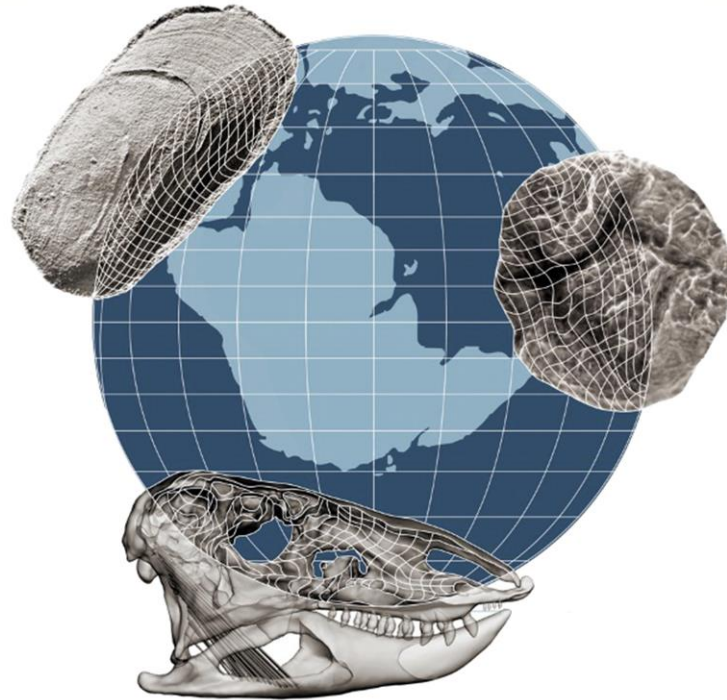




AMEGHINIANA

A GONDWANAN PALEONTOLOGICAL JOURNAL



This file is an uncorrected accepted manuscript (i.e., postprint). Please be aware that during the production process this version will definitively change. This postprint will be removed once the paper is officially published.

All legal disclaimers that apply to the journal pertain.

Submitted: 7 June 2023 - **Accepted:** 8 September 2023 - **Posted online:** 18 September 2023

To link and cite this article:

doi: [10.5710/AMGH.08.09.2023.3567](https://doi.org/10.5710/AMGH.08.09.2023.3567)

PLEASE SCROLL DOWN FOR ARTICLE

1 **NEW DATA ON THE OSTEOLOGY AND DEVELOPMENT OF**
2 ***AVITABATRACHUS ULIANA* (ANURA, XENOANURA), A PIPIMORPH FROM**
3 **THE CANDELEROS FORMATION, MID CRETACEOUS OF**
4 **NORTHWESTERN PATAGONIA, ARGENTINA**

5 ANA MARIA BÁEZ^{1, 3}, AND GUILLERMO FIDEL TURAZZINI^{2, 3}

6 ¹Museo Argentino de Ciencias Naturales, Av. Angel Gallardo 470, CP 1405, Ciudad
7 Autónoma de Buenos Aires, Argentina. baezanam@yahoo.com.ar

8 ²Departamento de Biodiversidad y Biología Experimental (DBBE), Universidad de
9 Buenos Aires, Intendente Güiraldes 2160, Pabellón II, Piso 2, CM2 of. 4, Ciudad
10 Universitaria, CP 1428. Ciudad Autónoma de Buenos Aires, Argentina.
11 gfturazzini@gmail.com

12 ³Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET)

13

14 22 pages; 6 figs.

15

16 Running Header: BÁEZ & TURAZZINI: OSTEOLOGY AND DEVELOPMENT OF
17 THE ANURAN *AVITABATRACHUS*

18 Short Description: The sacro-urostylic complex of the holotype and newly identified
19 tadpole remains of the mid-Cretaceous pipimorph anuran *Avitabatrachus uliana* are
20 discussed herein.

21

22 Corresponding author: A.M. Báez, baezanam@yahoo.com.ar

23

24

25

26

27 **Abstract.** Re-examination of the type skeleton of the pipimorph frog *Avitabatrachus*
28 *uliana* from the Candeleros Formation of northwestern Patagonia and consideration of
29 recent evidence on the development of the sacro-urostylic complex in living anurans,
30 leads to a reinterpretation of the pattern of contact of sacrum and urostyle in young post
31 metamorphs of this Cenomanian taxon and re-consideration of its diagnostic features.
32 This re-examination of the slab on which the type specimen is preserved also enabled us
33 to identify remains that represent a metamorphosing individual of the same species and
34 provide evidence for the plesiomorphic configuration of the parasphenoid and the
35 separate first two presacral vertebrae preceding fusion to one another, as in some other
36 Cretaceous pipimorphs.

37 **Keywords.** Mid-Cretaceous. Patagonia. Xenoanura. Pipimorpha. *Avitabatrachus*.
38 Sacro-urostylic complex.

39 **Resumen.** NUEVOS DATOS SOBRE LA OSTEOLOGIA Y DESARROLLO DE
40 *AVITABATRACHUS ULIANA* (ANURA, XENOANURA), PIPIMORFO DE LA
41 FORMACION CANDELEROS, CRETACICO MEDIO DEL NOROESTE DE
42 PATAGONIA, ARGENTINA. La revisión de los restos del ejemplar tipo del anuro
43 pipimorfo *Avitabatrachus uliana* Báez, Trueb, and Calvo, 2000 proveniente de la
44 Formación Candeleros del noroeste de Patagonia y la consideración de evidencia
45 reciente sobre el desarrollo del complejo sacro-urostílico en los anuros vivientes
46 condujo a la re-interpretación del patrón de contacto entre sacro y urostilo, al menos en
47 jóvenes individuos postmetamórficos de este taxón cenomaniano y a la reconsideración
48 de sus caracteres diagnósticos. Esta revisión de la laja en la que se preserva el ejemplar
49 tipo también nos permitió identificar restos que pertenecen a un individuo en
50 metamorfosis de la misma especie y que proveen evidencia de la configuración

- 51 plesiomórfica del paraesfenoides y de la separación de las primeras dos vértebras
- 52 presacras antes de su fusión subsecuente, tal como ocurre en algunos otros pipimorfos
- 53 cretácicos.
- 54 **Palabras clave.** Cretácico medio. Patagonia. Xenonura. Pipimorpha. *Avitabatrachus*.
- 55 Complejo sacro-urostílico.
- 56

57 IN 2000, BÁEZ, TRUEB, & CALVO described cranial and postcranial fossil remains that at
58 the time constituted the earliest record of pipimorph frogs (*sensu* Ford and Cannatella,
59 1993) from South America (Báez *et al.*, 2000), an anuran evolutionary lineage
60 represented today by crown-group Pipidae and distributed in tropical South America,
61 east of the Andes (*Pipa* Laurenti, 1768), and sub-Saharan Africa (*Xenopus* Wagler,
62 1827, *Hymenochirus* Boulenger, 1896, and *Pseudhymenochirus* Chabanaud, 1920).
63 These remains were recovered from beds of the lower part of the middle-upper section
64 of the Albian?- Cenomanian Candeleros Formation (Báez *et al.*, 2022; Garrido pers.
65 com. 2020), in the environs of the Ezequiel Ramos Mexia Reservoir, near the boundary
66 between Neuquén and Río Negro provinces, Argentina (Fig. 1). A new pipimorph genus
67 and species, *Avitabatrachus uliana*, was erected (Báez *et al.*, 2000) on the basis of the
68 dispersed, but partially articulated and associated, skeletal elements of one individual
69 (MUCPv123) that unquestionably had completed metamorphosis and whose snout-vent
70 length was estimated at 35 mm. In the original paper it was stated that some bones of
71 the type specimen were incompletely preserved and others were missing, and that a
72 second individual also was preserved on the same slab (Báez *et al.*, 2000). Most of the
73 preserved elements of the holotype are exposed in ventral view and a tentative
74 restoration of the holotype was depicted in the original publication (Báez *et al.*, 2000;
75 figure 4).

76 Subsequent discovery of an articulated vertebral column and a few other
77 postcranial elements of an adult pipimorph (MMCh Pv259), also from the lower part of
78 the middle section of the Candeleros Formation at a nearby locality, and comparisons of
79 this specimen with the holotype of *Avitabatrachus uliana* led to the suspicion that the
80 disarticulated fused sacrum and urostyle of the latter specimen had been erroneously
81 interpreted and that the sacral vertebra is, in fact, missing (Báez *et al.*, 2022; Báez,

82 2022). It was also suggested that the holotype of *A. uliana* might be a young
83 postmetamorph partly because the wavy transverse processes and ribs born by vertebrae
84 III and IV possibly indicated a still incomplete ossification.

85 Re-examination of the slab containing the holotype of *Avitabatrachus uliana* and
86 recent evidence provided by studies on the morphogenesis of the sacro-urostylic
87 complex in extant anurans allow us to shed new light on the identity of the bone
88 previously interpreted as the fused sacrum and urostyle and, consequently, to modify
89 the diagnosis of the species accordingly in the present note. Our re-examination also led
90 to identify the dispersed remains of an additional individual on the same slab, as
91 mentioned in passing in the original publication (Báez *et al.*, 2000), as a
92 metamorphosing tadpole of *A. uliana*. That specimen is described and briefly discussed
93 below.

94 **Institutional abbreviations.** **HUJZ**, Department of Evolution, Systematics and
95 Ecology, Hebrew University, Jerusalem, Israel; **KU**, University of Kansas, Museum of
96 Natural History and Biodiversity Center, Herpetology, Lawrence, Kansas, USA;
97 **MACN Pv N**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia,
98 Paleontología Vertebrados, Colección Neuquén, Buenos Aires, Argentina; **MMCh Pv**,
99 Museo Municipal Ernesto Bachmann, Paleontología Vertebrados, Villa El Chocón,
100 Neuquén province, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard
101 University, Cambridge, Mass, USA; **MUCPv**, Museo de Ciencias Naturales de la
102 Universidad Nacional del Comahue, Neuquén, Neuquén province, Argentina; **PVL**,
103 Paleontología Vertebrados, Instituto Miguel Lillo, Tucumán, Tucumán province,
104 Argentina.

105 **Material and Methods**

106 The specimens herein studied are housed at the vertebrate paleontology section of the
107 Museo de Geología y Paleontología of the Universidad Nacional del Comahue
108 (MUCPv). Because the type material and the referred specimen are on the same slab,
109 their collection numbers are distinguished herein as MUCPv 123 and MUCPv 123a
110 respectively. Drawings were executed under a Nikon M8 stereomicroscope, with a
111 camera-lucida attachment. Osteological terminology mainly follows those of Bolkay
112 (1919), Trueb (1973, 1996), Roček (2003), and iliac nomenclature follows Gómez and
113 Turazzini (2016). We did not stage the tadpole by reference to tables by Nieuwkoop and
114 Faber (1956) for *Xenopus laevis* (Daudin) because the specimen is not well enough
115 preserved. Age is not known and size is regarded as a reasonably good approximation in
116 most organisms (Kluge, 1988), although it has been considered problematic in anurans
117 (Yeh, 2002).

118 SYSTEMATIC PALEONTOLOGY

119 ANURA Fischer, 1813

120 XENOANURA Savage, 1973

121 PIPIMORPHA Ford & Cannatella, 1993

122 *Avitabatrachus* Báez, Trueb, & Calvo, 2000

123 **Type species.** *Avitabatrachus uliana*

124 **Diagnosis.** As for the type and only known species.

125 *Avitabatrachus uliana* Báez, Trueb, & Calvo, 2000

126 **Type material.** MUCPv 123. Associated remains of a post metamorphic individual.

127 **Referred specimens.** MUCPv 123a. Few associated bones that presumably belong to a
128 single individual; tadpole.

129 **Geographic occurrence.** El Gigante site, southeastern margin of the Ezequiel Ramos
130 Mexia Reservoir, Río Negro Province, Argentina.

131 **Stratigraphic occurrence.** Middle-upper section of the Candeleros Formation.
132 **Revised diagnosis.** Moderately small pipimorph frog (sensu Ford & Cannatella, 1993)
133 that shares with crown-group Pipidae conch-like squamosals and articulations for the
134 lower jaw at the anterolateral corners of otic capsules; sacrum and urostyle not fused to
135 one another in tadpoles and young juveniles, probably fully fused in grown adults; it
136 differs from all pipimorph taxa in having distinct flanges along the posterior halves of
137 the prootics medial to the inner ear region in adults and from those of crown-group taxa
138 also in the presence of four posterior presacral vertebrae that bear wide and distally
139 acuminate transverse processes that are not strongly directed anteriorly. Differs further
140 from *Saltenia* and *Shelania* in the presence of toothed maxillae and rectangular
141 pterygoid otic plates, and from *Saltenia* also in the fusion of the first two vertebrae in
142 postmetamorphs. The narrow cultriform process of parasphenoid in the orbital region
143 additionally distinguishes it from species of *Pipa*, *Hymenochirus*, and
144 *Pseudhymenochirus*.

145 **Comparative description of selected features of the type specimen**

146 As noted above, careful re-examination of the slab containing the remains of the
147 type specimen clarifies the identity of the bone that was interpreted previously as the
148 fused sacrum and urostyle by Báez *et al.* (2000). The ventral exposure of this bone
149 shows that the lateral margins of the hypochord are still discernible along the element,
150 denoting that it is not still fully synostotically fused to the coccyx. The anterior terminus
151 of the hypochord clearly surpasses the anterior border of the bone (Fig. 2.1– 2.2),
152 presumably reaching the preceding component of the axial column. A recent study of
153 the ontogeny of the sacro-urostylic region in a large number of living anuran taxa by
154 Pugener & Maglia (2009) led to the conclusion that in species with fused sacrum and
155 urostyle in adult stages (*e.g.*, *Xenopus laevis* (Daudin) 1802 and *Hymenochirus curtipes*

156 Noble, 1925) the hypochord extends anteriorly to the level of the overlying sacral
157 centrum before fusion with this latter element during metamorphosis, whereas in
158 species with unfused sacrum and urostyle the hypochord never exceeds the postsacral
159 vertebra. Lateral webbings may develop by the coccyx to join the expanded sacral
160 diapophyses, causing loss of mobility between the sacrum and urostyle in anurans with
161 an adult aquatic lifestyle such as those mentioned above; this condition appears to be
162 advantageous for swimming (Emerson, 1979; Emerson & De Jongh, 1980; Trueb, 1996;
163 Pugener & Maglia, 2009, among others). The foregoing evidence indicates that the
164 preserved disarticulated element of the type specimen of *A. uliana* is actually the
165 urostyle not yet fused with the sacrum and the previously identified “sacral
166 diapophyses” are the distally incomplete bony webbings developed by the anterior
167 postsacral vertebrae, which form the coccyx. In fact, the sacral vertebra of the holotype
168 of *Avitabatrachus uliana*, a post metamorph, is missing and the bony webbings might
169 have extended to ultimately fuse with the sacral diapophyses, thus limiting the
170 movement at the articulation of sacrum and urostyle. In this regard, it is noteworthy that
171 an adult vertebral column (MMCh Pv259) from the same stratigraphic unit, possibly
172 referable to *Avitabatrachus*, clearly has traces of a ventral suture between the sacrum
173 and urostyle (Báez *et al.*, 2022). In this individual mobility between these elements was
174 impeded by fusion of the bony webbings of post sacral vertebrae with the distally
175 expanded sacral diapophyses. It is also worthy of note that the specimen MACN Pv
176 N96, also from the Candeleros Formation and belonging to a metamorphosing
177 pipimorph, has two well-developed post sacral neural arch laminae bearing transverse
178 processes (Báez *et al.*, 2007). In this regard it is also significant that the holotype of the
179 Aptian postmetamorph pipimorph *Cratopipa novaolindensis* Souza Carvalho, Agnolin,
180 Aranciaga Rolando, Novas, Xavier-Neto, Freitas, & Ferreira Gomes de Andrade, 2019

181 from Brazil has a discernible postsacral neural arch bearing transverse processes (Báez
182 *et al.*, 2021). In turn, full synostotic fusion of the hypochord with the coccyx and
183 sacrum may occur relatively late in ontogeny, after the completion of metamorphosis, at
184 least in some fossil pipimorphs such as the Eocene *Shelania pascuali* Casamiquela,
185 1960 (Fig. 2. 3; parenthetically figure 2 in Báez & Trueb, 1997 depicts the actual
186 holotype of the species and not a peel) and Oligocene *Palaeobatrachus* Tschudi, 1838
187 (Roček, 2003). Moreover, in some members of the latter genus the protruding anterior
188 terminus of the hypochord remains clearly discernible on the ventral surface of the
189 sacral centrum even in well-ossified adults (Fig. 2. 4).

190 **Comparative description of remains in the same slab that represent an**
191 **immature additional individual**

192 All the bones referred to this individual (MUCPv123a) differ from the ones that
193 belong to the described holotype (Báez *et al.*, 2000) not only in their proportionally
194 much smaller sizes but also in their textural heterogeneity and irregular shades of grey
195 with some vivid red deposits that suggest a lesser degree of mineralization. The absence
196 of duplicate elements and the proportions of those preserved point to the conclusion that
197 these remains belong to a single individual. Available evidence suggests that this
198 individual was a metamorphosing, free-swimming tadpole. Comparisons of these
199 remains with those of known immature pipimorphs, mainly putative mid-Cretaceous
200 members of the stem group or crown-group taxa, based on literature as well as personal
201 examination of cited specimens, are presented below.

202 **Skull.** The relatively large otic capsules (MUC Pv123a), exposed in ventral
203 aspect, are partially preserved showing the bulging inner ear regions and, thus,
204 providing evidence for the lack of parasphenoid subotic alae (Fig. 3.1–3.2). The otic
205 capsules are separated from one another owing to the lack of medial ossification of the

206 contralateral exoccipitals and prootics, whereas the margin of the foramen magnum is
207 not completely ossified. A posteriorly convex piece of bone is discernible between the
208 otic capsules, posterodorsal to the latter; it probably belongs to the frontoparietal, an
209 azygous bone in all xenoanurans (*Rhinophrynus dorsalis* Dumeril & Bibron, 1841+
210 Pipidae Gray, 1825) (Cannatella & Trueb, 1988a). The incomplete parasphenoid is
211 exposed ventrally between the otic capsules (Fig. 3.1–3.2). The anteroposterior length
212 of the preserved portion of the parasphenoid of this specimen nearly equals that of the
213 underlying otic capsules, suggesting that the anterior long, thick, narrow cultriform
214 process observed in the holotype (Báez *et al.*, 2000) is not preserved. The most posterior
215 part of the parasphenoid is paddle-shaped (parasphenoid lateral expansions of
216 Cannatella & Trueb, 1988a) and becomes broader along the anterior portion of the otic
217 capsules (Fig. 4.3, 4.6). This broader part has slightly concave lateral margins and
218 extends just anterior to the otic capsules. This broad portion is preserved in the holotype
219 but the paddle-shaped portion is missing (Báez *et al.*, 2000; figure 5; Fig. 3.3). The
220 parasphenoid of tadpoles of the Aptian *Thoraciliacus rostriceps* Nevo, 1968 from Israel
221 have a similar distinct broad corpus in the region between the otic capsules (Roček
222 & Van Dijk, 2006; figure 1C, D; Fig. 4.1, 4.4), recalling the condition of *Rhinophrynus*
223 *dorsalis* (Trueb & Cannatella, 1982; Báez, 1996). This configuration, which might
224 represent a plesiomorphic state for pipimorphs, is unlike the one depicted in tadpoles
225 (NF stage 64) of *Xenopus laevis* by Trueb & Hanken (1992; figure 6) and present in
226 those of *Shelania pascuali* (Fig. 4.2, 4.5) in which a narrow portion of this bone extends
227 throughout the length of the otic capsules. However, a distinct paddle-like posterior
228 portion that extends along the auditory region and nearly reaches the ventral margin of
229 the foramen magnum occurs in some adults of *Xenopus* species (*e.g.*, *X. mulleri* (Peters)
230 1944 (MCZ 16311), *X. vestitus* Laurent, 1972 (KU 206873), *X. gilli* Rose & Hewitt,

231 1927 (KU 206865), *X. epitropicalis* Fischberg, Colombelli & Piccard, 1982 (KU
232 195660, Cannatella & Trueb, 1988a; figure 2) but it is undiscernible in other individuals
233 owing to the fusion of the parasphenoid with overlying bones. In contrast, the
234 parasphenoid of tadpoles of *Pipa carvalhoi* (Miranda-Ribeiro) 1937 (Sokol, 1977; plate
235 7) has a noticeably short posterior process, whereas those of *Hymenochirus boettgeri*
236 (Sokol, 1962), *H. curtipes* Noble, 1924 (KU 201134, pers. obs.), and
237 *Pseudhymenochirus merlini* Chabanaud, 1920 (Klinger-Strobel *et al.*, 2020; figure 2F)
238 lack this portion. The parasphenoid in embryos of the direct-developing *Pipa pipa*
239 (Linnaeus) 1758 at the end of metamorphic climax has an acuminate posterior end
240 (Trueb *et al.*, 2000).

241 **Axial skeleton.** One isolated vertebra partially overlying the right otic capsule is
242 preserved and is identified as v II in posterior view (Fig. 5.1– 5.2). It has a large neural
243 canal, laterally bounded by high neural arch pedicels, and bears narrow and relatively
244 short, straight transverse processes that lack the flat distal expansion present in the type
245 specimen. The centrum is dorsoventrally shallow, lacks a discernable notochordal canal,
246 and bears an unfinished articular cotyle, suggesting an epichordal pattern of vertebral
247 development and opisthocoelous condition. Behind the neural arch of this vertebra,
248 there is an impression of an overall convex margin that might correspond to the ventral
249 surface of the centrum of the first presacral rotated posteriorly (Fig. 5.1– 5.2).
250 Moreover, additional poorly preserved bony remains of the short atlas are discernable
251 slightly anterior of the neural arch of v II (Fig. 5). These two vertebrae are separate
252 unlike the fused condition of the type specimen of *A. uliana* (Báez *et al.*, 2000; figure 3)
253 and in the individual probably at the end of metamorphosis from the same formation in
254 the vicinity of Villa El Chocón (Báez *et al.*, 2007; figure 2A). Immature individuals
255 showing evidence of separate vertebrae I and II that subsequently synostotically fuse to

256 one another were presented for the Aptian *Thoraciliacus* (Trueb, 1999) and for
257 *Eoxenopoides reuningi* Haughton, 1931 from putative Upper Cretaceous or Paleogene
258 deposits of South Africa (Estes, 1977; Van Dijk, 1995). Presacrals I and II are also
259 separate from one another in tadpoles of the Early Cretaceous *Shomronella jordanica*
260 Estes, Spinar & Nevo, 1978 from Israel, the atlas occasionally bearing a transverse
261 process (Estes *et al.*, 1978; Roček & Van Dijk, 2006; figures 3E, J₂). In some crown-
262 group taxa, such as *Pipa*, *Hymenochirus*, and *Pseudhymenochirus*, the first presacral
263 vertebra is short and bears transverse processes and spinal nerve foramina for SN I+II,
264 suggesting that it represents fused presacrals I and II (Cannatella & Trueb, 1988b).
265 However, only a single cartilaginous element is present early in development in the few
266 species for which data are available, such as *H. curtipes* (Pugener, 2002) and
267 *Pseudhymenochirus merlinii* (Klinger-Strobel *et al.*, 2020). The opisthocoeleous
268 condition of the vertebral centrum also occurs in the type specimen of *Avitabatrachus*
269 *uliana* and in the early Cretaceous *Thoraciliacus* (Nevo, 1968; Trueb, 1999), as well as
270 in all pipids. In turn, the presumably epichordal pattern of development, present in
271 crown-group taxa, contrasts with the perichordal pattern of *Rhinophrynus dorsalis*
272 (Kluge and Farris, 1969) and *Thoraciliacus* (Nevo, 1968; Trueb, 1999), the latter of
273 which probably represents the plesiomorphic condition for pipimorphs (Báez, 2013).

274 **Pelvic girdle.** An isolated left ilium, about 6 mm in total length, is preserved
275 near the otic capsules (Fig. 6.2–6.3). It is exposed in lateral (acetabular) aspect, showing
276 the posterior body that bears the anterior part of the acetabulum as well as a great
277 portion of the anterior shaft. There is no evidence for the presence of a dorsal crest
278 along the ilial shaft, which also is absent in the type specimen of *Avitabatrachus uliana*
279 (Fig. 6.1). The dorsal prominence is slightly incomplete but it is longer than high and
280 both its anterior and posterior margins slope downwards at a low angle. Its apex lies

281 slightly anterior of the level of the anterior margin of the acetabular fossa. The
282 acetabular fossa is higher than long, and has an extruded anteroventral margin and an
283 even dorsal one (Fig. 6.2). The ventral acetabular expansion is narrow in acetabular
284 view; its anterior margin and the ventral margin of the iliac shaft form a wide angle. In
285 contrast, the dorsal acetabular expansion has a distinct dorsal vector. These features
286 occur in the ilium of the holotype of *Avitabatrachus uliana* (Báez *et al.*, 2012; figure 4).
287 Although few features of the ilium of *Thoraciliacus rostriceps* are known, the lack of a
288 dorsal crest along the iliac shaft was commented on by Trueb (1999) in her revision of
289 the species. Adult individuals of the coeval *Nevobatrachus* (replacement name for
290 *Cordicephalus* because the latter was preoccupied; Mahoney, 2019) also lack any
291 indication of prominent flanges or crests on the iliac shaft. Additionally, in
292 *Nevobatrachus*, the dorsal prominence is low and wide-based and distinct infra-and
293 supracetabular expansions are exposed in acetabular view (Trueb & Báez, 2006).

294 **Appendicular skeleton.** Although not figured here, some disarticulated
295 components of the appendicular skeleton that presumably belong to the same immature
296 individual are discernible on the slab. However, their poor preservation precludes
297 detailed descriptions and only the anteroposterior length of some of these elements,
298 which lack ossified epiphyses, can be roughly measured. The humerus (7 mm), the
299 radioulna (4 mm), and metacarpal (2.5 mm) are present among the forelimb elements,
300 whereas only the femur, tibiofibula (nearly 9 mm), tibiofibulare, and one metatarsal can
301 be identified among the hindlimb bones.

302 **CONCLUSIONS**

303 The type specimen of the pipimorph *Avitabatrachus uliana* (Báez *et al.*, 2000) from the
304 mid Cretaceous Candeleros Formation was originally described as having a fused
305 sacrum and urostyle, which is considered a derived feature for adult pipids (Cannatella

306 & Trueb, 1988a, b). Re-examination of this specimen, probably a young
307 postmetamorph, allowed us to confirm that the urostyle is not fully fused to the sacral
308 vertebra, the latter of which is actually missing in this specimen. Since changes in
309 morphological traits are necessarily mediated by changes in the processes that generate
310 them (DiFrisco & Jaeger, 2021), the anteriorly projecting tip of the hypochord suggests
311 that, as in extant pipids, the fused sacrum and urostyle in adults is the result of a
312 developmental mode in which the hypochord extends to and fuses with the sacral
313 centrum, as proposed by Pugener & Maglia (2009). In this contribution we also describe
314 some poorly ossified additional remains that probably belong to a metamorphosing
315 tadpole of this species. The distinct corpus of the parasphenoid of this individual is
316 unlike that of living pipids and, conversely, recalls the plesiomorphic configuration for
317 xenoanurans. This study also furnishes evidence for the separate condition of presacrals
318 I and II preceding fusion, as in some other Cretaceous pipimorph taxa, revealing
319 insights into the ontogenetic development in this group.

320

321 **ACKNOWLEDGMENTS**

322 We would like to express our gratitude to the late Jorge Calvo (Proyecto Dino,
323 Universidad Nacional del Comahue, Lago Barreales) for his help and hospitality to
324 AMB, providing access to the material under his care in the Lago Barreales facility,
325 Neuquén, Argentina. We are also thankful to the reviewers James Gardner (Tyrrell
326 Museum, Drumheller, Alberta, Canada) and Paula Muzzopappa (Fundación Felix de
327 Azara, Buenos Aires, Argentina), as well as the handling editor Martin Ezcurra (Museo
328 argentino de Ciencias Naturales) for their thoughtful comments that improved the
329 manuscript. The leading author also thanks Linda Trueb (University of Kansas, USA)
330 for her generosity, permanent encouragement, and lifelong friendship.

- 332 Báez, A. M. (1996). The fossil record of the Pipidae (Chapter 18). In R. C. Tinsley & H.
333 R. Kobel (Eds.), *The biology of Xenopus*. The Zoological Society of London
334 (pp. 329–347). Clarendon Press.
- 335 Báez, A. M. (2013). Anurans from the Early Cretaceous Lagerstätte of Las Hoyas,
336 Spain: New evidence on the Mesozoic diversification of crown-clade Anura.
337 *Cretaceous Research*, *41*, 90–106.
- 338 Báez, A. M. (2022, November 2–5). *Preliminary report on recent finds from the*
339 *Albian?-Cenomanian Candeleros Formation of northwestern Patagonia,*
340 *Argentina, and their bearing on the evolution of pipimorph frogs (Anura,*
341 *Xenoanura)*. [Poster presentation] Program and Abstracts of the 82nd Annual
342 Meeting of the Society of Vertebrate Paleontology, Toronto, Canada.
- 343 Báez, A. M., Gómez, R. O., & Taglioretti, M. L. (2012). The archaic ilial morphology
344 of an enigmatic pipid frog from the upper Pleistocene of the South American
345 pampas. *Journal of Vertebrate Paleontology*, *32* (2), 304–314.
- 346 Báez, A. M., Muzzopappa, P., & Araújo, O. G. S. (2022). New remains from the
347 Cenomanian Candeleros Formation, Neuquen Basin (Patagonia, Argentina)
348 provide insights into the formation of the sacro-urostylic complex in early
349 pipimorph frogs (Amphibia, Anura). *Cretaceous Research*, *129*, 105026.
- 350 Báez, A. M., Muzzopappa, P., & Moura, G. J. B. de (2021). The earliest records of
351 pipimorph frogs from South America (Aptian, Crato Formation, Brazil): A
352 critical evaluation. *Cretaceous Research*, *121*, 104728.
- 353 Báez, A. M., Muzzopappa, P., & Nicoli, L. (2007). Anurans from the Candeleros
354 Formation (?Cenomanian-Turonian) of west-central Argentina: new evidence
355 for pipoid evolution. *Cretaceous Research*, *28*, 1005–1016.
- 356 Báez, A. M. & Trueb, L., 1997. Redescription of the Paleogene *Shelania pascuali* from
357 Patagonia and Its Bearing on the Relationships of Fossil and Recent Pipoid
358 Frogs. *Scientific Papers*, Natural History Museum, University of Kansas, *4*, 1–
359 41.
- 360 Báez, A. M., Trueb, L., & Calvo, J. (2000). The earliest known pipoid frog from South
361 America: a new genus from the middle Cretaceous of Argentina. *Journal of*
362 *Vertebrate Paleontology*, *20*, 490–500.

- 363 Bolkay, S. J. (1919). Osnove uporedne osteologije anurskih batrahija sa dodatkom o
 364 porijeklu Anura i sa slikom narajnova sistema istih. *Glasnik Zemaljskov Muzeja*
 365 *Bosni Hercegovini*, 31, 277–353.
- 366 Boulenger, G.A. (1896). A new genus of aglossal batrachian. *The Annals and Magazine*
 367 *of Natural History Ser VI*, 420.
- 368 Cannatella, D. C. & Trueb, L. (1988a). Evolution of pipoid frogs: intergeneric
 369 relationships of the aquatic frog family Pipidae (Anura). *Zoological Journal of*
 370 *the Linnean Society of London*, 94, 1–38.
- 371 Cannatella, D. C., & Trueb, L. (1988b). Evolution of pipoid frogs: morphology and
 372 phylogenetic relationships of *Pseudhymenochirus*. *Journal of Herpetology*, 22,
 373 439–456.
- 374 Carvalho, I. S., Agnolin, F., Aranciaga Rolando, M., Novas, F. E., Xavier-Neto, J.,
 375 Freitas, F. I. & Gomes de Andrade, J. A. F. (2019). A new genus of pipimorph
 376 frog (Anura) from the Early Cretaceous Crato Formation (Aptian) and the
 377 evolution of South American tongueless frogs. *Journal of South American Earth*
 378 *Sciences*, 92, 222–233.
- 379 Casamiquela, R. M. (1960). Datos preliminares sobre un pipoideo fósil de Patagonia.
 380 *Actas y Trabajos del Primer Congreso Sudamericano de Zoología*, 1, 17–22.
- 381 Chabanaud, P. (1920). Contributions a l' étude de la faune herpétologique de l'Afrique
 382 Occidentale. Note préliminaire sur les resultats d'une misión scientifique en
 383 Guinée Francaise (1919–1920). *Bulletin du Comité d'Études Historiques et*
 384 *Scientifiques de l'Afrique occidental Française 1920*, 489–497.
- 385 Daudin, F. M. (1802). *Histoire Naturelle des Rainettes, des Grenouilles et des*
 386 *Crapauds*. Lerrault, Paris.
- 387 DiFrisco J. & Jaeger J. (2021). Homology of process: developmental dynamics in
 388 comparative biology. *Interface Focus*, 11, 20210007.
- 389 Duméril, A. M. C. & Bibron, G. (1941). *Erpétologie Générale ou Histoire Naturelle*
 390 *Complète des Reptiles 9*. Librairie Roret, Paris.
- 391 Emerson, S. (1979). The iliosacral articulation in frogs: form and function. *Biological*
 392 *Journal of the Linnean Society*, 11, 153–168.
- 393 Emerson, S., & De Jongh, J. (1980). Muscle activity at the iliosacral articulation on
 394 frogs. *Journal of Morphology*, 166, 129–144.
- 395 Estes, R. (1977). Relationships of the South African fossil frog *Eoxenopoides reuningi*
 396 (Anura, Pipidae). *Annals of the South African Museum*, 73, 49–80.

- 397 Estes, R., Spinar, Z. V., & Nevo, E. (1978). Early Cretaceous pipid tadpoles from Israel
398 (Amphibia: Anura). *Herpetologica*, 34, 374–393.
- 399 Fischberg, M., Colombelli, B. & Picard, J. J. (1982). Diagnose préliminaire d'une
400 espèce nouvelle de *Xenopus* du Zaïre. *Alytes*, 1, 53–55.
- 401 Fischer, G. (1813). *Zoognosia tabulis synopticis illustrata, in usum prælectionum*
402 *Academiæ Imperialis Medico-Chirurgicæ Mosquensis edita. 3rd edition,*
403 *Volume I.* Nicolai Sergeidis Vsevolozsky, Moscow.
- 404 Ford, L., & Cannatella, D. C. (1993). The major clades of frogs. *Herpetological*
405 *Monographs*, 7, 94–117.
- 406 Gómez, R. O., & Turazzini, G. F. (2016). An overview of the ilium of anurans
407 (Lissamphibia, Salientia), with a critical appraisal of the terminology and
408 primary homology of main ilial features. *Journal of Vertebrate Paleontology*,
409 36, e1030023.
- 410 Gray, J. E. (1825). A synopsis of the genera of reptiles and Amphibia, with a
411 description of some new species. *Annals of Philosophy Series 2*, 10, 193–217.
- 412 Haughton, S. (1931). On a collection of fossil frogs from the clays at Banke.
413 *Transactions of the Royal Society of South Africa*, 19, 233–249.
- 414 Klinger-Strobel, M., Olsson, L., Glaw, F., & Müller, H. (2020). Development of the
415 skeleton in the dwarf clawed frog *Pseudhymenochirus merlini* (Amphibia: Anura:
416 Pipidae). *Vertebrate Zoology*, 70, 435–446.
- 417 Kluge, A. G. (1988). The characterization of ontogeny. In C. J. Humphries (Ed.)
418 *Ontogeny and Systematics* (pp 57–381) Columbia University Press, New York.
- 419 Kluge, A. G., & Farris, J. S. (1969). Quantitative phyletics and the evolution of anurans.
420 *Systematic Zoology*, 18, 1–32.
- 421 Laurent, R. F. (1972). Amphibiens. *Exploration de Parc national Virunga. Ser 2*, 1–
422 125.
- 423 Laurenti, J. N. (1768). *Specimen medicum exhibens synopsis reptilium emendatum cum*
424 *experimentis circa venena et antidota.* Reptilium Austracorum, Wien.
- 425 Linnaeus, C. (1758). *Systema Naturae per Regna Tria Naturae, Secundum Classes,*
426 *Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, I,*
427 L. Salvii, Stockholm, Sweden.
- 428 Mahoney, S. (2019). *Cordicephalus* Nevo, 1968 (Amphibia, Anura, Pipimorpha), is a
429 junior homonym of *Cordicephalus* Wardle, 1947 (Rhabditophora, Cestoda,

430 Diphyllbothriidae). *Journal of Vertebrate Paleontology*, 39, DOI:
431 10.1080/02724634.2019.1593186.

432 Miranda Ribeiro, A. (1937). Sobre uma coleção de vertebrados do nordeste brasileiro:
433 Primera Parte: peixes e batracios. *O Campo*, Rio de Janeiro, 54–56.

434 Nevo, E. (1968). Pipid frogs from the Early Cretaceous of Israel and pipid evolution.
435 *Bulletin of the Museum of Comparative Zoology*, 136, 255–318.

436 Nieuwkoop, P. D. & Faber, J. (1956). *Normal Table of Xenopus laevis (Daudin). A*
437 *systematical and chronological survey of the development from the fertilized egg*
438 *till the end of metamorphosis*. North Holland Publishing Company, Amsterdam.

439 Noble, G. K. (1924). Contributions to the herpetology of the Belgian Congo based on
440 the collection of the American Museum Congo Expedition. Part III Amphibia.
441 *Bulletin of the American Museum of Natural History*, 49, 147–347.

442 Peters, W. C. H. (1844). Über einige neue Fische und Amphibien aus Angola und
443 Mozambique. *Monatsberichter der Koniglichen Preussische Akademie des*
444 *Wissenschaften zu Berlin*, 1844, 32–37.

445 Pugener, L. A. (2002). *The vertebral column and spinal nerves of anurans*.
446 [Unpublished PhD dissertation]. University of Kansas.

447 Pugener, L. A. & Maglia, A. M. (2009). Developmental evolution of the anuran sacro-
448 urostylic complex. *South American Journal of Herpetology*, 43, 193–209.

449 Rage, J-C., & Dutheil, D. B. (2008). Amphibians and squamates from the Cretaceous
450 (Cenomanian) of Morocco. A preliminary study, with description of a new genus
451 of pipid frog. *Palaeontographica, Abteilung A: Palaeozoologie-Stratigraphie*,
452 285, 1–22.

453 Roček, Z. (2003). Larval development and evolutionary origin of the anuran skull. In H.
454 Heatwole, & M. Davies (Eds.). *Amphibian Biology, vol. 5. Osteology*. (pp.
455 1877–1995). Surrey Beatty and Sons.

456 Roček, Z., & Van Dijk, E. (2006). Patterns of larval development in Cretaceous pipid
457 frogs. *Acta Palaeontologica Polonica*, 51, 111–126.

458 Rose, W. & Hewitt, J. (1927). Description of a new species of *Xenopus* from the Cape
459 Peninsula. *Transactions of the Royal Society of South Africa*, 14, 343–346.

460 Savage, J. M. (1973). The geographic distribution of frogs: patterns and predictions.
461 (Chapter 13). In L. H. Vial (Ed.), *Evolutionary Biology of the Anurans*.
462 *Contemporary Research on Major Problems*. (pp. 351–445). University of
463 Missouri Press.

- 464 Sokol, O. (1962). The tadpole of *Hymenochirus boettgeri* (Tornier). *Copeia*, 1962, 273–
465 284.
- 466 Sokol, O. (1977). The free-swimming *Pipa* larvae with a review of *Pipa* larvae and
467 pipid phylogeny (Anura: Pipidae). *Journal of Morphology*, 154, 354–426.
- 468 Tornier, G. (1896). Reptilien, Amphibien. In K. Möbius (Ed.). Die Thierwelt Ost-
469 Afrikas (pp. 1–164). Dietrich Reimer, Berlin.
- 470 Trueb, L. (1973). Bones, frogs, and evolution (Chapter 2). In J. E. Vial (Ed.).
471 *Evolutionary Biology of the Anurans*. (pp. 65–132). University of Missouri
472 Press.
- 473 Trueb, L. (1996). Historical constraints and morphological novelties in the evolution of
474 the skeletal system of pipid frogs (Anura: Pipidae) (Chapter 19). In R. C.
475 Tinsley, & H. R. Kobel (Eds.). *The biology of Xenopus*. (pp. 349–377). The
476 Zoological Society of London, Clarendon Press.
- 477 Trueb, L. (1999). The Early Cretaceous pipoid anuran *Thoraciliacus*: redescription,
478 reevaluation, and taxonomic status. *Herpetologica*, 55, 139–157.
- 479 Trueb, L., & Báez, A. M. (2006). Revision of the Early Cretaceous *Cordicephalus* from
480 Israel and an assessment of its relationships among pipoid frogs. *Journal of*
481 *Vertebrate Paleontology*, 26, 44–59.
- 482 Trueb, L., & Cannatella, D. C. (1982). The cranial osteology and hyolaryngeal
483 apparatus of *Rhinophrynus dorsalis* (Anura: Rhinophrynidae) with comparisons
484 to Recent pipid frogs. *Journal of Morphology*, 171, 11–40.
- 485 Trueb, L., & Cannatella, D. C. (1986). Systematics, morphology, and phylogeny of
486 genus *Pipa*. *Herpetology*, 42, 412–449.
- 487 Trueb, L., Hanken, J. (1992). Skeletal development in *Xenopus laevis* (Anura: Pipidae).
488 *Journal of Morphology*, 214, 1–41.
- 489 Trueb, L., Pugener, A., & Maglia, A. M. (2000). Ontogeny of the bizarre: an
490 osteological description of *Pipa pipa* (Anura: Pipidae), with an account of
491 skeletal development in the species. *Journal of Morphology*, 243, 75–104.
- 492 Tschudi, J.J. (1838). *Classification der Batrachier, mit Berücksichtigung der fossilen*
493 *Thiere diese Abtheilung der Reptilien*, 3–100, Petitpierre, Neuchâtel.
- 494 Van Dijk, D. E. (1995). Fossil Anura from southern Africa. *Madoqua*, 19, 57–60.
- 495 Wagler, J. (1827). Untitled footnote. *Isis von Oken*, 20, 726.
- 496 Yeh, J. (2002). The evolution of development: two portraits of skull ossifications in
497 pipoid frogs. *Evolution*, 56, 2484–2498.

498 **FIGURE CAPTIONS**

499 **Figure 1.** Location of the El Gigante fossil site along the margin of the Ezequiel
500 Ramos Mexia Reservoir, near the boundary between Río Negro and Neuquén provinces,
501 Argentina, from which the type of *Avitabatrachus uliana* (MUCPv 123) and referred
502 specimen (MUCPv 123a) were recovered.

503 **Figure 2.** Comparative sacro-urostylic region of select pipimorph taxa. **1–2**
504 *Avitabatrachus uliana* (MUCPv 123, holotype). Disarticulated urostyle with traces of
505 hypochord margins. **3**, *Shelania pascuali* (PVL 2186, holotype). Latex peel of the
506 holotype, which belongs to an individual that might be at the end of metamorphosis in
507 ventral aspect, showing the ossified hypochord not fully fused to the coccyx. **4**,
508 *Palaeobatrachus* sp. (KU 124939). Latex peel of mature individual in ventral aspect,
509 showing the anterior terminus of the hypochord reaching the sacral vertebra (IX), part
510 of synsacrum. **coc**, coccyx; **hyp**, hypochord. Scale bar equals 2 mm.

511 **Figure 3.** *Avitabatrachus uliana* (MUCPv123a). Tadpole remains. **1**,
512 *Avitabatrachus uliana* (MUCPv123a). Partial otic capsules, parasphenoid, and two
513 anterior-most presacral vertebrae of metamorphosing individual in ventral view. **2**,
514 Schematic drawing of same remains. **3**, left, partial parasphenoid of tadpole; center,
515 tentative restoration of parasphenoid of tadpole; right, parasphenoid of holotype
516 (MUCPv 123). **fp**, frontoparietal; **ps**, parasphenoid; **ps1**, presacral vertebra 1; **ps2**,
517 presacral vertebra 2; **roc/loc**, right/left otic capsule. Scale bar equals 2 mm.

518 **Figure 4.** Comparative parasphenoid morphology in select pipimorph taxa. **1–4**,
519 *Thoraciliacus rostriceps* (HUJZ Th 03). Ventral aspect of metamorphosing individual,
520 stage NF 60 (modified from Roček and Van Dijk, 2006); restoration of the same. **2–5**,
521 *Shelania pascuali* (PVL 4009), ventral aspect of the parasphenoid in metamorphosing

522 individuals; restoration of the same; **3–6**, *Avitabatrachus uliana* (MUCPv123a).

523 Parasphenoid in ventral aspect; restoration of the same. Scale bar equals 2 mm.

524 **Figure 5.** *Avitabatrachus uliana* (MUCPv123a). 1, Anterior-most two presacral

525 vertebrae. **2**, interpretive drawing of the same. **cen**, vertebral centrum of ps 1; **ped**,

526 pedicel; **ps1**, presacral vertebra 1; **ps2**, presacral vertebra 2; **rm**, red mark; **trp**,

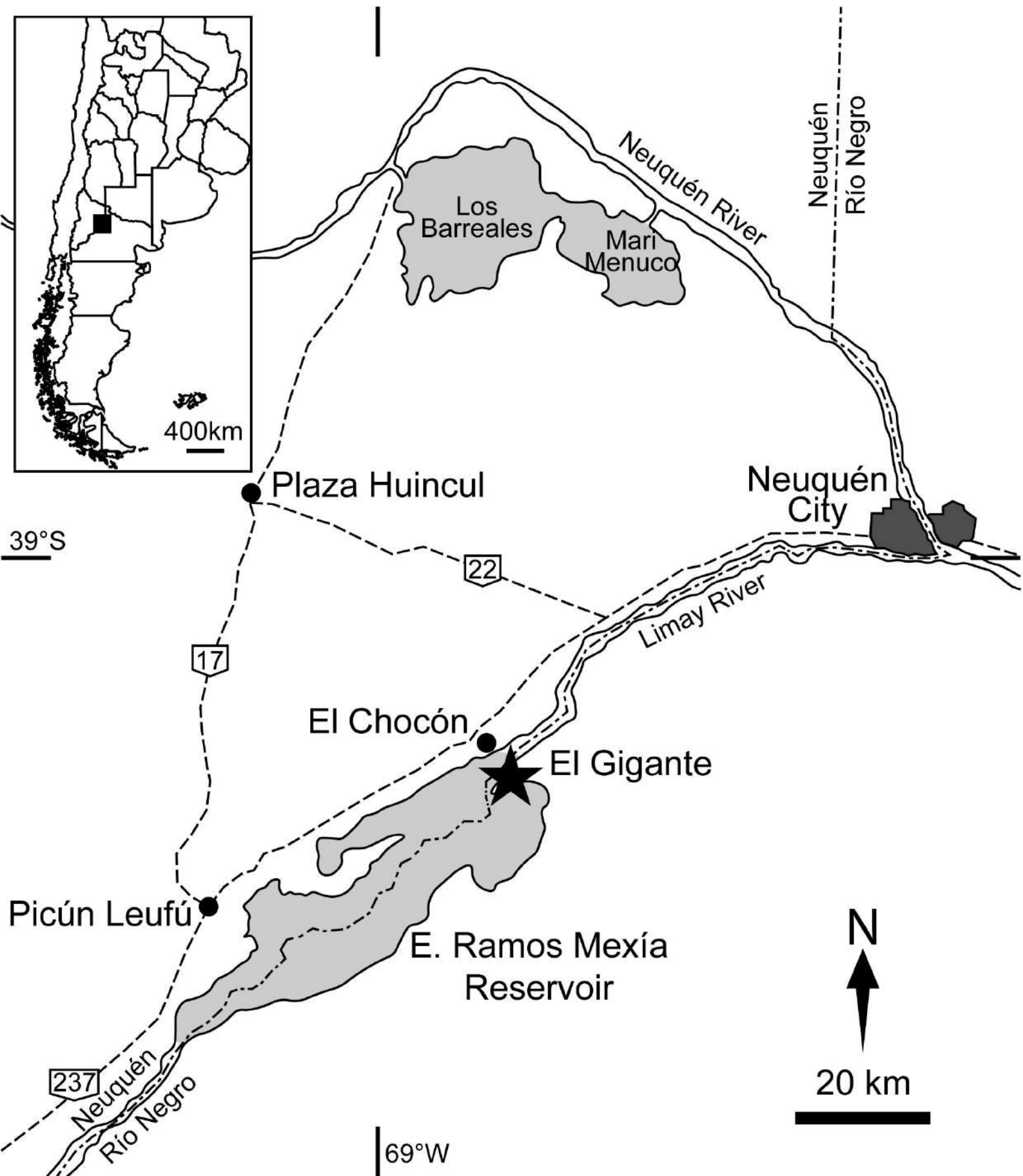
527 transverse process; Scale bar equals 2 mm.

528 **Figure 6.** *Avitabatrachus uliana*. **1**, left ilium of holotype (MUCPv123); **2**, Left

529 ilium of metamorphosing individual (MUCPv123a) exposed in lateral (acetabular)

530 view; **3**, interpretive drawing of 2. **af**, acetabular fossa; **dae**, dorsal acetabular

531 expansion; **dp**, dorsal prominence; **is**, iliac shaft. Scale bar equals 2 mm.



1

