

Cretaceous Research 28 (2007) 1005-1016

CRETACEOUS RESEARCH

www.elsevier.com/locate/CretRes

Anurans from the Candeleros Formation (?Cenomanian-Turonian) of west-central Argentina: new evidence for pipoid evolution

Ana M. Báez*, Paula Muzzopappa, Laura Nicoli

Universidad de Buenos Aires, Facultad de Ciencias Exactas, Departamento de Ciencias Geológicas, Pabellón 2, Ciudad Universitaria, Buenos Aires 1428, Argentina

> Received 5 June 2006; accepted in revised form 17 January 2007 Available online 10 July 2007

Abstract

The fluvio-lacustrine deposits of the ?Cenomanian-Turonian Candeleros Formation in the northwestern fringe of Patagonia have yielded numerous remains of vertebrates, including anurans. A new, partially articulated immature specimen of a small pipimorph pipoid from the upper part of this unit is described herein. Although incompletely preserved, the morphology and proportions of the skeleton are strongly reminiscent of corresponding elements of the holotype of *Avitabatrachus uliana* from the lower section of the same formation at a nearby locality, thus suggesting that these specimens might represent the same, or a closely related, taxon. The new specimen is a metamorphosing individual: it has a zygapophyseal articulation between the sacrum and the neural arch of a postsacral vertebra that bears conspicuous transverse processes, and four pairs of ribs. These traits are not present in the available material of *A. uliana*, but they might have occurred within the normal range of variation of a single species. Although the generic and specific allocation of the new material is uncertain, a parsimony analysis performed to clarify the relationships of *A. uliana* supports a phylogenetic placement of this taxon outside the crown Pipidae. The evidence provided by the Candeleros anurans confirms the presence of stem pipids in Patagonia in the early Late Cretaceous.

Keywords: Pipoidea; Pipidae; Avitabatrachus; Cretaceous; Patagonia; Candeleros Formation

1. Introduction

The available evidence furnished by the fossil record indicates that, in the Kimmeridgian, pipoid frogs had already diverged into the lineages represented today by the fossorial rhinophrynids and aquatic pipids (Henrici, 1998). Unquestionable fossil occurrences of the latter clade indicate that, by the Senonian, they were widely distributed in Africa and South America, where their extant representatives live (Báez, 1996; Trueb et al., 2005). However, the early evolution of the stem-pipid lineage has only sparsely been documented to date and the history of the numerous anatomical

* Corresponding author.

E-mail address: baez@gl.fcen.uba.ar (A.M. Báez).

modifications for a wholly aquatic existence is still incompletely understood.

Despite the fact that anuran remains are virtually unknown in pre-Senonian Cretaceous beds of Patagonia, the lower section of the ?Cenomanian-Turonian Candeleros Formation has provided the oldest well-documented record of pipoid frogs from South America. Disarticulated and partially articulated remains of at least two individuals were collected from continental red sandstones of the Neuquén Basin and referred to the new pipoid *Avitabatrachus uliana* (Báez et al., 2000) (Fig. 1). *Avitabatrachus* was originally proposed as a stem pipid, possibly crownward with respect to the Aptian *Thoraciliacus* and *Cordicephalus* from Israel (Nevo, 1968; Trueb and Hanken, 1992; Trueb, 1999; Trueb and Báez, 2006), although the taxonomic placements of the latter two taxa were in need of revision. Here we describe new pipoid remains

^{0195-6671/\$ -} see front matter @ 2007 Elsevier Ltd. All rights reserved. doi:10.1016/j.cretres.2007.01.004



Fig. 1. Geographical location of the El Gigante and El Chocón localities that yielded the holotype of *Avitabatrachus uliana* (MUCPv 123) and the pipimorph material described herein (MACN PV N96 and 103), respectively.

from the upper section of the Candeleros Formation, which were discovered in association with a diplodocoid sauropod by José F. Bonaparte in 1988 (Calvo and Bonaparte, 1988). The material was recovered from a fossil locality geographically close to the site that yielded the holotype of *Avitabatrachus*. Although we were unable to ascertain whether these specimens are conspecific, we performed a parsimony analysis to investigate the phylogenetic position of *Avitabatrachus uliana* and its bearing on pipoid evolutionary history, based on the material of this species that had been previously described (Báez et al., 2000).

2. Geological framework

The Candeleros Formation is part of the thick sedimentary infill of the Neuquén Basin, a back-arc depocentre implanted on Palaeozoic and older continental crust, located near the western margin of southern South America (Fig. 1). The basin was periodically drowned during the Jurassic and Early Cretaceous, but the marine influx from the Pacific Ocean was cut off as a result of the renewed tectonic activity and inversion that affected the region in the mid Cretaceous. This was accompanied by the deposition of widespread red beds of the Neuquén Group, which comprise, from top to bottom, the Río Colorado, Río Neuquén, and Río Limay subgroups (formerly units of formation status). The basal division of the latter subgroup is the Candeleros Formation, which consists of an upward-fining succession that attains a thickness of nearly 300 m. It is mainly composed of massive coarse- and medium-grained, violet to dark red sandstones and conglomerates (Cazau and Uliana, 1973; Leanza and Hugo, 2001). Dark-brownish siltstones and claystones occur in thin beds, some representing swampy conditions, whereas palaeosols are frequent in some horizons. Deposition of this unit probably took place in braided and meandering fluvial systems (Leanza and Hugo, 2001). In the area of the Ezequiel Ramos Mexía reservoir, sedimentological study of Candeleros exposures shows that the fluvial environment included some shallow bodies of water that were seasonally flooded (Calvo and Gazzera, 1989; Ortega et al., 2000).

The Candeleros Formation is devoid of age-diagnostic fossils but its age has been considered post-Albian by most authors on the basis of stratigraphic relationships. The unconformity that occurs between this depositional sequence and the underlying Lohan Cura Formation has been considered earliest Cenomanian (Vergani et al., 1995; Leanza et al., 2004). This age agrees with the presence of Albian microfossils in sediments of the Huitrin-Rayoso Group (Volkheimer and Salas, 1976), 800 m below the unconformity that separates the bottom of the Neuquén Group from older rocks. However, based on the presence of putative iguanodontid footprints, Calvo (1991) proposed that the Candeleros Formation started to accumulate in the Albian. A pre-Cenomanian age for this unit was also suggested by the ?Albian-Cenomanian dating of a palynological assemblage from the overlying Huincul Formation in the northern part of the basin (Vallati, 2001). In turn, this age estimate of the Huincul Formation is not consistent with the 88.0 ± 3.9 Ma datum (Late Turonian-Coniacian, according to the geological time scale of Gradstein et al., 2004) obtained by fission-track dating. This dating was performed on zircon crystals discovered within a tuffaceous bed that lies 16 m above the conformable contact between the Candeleros and Huincul formations (Corbella et al., 2004). Based on the latter result, it is inferred that the minimun age of the Candeleros Formation could range well into the Turonian, and that this unit might be younger than previously thought.

The Candeleros Formation has yielded a taxonomically diverse assortment of tetrapod remains, although the fossils have been collected in several exposures from different stratigraphic levels within the sequence. Outcrops of the lower part of the unit at the El Gigante locality (Fig. 1), on the northeastern margin of the Ezequiel Ramos Mexía reservoir, have produced the holotype of the pipoid frog Avitabatrachus uliana (Báez et al., 2000) and isolated remains of turtles. Most other finds from the lower Candeleros Fomation were recovered at the geographically close El Chocón locality or its vicinity: these include a small crocodyliform (Ortega et al., 2000), and sauropod (Calvo and Bonaparte, 1991) and theropod dinosaurs (Coria and Currie, 2002). Exposures of the upper part of the Candeleros Formation at the El Chocón fossiliferous site (Fig. 1) yielded the pipoid material described here. These anuran remains were discovered in association with the rebbachisaurid sauropod Limaysaurus tessonei, originally described as Rebbachisaurus tessonei (Calvo and Salgado, 1995; Salgado et al., 2004). Chelid turtles also have been reported from the upper part of this formation in the El Chocón locality (Lapparent de Broin et al., 1997; Lapparent de Broin and de la Fuente, 2001). Recently, a taxonomically diverse fauna that includes ceratodontid lungfishes, fragmentary remains of anurans, chelid turtles,

sphenodontians, snakes, araripesuchian crocodyliforms, saurischian dinosaurs, and dryolestoid mammals were discovered in outcrops of the Candeleros Formation south of the Ezequiel Ramos Mexía reservoir (Apesteguía et al., 2001; Pol and Apesteguía, 2005). These fossiliferous beds occur near the top of this unit (Apesteguía and Zaher, 2006) and the samples were collected at La Buitrera and other geographically close sites.

3. Systematic palaeontology

Institutional Abbreviations: MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina. MUCPv, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Sección Paleontología de Vertebrados, Neuquén, Argentina.

Anura Rafinesque, 1815 Pipoidea Fitzinger 1843 Pipimorpha Ford and Cannatella, 1993 Genus and species, indeterminate

Material. The specimen is a single articulated skeleton (MACN Pv N96), lacking the most anterior part of the skull, the upper and lower jaws, the forelimbs, and the hind autopodia (Fig. 2). A few disarticulated remains belong to other individuals. The specimen is preserved as part (a) and counterpart (b) on a piece of massive, reddish-brown siltstone. An exceptionally well preserved right otic capsule (MACN Pv N103, Fig. 3) was removed from the matrix and prepared mechanically to reveal additional anatomical information.

Locality and stratigraphic horizon. 5 km SW of the town Villa El Chocón, Neuquén Province, Argentina. Upper part of the Candeleros Formation, Río Limay Subgroup, Neuquén Group; ?Cenomanian-Turonian.

Description

The description below is based on the most complete skeleton unless otherwise noted. The snout-vent length of this skeleton is calculated to be approximately 25 mm. Comparisons with the developmental sequence of extant (Xenopus laevis, Trueb and Hanken, 1992) and extinct (Shomronella, Estes et al., 1978; Chipman and Tchernov, 2002; Palaeobatrachus, Roček, 2003) pipoids helped us estimate the ontogenetic stage of this specimen. The expanded configuration of the bony sacral diapophyses, the completely ossified transverse processes of all posterior presacrals, and the general high degree of ossification of ilia, femora and tibiofibulae suggest that it had completed metamorphosis. In contrast, the poor ossification of the braincase in the orbital region suggests that the individual might have been premetamorphic. Furthermore, the short, wide neural arches and their collapsed condition along the midline (suggesting weak medial fusion of the two halves), and the presence of ribs that are still unfused to the transverse processes, also indicate that the specimen is just at the end of metamorphosis. The relative delay in the ossification of the cranial skeleton with respect to the vertebral column, when compared with the osteogenesis of *Xenopus laevis*, also occurs in the Early Cretaceous pipoid *Shomronella* (Estes et al., 1978).

Cranial skeleton. The skull is incomplete: only parts of the azygous frontoparietal, parasphenoid, and pterygoids, and the otic capsules, are preserved. Although the frontoparietal is exposed in ventral view, no impressions of the dorsal endocranial pattern (sensu Špinar, 1976) are evident. The anterior portion of this bone is missing, whereas its most posterior part is obscured by the large otic capsules. We cannot therefore describe the overall shape of the frontoparietal or its relationships with neighboring bones. However, the portion preserved in the orbital region shows the frontoparietal to be broad, forming an extensive dorsal table, and having margins that diverge slightly posterolaterally lateral (Fig. 2B). It is also evident that the frontoparietal was not fused to the underlying sphenethmoid. The latter element is not preserved and might still have been cartilaginous or poorly ossified. The otic capsules are quadrangular and well ossified, indicating that the prootics and exoccipitals are fused (otoccipitals auctorum). Examination of MACN Pv N103 (Fig. 3), which belongs to a larger, and probably older, individual, provides further information on this structure. The relatively flat roof of each otic capsule lacks crests. although a rounded protuberant rim along its anterior, medial, and posterior borders is evident. A well-developed process projects posterolaterally from the roof of the otic capsule: a similar process in juvenile Xenopus laevis was described as a muscular process of the auditory capsule by Trueb and Hanken (1992).

Posteromedially, the roof of the otic capsule extends over the occipital condyles: this condition, together with the straight anterior margin of the atlantal neural arch (described below), implies that there was almost no dorsal exposure of the spinal cord in life. Ventrally, a depressed area that broadens medially occurs across the most anterior portion of the otic capsule: this wide channel probably housed the Eustachian tube (Figs. 2B, 3). Posterior to the Eustachian canal, a bulbous area corresponds to the inner ear region. It is noteworthy that this area is distinctly more prominent in the articulated specimen than in the isolated otic capsule, which, as noted above, likely belongs to an older individual. Owing to its fragility, the medial wall could not be cleaned of sediment to reveal the condition of the foramina. The posterior wall of the otic capsule is pierced by the large foramen magnum, which is bordered on both sides by the posterolaterally oriented occipital condyles. Lateral to each condyle, the jugal foramen (through which the glossopharyngeal and vagus nerves leave the braincase) is evident at the bottom of the condyloid fossa. Dorsolateral to the jugal foramen, a single opening might correspond to the inferior perilymphatic foramen, although it is not possible to ascertain the presence or absence of the superior foramen. Fragments of the



Fig. 2. A. Photograph (left) and interpretive drawing (right) of MACN Pv N96a. Hatched areas are pieces of bone preserved on MACN Pv N96b. Dash-lines indicate probable outlines of bones. B. Photograph (left) and interpretive drawing (right) of the cranial region of MACN Pv N96b.

parasphenoid are crushed against the ventral surfaces of the frontoparietal, and the medial portions of the otic capsules (Fig. 2B). Despite its fragmentary condition, which prevents an assessment of its anterior extent and shape, it is possible to determine that the parasphenoid lacked subotic alae and that it terminated posteriorly near the ventral margin of the foramen magnum, as evidenced by the scar that it left on the ventral surfaces of the otic capsules (Fig. 2B). The pterygoids are relatively flat, triradiate bones. The tip of the anterior ramus is missing: its posterior portion is broad and has a convex lateral margin. The medial and posterior rami are nearly equal in length. A piece of a laminar bone preserved on the ventral surface of the left otic capsule, interpreted by us as part of the pterygoid, suggests that these rami formed an otic plate, although the element is too poorly preserved to determine its original shape.

Postcranial skeleton. The vertebral column is composed of seven discrete presacral vertebrae (Figs. 2A, 4). The first element bears transverse processes: this suggests that the first two vertebrae might be fused and that eight presacrals might be formed during development. The neural arches are short

and wide: while most appear crushed along the midline, the arches seem to have been imbricated. The transverse processes of the four anterior presacrals are well developed. Those of the first element, heretofore termed atlas, are directed slightly anteriorly and uniform in width throughout the length of the preserved portion. The atlantal neural arch is smooth dorsally and its anterior margin is straight. The most anterior part of the atlantal centrum is exposed posterior to the otic capsules: its convex shape indicates that an intercotylar notch was absent. The following three vertebrae (interpreted as Vertebrae III, IV, and V) bear elongate, laterally blunt transverse processes. Slender, long ribs occur laterally to these transverse processes. The ossified ribs and transverse processes of Vertebra III are in contact: in contrast, those of Vertebrae IV and V are separated by a gap, probably indicating that the lateral tip of the transverse process and the proximal epiphyses of the adjacent rib were still cartilaginous. The ribs on Vertebra III and Vertebra IV are expanded at their lateral tips and are more robust than those on Vertebra V. The last three presacrals (Vertebrae VI, VII, and VIII) bear well-ossified, anteriorly directed,



Fig. 3. SEM photomicrograph of right otic capsule (MACN Pv N103) in ventral view.



Fig. 4. Partial restoration of the skeleton of MACN Pv N96 in dorsal view.

and broad scapular blade with a straight leading edge that forms an obtuse angle with the suprascapular margin of the bone. In contrast, the suprascapular margin forms a narrow angle with the posterior edge of the scapula, a configuration

short transverse processes. These processes are distinctly wide-based and with acuminate lateral tips. The sacral vertebra is formed by a single vertebra (Ver-

tebra IX). The sacral diapophyses are symmetrical and moderately expanded: their lateral margins are slightly convex (Figs. 2A, 4). A narrow band of a lighter shade than the rest of the sacral vertebra, suggesting incomplete mineralization, occurs along the lateral margin of each diapophysis. The neural arch of the sacral vertebra, unlike those of the presacrals, lacks a spinous process posteromedially. Posterolaterally, this vertebra bears postzygapophyses for the articulation with the prezygapophyses of a postsacral element (Fig. 5). This postsacral element has a neural arch with well-developed transverse processes. However, owing to its fragility, it was not possible to expose this element ventrally to ascertain whether it also posseses a discrete centrum. Posterodorsally, the rudimentary neural arch of another vertebra is present in front of the ossified unsegmented posterior part of the urostyle. This neural arch was probably, in life, joined to the adjacent elements by bridges of cartilage. In lateral aspect, a spinal nerve foramen is visible at the level of the caudal margin of the posterior postsacral neural arch.

We are unable to ascertain whether the pectoral girdle was arciferal or firmisternal, because only a few isolated components of this structure are preserved. These include the left scapula and coracoid, and the medial end of the right clavicle, all exposed in dorsal view. The scapula is flat and has a short



Fig. 5. Sacrourostylar region (dorsal view) of MACN Pv N96a.

that results from the marked posterior flaring of the scapular blade. Medially, the partes acromialis and glenoidalis are developed in the same plane and are widely separated by a rounded cleft, which is clearly visible in dorsal view (Fig. 2A). The anterior border of the pars acromialis is distinctly convex and the clavicle was not fused to it. The dorsal surface of the pars glenoidalis is flat. The coracoid length is nearly three times its sternal width. Both lateral and medial ends are slightly expanded: the similar degree of these expansions confers a symmetrical overall aspect to the bone. The acromial end of the clavicle has a hook-like shape, indicating that this bone overlapped the convex anterior edge of the pars acromialis of the scapula. The disarticulated right humerus is visible near the skull (Fig. 2A): it is evident that it is relatively long and straight, but both its ends are too poorly preserved to be described in detail.

The pelvic girdle is represented by the partially articulated ilia. The ilium has a rod-like shaft that lacks a dorsal crest. A low, but long-based, dorsal prominence stands out from the dorsal margin of the shaft near the acetabulum. The ilial acetabular portion, partially exposed medially, is moderately expanded. An interiliac tuberosity is absent, at least dorsally.

The preserved hind-limb bones are long and slender. The femur is slightly sigmoidal and its proximal head is unossified. The tibiofibula is as long as the femur and the sulcus on the tibiofibula is not visible owing to the position in which this bone is exposed.

Taxonomic placement

The specimen MACN Pv N96 clearly represents a pipoid taxon based on the azygous frontoparietal and the lanceolate parasphenoid that lacks subotic alae. Furthermore, the smooth ventral surface of MACN Pv N103 indicates that the parasphenoid did not extend laterally under the inner ear region. These character states have been considered synapomorphies of Pipoidea in recent phylogenetic analyses (Báez and Púgener, 1998, 2003; Báez and Harrison, 2005; Trueb and Báez, 2006). Moreover, the short and posteriorly flared scapular blade, and the otic capsule modified for subaquatic hearing, indicate that the remains belong to a pipimorph (i.e., more closely related to crown Pipidae than to crown Rhinophrynidae, Ford and Cannatella, 1993). The morphology and skeletal proportions of these specimens are reminiscent of those of Avitabatrachus uliana (Báez et al., 2000), the stratigraphically and geographically closest pipimorph occurrence. However, detailed comparison with this taxon is difficult because of the incomplete nature of the available material of Avitabatrachus and the few elements that are similarly exposed. In addition, it is noteworthy that these specimens presumably belong to slightly different developmental stages: the holotype of Avitabatrachus probably being somewhat older, as indicated not only by its greater size but also by its more completely ossified bones. In both, the otic capsules are prominent and their anteroventral surfaces are excavated to accommodate the elongate Eustachian tubes, although the medial flanges described on the floor of the otic capsules of *Avitabatrachus* are not evident in the specimens described here. As in *Avitabatrachus*, the roof of the otic capsules lacks a transverse crest. The positions of the condyloid fossae and jugal foramina are similar, but the perilymphatic foramina are unknown in *Avitabatrachus* because the only otic capsule exposed appropriately to examine this trait is broken.

The scapula of MACN Pv N96 is slightly wider than that of *Avitabatrachus*. It is about one and a half times wider than it is long, whereas in the latter taxon it is almost as long as wide. MACN Pv N96 resembles *Avitabatrachus* in having an anteroposteriorly expanded pars acromialis: this scapular configuration is unlike that of other mid-Cretaceous pipimorphs such as *Thoraciliacus* and *Cordicephalus* (Nevo, 1968; Trueb, 1999; Trueb and Báez, 2006). All these taxa share the presence of a distinct notch between the partes acromialis and glenoidalis. Conversely, palaeobatrachids differ in lacking a bicapitate and posteriorly flared scapula.

The vertebral column of MACN Pv N96 differs from that of Avitabatrachus in the presence of acuminate transverse processes on the last three presacrals, instead of on the posterior four. In Avitabatrachus the atlas and the following two vertebrae bear long and blunt transverse processes with indications that they include fused ribs, whereas in MACN Pv N96 transverse processes occur on the atlas and the following three vertebrae, the latter associated with free ribs. Assuming that in both specimens the first vertebra is a composite of the atlas and Vertebra II, an additional pair of ribs on Vertebra V occurs in MACN Pv N96. This condition was described as an occasional intrapopulational variant in fossil and living "archaeobatrachian" taxa, such as Shomronella jordanica (Estes et al., 1978; Chipman and Tchernov, 2002), and Ascaphus truei (Ritland, 1955). However, the presence of four pairs of ribs that fuse to the transverse processes of Vertebrae II-V during ontogeny was considered the normal state in Thoraciliacus (Nevo, 1968), whereas five pairs occur invariably in Cenozoic palaeobatrachids (Roček, 2003) and occasionally in the basal Jurassic anuran Notobatrachus degiustoi (Estes and Reig, 1973). As in Avitabatrachus and Thoraciliacus, the transverse processes of the posterior presacrals of MACN Pv N96 have distinctly wide bases, differing from the more slender posterior transverse processes of other extinct and extant pipimorph taxa, such as Cordicephalus, Saltenia, Xenopus, and Pipa. These posterior transverse processes have a more perpendicular orientation with respect to the longitudinal axis than those of living pipids, in which the processes are oriented at an acute angle to this axis. A postdisplacement in the onset of the differentiation of the transverse processes has been proposed to account for the intracolumnar differences between anterior and posterior presacral transverse processes and, perhaps, for the loss of ribs in anurans (Blanco and Sanchiz, 2000). This hypothesis predicts less reduced posterior transverse processes and a higher number of ribs in basal forms, an inference that seems to be in accordance with the available palaeontological evidence. These trends, however, may have occurred independently in different anuran lineages.

In the holotype of Avitabatrachus uliana, the sacral vertebra, exposed in ventral view, is fused to the urostyle, as is the case in extant and extinct pipids (Báez and Harrison, 2005). In MACN Pv N96 the sacral vertebra is exposed in dorsal view and articulates with the neural arch of a well-ossified postsacral element. The occurrence of bony neural arches of Vertebra X having a zygapophyseal joint with the sacrum is a situation not described in studies of the ontogenetic and individual variation of the sacral region in extant pipids. In Xenopus laevis (the only pipid taxon for which this information is known in detail), the sacral and three pairs of postsacral neural arches (corresponding to Vertebrae X, XI, and XII) chondrify independently (Smit, 1953). At early metamorphosis, the postsacral neural arches fuse synchondrotically into a pair of elongated structures joined by the extensively ossified Vertebra X (Ročková and Roček, 2005). At this developmental stage, fusion of well-formed zygapophyses between the sacrum and Vertebra X (the only zygapophyseal articulation formed posterior to the sacral vertebra), has already occurred (Smit, 1953). Ossification proceeds in an anteriorposterior direction as in the rest of the vertebral column and fusion of the postsacrals is complete by the end of metamorphosis. However, occasionally, incomplete ossification may cause the transient appearance of bony postsacral neural arches in juveniles, although these elements are joined by cartilage (Kovalenko, 1999). Even rarer (recorded in 2 out of 1695 late larvae or early juveniles by Kovalenko, 1999), is the mobile articulation between sacrum and urostyle when the sacrum is formed by Vertebra IX (Kovalenko, 1999). Among extinct pipoid taxa, transient distinct neural arches at the anterior end of a fused or mobile urostyle have been described (Špinar, 1972; Báez and Púgener, 1998). In contrast, the presence of one or two complete postsacral vertebrae in Thoraciliacus, which has a mobile sacrourostylar articulation, was considered the normal adult condition by Nevo (1968). However, this was not confirmed in the revision of this taxon by Trueb (1999), although illustrations of Thoraciliacus in Nevo's paper depict neural arches with vestigial transverse processes and zygapophyses posteriorly to the sacrum in some (immature?) individuals (Nevo, 1968, plate 6B). In this regard it is pertinent to recall that in Notobatrachus degiustoi the occasional presence of one discrete postsacral vertebra, including centrum and bearing prezygapophyses and transverse processes, has been reported in adults (Báez and Basso, 1996; Báez and Nicoli, 2004). In contrast, a postsacral neural arch bearing prezygapophyses is an infrequent variant in Ascaphus (Ritland, 1955) and also in some neobatrachians (e.g. Bufo bufo and Rana sp., Böhme, 1982).

It seems likely that progress in the osteogenesis of MACN Pv N96 would have led to the complete coalescence of the neural arches of Vertebrae X and XI to form the anterodorsal part of the urostyle. The ultimate fusion of arches of Vertebrae IX and X is less certain, although in any case the lack of

complete fusion of the anterior postsacrals (which appear to have already coalesced with the hypochord), contrasts with the well-ossified, dilated sacral diapophyses. Possibly, the sacrum and urostyle remained unfused until postmetamorphic stages: later than they do in extant *Xenopus* (Trueb and Hanken, 1992). This might also explain the variability perceived in this region in *Thoraciliacus* and *Cordicephalus* (Nevo, 1968; Trueb and Báez, 2006).

The high degree of variation of the anuran sacrourostylar region (Trueb, 1977; Kovalenko and Danylevskaya, 1994; Kovalenko, 1999) advises caution in using characters of this part of the skeleton taxonomically. In the present case, distinct neural arches bearing transverse processes and prezygapophyses posterior to the sacrum, as well as an additional pair of ribs, might occur within the range of variation of a single species, either as transient juvenile features or individual variants. However, are the holotype of Avitabatrachus uliana and the specimens from El Chocón conspecific? The horizons that yielded these specimens are clearly diachronous: the stratigraphic interval that separates them might represent between 10 and 7 Ma, depending on whether the clastics of the Neuquén sequence started to accumulate around 97 Ma (Orchuela and Ploszkiewicz, 1984) or 94 Ma (Uliana and Legarreta, 1993). In addition, the range of morphological variation of A. uliana is unknown, as this taxon is based primarily on a single specimen. Despite the close morphological similarity with Avitabatrachus, minor differences in the shapes of the atlantal transverse processes and the parasphenoid are present. Furthermore, there is no evidence of the flanges on the ventral surface of the prootics that characterize Avitabatrachus. On the other hand, as discussed above, apart from the general pipimorph traits, a different combination of features clearly differentiate this material from all other taxa included in this lineage. In sum, the available information is insufficient to determine unambiguously its generic allocation: hence, the material described here is considered a non-palaeobatrachid pipimorph, genus and species indeterminate.

4. The phylogenetic relationships of Avitabatrachus

Even if the generic and specific allocation of the available specimens from the upper section of the Candeleros Formation cannot be determined with confidence at present, it is pertinent to assess the taxonomic placement of *Avitabatrachus uliana*. Although the pipimorph affinities of *Avitabatrachus* were previously noted by Báez et al. (2000), this taxon was not included in recent phylogenetic analyses. Therefore, we performed a parsimony analysis based mainly on the matrix of Báez and Harrison (2005) and Trueb and Báez (2006), with the addition of two characters (37 and 52, see Appendix 1). The scoring for *A. uliana* was based on the holotype only, although all of its character states match those that could also be scored for MACN Pv N96, except the nature of the sacrourostylar articulation. We also included the pipimorphs *Vulcanobatrachus mandelai* from the Upper Cretaceous of South Africa, *Neusibatrachus wilferti* from the Lower Cretaceous of Spain, and the extant basal neobatrachian *Limnodynastes ornatus*. Character states for *Vulcanobatrachus* were taken from the description of Trueb et al. (2005), whereas those for the latter two taxa were obtained from personal observations. Characters for *Thoraciliacus* were scored in accordance with the matrix of Trueb and Báez (2006). Ambiguous evidence with regard to the states in *Thoraciliacus* (e.g., characters 8, 34, 51, 56) was denoted by a "?". The vomers (character 21) are poorly preserved in this taxon, although the triradiate outline described by Nevo (1968) and Trueb (1999) indicates a position medial and posterior to the choanae (state 0). The vertebral centra were scored as notochordal (character 43, state 0) because they exhibit a condition similar to that of *Rhinophrynus* (Trueb, 1999), in which a notochordal canal is present. The few specimens of *Thora-ciliacus* in the Museum of Natural History of the University of Kansas examined by one of us (A.M.B.), although poorly preserved, lack evidence of modification of the ventral surface of the otic capsule for the Eustachian tube (character 12, state 0), and the pterygoid does not form an otic plate according to Trueb (1999). Character 18 (maxillary partes) for *Thoraciliacus* was confidently scored as 0 in this analysis. The matrix (Appendix 2) was run in PAUP, version 4.0b10 (Swofford, 2002), using the branch-and-bound algorithm. Multistate characters were treated as unordered and of equal weight. The analysis produced six most parsimonious trees, each of 136 steps, CI of 0.537, and RI of 0.816. A strict consensus of these trees is shown in Fig. 6. These trees differ in the interrelationships within a clade of several South



Fig. 6. Strict consensus of the six most parsimonious trees obtained in the analysis of matrix shown in Appendix 2. The extant taxa are in bold type. The numbers next to the nodes represent the decay indices (Bremer indices).

American extinct species represented by fragmentary material, which also remained unresolved in previous analyses (e.g., Báez and Púgener, 2003; Trueb and Báez, 2006), as did the placement of the outgroups Bombina variegata and Discoglossus pictus. The position of Neusibatrachus fluctuates between being the sister-taxon of pipoids and that of pipimorphs: this analysis thus confirms the pipoid affinities of this taxon suggested by Gao and Chen (2004). In contrast, we could not corroborate the close relationship of Vulcanobatrachus and pipines suggested by Trueb et al. (2005). In all trees, Avitabatrachus appears as the sister taxon of crown Pipidae. This position is supported by the possession of four unequivocal synapomorphies shared with pipids (maxilla lacking distinct partes in the orbital region ($CI_{(ch18)} = 1$), conch-shaped squamosal ($CI_{(ch26)} = 1$), well-developed Eustachian canal ($CI_{(ch12)} = 0.667$), and fused sacrum and urostyle $(CI_{(ch48)} = 1))$, and the plesiomorphic state (optic foramen not completely bound in bone, weak coronoid process on the lower jaw, posteromedial process of the hyoid expanded anteriorly, and presence of ilial preacetabular expansion) of four pipid synapomorphies. However, there is a poor resolution of the relationships of the stem-pipid taxa, as the low decay indices show, probably owing to high degrees of homoplasy and uncertainty with regard to many traits.

5. Conclusions

The anuran material so far discovered in the Candeleros Formation provides significant information on the evolutionary history of pipoid anurans. Some of the derived character states that Avitabatrachus shares with crown pipids have been interpreted as advantageous in the aquatic milieu. The sacrourostylar fusion might give rigidity to the trunk, probably increasing the effectiveness of the anterior thrust by the hind-limbs (Trueb, 1996). Furthermore, the conch-shaped squamosal, with the incorporated tympanic annulus, implies a rigid support of the tympanum. This morphological specialization might be functionally important for underwater hearing (Lombard and Hetherington, 1993). However, the broadly expanded anterior ends of the posteromedial processes of the hyoid indicate that the hyoid plate was not reduced, unlike the condition in extant pipids (Ridewood, 1898). This suggests that the hypotranchial skeleton of Avitabatrachus was not as highly modified as in the latter, probably still retaining a broad hyoglossal sinus instead of having a small foramen for the reduced tongue muscles resulting from the aglossal condition. In this regard, it is noteworthy that in at least some extinct South American taxa for which the posteromedial processes are known, such as the Late Cretaceous Saltenia ibanezi and Palaeogene Shelania pascuali, the great length and club-like shape of these processes indicate that a major modification of the hyoid, and perhaps the larynx, had taken place. This also seems to be documented by the African Vulcanobatrachus, although this material is poorly preserved.

The specimens from the upper section of the Candeleros Formation, even though of uncertain generic allocation, clearly pertain to the pipimorph lineage. The conditions in the number of ribs and the anterior sacrourostylar region shown in the single articulated individual described here might represent variant configurations that are not part of the standard adult morphology of extant pipids, and which might have been lost during pipimorph phylogenesis.

Acknowledgments

We thank José F. Bonaparte for the opportunity to study this interesting specimen and Alejandro Kramarz (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina) for the loan of materials under his care. We acknowledge the contributions of Santiago Reuil for his competent preparation of the specimens and of Raúl Gómez for the execution of the drawings. We also thank Linda Trueb (University of Kansas, U.S.A.) and Darren Naish (University of Portsmouth, U.K.) for the pertinent comments on the manuscript. This research was supported by a grant of Universidad de Buenos Aires (TX 090) to AMB.

References

- Apesteguía, S., De Valais, S., González, J., Gallina, P., Agnolín, F., 2001. The tetrapod fauna of "La Buitrera", a new locality from the Candeleros Formation (Lower Cenomanian) of North Patagonia, Argentina. Journal of Vertebrate Paleontology 21, 29A.
- Apesteguía, S., Zaher, H., 2006. A Cretaceous terrestrial snake with robust hindlimbs and a sacrum. Nature 440, 1037–1040.
- Báez, A.M., 1996. The fossil record of the Pipidae. In: Tinsley, R.C., Kobel, H.R. (Eds.), The Biology of *Xenopus*. The Zoological Society of London, Oxford, pp. 329–347.
- Báez, A.M., Basso, N.G., 1996. The earliest known frogs of the Jurassic of South America: review and cladistic appraisal of their relationships. Müncher Geowissenschaftliche Abhandlungen, Reihe A (Geologie Palaontologie) 30, 131–158.
- Báez, A.M., Harrison, T., 2005. A new pipine frog from an Eocene crater lake in north-central Tanzania. Palaeontology 48, 723–737.
- Báez, A.M., Nicoli, L., 2004. A new look at an old frog: the Jurassic Notobatrachus Reig from Patagonia. Ameghiniana 41, 257–270.
- Báez, A.M., Púgener, L.A., 1998. A new Paleogene pipid frog from northwestern Patagonia. Journal of Vertebrate Paleontology 18, 511–524.
- Báez, A.M., Púgener, L.A., 2003. Ontogeny of a new Palaeogene pipid frog from southern South America and xenopodinomorph evolution. Zoological Journal of the Linnean Society 139, 439–476.
- Báez, A.M., Trueb, L., Calvo, J.O., 2000. The earliest known pipoid frog from South America: a new genus from the middle Cretaceous of Argentina. Journal of Vertebrate Paleontology 20, 490–500.
- Blanco, M.J., Sanchiz, F.B., 2000. Evolutionary mechanisms of rib loss in anurans: a comparative developmental approach. Journal of Morphology 244, 57–67.
- Böhme, G., 1982. Osteologische Anomalien bei anuren Amphibien (Salientia). Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematisch-naturwissenschaftliche Reihe 31, 201–207.
- Calvo, J.O., 1991. Huellas de dinosaurios en la Formación Río Limay (Albiano-Cenomaniano?), Picún Leufú, Provincia de Neuquén, República Argentina. (Ornithischia-Saurischia: Sauropoda-Theropoda). Ameghiniana 28, 241–258.

- Calvo, J.O., Bonaparte, J.F., 1988. Nuevos hallazgos de saurópodos en el Miembro Candeleros de la Formación Río Limay (Cretácico), Grupo Neuquén, Argentina. V Jornadas Argentinas de Paleontología de Vertebrados, La Plata, Actas, 12.
- Calvo, J.O., Bonaparte, J.F., 1991. Andesaurus delgadoi gen. et sp. nov. (Saurischia-Sauropoda), dinosaurio Titanosauridae de la Formación Río Limay (Albiano-Cenomaniano), Neuquén, Argentina. Ameghiniana 28, 303–310.
- Calvo, J.O., Gazzera, C.E., 1989. Paleoecología en el sector inferior del Miembro Candeleros (Fm. Rio Limay, Grupo Neuquén, Cretácico) en el área del lago Exequiel Ramos Mexía, Provincia del Neuquén, Patagonia, Argentina. VI Jornadas Argentinas de Paleontología de Vertebrados, San Juan, Resúmenes, 3–5.
- Calvo, J.O., Salgado, L., 1995. *Rebbachisaurus tessonei* sp.nov. A new Sauropoda from the Albian-Cenomanian of Argentina: new evidence on the origin of the Diplodocidae. GAIA 11, 13–33.
- Cazau, L., Uliana, M.A., 1973. El Cretácico Superior continental de la Cuenca Neuquina. V Congreso Geológico Argentino, Buenos Aires, Actas 3, 131– 163.
- Chipman, A.D., Tchernov, E., 2002. Ancient ontogenies: larval development of the Lower Cretaceous anuran *Shomronella jordanica* (Amphibia: Pipoidea). Evolution and Development 4, 86–95.
- Corbella, H., Novas, F.E., Apesteguía, S., Leanza, H.A., 2004. First fissiontrack age for the dinosaur-bearing Neuquén Group (Upper Cretaceous), Neuquén Basin, Argentina. Revista del Museo Argentino de Ciencias Naturales, n.s. 6, 227–232.
- Coria, R.A., Currie, P.J., 2002. The braincase of *Giganotosaurus carolinii* (Dinosauria: Theropoda) from the Upper Cretaceous of Argentina. Journal of Vertebrate Paleontology 22, 802–811.
- Estes, R., Reig, O.A., 1973. The early fossil record of frogs: a review of th evidence. In: Vial, J.L. (Ed.), Evolutionary Biology of the Anurans. University of Missouri Press, Columbia, p. 163.
- Estes, R., Špinar, Z.V., Nevo, E., 1978. Early Cretaceous pipid tadpoles from Israel (Amphibia: Anura). Herpetologica 34, 374–393.
- Ford, L.S., Cannatella, D.C., 1993. The major clades of frogs. Herpetological Monographs 7, 94–117.
- Gao, K.-Q., Chen, S., 2004. A new frog (Amphibia: Anura) from the Lower Cretaceous of western Lioning, China. Cretaceous Research 25, 761– 769.
- Gradstein, F.M., Ogg, J.G., Smith, A.G., Agterberg, F.P., et al. (36 other authors), 2004. A Geologic Time Scale 2004. Cambridge University Press, 589 pp.
- Henrici, A.C., 1998. A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah. Journal of Vertebrate Paleontology 18, 321–332.
- Kovalenko, E.E., 1999. The structure of the sacrourostyle region in the family Pipidae (Anura, Amphibia). Russian Journal of Zoology 3, 32–42.
- Kovalenko, E.E., Danylevskaya, S.E., 1994. On unique forms of anomalous sacral structure in tailess amphibians. Russian Journal of Herpetology 1, 30– 36.
- Lapparent de Broin, F. de, de la Fuente, M.S., 2001. Oldest world Chelidae (Chelonii, Pleurodira), from the Cretaceous of Patagonia, Argentina. Comptes Rendus Acadèmie des Sciences Paris, Sciences de la Terre et des planètes/Earth and Planetary Sciences 333, 463–470.
- Lapparent de Broin, F. de, de la Fuente, M.S., Calvo, J.O., 1997. Presencia de los más antiguos quélidos (tortugas pleurodiras) en el Cretácico inferior de El Chocón, Provincia del Neuquén, Argentina. Ameghiniana 34, 538.
- Leanza, H.A., Apesteguía, S., Novas, F.E., de la Fuente, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. Cretaceous Research 25, 61–87.
- Leanza, H.A., Hugo, C.A., 2001. Cretaceous red beds from southern Neuquén Basin (Argentina): age, distribution and stratigraphic discontinuities. Asociación Paleontológica Argentina, Publicación Especial 7 VII International Symposium of Mesozoic Terrestrial Ecosystems, 117–122.
- Lombard, R.E., Hetherington, T.E., 1993. Structural basis of hearing and sound transmission. In: Hanken, J., Hall, B.K. (Eds.), The Skull, vol. 3. University of Chicago Press, Chicago, pp. 241–302.

- Nevo, E., 1968. Pipid frogs from the Early Cretaceous of Israel and pipid evolution. Bulletin of the Museum of Comparative Zoology, Harvard University 136, 255–318.
- Orchuela, I.A., Ploszkiewicz, J.V., 1984. La Cuenca Neuquina. IX Congreso Geológico Argentino. Secretaría de Minería de la Nación Argentina, San Carlos de Bariloche, Relatorio, 163–188.
- Ortega, F., Gasparini, Z., Buscalioni, A.D., Calvo, J.O., 2000. A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). Journal of Vertebrate Paleontology 20, 57–76.
- Pol, D., Apesteguía, S., 2005. New Araripesuchus remains from the early Late Cretaceous (Cenomanian–Turonian) of Patagonia. American Museum Novitates, 38 pp.
- Ridewood, W.G., 1898. On the structure and development of the hyobranchial skeleton and larynx with remarks on the affinities of the Aglossa. Journal of the Linnean Society of London 26, 53–128.
- Ritland, R.M., 1955. Studies on the post-cranial morphology of Ascaphus truei. Journal of Morphology 97, 119–174.
- Roček, Z., 2003. Larval development in Oligocene palaeobatrachid frogs. Acta Palaeontologica Polonica 48, 595–607.
- Ročková, H., Roček, Z., 2005. Development of the pelvis and posterior part of the vertebral column in the Anura. Journal of Anatomy 206, 17–35.
- Salgado, L., Garrido, A., Cocca, S.E., Cocca, J.R., 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada del León (Lohan Cura Formation), Neuquén Province, Northwestern Patagonia, Argentina. Journal of Vertebrate Paleontology 24, 903–912.
- Smit, A.L., 1953. The ontogenesis of the vertebral column of *Xenopus laevis* (Daudin) with special reference to the segmentation of the metotic region of the skull. Annals of the University of Stellenbosch 29, 79–136.
- Špinar, Z.V., 1972. Tertiary Frogs from Central Europe. W. Junk, The Hague, 286 pp.
- Špinar, Z.V., 1976. Endolymphatic sacs and dorsal endocranial pattern: their significance for systematics and phylogeny of frogs. Vestnik Ustredniho ustavu geologickeho 51, 285–290.
- Swofford, D.L., 2002. PAUP version 4.0b10: Phylogenetic Analysis Using Parsimony. Sinauer Associates, Sunderland, Massachusetts.
- Trueb, L., 1977. Osteology and anuran systematics: intrapopulational variation in *Hyla lanciformis*. Systematic Zoology 26, 165–184.
- Trueb, L., 1996. Historical constraints and morphological novelties in the evolution of the skeletal system of pipid frogs (Anura, Pipidae). In: Tinsley, R.C., Kobel, H.R. (Eds.), The Biology of *Xenopus*. Clarendon Press, Oxford, pp. 377–449.
- Trueb, L., 1999. The Early Cretaceous pipoid anuran, *Thoraciliacus*: redescription, revaluation, and taxonomic status. Herpetologica 55, 139– 157.
- Trueb, L., Báez, A.M., 2006. Revision of the Early Cretaceous *Cordicephalus* from Israel and an assessment of its relationships among pipoid frogs. Journal of Vertebrate Paleontology 26, 44–59.
- Trueb, L., Hanken, J., 1992. Skeletal development in *Xenopus laevis* (Anura: Pipidae). Journal of Morphology 214, 1–41.
- Trueb, L., Ross, C.F., Smith, R., 2005. A new pipoid anuran from the Late Cretaceous of South Africa. Journal of Vertebrate Paleontology 25, 533–547.
- Uliana, M.A., Legarreta, L., 1993. Hidrocarbons habitat in a Triassicto-Cretaceous Sub-Andean setting: Neuquén Basin, Argentina. Journal of Petroleum Geology 16, 397–420.
- Vallati, P., 2001. Middle Cretaceous microflora from the Huincul Formation ("Dinosaurian Beds") in the Neuquén Basin, Patagonia, Argentina. Palynology 25, 179–197.
- Vergani, G.D., Tankard, A.J., Belotti, H.J., Welsink, H.J., 1995. Tectonic evolution and paleogeography of the Neuquén Basin, Argentina. In: Tankard, A.J., Suárez, R., Welsink, H.J. (Eds.), Petroleum basins of South America. American Association of Petroleum Geologists Memoir 62, pp. 383–402.
- Volkheimer, W., Salas, A., 1976. Estudio palinológico de la Formación Huitrín, Cretácico de la Cuenca Neuquina, en su localidad tipo. VI Congreso Geológico Argentino. Gráfica Fluminense, Bahía Blanca, 431–453.

Appendix 1

Cranial characters

- 1. Skull shape in lateral profile: 0, rounded; 1, wedge-shaped.
- 2. Length of rostrum: 0, one-third, or more, of the skull length; 1, one quarter, or less, of the skull length.
- 3. Nasals: 0, paired; 1, fused.
- 4. Frontoparietals and nasals, relationship: 0, not overlapping; 1, overlapping.
- 5. Frontoparietals: 0, paired; 1, fused.
- 6. Frontoparietals, posterolateral extensions: 0, absent; 1, present.
- 7. Frontoparietal fenestra, anterior margin: 0, sphenethmoidal ossification composes anterior margin; 1, anterior margin cartilaginous.
- 8. Olfactory foramina: 0, bound completely or partially in bone; 1, bound in cartilage.
- 9. Planum antorbitale: 0, partially or completely cartilaginous; 1, completely ossified/mineralized between sphenethmoid medially and maxillary arcade laterally.
- 10. Margins of the optic foramina: 0, composed of cartilage and sphenethmoidal ossification; 1, composed completely of sphenethmoidal ossification.
- 11. Floor of the braincase in the orbital region: 0, rounded; 1, distinctly angled.
- 12. Eustachian canal: 0, absent; 1, present a deep furrow in prootic; 2, present as shallow anterior depression in prootic.
- 13. Inferior perilymphatic foramina: 0, present, not ventral to jugular foramina; 1, present, ventral to jugular foramina; 2, absent.
- 14. Superior perilymphatic foramina: 0, present; 1, absent.
- 15. Premaxilla, palatine process: 0: not daggerlike; 1: daggerlike.
- 16. Maxilla, pars facialis: 0, not or slightly overlapping premaxilla; 1, overlapping premaxilla with pointed process that reaches alary process; 2, nearly or completely covering premaxilla anteriorly.
- 17. Maxilla, antorbital process: 0, absent; 1, present.
- 18. Maxilla, partes in the orbital region: 0, distinct; 1, not distinct.
- 19. Maxillary arcade: 0, complete; 1, incomplete.
- 20. Septomaxillae: 0, small and complex; 1, large and arcuate. (continued)
- 21. Vomers: 0, medial to the choanae; 1, posterior to the choanae only; 2, absent.
- 22. Parasphenoid, relationship to braincase: 0, not fused; 1, partially or completely fused.
- 23. Parasphenoid, alae: 0, present; 1, absent.
- 24. Parasphenoid, anterior extent: 0, not reaching maxillary arcade; 1, reaching maxillary arcade.
- 25. Parasphenoid, posteromedial extent: 0, extending near the ventral margin of the foramen magnum; 1, ending well anteriorly to the ventral margin of the foramen magnum.
- 26. Squamosal, shape: 0, T-shaped without stapedial process; 1, T-shaped with stapedial process; 2, conch-shaped.
- 27. Squamosal, zygomatic ramus: 0, well developed; 1, reduced or absent.
- 28. Pterygoid knob: 0, absent; 1, present.
- 29. Pterygoid, position of the anterior ramus: 0, medial to maxilla; 1, dorsal to maxilla;2, anterior ramus absent.
- 30. Pterygoid, medial ramus: 0, present, lacking indentation; 1, present, with indentation; 2, absent.
- 31. Pterygoid, configuration in otic region: 0, not expanded; 1, expanded to form an otic plate.
- 32. Pterygoid, contact between medial ramus and parasphenoid: 0 limited or no contact; 1, extensive contact.
- 33. Pterygoid, fusion of pterygoid and otic capsule: 0, not fused; 1, fused.
- 34. Angulosplenial, coronoid process: 0, poorly developed; 1, blade-like.
- 35. Mentomeckelian bone: 0, present; 1, absent.
- 36. Jaw articulation, position: 0, lateral to the otic capsule; 1, at the anterior margin of the otic capsule.
- 37. Teeth: 0, pedicellate, 1, non-pedicellate, 2, absent.

Hyobranchium

- 38. Posteromedial process, length: 0, length less than half the anteroposterior length of the lower jaw; 1, length more than half the anteroposterior length of the lower jaw.
- 39. Posteromedial process, anterior end: 0, wider than posterior end; 1, narrower than posterior end.
- 40. Parahyoid bone: 0, present; 1, absent.
- 41. Ceratohyal (= hyale): 0, not ossified; 1, ossified.

Postcranial characters

- 42. Vertebral centra, shape: 0, cylindrical; 1, depressed.
- 43. Vertebral centra, articulation facets: 0, notochordal; 1, opisthocoelous; 2, procoelous.
- 44. Postzygapophyses, articulation facets: 0, flat; 1, with grooves and ridges; 2, curved ventrally.
- 45. Presacral vertebrae, neural spines: 0, sagittal; 1, parasagittal.
- 46. Presacral Vertebrae I and II: 0, separate, weak or no imbrication; 1, separate, broad imbrication; 2, fused.
- 47. Ribs: 0, free ribs present in larvae and adults; 1, free ribs present in larvae and fused to transverse processes in adults; 2, ribs absent in larvae and adults.
- 48. Sacrum and urostyle: 0, not fused; 1, fused.
- 49. Clavicle, relationship to scapula: 0, lateral end contacts medial edge of pars acromialis; 1, lateral end overlaps anterior edge of scapula; 2, lateral end is fused to scapula.

50. Clavicle, medial end: 0, not expanded; 1, expanded.

- 51. Scapula, proportions: 0, glenoid area one-third total length of the scapula; 1, glenoid area more than one-third total length of the scapula.
- 52. Scapula, medial notch: 0, present, 1, absent.
- 53. Cleithrum: 0, not covering the posterior edge of the suprascapular cartilage; 1, covering part of the posterior edge of the suprascapular cartilage.
- 54. Coracoid, sternal expansion relative to coracoid length: 0, sternal expansion less than half the length of the coracoid; 1, sternal expansion nearly half the length of the coracoid; 2, sternal expansion nearly the length of the coracoid.
- 55. Ilium, supra-acetabular expansion: 0, present; 1, absent.
- 56. Ilium, preacetabular expansion: 0:present; 1, absent.
- 57. Pubis: 0, cartilaginous; 1, ossified.

58. Distal os sesamoides tarsale: 0, absent; 1, present.

Appendix 2

Data matrix of the 58 characters coded among the five outgroup taxa and the 19 ingroup taxa

			5				10)			15			2	20			2	25			3	0			35	5			40			4	5			50)		5	5	58
Ascaphus truei	0 0	0	0 0	0	2	1 (0 0	0	0	2 (0	0 0	0 0	1 () (0 0	0	0 0) (0 0	0	0 0	0	0	0	0 0	0	1	0 0	0 0	0 0) ()	0.0	0	0	0	1 0	1	1 0	1 (0	0 0
Avitabatrachus uliana	? 1	0	1 1	0	?() 1	0	0	1	??	?	? '	? 1	1 ?	?'	? 0	1	??	? 2	2 0	0	? 0	1	0	0	0?	1	?	0 0)?	?	1	0 0	2	1	1	1 0	1	0 ?	0.0	0	??
Bombina variegata	0 0	0	0 0	0	0 (0 0	0 (0	0	0 0	0 (0 0	0 0	0 0) (0 0	0	0.0) (0 0	0	0 0	0	0	0	1 0	0	0	0 1	0	0	11	0 0	0	0	0	0 0	1	0 0	0.0	0	0 ?
Chelomophrynus bayi	0 ?	0	? 1	0	?() (0 0	?	0	0 0	0	0 (0 0	0 ?	? (0 0	1	0 0) () 1	0	??	?	?	?	0?	?	2	0 1	0	0 0) ()	0 0	1	2	0	10	0	0 0	10	0	??
Cordicephalus gracilis	0 1	0	0 1	0	0 () ()?	0	2	??	0	0	10	1 () (0 0	1	1 () (0 0	0	0 0	1	0	0	01	0	0	0 ?	??	0	1	0 0	2	1	0	1 0	1	0 0	0.0	?	1 0
Discoglossus pictus	0 0	0	0 0	0	0 () (0 0	0	0	0 0	0	0 (0 0	0 0) (0 0	0	0 0) (0 0	0	0 0	0	0	0	0 0	0	0	0 0	0 (0 () 1	0 0	0	0	0	0 0	1	0 0	1 (0	0 0
Eoxenopoides reuningi	0 1	0	1 1	0	0 (01	1	1	1	??	0	1 () 1	1 ?	?	11	1	1 () 2	2 1	0	1 0	1	0	0	11	0	2	? ?	??	0	l 1	0 0	2	1	1	? 0	0	? (0.0	1	1 0
Hymenochirus boettgeri	11	0	1 1	0	1 (01	1	1	1 :	2 0) 1	2 () 1	1 1	1 2	2 1	1	0 1		2 1	0	2 0	1	1	1	11	1	2	0 1	1	1	l 1	2 1	2	1	1	2 0	0	0 0	21	1	1 1
Limnodynastes ornatus	0 0	0	0 0	1	0 (0 0	0 0	0	0	0 0	0	0	10	0 0) (0 0	0	0 0) ()?	0	0 0	0	0	0	1 0	0	0	0 1	1	0 () 2	0 0	2	2	0	2 0	0	0 0	0.0	0	0 ?
Llankibatrachus truebae	01	0	1 1	0	?'	? ?	21	0	1	??	0	? :	11	1 1	l'	? 1	1	1 () 2	2 0	1	1 1	1	?	?	11	0	?	1 1	?	0	1	0 0	2	1	1	2 0	1	0 1	0 1	1	? 0
Neusibatrachus wilferti	? 1	0	? 1	0	0'	? (0 0	?	0	? ?	0	0 (0 0	0 ?	? (0 0	1	0 ?	? (0 0	?	0 0	0	0	0	? 0	0	0	? ?	0 9	? () 2	? 0	2	?	0	1 0	0	1 ?	0 0	?	??
Pachycentrata taqueti	1 ?	?	? 1	1	? () 1	1	1	1	??	?	? 1	??	? ?	? 2	2 1	1	0 1		??	0	??	1	1	0	? 1	0	?	??	??	0	1	2 1	2	?	1	??	0	??	? ?	?	??
Palaeobatrachus grandipes	01	0	01	0	0 () (0 0	1	2	0 0	0	1 (0 0	1 () (0 0	1	1 ()	10	1	0 0	1	0	0	0 0	0	2	0 0	0 (0	12	0 0	2	1	0	1 0	1	1 0	10	0	1 0
Pelobates cultripes	0.0	0	0 1	1	0 (0 0	0 (0	0	0.0	0	0 0	0 0	0.0) (0 0	0	0.0) (0 0	0	0 0	0	0	0	0 0	0	0	0 0) 1	0 () 2	0.0	0	2	0	0 0	0	0 0	10	0	0 0
Pipa carvalhoi	1 1	0	1 1	0	1 () () 1	1	1	2 0	0 (1 () 1	1 1	1 1	21	1	1 1	1 2	21	0	1 0	1	0	0	1 1	1	1	0 1	1	0	1	0 1	2	1	1	1 0	0	1 0	21	1	11
Pseudhymenochirus merlini	11	0	? 1	0	1 (0 1	1	1	1 1	2 () 1	2 () 1	1 1	1 2	21	1	0 1	1 2	2 1	0	2 0	1	1	1	11	1	2	1 1	1	1	1	2 1	2	1	1	2 0	0	0 0	21	1	11
Rhinophrynus dorsalis	0 0	0	1 1	0	0 () (0 0	1	0	0 0	0	0 (0 0	0 0) (0 0	1	0 0) () 1	0	02	?	?	0	01	1	2	0 0	0 0	0 (0 0	0 0	1	2	0	1 0	0	0 0	10	0	0 0
Saltenia ibanezi	? 1	0	1 1	0	0 () () 1	0	1	? ?	0	1	1?	1 ?	?	1 1	1	1 0) (2 1	1	0?	1	0	0	1 1	1	2	1 1	?	0	1	0 0	0	1	1	1 0	1	0 ?	0.0	1	??
'Shelania' laurenti	0 ?	0	11	0	0 () () 1	0	1	1 1	?	? :	11	1 ?	?	11	1	? () 2	2?	1	??	?	?	?	1?	?	?	??	??	0	1	0 0	2	1	1	2 ?	1	??	? 1	1	??
Shelania pascuali	01	1	1 1	0	0 () () 1	0	1	? ?	0	1	11	1 1	1	1 1	1	1 0) 2	2 0	1	0 1	1	0	0	11	0	2	1 1	1	0	1	0 0	0	1	1	1 0	1	0 1	0 1	1	10
Silurana tropicalis	01	0	1 1	0	1	1 () 1	0	1	0 1	0	1 () 1	1 1	1 1	2 1	1	1 0) 2	2 0	1	1 1	1	0	0	11	0	1	1 1	1	0	1	10	0	1	1	2 1	1	0 1	0 1	1	10
Singidella latecostata	1 1	0	? 1	1	?() 1	1	1	1	??	0	2 () 1	1 1	1 1	21	1	0 1	1 2	2 1	0	10	1	1	0	??	0	2	0 1	?	0	1	2 1	2	1	1	2 ?	0	0 ?	11	1	? 1
Thoraciliacus rostriceps	0 1	0	1 1	0	?'	? (0 0	0	0	??	0	? :	1?	1 ?	? (0 0	1	1 () (0 0	0	0 0	0	0	0	? 1	0	0	??	??	0 (0 0	0 0	02	21	0	1 0	?	0 ?	0 0	?	1?
Vulcanobatrachus mandelai	0 1	0	? 1	0	1'	? ()?	0	2	??	?	? :	1?	1 ?	? 2	2 1	1	1 ?	? 1	2 1	0	0?	?	0	0	11	1	2	1 1	?	?	1?	0 0	2	1	1	1 0	1	0 ?	0 ?	1	??
Xenopus laevis	0 1	1	1 1	0	1	1 () 1	0	1	0 1	0	1 () 1	1 1	L :	1 1	1	1 () 2	2 0	1	1 1	1	0	0	1 1	0	1	1 1	1	0	1	1 0	0	1	1	2 1	1	0 1	0 1	1	$1 \ 0$
'Xenopus' romeri	01	1	1 1	0	0 () () 1	0	1	1 1	?	? :	??	? ?	?	1 1	1	? 0) '	??	1	??	?	?	0	??	?	?	? ?	??	0	1	0 0	2	?	1	2 ?	1	0 ?	? 1	1	??