Schematic drawing of the right carpus of *Ascaphus truei* Stejneger, 1899 (CMN 21868, cleared and stained). 7, Schematic drawing of the right carpus of *LeiopeIma hamiltoni* McCulloch, 1919. (CMN 29597-4, cleared and stained). Scale bar: 2 mm.

the bone; in addition, comparison with *N. degiustoi* suggests that even if teeth were present on the most anterior portion of the maxilla, they would have had a different morphology and attachment from those of the latter species. In *N. degiustoi*, the pillars of bone (pedicels?) that support the small crowns are labio-lingually broad and low (Fig. 3.5, 3.6), whereas in *N. reigi* that part of the maxilla is distinctly thin (Fig. 3.4). Although true teeth do not develop before metamorphosis in anurans (Castanet et al., 2003), the complete ossification and size of the specimen from the Cañadón Asfalto Formation make the edentulous condition hardly attributable to immaturity. Moreover, the quadratojugal, which usually ossifies late in development in extant frogs (Trueb, 1985; Roček, 2003), is present in *N. reigi*, but it has not been observed in any specimen of *N. degiustoi* (Estes and Reig, 1973; Báez and Basso, 1996; Báez and Nicoli, 2004) even though its pars articularis quadrata is more ossified than it is in the new species. Additionally, the pars palatina of the maxilla forms a more distinct pterygoid process than in *N. degiustoi* (Fig. 2.1–2.3).

These data confirm the existence of a different species of *Notobatrachus* about 500 km northwest of the northern limit of the known geographical distribution of *N. degiustoi* (Fig. 1.1). It is noteworthy that the lacustrine rocks that yielded specimens of *N. degiustoi* in its type locality interdigitate with ignimbrites for which a Rb-Sr whole-rock isochron of 168 ± 2 Ma was obtained (Pankhurst et al., 1998; Pankhurst et al., 2000). This indicates a Middle Jurassic age for these deposits and, thus, the possible contemporaneity of the horizons that yielded *Notobatrachus* in the Deseado Massif, northeastern Santa Cruz, and Cañadón Asfalto Basin, northwestern Chubut. These frog-bearing volcaniclastic successions are part of the infillings of a series of halfgrabens that were formed under extensional tectonics during the early stages of the separation of the South American and African plates (Geuna et al., 2000; Franzese et al., 2003; Echavarría et al., 2005). As this new record shows, our knowledge of the early history of the salientian amphibians in South America is confined entirely to the southern end of the continent where, in the Middle Jurassic, taxonomically-monotonous populations of the large *Notobatrachus* thrived in lacustrine environments. However, this reflects collecting biases, because in the past, small vertebrates frequently were overlooked by collectors. As more attention is paid to fossil microfaunas, we anticipate that a change in this trend during the last few years permits us to foresee a different picture emerging in the near future.

REFERENCES

BÁEZ, A. M. AND N. G. BASSO. 1996. The earliest known frogs of the Jurassic of South America: Review and cladistic appraisal of their relationship. Munchner Geowissenschaftliche Abhandlungen, Reihe A (Geologie Palaontologie), 30:131–158.

BÁEZ, A. M. AND L. NICOLI. 2004. A new look at an old frog: The Jurassic *Notobatrachus* Reig from Patagonia. Ameghiniana, 41(3):257–270.

BONAPARTE, J. F. 1986. Les Dinosaures (Carnosaures, Allosauridés, Sauropodes, Cetiosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentine). Annales de Paléontologie (Vert.-Invert.), 72:247–289.

CABALIERI, N. G., C. ARMELLA, AND D. G. SILVA NIETO. 2005. Saline paleolake of the Cañadón Asfalto Formation (Middle-Upper Jurassic), Cerro Condor, Chubut province (Patagonia), Argentina. Facies, 51:350–364.

CASTANET, J., H. FRANCILLON-VIEILLOT, H. DE RICQLÉS, AND L. SYLBERBERG. 2003. The skeletal histology of amphibians, p. 1598–1683. *In*: H. Heatwole (ed.), Amphibian Biology. Volume 5. Osteology. Surrey Beatty and Sons, Chipping Norton, Australia.

ECHAVARRÍA, L. E., I. B. SCHALAMUK, AND R. 0. ETCHEVERRY. 2005. Geological and tectonic setting of Deseado Massif epithermal deposits, Argentina, based on El Dorado—280 Montserrat. Journal of South American Earth Sciences, 19:415–432.

ESTES, R. AND O. A. REIG. 1973. The early fossil record of frogs: A review of the evidence, p. 282, 11–36. *In*: J. L. Vial (ed.), Evolutionary Biology of the Anurans, Contemporary Research on Major Problems. University of Missouri Press, Columbia.

EVANS, S. E. AND A. R. MILNER. 1993. Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. Journal of Vertebrate Paleontology, 13:24–30.

EVANS, S. E., A. R. MILNER, AND F. MUSSET. 1990. A discoglossid frog from the Middle Jurassic of England. Palaeontology, 33:299–311.

FABREZI, M. 1992. El carpo de los anuros. Alytes, 10:1–29.

FABREZI, M. AND P. ALBERCH. 1996. The carpal elements of anurans. Herpetologica, 1:188–204.

FIGARI, E. G. AND S. D. COURTADE. 1993. Evolución tectosedimentaria de la cuenca de Cañadón Asfalto, Chubut, Argentina. Actas 12° Congreso Geológico Argentino, Buenos Aires, 1:66–77.

FRANZESE, J., L. SPALLETTI, I. GÓMEZ PÉREZ, AND D. MACDONALD. 2003. Tectonic and paleoenviromental evolution of Mesozoic sedimentary basins along the Andean foothills of Argentina (32°–54°S). Journal of South American Earth Sciences, 16:81–90.

GAO, K.-Q. AND S. CHEN. 2004. A new frog (Amphibia: Anura) from the Lower Cretaceous of western Liaoning, China. Cretaceous Research, 25: 761–769.

GAO, K.-Q. AND Y. WANG. 2001. Mesozoic anurans from Liaoning Province, China, and phylogenetic relationships of archaeobatrachian anuran clades. Journal of Vertebrate Paleontology, 21:460–473.

GEUNA, S. E., R. SOMOZA, H. VIZAN, E. G. FIGARI, AND C. A. RINALDI. 2000. Paleomagnetism of Jurassic and Cretaceous rocks in central Patagonia: A key to constrain the timing of rotations during the breakup of southwestern Gondwana? Earth and Planetary Science Letters, 181:145–160.

HENRICI, A. 1998. A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah. Journal of Vertebrate Paleontology, 18:321–332.

JENKINS, F. A. AND N. H. SHUBIN. 1998. *Prosalirus bitis* and the anuran caudopelvic mechanism. Journal of Vertebrate Paleontology, 18:495–510.

LAURENTI, J. N. 1768. Specimen medicum, exhibens synopsin Reptilium emendatum cum experimentis circa venena et antidota Reptilium Austriacorum. J. T. de Trattem, Wien, 214 p.

LINNEAUS, C. 1758. Systema Naturae (10th edition). L. Salvii, Stockholm, 824 p.

MARTIN, T. AND O. W. M. RAUHUT. 2005. Mandible and dentition of *Asfaltomylos patagonicus* (Australosphenida, Mammalia) and the evolution of tribosphenic teeth. Journal of Vertebrate Paleontology, 25:414–425.

MUSACCHIO, E. 1995. Estratigrafia y micropaleontología del Jurásico y el Cretácico en la comarca del valle medio del río Chubut, Argentina. Actas 6° Congreso de Paleontología y Bioestratigrafía, Trelew: 179–187.

MUSACCHIO, E. A., C. BEROS, AND I. PUJANA. 1990. Microfósiles continentales del Jurásico y el Cretácico en Chubut y su contribución a la bioestratigrafia de la Cuenca del Golfo de San Jorge, Argentina, p. 355–371. *In*: W. Volkheimer (ed.), Bioestratigrafia de los Sistemas Regionales del Jurásico y Cretácico de América del Sur. Volume 2. CRICYT, Mendoza.

PAGE, R., A. ARDOLINO, R. E. DE BARRIO, M. FRANCHI, A. LIZUAIN, S. PAGE, AND D. SILVA NIETO. 1999. Estratigrafía del Jurásico y Cretácico del Macizo de Somun Cura, Provincias de Río Negro y Chubut, p. 460–488. *In*: R. Caminos (ed.), Geología Argentina. Instituto de Geología y Recursos Minerales, Buenos Aires.

PANKHURST, R. J., P. T. LEAT, P. SRUOGA, C. W. RAPELA, M. MARQUEZ, B. C. STOREY, AND T. R. RILEY. 1998. The Chon Aike province of Patagonia and related rocks in West Antarctica: A silicic large igneous province. Journal of Volcanology and Geothermal Research, 81:113–136.

PANKHURST, R. J., R. RILEY, C. M. FANNING, AND S. P. KELLEY. 2000. Episodic silicic volcanism in Patagonia and the Antarctic Peninsula: Chronology of magmatism associated with the break-up of Gondwana. Journal of Petrology, 41:605–625.

RAUHUT, O. W. M. 2005. Osteology and relationships of a new theropod dinosaur from the Middle Jurassic of Patagonia. Palaeontology, 48:87–110.

RAUHUT, O. W. M., T. MARTIN, E. ORTIZ-JAUREGUIZAR, AND P. PUERTA. 2002. A Jurassic mammal from South America. Nature, 416:165–168.

REIG, O.A. 1961. 339 Noticia sobre un nuevo anuro fósil del Jurásico de Santa Cruz (Patagonia). Ameghiniana, 2:73–78.

ROČEK, Z. 2000. Mesozoic Anurans, p. 1295–1331. *In*: H. Heatwole and R. Carroll (eds.), Amphibian Biology. Volume 4. Surrey Beatty & Sons, Chipping Norton, Australia.

ROČEK, Z. 2003. Larval development and evolutionary origin of the anuran skull, p. 1877–1995. *In*: H. Heatwole and M. Davies (eds.), Amphibian Biology. Volume 5. Surrey Beatty & Sons, Chipping Norton, Australia.

ROELANTS, K. AND F. BOSSUYT. 2005. Archaeobatrachian paraphyly and Pangean diversification of crown-group frogs. Systematic Biology, 54:111–126.

SANCHIZ, B. 1998. Handbuch der paleoherpetologie-Encyclopedia of Paleoherpetology, 4. Verlag Dr. Friederich Pfeil, Munich, 276 p.

SAN MAURO, D., M. VENCES, M. ALCOBENDAS, R. ZARDOYA, AND A. MEYER. 2005. Initial diversification of living amphibians predated the breakup of Pangea. American Naturalist, 165:590–599.

SHUBIN, N. AND P. ALBERCH. 1986. A morphogenetic approach on the origin and basic organization of the tetrapod limb. Evolutionary Biology, 20:319–387.

SILVA NIETO, D., N. CABALIERI, F. SALANI, M. MARQUEZ, E. GONZALEZ DIAZ, AND A. COLUCCIA. 2002. Hoja Geológica 4369-27 Cerro Cóndor, Provincia del Chubut. Instituto de Geología y Recursos Minerales Servicio Geológico Minero Argentino, Boletín N 328, Buenos Aires, 68 p.

SILVA NIETO, D., N. CABALIERI, AND F. SALANI. 2003. Stratigraphy of the Cañadón Asfalto Formation (Callovian-Oxfordian), Chubut province, Argentine. Ameghiniana, 40:46R.

STIPANICIC, P. N. AND M. I. R. BONETTI. 1970. Posiciones estratigráficas y edades de las principales floras jurásicas argentinas. II Floras doggerianas y málmicas. Ameghiniana, 7:101–118.

STIPANICIC, P. N. AND O. A. REIG. 1955. Breve noticia sobre el hallazgo de anuros en el denominado "Complejo porfírico de la Patagonia extraaandina," con consideraciones acerca de la composición geológica del mismo. Revista de la Asociación Geológica Argentina, 10:215–233.

STIPANICIC, P. N. AND O. A. REIG. 1957. El "Complejo porfírico de la Patagonia extraandina" y su fauna de anuros. Acta Geológica Lilloana, 1: 185–298.

STIPANICIC, P. N., F. RODRIGO, O. BAULIES, AND C. MARTINEZ. 1968. Las formaciones presenonianas en el denominado Macizo Nordpatagónico y regiones adyacentes. Revista de la Asociación Geológica Argentina, 23(2): 67–98.

TASCH, P. AND W. VOLKHEIMER. 1970. Jurassic conchostracans from Patagonia. University of Kansas, Paleontological Contributions, Paper 50, Kansas.

TRUEB, L. 1985. A summary of osteocranial development in anurans with notes on the sequence of cranial ossification in *Rhinophrynus dorsalis* (Anura: Pipoidea: Rhinophrynidae). South African Journal of Science, 81:181–185.