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A new look at an old frog: the Jurassic *Notobatrachus* Reig from Patagonia

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Abstract. About 100 specimens of the stem-anuran *Notobatrachus degiustoi*, from several localities of the Middle-Late Jurassic La Matilde Formation of southern Patagonia, were examined. This was aimed at clarifying numerous controversial aspects of its anatomy and executing an updated restoration of its skeleton, presented herein. Additionally, the few available immature specimens provide some data on the osteogenesis of this evolutionarily significant taxon. This study also revealed variation in the morphology of the adult sacral region, this variation being more evident among the specimens from one of the localities.

Resumen. UNA NUEVA MIRADA A UNA ANTIGUA RANA: *NOTOBATRACHUS* REIG DEL JURÁSICO DE PATAGONIA. Fueron examinados alrededor de 100 ejemplares del stem-anuro *Notobatrachus degiustoi* provenientes de varias localidades de la Formación La Matilde (Jurásico Medio-Superior) en el extremo sur de Patagonia. Este análisis tuvo como objetivo clarificar numerosos aspectos controvertidos de su anatomía y elaborar una reconstrucción actualizada de su esqueleto, presentada aquí. Además, los pocos especímenes inmaduros disponibles proveyeron datos acerca de la osteogénesis de este taxón evolutivamente significativo. Este estudio reveló también variación en la morfología adulta de la región sacra, siendo esta variación más evidente entre los ejemplares provenientes de una de las localidades.

Key words. *Notobatrachus.* La Matilde Formation. Jurassic. Patagonia. Salientia. Anura.

Palabras clave. *Notobatrachus.* Formación La Matilde. Jurásico. Patagonia. Salientia. Anura.

Introduction

The interpretation of the Early Triassic *Triadobatrachus* from Madagascar as a relative of anurans (Piveteau, 1937; Estes and Reig, 1973; Rage and Roček, 1989) implies that the lineage leading to the crown-group Anura (*sensu* Ford and Cannatella, 1993) must have appeared and begun to diversify at that time. Many character states of *Triadobatrachus* have been debated (Hecht, 1962; Griffiths, 1956, 1963; Estes and Reig, 1973; Roček and Rage, 2000), but most authors agree that the presence of the frontoparietal, an anteriorly elongated ilial shaft, and a reduced number of presacral vertebrae, among other features, are shared-derived characters with Anura and, thus, support the clade Salientia (Trueb and Cloutier, 1991; Milner, 1993, 2000; Ford and Cannatella, 1993). The recent discovery of amphibian remains that bear some derived features of Salientia in the Early Triassic of Poland (Evans and Borsuk-Bialynicka, 1998; Borsuk-Bialynicka and Evans, 2002) has lent additional support to the early origin of the group. However, there is a gap of nearly 45 million years in our knowledge of the history of the salientian clade, because the next earliest recorded salientian, *Prosalirus bitis*, occurs in the Pliensbachian of North America (Shubin and Jenkins, 1995; Jenkins and Shubin, 1998). Moreover, *Prosalirus*, as well as most other described finds of Jurassic age (*e.g.*, Sanchiz, 1998; Roček, 2000), consists of fragmentary, partially articulated specimens or isolated bones. By contrast, the Callovian-Oxfordian *Notobatrachus degiustoi* Reig from southern Patagonia is mostly represented by numerous, unusually well preserved impressions of articulated, or partially articulated, skeletons; thus, it is the best-represented Jurassic salientian taxon known to date.

Notobatrachus was first described and discussed by Reig (in Stipanicic and Reig, 1955, 1957). The original materials, as well as additional specimens, were studied later by Casamiquela (1961), Estes and Reig (1973), and Báez and Basso (1996). The latter two authors also performed a phylogenetic analysis to evaluate the taxonomic placement of *Notobatrachus* and proposed the sister-group relationship of this genus and the crown-group Anura (Báez and Basso, 1996). This conclusion subsequently was discussed by Gao and Wang (2001) in their paper on two new Early Cretaceous salientian taxa from China.

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Despite the exceptional preservation of *Notobatrachus degiustoi*, the available restorations of this species contain several inaccuracies. Many characteristics depicted in the restoration of Reig (in Stipanicic and Reig, 1957) were reinterpreted by later authors (*e.g.*, Estes and Reig, 1973; Báez and Basso, 1996). Also, the recent reconstruction by Roček (2000) is incomplete and depicts juvenile features that are absent in mature individuals. In the present study we examined numerous specimens of *Notobatrachus*, including undescribed material, with the aim at clarifying controversial anatomical features and preparing an updated restoration of this evolutionarily significant taxon. In addition, we comment on its ontogenetic, individual, and geographic variation. Because current phylogenetic hypotheses place *Notobatrachus* either as a stem-anuran (*i.e.* outside the node that includes all living anurans) (Báez and Basso, 1996; Gao and Wang, 2001) or as an extinct relative of the extant *Leiopelma* (Estes and Reig, 1973; Sanchiz, 1998), we have included some preliminary comparisons with stem and basal anurans. However, a parsimony analysis, including *Notobatrachus* and other extinct and living salientians, is ongoing and will be published elsewhere.

Geologic setting and preservation remarks

All the specimens of *Notobatrachus* that we studied were obtained in isolated outcrops of the Middle to Late Jurassic La Matilde Formation in the Deseado Massif region, in Santa Cruz Province, Argentina (figure 1). This volcaniclastic sequence, together with the largely volcanic Chon Aike Formation, compose the Bahia Laura Group, which rests unconformably on Liassic, or older, units and, in turn, is overlain by post-Jurassic strata (De Barrio *et al.*, 1999). The La Matilde Formation was interpreted to represent a low-energy fluvial setting associated with an active volcanic environment, with swamps and waterbodies probably having developed in the adjacent floodplain (Mazzoni *et al.*, 1981; Panza, 1995). In addition to frogs, abundant and taxonomically diverse plant remains, as well as conchostracans, bivalves, and insects have been recovered from different levels of this sequence (Feruglio, 1949; Stipanic and Reig, 1957; Stipanicic and Bonetti, 1970; Baldoni, 1981).

Owing to the lack of reliable age-diagnostic fossils, the age of the La Matilde Formation is largely based on the radiometric dating of volcanics of the Chon-Aike Formation that interdigitates with it (Panza, 1993; De Barrio *et al.*, 1999). Whole-rock K-Ar dates ranging from 161 ± 10 to 138 ± 10 Ma were obtained from samples at Gran Bajo de San Julián (Spalletti *et al.*, 1982). Rb-Sr whole-rock analyses were also carried out on several lavas and associated ignimbrites from the eastern outcrops of the Chon Aike Formation, resulting in an isochron of 168.2 Ma (Pankhurst *et al.*, 1993). These, and other isotopic dates (De Barrio *et al.*, 1999), indicate a Bathonian-Oxfordian age, with an exceptional value in the earliest Cretaceous, according to the time scale of Gradstein *et al.* (1995). These results suggest that the magmatic event that originated the volcanics of the Chon-Aike Formation persisted at least throughout the late Middle and early Late Jurassic. In this regard, it was proposed that this formation is a diachronous unit that becomes older as one progresses northward (Pankhurst *et al.*, 1993). However, the stratigraphic position of the frog-bearing beds with respect to the dated volcanic rocks remains ambiguous.

All the frog specimens from the eastern area of exposures of the La Matilde Formation (Estancia La Matilde, Estancia El Malacara and Estancia La Trabajosa; figure 1) that we examined occur on fine-grained, light-gray, tuffaceous sandstones deposited in alternating thin layers of light and dark color. The light-colored layers are 2-4 mm thick and are composed of yellowish-brown, fine-grained, silty sandstones. These layers alternate with darker-colored shales that make up layers up to 2 mm thick. The contact between sand and shale layers is rather sharp. No features of subaereal exposure were observed. The frog remains, preserved as impressions, show a high degree of articulation and, in many cas-

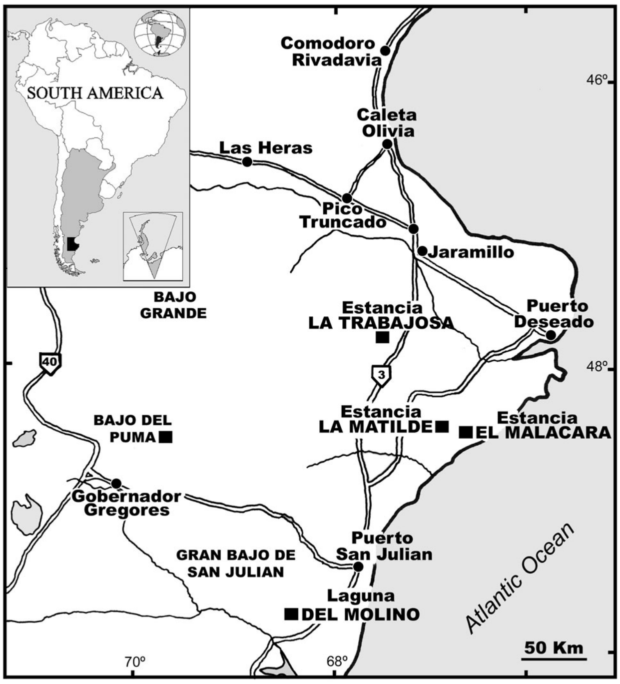

Figure 1. Map of southern Patagonia showing location of frog fossil sites of the La Matilde Formation, indicated by black squares / *Mapa del sur de Patagonia mostrando la ubicación de las localidades fosilíferas con anuros de la Formación La Matilde, indicadas con cuadrados negros.*

es, include bones that are easily detached from the skeleton, such as phalanges of fore- and hind limbs. In disarticulated specimens, the degree of dispersion is low; the different elements are found relatively near one another. Nevertheless, many bones are crushed and show evidence of dorsoventral flattening and compression. This might have led to some distortion of the original morphology.

By contrast, the anuran remains from Laguna del Molino (in the most southern fringe of the La Matilde Formation outcrops) occur in dark gray, silicified tuffs. There is an alternation between 0.5-mm-thick, black shale layers and 3-mm-thick layers of fine- to medium-grained sandstones that are lighter in color. These sandstone layers have intraclasts made up of the underlying shales. A conspicuous concentration of conchostracan and bivalve shells (Feruglio, 1949; Gallego, 1994) occurs in the sandy layers together with partially articulated and isolated anuran bones. The bones, preserved as impressions, lack any signs of abrasion or of strong compression. Although mostly disarticulated, bones from the same structural region frequently can be found relatively near each other. In one case, bones of two individuals are intermingled and oriented at different angles.

The occurrence of interlayered bedding in both types of frog-bearing deposits indicates changes in the transport or production of sediments probably owing to seasonal changes. This lamination also suggests that these beds formed in a low-energy, quiet-water setting with little or no infauna. However, at Laguna del Molino the sandy layer of the couplet is comparatively coarse-grained and demonstrates the operation of tractive forces, representing a depositional event of higher energy. These coarser layers may correspond to episodic underflows that transported the fossils from the more marginal zone of the waterbody. This might explain the abundance of conchostracans in these layers, because these typically benthic organisms live in shallow, ephemeral freshwater environments (Vannier *et al.*, 2003). Moreover, extant conchostracans exhibit reproductive adaptations to enviromental stress and ephemeral conditions. Their resting eggs are deposited in mud and hatch synchronically by a sudden imput of water, resulting in characteristic low diversity, high density assemblages (Vannier *et al.*, 2003). In addition, the darker colors of the sediments in this locality relative to those of the other frog-bearing sites might reflect a higher relative proportion of organic matter and anoxic or near-anoxic conditions. The high degree of articulation of the specimens from the northern outcrops suggests either rapid burial and/or anoxic conditions that prevented the action of scavengers.

The dissimilar modes in which the frog remains from the two fossiliferous areas are preserved reflect different taphonomic histories and are persuasive evidence of the presence of disparate depositional environments at the two outcrop areas, located about 200 km apart.

Material

We examined about 100 specimens housed in several institutions (Appendix I). Undescribed anuran remains have been reported from the most western outcrops of the La Matilde Formation, at Estancia El Puma (De Giusto *et al.*, 1980), but we were unable to locate these specimens.

Because specimens of *Notobatrachus* are preserved as impressions lacking any evidence of soft structures, we prepared latex casts of as many specimens as possible. In a few cases, pieces of bone partially filling the impressions were eliminated by mechanical abrasion before preparing the cast. Casts were made with silicones RTV-581 and RTV-585 (Contident, Buenos Aires).

Most of these specimens are postmetamorphic individuals, snout-vent length between 90 mm and 150 mm. The youngest stage of development in our sample is represented by CPBA-V-14003, which consists of disarticulated cranial and postcranial elements of a single individual. This specimen may correspond either to a late metamorphosing tadpole or an early postmetamorphic individual. The skull is weakly ossified in contrast to the postcranial skeleton; thus, several cranial elements, such as pterygoids and squamosals, if present, may have been still too poorly mineralized to be preserved. The parasphenoid and paired frontoparietals, nasals, and maxillae are already present; the axial skeleton is represented by several vertebrae bearing paired neural arches with well-developed transverse processes and no indication of ribs. All the components of the pectoral girdle are ossified, as are the long bones of fore- and hind limbs, although it is evident that both ends of these latter elements were still cartilaginous. Specimen MLP 55-VI-1-4 (formerly 55-VI-1-3) represents a slightly more advanced stage of development. It has several juvenile features, such as narrow, anteriorly acuminate frontoparietals that are partially fused to each other, weakly ossified otic capsules, an anteriorly positioned jaw articulation, unfused neural arches, and overall small size.

The relative proportions of the different structural parts of the restored skeleton of *Notobatrachus degiustoi*, as depicted in figures 2 and 3, are based on articulated specimens (*e.g.*, the holotype MACN 17720, figure 4; MACN 17721; MLP 54-XI-18). These specimens were collected at Cañadón de La Matilde (or Estancia La Matilde, 48º 25′ S 66º 45′ O) from a single fossiliferous level and correspond to adult, middle-

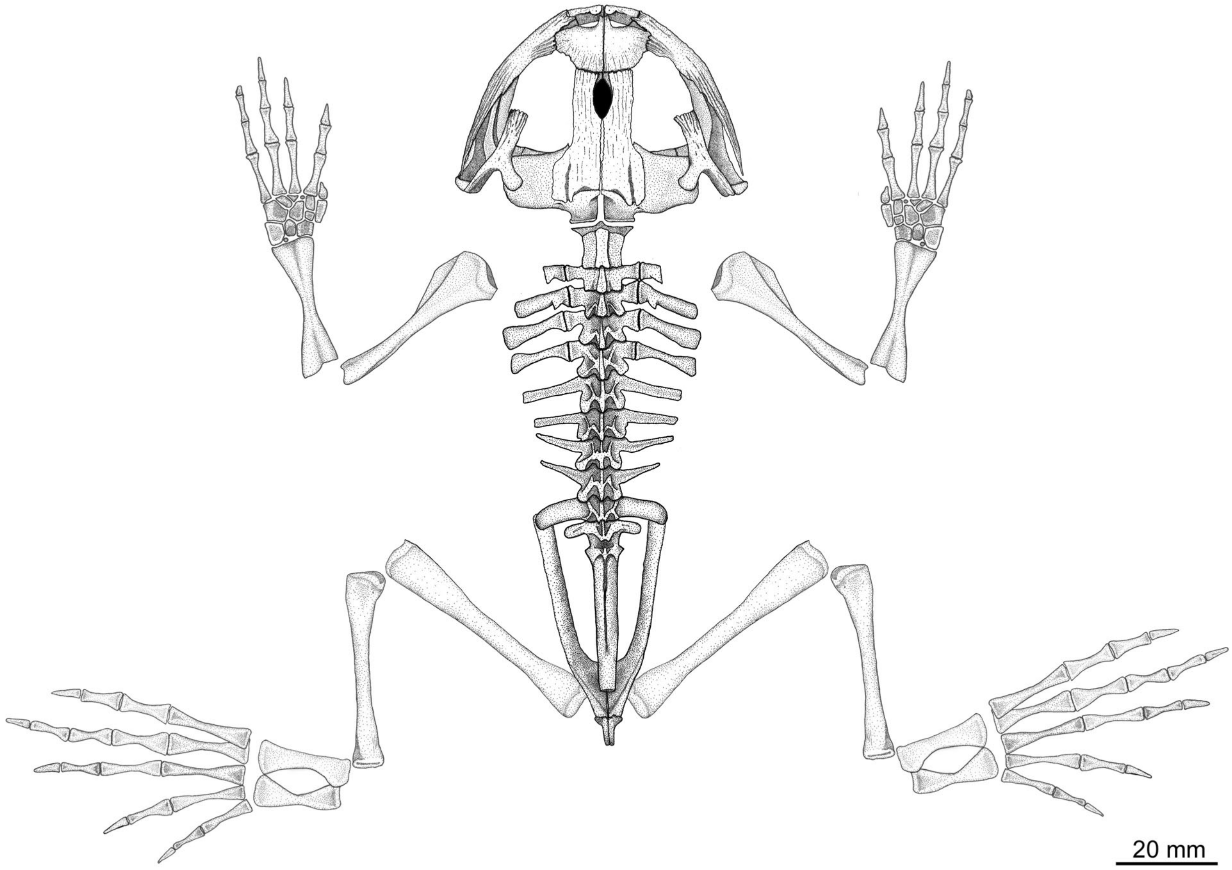

Figure 2. Restoration of *Notobatrachus degiustoi* Reig in dorsal aspect. Pectoral girdle and hyobranchial skeleton not shown / *Reconstrucción de* Notobatrachus degiustoi *Reig en vista dorsal. Cintura pectoral y esqueleto hiobranquial no representados.*

sized (129-117 mm of snout-vent length) individuals. Drawings were made with the use of a camera lucida attached to a Zeiss Stemi SV 11 binocular microscope. The restoration is a composite based on several specimens from the type locality. Comments on the skeletal anatomy of *Notobatrachus* refer to specimens examined from all localities, unless stated otherwise.

Comments on selected aspects of the skeleton of *Notobatrachus* and its ontogenetic, individual, and geographic variation

The skull is depressed and relatively wider than long. Most dermal cranial bones are ornamented with patches of well-defined ridges and grooves. In addition, in the largest individuals, the surfaces of these bones bear irregular, low rugosities. Ontogenetic variation in the shape of the skull is evident among the specimens of *Notobatrachus* examined. In juveniles (*e.g.*, MLP 55-6-1-4; CPBA-V 14024, MPEF-PV 1254), the skull is relatively longer than wide and the snout is slightly pointed anteriorly, whereas in larger adults the snout is broadly rounded.

The premaxilla bears a relatively wide *pars palatina*. Báez and Basso (1996) described a premaxillary palatine process based on the impression of a ventrally exposed premaxilla (CPBA-V 14001a). However, it is noteworthy that in other specimens the premaxillae clearly lack these processes (*e.g.*, CTES-Pz 5739B; figure 5.B). In most impressions of the ventral aspect of the skull, the premaxilla is obscured by the articulated lower jaw, and thus it is difficult to estimate the degree of variation of this condition. The *pars facialis* of each premaxilla bears a medial alary process, which is narrowly separated from the contralateral component. According to Estes and Reig (1973) and Báez and Basso (1996), the alary processes are in contact with the rostral processes of the nasals. Actually, the most anterior portion of the skull is frequently disarticulated and the alary processes usually are poorly exposed or broken. Estes and Reig (1973: 57) commented that the alary processes (= nasal or ascending processes *auctorum*) are well preserved in an immature specimen housed in the La Plata Museum. We identified this specimen as MLP 55-VI-1-4 (figure 5.C) and corroborated the medial position of the alary processes,

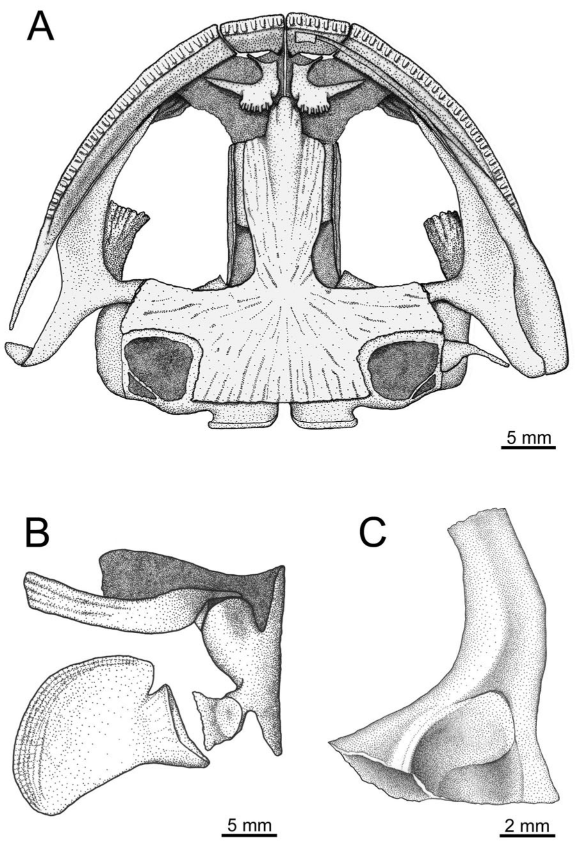

Figure 3. Restoration of *Notobatrachus degiustoi* Reig. **A,** skull in ventral aspect; **B,** pectoral girdle in ventral view (cartilages not shown), note that the bones are shown in their presumable natural position; **C,** ilium in mediolateral aspect / *Reconstrucción de* Notobatrachus degiustoi *Reig.* ***A,*** *cráneo en vista ventral (cartílagos omitidos), nótese que los huesos se muestran en su presunta posición natural;* ***B,*** *cintura pectoral en vista ventral;* ***C,*** *ilión en vista mediolateral.*

which may have barely contacted the rostral processes of the nasal bones.

The posterior terminus of the long maxilla is located near the bony *pars articularis* of the palatoquadrate. As stated in previous studies, the quadratojugal is absent. The maxillae are distinctly short in Roček's (2000) restoration probably because his restoration is based on a cast of a recently metamorphosed individual (MLP 55-VI-1-4 discussed above). In this specimen the *pars articularis* is located at the level of the posterior margin of the orbit, more anterior in position than it is in adults. Isolated maxillae from the type locality of *N. degiustoi*, as well as from Laguna del Molino, show that the *pars facialis* formed an anteromedial process that surrounded the lateral margin of the premaxilary *pars facialis* when these bones were in articulation (figure 5.A).

The adult nasals are extensive, winglike bones that are in contact with each other throughout their medial margins (figure 5.A). Laterally, each nasal is in broad contact with the *pars facialis* of the maxilla from the preorbital process of the latter bone forward, as the nasal lacks a distinct slender maxillary process. Posteriorly, the nasals articulate with the frontoparietals. In the holotype, the nasals seem to overlap the frontoparietals broadly; this condition was figured in the restoration by Estes and Reig (1973), but we could not corroborate this extensive overlap of nasals and frontoparietals in any other specimen that we examined. Moreover, in the holotype the frontoparietals, as well as the parasphenoid, have been shifted forward. An oval excavated area is visible at the anterior part of the ventral surface of each nasal (figure 6.A). Distinct convexities on the anterodorsal surface of the nasals correspond to these concave areas (figure 5.A), which might have partially accommodated the olfactory capsules as suggested by Estes and Reig (1973). Hence, if these excavated areas on the anteroventral surfaces of the nasals mark the position of the tapering *processus prenasalis medius* and the *cartilage obliqua* of the endocraniun of *Notabatrachus*, the olfactory capsules might have been located as far laterally as in the most basal living anurans *Ascaphus* and *Leiopelma* and, consequently, the *septum nasi* was as wide as in these two extant genera. The septum was cartilaginous as those of *Ascaphus* and *Leiopelma*, but unlike that of *Prosalirus*. The far anterior extent of the nasals indicates that the *external naris* opened more anteriorly than in *Leiopelma*. In young, postmetamorphic *Notobatrachus*, the nasals articulate with each other only along the central portions of their medial margins and are well separated from the frontoparietals. The shape of the latter bones also varies with age; those of young individuals have narrower anterior ends than the frontoparietals of larger frogs (figure 5.C).

The sphenethmoidal ossification remains bilaterally paired throughout life in most individuals of *Notobatrachus*, except a few large, hypertrophied individuals in which the halves are synostotically fused anteroventrally (*e.g.*, PVL 2194) as described by Estes and Reig (1973) and Báez and Basso (1996). Roček (2000) suggested that the adult, paired condition resulted from "*post-mortem* breakage and subsequent shift of both fragments". However, the paired condition is evident in several specimens of *Notobatrachus* (*e.g.*, MACN 17720, CTES-Pz 5739a) in which the smoothly rounded midventral margins of bilateral sphenethmoidal ossifications clearly indicate that the bones are not broken (figure 5.A). It is also noteworthy that a paired sphenethmoid is present in *Ascaphus* (figure 7.A-B) and *Leiopelma* (Jurgens, 1971; van Eeden, 1951), although an unpaired sphenethmoid occurs in *Triadobatrachus* (Rage and Roček, 1989) and *Prosalirus* (Jenkins and Shubin, 1998). Rocek (2000) probably based his assertion that a sin-

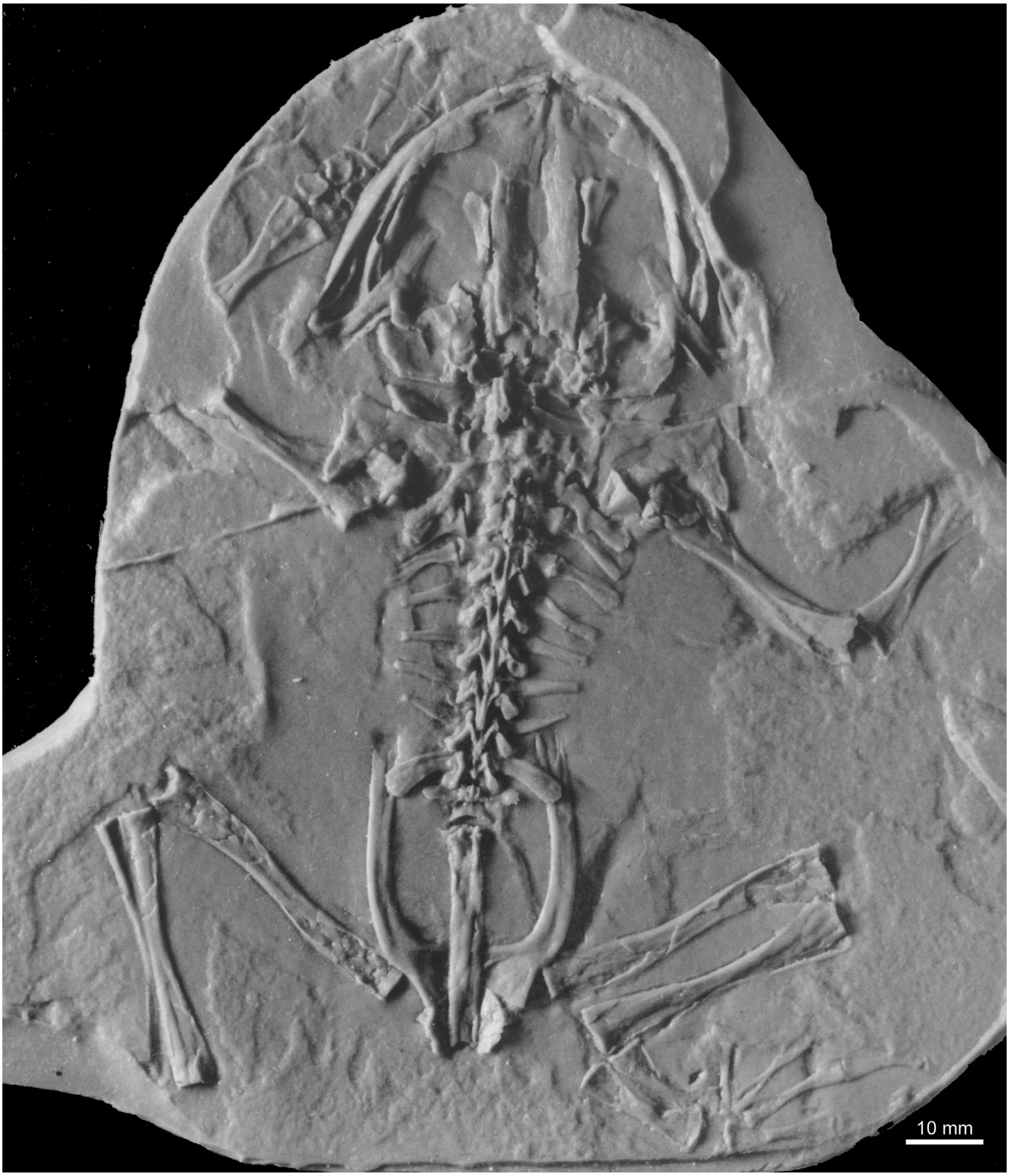

Figure 4. ***Notobatrachus degiustoi***. Cast of dorsal impression (MACN 17720, holotype) / *Molde de impresión dorsal (MACN 17720, holotipo).*

gle sphenethmoid is present in *Notobatrachus* on a cast of an unidentified specimen (*op. cit.*, figure 5) in which a single bone, interpreted by this author as the large sphenethmoid, is visible through the frontoparietal fontanelle. This specimen seems to correspond to MLP 55-VI-1-4 (figure 5.C) figured previously as an immature example (Roček, 1988). In this specimen, the element identified as the dorsally exposed sphenethmoid (Roček, 2000) extends as an uninterrupted sheet of bone from the posterior part of the nasals to the posterior terminus of the space between the frontoparietals, at the level of the posterior margin of the orbit, where it disappears beneath the otic capsules. More likely, this bone corresponds to the cultriform process of the parasphenoid exposed in dorsal aspect owing to the still cartilaginous, or poorly ossified, condition of the sphenethmoid (figure 5.C). In this regard, it should be noted that the sphenethmoid starts to ossify late in development or after completion of metamorphosis in most anurans for which the osteogenesis of this element is known (Trueb, 1985; Trueb *et al.*, 2000).

In all specimens of *Notobatrachus* examined, the zygomatic ramus of each squamosal is directed anteromedially and is usually visible on each side of the braincase in specimens exposed in ventral view (figures 3.A and 4). *Post-mortem* deformation might have displaced the squamosals such that the zygomatic ramus no longer articulated with the maxilla; however, we noted that even in isolated squamosals, the zygomatic ramus has distinct medial orientation that would have prevented contact with the maxilla.

The vomers are anterior palatal bones that are narrowly separated from one another medially when in their natural position (figure 5.B). These bones resemble the vomers of *Leiopelma* (*e.g.*, *Leiopelma*

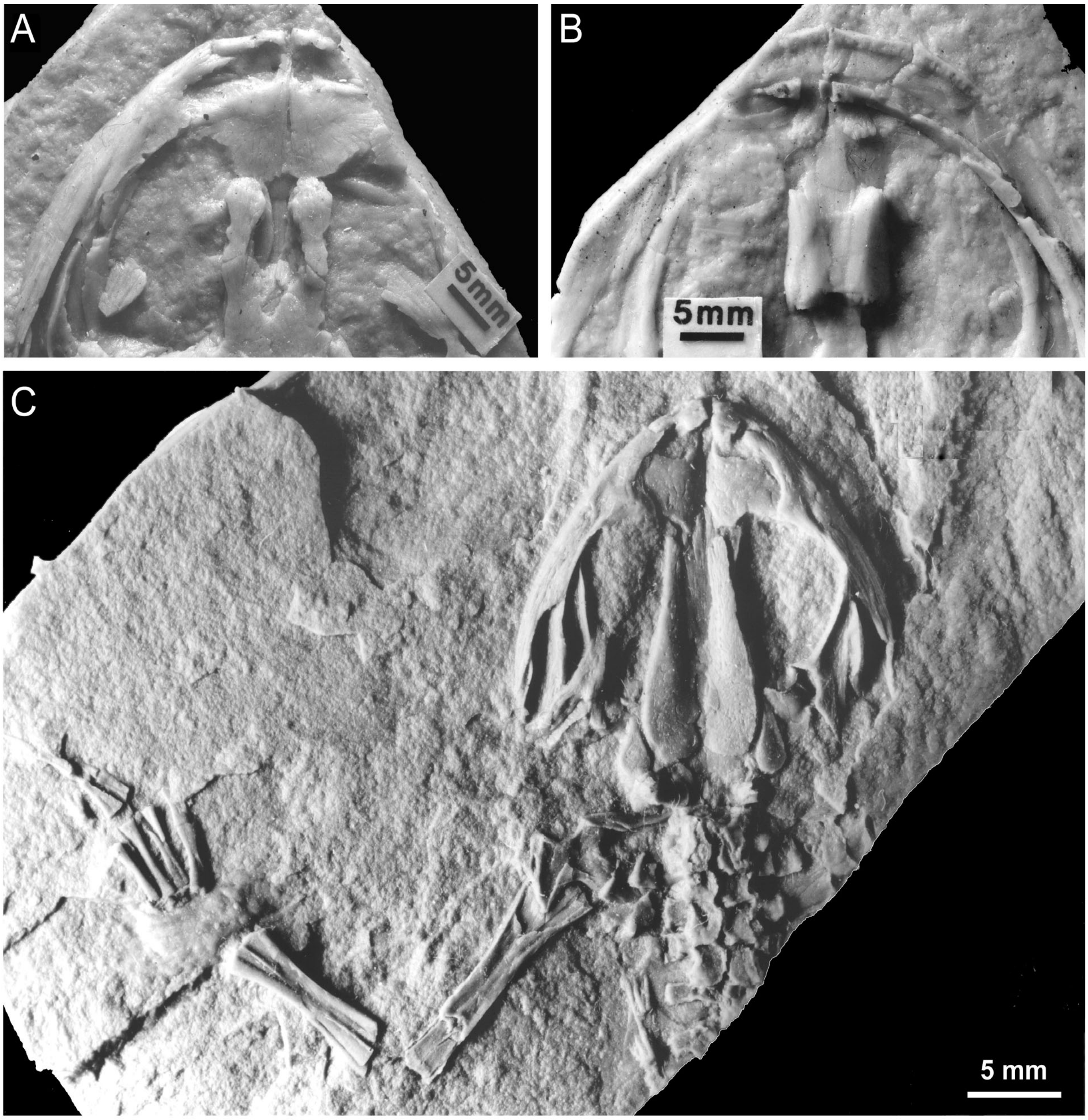

Figure 5. ***Notobatrachus degiustoi.*** **A,** anterior portion of skull in dorsal aspect (cast of CTES-Pz 5739B); **B,** anterior portion of skull in ventral aspect (cast of CTES-Pz 5739A); **C,** dorsal aspect of juvenile (cast of MLP 55-VI-1-4) / ***A,*** *parte anterior del cráneo en vista dorsal (molde de CTES-Pz 5739B);* ***B,*** *parte anterior del cráneo en vista ventral (molde de CTES-Pz 5739A);* ***C,*** *vista dorsal de juvenil (molde de MLP 55-VI-1-4).*

hochstetteri, *L. archeyi*, A.M.B. pers. obs.) in having distinct dentigerous processes, and long, edentulous postchoanal processes. However, the vomers of *Notobatrachus* differ from those of *Leiopelma*, as well as from those of *Ascaphus*, in being more anterior and medial in position. Also, the angle determined by the corpus and the postchoanal process is wider in *Notobatrachus* than in *Leiopelma*. Because the vomer usually forms the medial margin of the *fenestra exochoanalis* (*sensu* Roček, 1981), the position of this bone in *Notobatrachus* suggests that the choana was more anteriorly located in this frog than in *Ascaphus* and *Leiopelma*.

The cultriform process of the parasphenoid is unusual in having a trifurcate anterior end (Estes and Reig, 1973; Báez and Basso, 1996). The anterior portion of this process is narrow and reaches the level of the vomers. At the level of the anterior margin of the bony sphenethmoids, the cultriform process is expanded laterally to invest the ventral surface of these ossifications and form the floor of the braincase (figure 3.A). The width of the cultriform process diminishes posteriorly up to its union with the extensive corpus. The parasphenoid corpus is configured into anterolateral alae and a broad, truncate posteromedial plate. The posterior margins of the alae and the lateral margins of the plate parallel, and are narrowly separated from, the anterior and medial margins of the large openings in the floor of the otic capsules. Owing to postmortem crushing, the cultriform process seems to have three distinct parts in many specimens. In the youngest specimen available to us (CPBA-V- 14003), the parasphenoid is well ossified; the anteroventral surface of the cultriform process bears some longitudinal ridges and grooves as in more mature individuals, but the rectangular corpus lacks the posterolateral indentations characteristic of the latter (figure 3.A).

The premaxillary and maxillary teeth of *Notobatrachus* were described as pedicellate (Estes and Reig, 1973; Báez and Basso, 1996). Teeth are present in MLP 62-XII-11-4, MPEF 1264, and CPBA-V 14001b; in each of these specimens, the teeth are small, simple cones lacking the joint between pedicle and crown. Similar teeth occur in some living anurans (*e.g.*, *Xenopus*, Shaw, 1979; *Ascaphus*, Sanchiz pers. com. 2003), as well as in some extinct taxa, such as *Palaeobatrachus* (Vergnaud-Grazzini and Hoffstetter, 1972). The available latex molds do not preserve the tips of the teeth; therefore, it is difficult to ascertain if one or more cusps were present. However, a bicuspid maxillary tooth is preserved in one specimen from Laguna del Molino (CTES-Pz 7311). Usually, teeth, or their remains, are present in alternate tooth positions, thereby suggesting a slow replacement cycle.

The prootics and exoccipitals remain unfused to one another in juveniles (MLP 55-VI-1-4) and a few

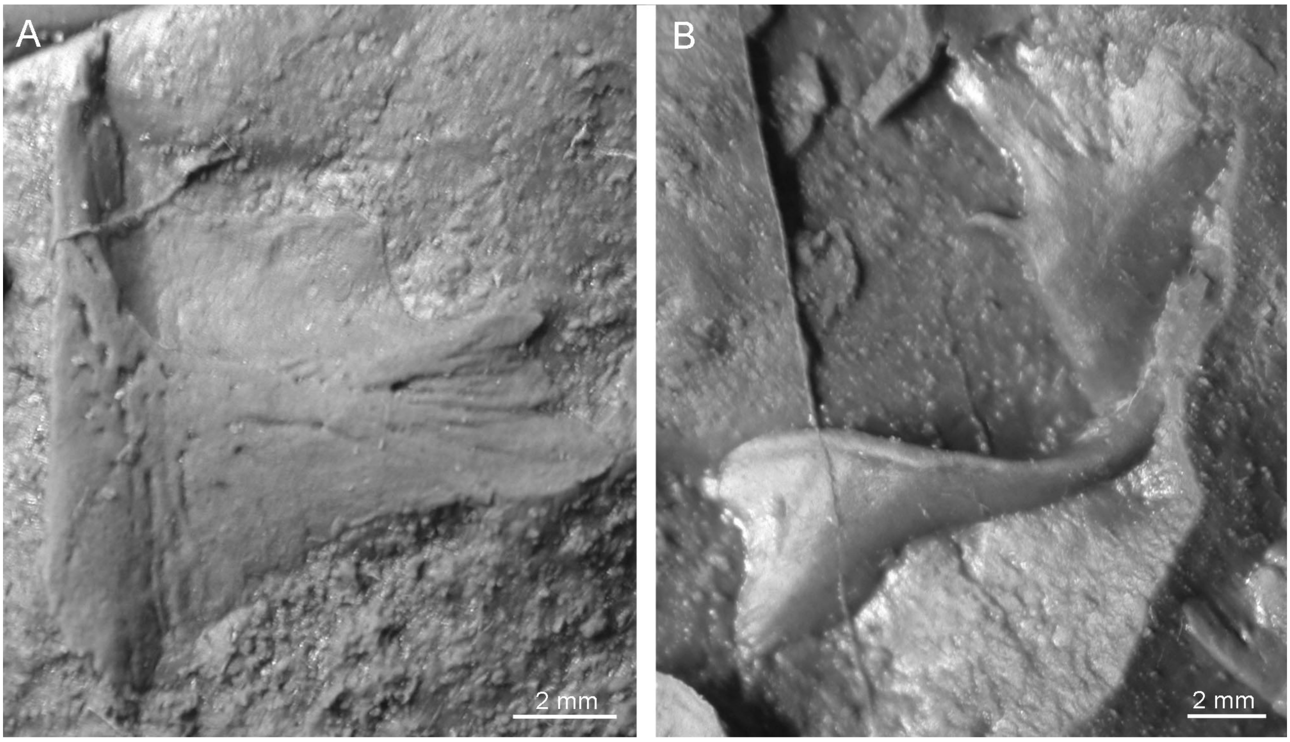

Figure 6. ***Notobatrachus*** sp. **A,** ventral aspect of nasal (cast of CTES-Pz 7312); **B,** right clavicle and thyrohyal (cast of CTEs-Pz 7311) / ***A,*** *aspecto ventral del nasal (molde de CTES-Pz 7312);* ***B,*** *clavícula y tirohial derechos (molde de CTES-Pz 7311).*

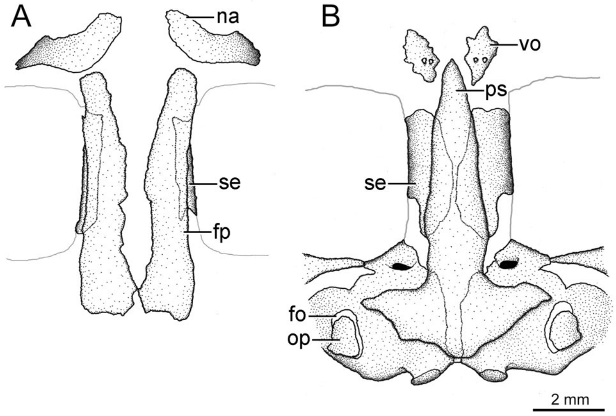

Figure 7. ***Ascaphus truei*** Stejneger (TNHC-53300, s-v length 35.11 mm; cleared and stained), partial view of skull. **A,** dorsal aspect; **B,** ventral aspect. Abbreviations: fo, fenestra ovalis; fp, frontoparietal; na, nasal; op, operculum; ps, parasphenoid; se, sphenethmoid; vo, vomer / *longitud corporal: 35.11 mm; diafanizado y teñido).* ***A,*** *vista dorsal;* ***B,*** *vista ventral. Abreviaturas: fo, fenestra ovalis; fp, frontoparietal; na, nasal; op, operculum; ps, paraesfenoides; se, esfenetmoides; vo, vomer.*

adult individuals (*e.g.* MACN 17721) in which a suture between these bones is visible. In most adult specimens, these elements seem to be fused, contrary to the restoration by Estes and Reig (1973, figures 1-4 and 1-5) and the opinion of Báez and Basso (1996). The prootics form most of the conspicuous otic capsules. The capsular roof is relatively flat, lacking well-developed epiotic eminences; it extends laterally to form the *crista parotica*, the lateral margin of which probably remained cartilaginous. A large, quadrangular opening with well-defined margins perforates the floor of each capsule. This opening might have been partially closed with cartilage and included the *fenestra ovalis* laterally. The latter foramen was closed by the footplate of the stapes, which is an approximately oval area of unfinished bone. Distally, the stapes bears a long, thin stylus. In contrast to *Prosalirus*, the stylus is devoid of processes and strongly curved.

The atlantal cotyles of *Notobatrachus* are clearly separated from each other by a pointed process that may bear a notochordal fossa in some specimens (*e.g.*, MACN 17121b). Although the cotyles extend medially onto the base of this process, they are not confluent and, therefore, do not form a single articular surface (*contra* Gao and Wang, 2001). The corresponding occipital condyles are distinctly separated from one another, thus, a portion of cartilaginous *solum synoticum* may have been exposed.

The posteromedial processes of the hyoid skeleton are stout bones preserved in many specimens either in their natural position (*e.g.*, MACN 17720-17721, MLP 62-XII-11-4) or isolated (*e.g.*, CTES-Pz 7311). Their anterior ends are widely expanded, whereas their narrow posterior portions frequently bear either a tubercle or a spine laterally (figure 6.B).

The sacral diapophyses are narrow in all the specimens from the type locality, as well as those from Estancia La Trabajosa and Estancia El Malacara (figure 1). However, there is some variation in the morphology of this anatomical region. Some specimens have diapophyses that are relatively flat and slightly deflected posteriorly (*e.g.*, MACN 18658, CTES-PZ 5740), but other specimens from the same fossiliferous bed (*e.g.* MACN 17721, PVL 2196) have sacral diapophyses perpendicular to the body midline. In addition, the sacral neural arches may have the same morphology as those of the presacral vertebrae, including the presence of postzygapophyses (MACN 17720, holotype), or they may be reduced, lacking these articulating structures (MACN 17721). Unlike the specimens from the northern fossiliferous sites, the specimens from Laguna del Molino show a marked variation in the degree of expansion of the sacral diapophyses. In PVL 250 (figures 8-9.A) the diapophyses are flat and distally expanded; this expansion is asymmetrical as it is distinctly greater in the posterior half than in the anterior half of each diapophysis. In addition, the transverse processes of the last two presacrals, as well as those of the discrete postsacral, are distinctly expanded. Another specimen from this fossiliferous bed, MACN 19178, has slightly expanded sacral diapophyses that are posteriorly directed (figure 9B), whereas other specimens (CTES-Pz 5754-5755) have narrow, posteriorly directed diapophyses similar to those of some specimens from the type locality (figure 9.C).

A discrete postsacral vertebra bearing short, robust transverse processes is occasionally present (*e.g.*, MACN 17720, MPEF-PV 1261, PVL 250; Báez and Basso, 1996; figure15). In other specimens, the anterior portion of the urostyle seems to be ventrally fused to this postsacral vertebra (*e.g.*, MACN 18658). The reduced neural arches of the succeeding vertebra, which may also bear extremely short transverse processes, are usually visible at the anterior end of the urostyle (Báez and Basso, 1996). Thus, the absence of transverse processes on the urostyle in *Notobatrachus* mentioned by Jones *et al.* (2003) is a misinterpretation. A medial dorsal keel occurs along the most anterior portion of the urostyle but more posteriorly a sulcus is present instead, as described by Estes and Reig (1973).

The overall shape of the scapula changes ontogenetically. The youngest stage represented in our sample has a nearly quadrangular scapula, the suprascapular margin being as long as the mediolateral width. In addition, the *partes acromialis* and

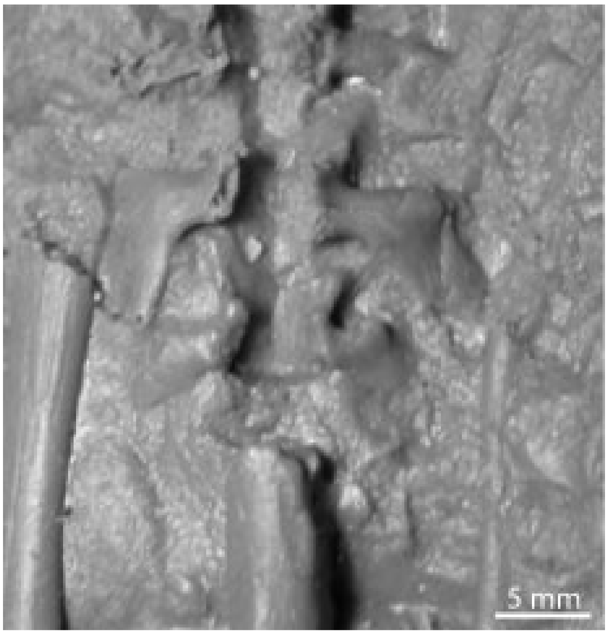

Figure 8. ***Notobatrachus*** sp. PVL 250. Note expanded sacral diapophyses and transverse processes of posterior vertebrae / *Note las diapófisis sacras y procesos transversos de las vértebras posteriores expandidos.*

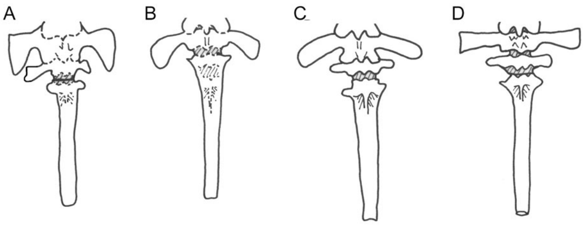

Figure 9. Schematic drawing of the variation in the sacrum and urostyle in *Notobatrachus*. **A,** PVL 250; **B,** MACN 19178; **C,** MACN 17720; D, MACN 17721. Not to same scale / *Dibujo esquemático de la variación del sacro y urostilo en* Notobatrachus. ***A,*** *PVL 250;* ***B,*** *MACN 19178;* ***C,*** *MACN 17720; D, MACN 17721. A diferentes escalas.*

glenoidalis, separated by a distinct notch, are equally developed (figure 10.A). Subsequently, the shape of the scapula changes; in slightly larger, and presumably older, individuals the suprascapular margin extends posteriorly beyond the level of the glenoid and the *pars acromialis* is expanded anteromedially (figure 10.B). This asymmetrical development of the *partes acromialis* and *glenoidalis* is more pronounced in mature individuals. Among the latter, some variation of the shape of the leading edge of the scapula is evident, this margin usually being more deeply concave in the specimens from the type locality than in those from Laguna del Molino (figure 10.C-D). In addition, the cleft that separates the *partes acromialis* and *glenoidalis* may disappear in large individuals (*e.g.*, MACN 17721, PVL 2196). As in *Leiopelma* and the Pliensbachian *Prosalirus* (Jenkins and Shubin, 1998), along with many pipoid frogs (*e.g.*, Báez, 1981, Henrici, 1991; Trueb, 1999), the cleft that separates the *partes acromialis* and *glenoidalis* is exposed in a ventrolateral view of the scapula, a condition considered plesiomorphic for anurans (Borsuk-Bialinicka and Evans, 2002). In some specimens the ventral surface of the *pars acromialis* bears a rounded ridge along its posterior margin, however, this ridge does not overhang into the glenoid cavity (*contra* Borsuk-Bialinicka and Evans, 2002: figure 9.D). The coracoid is plate-like, except for the short lateral portion that bears an elongated articular facet; this facet, set at a right angle with respect to the coracoid blade, formed the medial (ventral) bony wall of the glenoid cavity. The clavicle is unusual in being distinctly dorsoventrally curved (*e.g.*, MLP 89-XI-27-16 and 17; UNNE 5739B; figure 6.B) and in having a blunt, slightly expanded medial end, the ventral surface of which may bear a few ridges. The lateral end is robust and has a broad contact with the *pars acromialis* of the scapula. The great dorsoventral curvature of the clavicle is unlike that of all living anurans examined for this trait. This curvature may indicate that the glenoid cavity was more laterally oriented than in living anurans, a condition that is presumably plesiomorphic for this group. The dermal cleithrum invested part of the dorsal surface of the suprascapular cartilage and most of its anterior margin; therefore, it is more extensive than in *Triadobatrachus* (Rage and Roček, 1989), *Ascaphus*, and *Leiopelma* (De Vos, 1938).

Although the humerus and radioulna are robust bones, the distal end of the former, as well as the proximal end of the latter, are poorly ossified even in the largest specimens examined. The centrally placed, small humeral ball remained cartilaginous throughout life and the *fossa cubitalis* anteriorly adjacent to it is absent in all specimens that we examined.

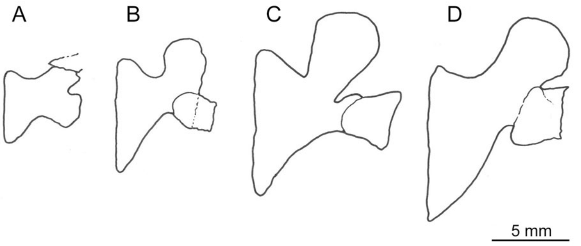

Figure 10. Schematic drawing of the variation of the scapular morphology in *Notobatrachus*. **A,** MLP 55-VI-1-4; **B,** RH; unnumbered specimen; **C,** MACN 17720; D, MLP 89-XI-27-16 / *Dibujo esquemático de la variación de la morfología escapular en* Notobatrachus. ***A,*** *MLP 55-VI-1-4;* ***B,*** *RH, ejemplar sin número;* ***C,*** *MACN 17720; D, MLP 89-XI-27-16.*

Similarly, the radioulna lacks a well-developed, ossified olecranon process.

Previous restorations of the pelvic girdle of *Notobatrachus degiustoi* (Estes and Reig, 1973; Roček, 2000) did not take into account the disarticulation of the halves of the pelvis (including ilia and ischia) and their rotation around their longitudinal axes in opposite directions. Thus, in dorsal impressions of the pelvic girdle the internal *(i.e.,* medial) aspects of both halves of the girdle are visible (figure 4), whereas in the ventral impressions the acetabular aspects are exposed. This fact accounts for the more rounded overall aspect of the pelvis in the restorations made by previous authors in contrast with the one presented herein (figure 2). The ilia lack dorsal crests and a dorsal tubercle is only weakly developed in a few individuals (*e.g.*, MACN 17722, CTES-Pz 7313, MLP 89-XI-27-8). This absence of a well-developed dorsal tubercle is as in *Prosalirus*, *Ascaphus*, and *Leiopelma*, but contrasts with the presence of a protuberant dorsal tubercle in the Triassic salientians *Tridobatrachus* (Rage and Roček, 1989) and *Czatkobatrachus* (Evans and Borsuk-Bialynicka, 1998). There is a striking resemblance between the acetabula of *Notobatrachus* (figure 3.C) and *Triadobatrachus* (Roček and Rage, 2000; figure 7.A) in the presence of a well-demarcated rough area of elongate shape, distinctly separated from a posterodorsal triangular region. In addition, in both taxa the acetabular fossa is shallow and its ventral margin extends along a laterally projecting portion of the ilial corpus, a crest or acetabular rim (*sensu* Evans and Milner, 1993) being absent. However, in *Notobatrachus*, the acetabular margins are better defined than in *Triadobatrachus* and the triangular posterodorsal region of the fossa is distinctly depressed unlike that of the latter genus.

Significance of the ontogenetic variation

All the immature specimens of *Notobatrachus degiustoi* available to us were collected in the northern frog-bearing outcrops of the La Matilde Formation; despite their rarity, they provide some information on the skeletal development of this species. However, few generalizations are possible because the ossification sequence may vary intraspecifically (Hanken and Hall, 1984) and, thus, examination of a more specimens would have been desirable. Also, pertinent comparative data are lacking, particularly with regard of the osteogenesis of postcranial bones. The weak ossification and small size of the paired sphenethmoid in the juvenile CPBA-V- 14024 and the absence of these endochondral bones in the younger specimens CPBA-V- 14003 and MLP 55-VI-1-4 suggest that the ossfication of the sphenethmoid occurred after completion of metamorphosis in *Notobatrachus*. The post metamorphic appearance of the bony sphenethmoid contrasts with its earlier formation near the end of metamorphosis in the living basal anuran *Ascaphus truei* (Yeh, 2001). In the latter species (Yeh, 2001), the ossification of the nasals starts after that of the prootics and sphenethmoid, thus being among the last cranial bones to appear. The presence of well-developed nasals, together with weakly ossified prootics and a presumably still cartilaginous sphenethmoid in MLP 55-VI-1-4, indicates that the ontogenetic trajectory of *N. degiustoi* was different from that of *Ascaphus* and resembled those of other archeobatrachians, such as *Bombina* (Hanken and Hall, 1984) and *Discoglossus* (Pugener and Maglia, 1997). The well-developed, edentulous maxilla in CPBA-V- 14003 suggests that teeth did not erupt until the end of metamorphosis as in most anurans (*e.g.*, Pugener and Maglia, 1997; Yeh, 2001).

In CPBA-V- 14003, the youngest specimen available to us, six postatlantal, anterior presacrals are preserved; all these vertebrae bear well ossified, large, blunt transverse processes, the distal ends of which probably were cartilaginous. The robustness of these processes suggests that they formed when the neural arches were still cartilaginous and probably ossified once they were well developed, following the generalized pattern described for the anterior presacrals (V2-V4) of discoglossids and other living frogs (Blanco and Sanchiz, 2000). It is also evident that ribs ossified after the transverse processes did. There is no indication of ribs in CPBA-V-14003, but small ribs occur distal to the transverse processes of V2, V3, and V4 in the next oldest specimen MLP 55-VI-1-4. In the latter specimen there is also evidence that ossification started in the cartilage adjacent to the transverse processes of V5 and V6. It is also interesting to note that, according to their degree of development, ribs presumably ossified in an anterior to posterior sequence unlike those of living rib-bearing anurans for which we have this information (Blanco and Sanchiz, 2000).

Even in the youngest specimen examined, the clavicle has a robust, bifurcate lateral end thereby indicating that this is the natural configuration, as described by Estes and Reig (1973). Báez and Basso (1996) reported that in several mature *Notobatrachus* the posterior prong of the bifurcated lateral end is separated from the rest of the clavicle by a distinct suture and suggested that ossification of the procoracoid cartilage might be involved in the formation of this process. The shape of the lateral end of the clavicle in an immature specimen of *Notobatrachus* (CPBA V 14003) and the fact that this cartilage is late in ossifying in *Leiopelma* (Stephenson, 1952) suggest that the apparent suture is more likely the result of postmortem breakage.

Significance of the intraspecific and geographic variation

Significant variation in the shape and orientation of the sacral diapophyses, a feature that has been widely used in anuran systematics, is evident in *Notobatrachus*. This variation is especially obvious among the few specimens from Laguna del Molino in which the sacrum is preserved and poses interesting questions with regard to their taxonomic status. Does this morphological variance represent different growth stages? Is there more than one species represented? Critical to this discussion is the interpretation as to whether the fossil samples represent single populations. Specimens in a fossil assemblage can be regarded as contemporaneous only within the interval of time represented, which depends on the sedimentary and taphonomic processes that produced the fossil-bearing stratum (Behrensmeyer and Hook, 1992). This time averaging can mix remains from different evolutionary stages and thus more variation than in an extant population may be expected. Although few analyses of intrapopulational skeletal variation have been conducted in living frogs, available studies show that the sacral region may vary in basal anurans (Ritland, 1955), as well as in neobatrachians (Trueb, 1977). As in *Notobatrachus*, a marked variation of the width and angle of the expansion of the adult sacral diapophyses was recorded in several populations of *Ascaphus* in which, in turn, the frequency of the different morphologies varies (Ritland, 1955). However, some of these populations of *Ascaphus* may belong to a separate species based on molecular data (Nielson *et al.*, 2001; García-Paris *et al.*, 2003). This contrasts with the notably low coefficient of intrapopulational variation of the angle formed by the leading edge of the sacral diapophyses and the longitudinal axis of the vertebral column shown by a species of *Hyla* (Trueb, 1977). Moreover, this stability was related to the observation that the shape and orientation of the sacral leading edge is established early in development (Trueb, 1977). In the case of Laguna del Molino, the presumably episodic nature of bone concentration in the 0.25 m-thick fossiliferous bed and taphonomic mode (Behrensmeyer and Hook, 1992) suggest a level of temporal resolution between $< 10^{o}$ to $10^{1,}$ *i.e.*, a very short time from a geological viewpoint. Unfortunately, although this allows populational level inferences, the rarity of specimens in which variation of the sacrum may be analyzed prevents determination as to wether the variation was continuous or discrete. It is also not possible to estimate the relative frequency of the different sacral shapes in order to make meaningful comparisons with the assemblage from the northern outcrop areas.

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Appendix I

Specimens examined

Institutional abbreviations

CPBA-V: Paleontología de Vertebrados, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina
CTES-Pz: Universidad Nacional del Noreste, Corrientes, Argentina.
MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.
MLP: Museo de La Plata, La Plata, Argentina.
MPEF-PV: Paleontología de Vertebrados, Museo Provincial Edigio Feruglio, Trelew, Argentina.
RH: Rafael Herbst, personal collection.
THHC: Texas Natural History Collection, University of Texas at Austin, U.S.A.

Fossil material

1) Cañadón de Estancia La Matilde, about 110 km SW of Puerto Deseado, Departamento de Deseado, Provincia de Santa Cruz, Argentina (type locality). La Matilde Formation (fossiliferous level I, section by Stipanicic in Stipanicic and Reig 1957).
CPBA-V 14001-14007. MACN 17720 (holotype)-17727, 18658-18669; 1867-18673; 18675; 18677. MLP 54-XI-18-1; 62-XII-1-1 to 4. MPEF-PV-1250- 1266. PVL 2196,2194.
2) Slopes west of Cañadón de Estancia La Matilde, about 110 km SW of Puerto Deseado, Departamento de Deseado, Provincia de Santa Cruz, Argentina. La Matilde Formation.
CTES-Pz 5739-5746.
3) Estancia El Malacara, about 100 km S of Puerto Deseado, Departamento de Deseado, Provincia de Santa Cruz, Argentina. La Matilde Formation.
CPBA-V 14024.
4) 20 Km N of Estancia La Trabajosa, 140 Km W of Puerto Deseado, Departamento de Deseado, Provincia de Santa Cruz, Argentina. La Matilde Formation.
MLP 55-VI-1-1 to 4.
5) Laguna del Molino, Gran Bajo de San Julián, Departamento de Magallanes, Provincia de Santa Cruz
MACN 19178. CTES-Pz 5747-5760; 7311-7318. MLP 89-XI-27-1 to 19. PVL 250, 261.

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