



Osteological development and homology of the prenasal bones in the neotropical toad *Rhinella fernandezae* (Anura: Bufonidae)



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ABSTRACT

Bufonid toads of the *Rhinella granulosa* species group are reported to have paired prenasal bones typically absent in other bufonids. The homology of the prenasal bone is explored throughout ontogeny herein by studying larvae, froglets, and adult *R. fernandezae*. I found that these putative bones are actually part of the enlarged and exposed anterior ends of the septomaxillae. An unpaired prenasal bone not previously described for other toads was found at the anterior end of the snout of *R. fernandezae*. Its position, origin, and shape indicate this bone is a homologue with the prenasal described for some casque-headed hylids.

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1. Introduction

Trueb (1970) coined the term “prenasal bone” to describe an unpaired dermal bone she found in the snout of some species of the casque-headed hylid genera *Aparasphenodon* Miranda Riberio (1920), and *Tripriion* Cope (1866). A decade later, Pregill (1981, 1982) described paired elements in the snouts of toads of the *Peltophryne peltoccephala* (Tschudi, 1839) and *Rhinella granulosa* (Spix, 1824) as “rostral bones.” Pramuk (2000) preferred the term “prenasal” rather than “rostral,” and provided a more detailed description of these bones for several species of the *Rhinella granulosa* species group. No similar paired rostral bones occur in other anurans or other lissamphibians (Roček, 2003).

Trueb (1970) considered the unpaired prenasal bone of casque-headed hylids to be neomorphic given the bone has no clear homology with respect to the similarly positioned ancient bones present in rhpidistians and early tetrapods (Vorobyeva, 2003). Similarly, Pregill (1981) and Pramuk (2000) thought that the paired prenasals of certain bufonids are also neomorphic. Herein, I compare the adult osteology, and the larval and postmetamorphic cranial development of two species representing two different species groups of *Rhinella* (Fitzinger, 1826) to assess the homology of the prenasal bones. *Rhinella fernandezae* (Gallardo, 1957) of the *R. granulosa* species group has prenasals, whereas *R. arenarum* (Hensel, 1867) which belongs to the *R. marina* (Linnaeus, 1758) species group lacks them.

2. Materials and methods

All specimens examined were housed at the amphibian collection of the Museo de La Plata (MLPA, Appendix A). The specimens (advanced larvae, froglets and adults) of both species were stained for bone (red) and cartilage (blue), and then cleared following the technique of Taylor and Van Dyke (1985). Thus, a bone was classified as chondral when it forms a matrix of red stain tissue within a pre-extant cartilaginous structure. On the contrary, a dermal bone usually appears either “floating” on a soft tissue matrix or tapering but never into pre-extant cartilaginous structures.

Larvae were staged according Gosner (1960), and froglets were ordered according their snout–vent length (SVL). General bone and cartilage terminology followed Duellman and Trueb (1994). Exceptions are the configuration of the septomaxillae for which I followed Roček (2003) and the cheek and otic bones which were named on the basis of the homology criteria proposed by Alcalde and Basso (2013). Terms relative to different kinds of bone ornamentation (exostosis, co-ossification) followed Trueb (1973).

3. Results

3.1. Adult morphology of the bones of the snout in *R. fernandezae* and *R. arenarum*

The species differed in the number of rostral bones. *Rhinella fernandezae* has five (premaxilla, maxilla, septomaxilla, nasal, and prenasal; Fig. 1A–H) whereas *R. arenarum*, which lacked a prenasal, has four. The additional unpaired dermal bone present in

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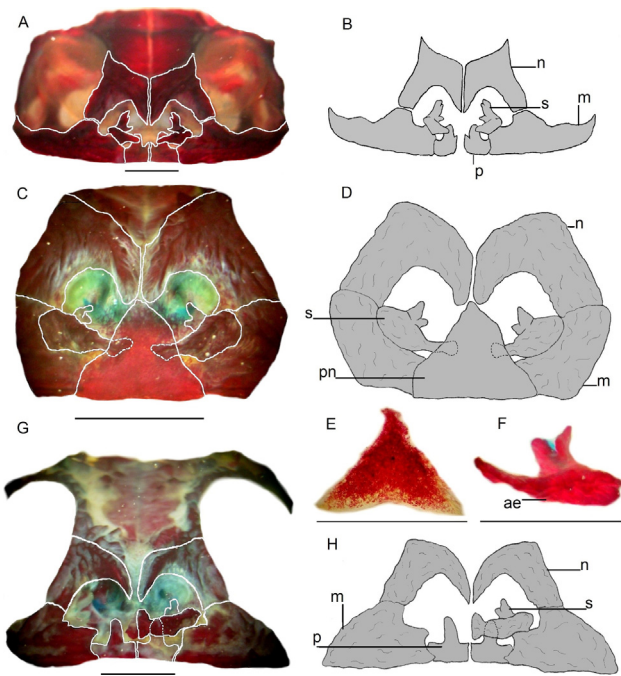


Fig. 1. Photo (A), and line drawn (B) of a 25 mm SVL froglet of *Rhinella fernandezae* (MLPA5770) in a frontal view of the rostral and snout bones previous ossification of the prenasal. Photo (C), and line drawn (D) of a 47 mm SVL female of *R. fernandezae* (MLPA5775) in a frontal view showing the complete set of rostral and snout bones of the species. Frontal view of the triangular unpaired prenasal (E) and of the right septomaxilla (F) which was removed from the specimen MLPA5775. Photo (G), and line drawn (H) of the MLPA5775 specimen of *R. fernandezae* in a frontal view once the prenasal and the right premaxilla were removed. All scale bars: 3 mm. References: ae: anterior end of the septomaxilla; m: maxilla; p: premaxilla; n: nasal; pn: prenasal; s: septomaxilla.

R. fernandezae was considered here to be a prenasal and its homology is discussed below. The most anterior bone of the snout is the unpaired, triangular prenasal in *R. fernandezae* (Fig. 1C–E). This bone obscured the anteromedial ends of the maxillae, the medial anterior ends of the septomaxillae and the entire premaxillae (Fig. 1C, D). The prenasal has no contact with the cartilages of the nasal capsules or the other bones of the snout.

The septomaxillae of both species laid entirely within the nasal capsules (except by their anterior ends on *R. fernandezae*) and were deeply integrated with nasal cartilages (Fig. 1A–D). The main body of each septomaxilla (also termed *pars horizontalis*) has three processes (Figs. 2 C, 3 C)—the infrafenestral, dorsal, and ventral. The nasolacrimal duct crossed the *pars horizontalis* via a groove between the ventral and dorsal processes rather than by a foramen as is usual in other anurans (Figs. 2 C, 3 C). The oblique cartilage is attached to the dorsal, ventral and infrafenestral processes of the septomaxilla (Fig. 2). The anterior and anterolateral faces of the body of the septomaxillae were highly exostosed and very developed in adult *R. fernandezae* (Fig. 2). The anterior ends of the septomaxillae of this species were exposed outside the nasal capsules and obscured the dorsal part of the alary processes of the premaxillae and the anteromedial ends of the maxillae (Fig. 1C, D and G, H). In large adult *R. fernandezae*, the anterior ends of the left and right septomaxillae may touch at midline (Fig. 1C, D). In *R. arenarum*, the anterior ends of the septomaxillae were few developed and scarcely exostosed; the septomaxillae of this species is located entirely within the nasal capsules and did not extend over the alary process of the premaxillae. The anteromedial faces of the *pars horizontalis* septomaxillae of both species formed the *margo libera*. The area between the *margo libera* and the medial face of the dorsal process formed the con-

tact crest (Figs. 2, 3), the point at which the cartilaginous *crista intermedia* and the septomaxilla met.

The paired, dermal, and edentate premaxilla comprised three non-exostosed parts—the *pars dentalis*, *pars palatina* and the alary process. Given the absence of a prenasal in *R. arenarum*, the entire premaxillae were visible frontally. The *pars dentalis* premaxillae and the anterior ends of the maxillae have a delicate connection. The medial flanges of both premaxillae were separated by connective tissue. Remaining parts of the premaxillae lacked bony contact with adjacent bones but some have contact with the nasal cartilages. The short, triangular *pars palatina* was in contact with the slightly calcified nasal floor, and the high, slender alary process was laid adjacent to the superior prenasal cartilage. The unique structural difference in the premaxillae of both species was the configuration of the *pars palatina*; it was bifid in *R. arenarum* with medial and lateral processes, but the lateral process was absent in *R. fernandezae*.

The heavily ossified, edentate, and slightly exostosed maxillae of *Rhinella arenarum* and *R. fernandezae* were in contact with other bones. It contacted the premaxilla (*pars dentalis*), vomer (anterior arm) and septomaxilla (anterior end) anteriorly, quadratojugal posteriorly, nasal anterodorsally, neopalatine anteromedially (point contact), and anterior arm of the pterygoid posteromedially (broad area of contact, wider in *R. fernandezae*).

The paired, dermal nasals of both species roofed the rostrum. Left and right nasals have a complete medial articulation with one another. Each nasal articulated the frontoparietal posteriorly, maxilla (*pars facialis*) laterally, and neopalatine ventrolaterally. Anteriorly, the nasal may be articulated either the alary process of the premaxilla (*R. arenarum*) or the anterior end of the septomaxilla (*R. fernandezae*). Exostosis and co-ossification were verified in both *Rhinella arenarum* and *R. fernandezae*, but they were more marked in the latter. The entire nasal of *R. fernandezae* is covered with dermal ornamentation that obscured both nasal–nasal and nasal–frontoparietal articulations. The dorsal lamina of the nasal of this species bore transverse ridges of exostosed bone, along with bony tubercles. In contrast, bony sculpturing in *R. arenarum* consisted of bony tubercles restricted to the cephalic crests of the nasal; the nasal and frontoparietal articulations are never obscured. The posteroventral face of the nasal invested the posterior part of the roof of the nasal capsule, which in turn, is invaded by the anterior growth of the sphenethmoid. Similarly, the posteromedial face of the maxillary process of the nasal has a delicate area of contact with the part of the sphenethmoid that invaded the anteorbital plate.

3.2. A development context for the homology of the prenasals. Ossification sequence and developmental features of the snout and rostral bones of *R. fernandezae* and *R. arenarum*

The premaxillae were the first snout bone to ossify in *Rhinella arenarum* and *R. fernandezae* (Table 1). The dermal, rectangular centre of each alary process of the premaxilla appeared between Stages 38 (*R. arenarum*) and 39 (*R. fernandezae*). The shape and developmental change of the premaxillae were almost the same in both species. Each centre invested the dorsal face of the corresponding trabecular horn. In Stage 43, the premaxillae reached adult configuration and position.

The nasals and septomaxillae appeared at different stages between species but at the same stage within each species (Stage 40: *R. fernandezae*; Stage 41: *R. arenarum*; Table 1); but intra-stage variation within each species indicated the septomaxillae ossify first. The *pars horizontalis* of both septomaxillae developed in the sides of the nasal capsule adjoining most anterior nasal cartilages (*crista intermedia*, alary cartilage) and covered the anteromedial ends of the nasal sacs. The U-shaped dermal centre of each nasal appeared on the dorsal face of the cartilaginous roof of the nasal

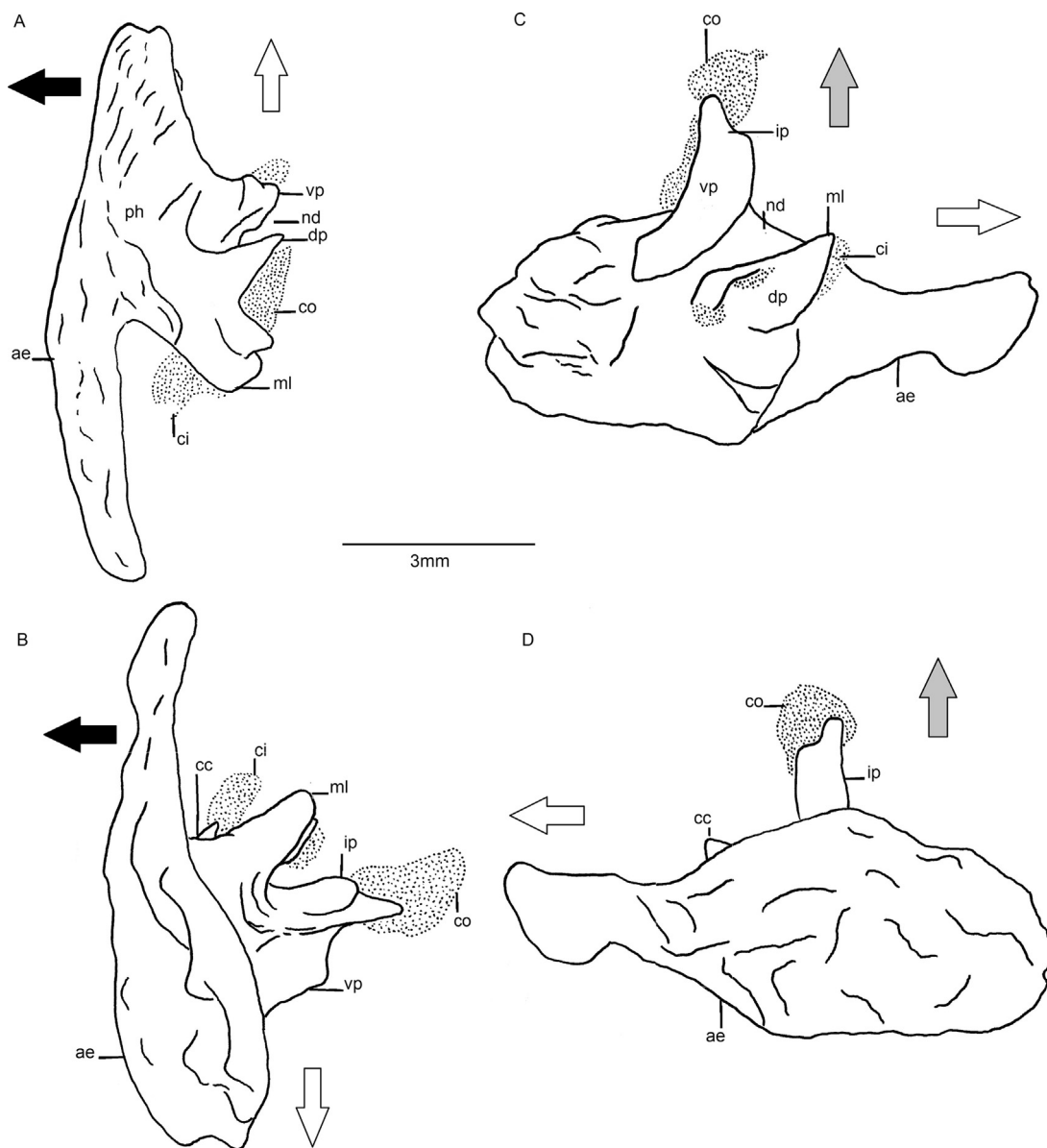


Fig. 2. (A) Ventral, (B) dorsal, (C) caudal, and (D) frontal views of the right septomaxilla of *Rhinella fernandezae* (MLPA5775). References: ae: anterior end of the septomaxilla; cc: contact crest; ci: *crista intermedia*; co: cartilage oblique; dp: dorsal process; ip: infrafenestral process; ml: *margo libera*; nd: nasolacrimal duct; ph: *pars horizontalis*; vp: ventral process. Arrows indicate anterior (black), dorsal (gray), and medial (white) sides of the structures.

capsule just anterior to the antorbital plate. The last rostral bones to ossify were the maxillae that were first represented by the square dermal centre of each *pars facialis*. It ossified in Stages 42 (*R. arenarum*) and 43 (*R. fernandezae*) and invested the subnasal crest laterally.

Both shape and position of the centres of the snout and rostral bones began to change in Stage 41 in both *Rhinella arenarum* and *R. fernandezae*. (1) The alary process of each premaxilla transitioned from an almost horizontal through an oblique to a vertical position in Stage 42. (2) The *partes dentalis* and *palatina* of each premaxilla began to grow from the ventral region of the alary process of both species in Stages 41 and 42. (3) The size of the *pars horizontalis* of each septomaxilla increased in Stages 42 and 43. (4) During Stage 42, the centre of each nasal in both species expanded anteroposteriorly and mediolaterally conserving the initial U-shape. (5) In Stage 43, each maxilla began to grow caudally along the lateral face of the pterygoid process. (6) The medial end of the *pars horizontalis* of each septomaxilla of *R. fernandezae* developed two processes dur-

ing Stage 43; the most ventral of them is the anterior end of the septomaxilla, which enlarged and projected anteriorly during Stage 45. In addition, the *pars horizontalis* of each septomaxilla projected laterally and caudally forming a semicircle. (7) The *pars dentalis* of each maxilla appeared postmetamorphically.

The postmetamorphic development of *Rhinella fernandezae* was characterized by an increase in bone to bone contact, along with an increasing dermal sculpturing. Contact between nasal and neopalatine and maxilla and septomaxilla was detected at the smallest available froglet's Stage (18 mm SVL). All froglets of *R. fernandezae* have advanced bone development (i.e., bone area, bone to bone contact, exostosis) than did similar-sized froglets of *R. arenarum*. All snout and rostral bones of the 18 mm SVL froglets of *R. fernandezae* were nearly articulated and bore marked ornamentation indicative of the adult condition of the species; these features were elaborated in the 25 mm SVL froglets of the species (Fig. 1A, B). The 13 and 28 mm SVL froglets of *R. arenarum* were poorly ossified in contrast to those of *R. fernandezae*. The amount of ossification in the smallest

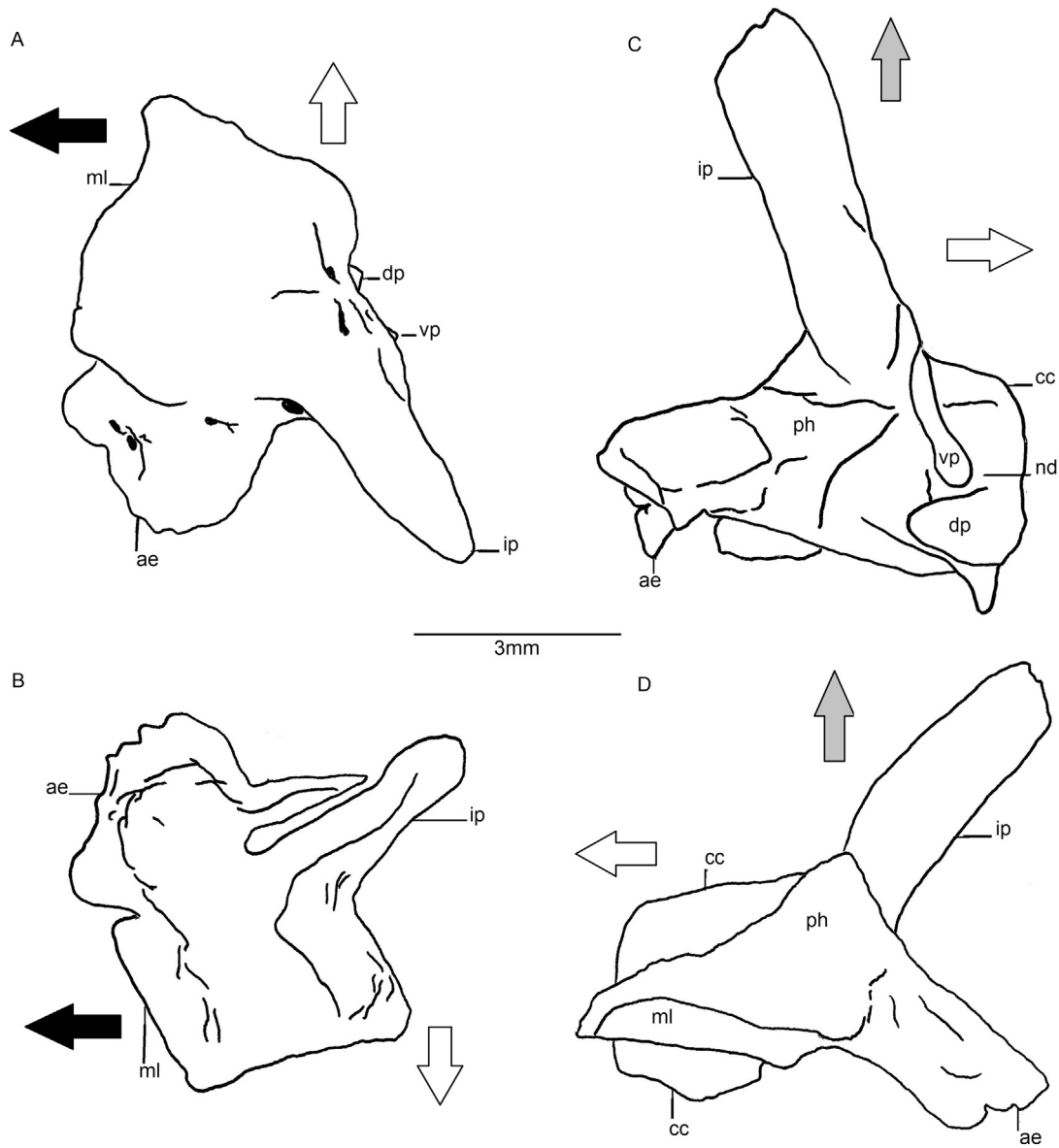


Fig. 3. (A) Ventral, (B) dorsal, (C) caudal, and (D) frontal views of the right septomaxilla of an adult female of *Rhinella arenarum* (MLPA5732). See Fig. 2 for references. Arrows indicate anterior (black), dorsal (gray), and medial (white) sides of the structures.

froglets of *R. arenarum* resembled that of advanced larvae, rather than adults. The only bone articulation was that between the maxilla and quadratojugal and bone sculpturing of the nasal, maxilla, and premaxilla appeared at 28 mm SVL froglets of *R. arenarum*. The 30 mm SVL specimens of this species have increased bone to bone contact, but few bony ornaments when compared with the adult dermal sculpturing.

The skull of the 35 mm SVL juveniles of *R. fernandaeze* resembled that of adults. At this size, some specimens have the unpaired triangular prenasal (Table 1), which was absent in *R. arenarum*.

4. Discussion

This study documented that elements formerly known as “paired prenasal bones” in *Rhinella fernandaeze*, were instead ossifications of the anterior end of the septomaxillae. It also revealed the presence of an unexpected bone, the prenasal, which until now was unknown for this toad group. The homology and systematic implications of such a bone in one species of the *R. granulosa* species group are discussed below.

The adult osteology and development of the rostral bones described herein demonstrated that elements termed either “rostrals” (Pregill, 1981) or “prenasals” (Pramuk, 2000) are not separated from the septomaxillae. Instead, these ossifications, which are particularly extensive in *R. fernandaeze*, represented the anterior end of each septomaxilla. *Rhinella fernandaeze* and *R. arenarum* shared most developmental features of the septomaxilla. (1) The ossification centre of each septomaxilla appeared in Stages 40 and 41, along with the development of the alary cartilage and the *crista intermedia*. (2) The sequence of ossification is first premaxilla, second septomaxilla, third nasal, and fourth maxilla. The species differed developmentally in the more rapid development of the septomaxillary processes in *R. fernandaeze* than in *R. arenarum*. The accelerated development of the septomaxilla in *R. fernandaeze* continued during postmetamorphic development and resulted into a significant increase in size of the element, which is particularly marked with respect to the anterior end of the bone.

The unpaired triangular bone I observed in all *Rhinella fernandaeze* larger than 35 mm SVL appeared postmetamorphically as a diffuse centre of dermal ossification. Its general shape, the unpaired

Table 1
Ossification sequence of the skull bones of *Rhinella fernandezae* and *R. arenarum*. Chondral bones are in boldface.

STAGE	<i>N</i>	<i>Rhinella fernandezae</i>	<i>N</i>	<i>Rhinella arenarum</i>
LARVAL DEVELOPMENT				
25–28	3		0	
35	2		0	
36	1	Frontoparietal (<i>f</i> ²)	2	
37	1	Exoccipital	2	Frontoparietal (<i>f</i> ²) – Exoccipital
38	1		5	1. Parasphenoid 2. Premaxilla
39	2	Parasphenoid – Premaxilla	0	
40	2	1. Septomaxilla – Opisthotic 2. Nasal	0	
41	0		8	1. Squamosal 2. Opisthotic – Prootic Septomaxilla – nasal – Angulosplenia 3. Dentary
42	1	Squamosal	6	1. Maxilla – Pterygoid 2. Tabular
43	4	1. Prootic 2. Maxilla – Dentary – Angulosplenia 3. Tabular	7	
44	1	Pterygoid	0	
45	5		1	
46	0		3	
FROGLET DEVELOPMENT				
13 mm	0		1	
15 mm	0		3	1. Mentomeckelian – Tirohyal 2. Vomer – Neopalatine
18 mm	3	Vomer – Tirohyal – Neopalatine – Mentomeckelian – Columella – Sphenethmoid	1	
25 mm	2		0	
28 mm	0		1	
30 mm	2		5	Quadratojugal – Columella
JUVENILE DEVELOPMENT				
35 mm	3	Unpaired triangular dermal element (Prenasal)	0	
ADULT DEVELOPMENT				
40–47 mm	3	Quadratojugal	0	
90 mm	0		2	Sphenethmoid

origin, its postmetamorphic development, and its position just in front to both premaxillae indicated this element is homologous with the prenasal bone of the casque-headed hylid genera *Aparasphenodon* and *Triprion* (Trueb, 1970).

Pramuk (2000) claimed that the presence of paired prenasal bones in the *Rhinella granulosa* species group supports the monophyly of the clade. The present results however clearly indicated the character needs to be re-described, but that it remains a synapomorphy of the species group. Thus, the character “prenasals present or absent” should be changed to “anterior end of the septomaxilla very developed and exposed anteriorly to the alary process of the premaxilla, or not.”

The presence of an unpaired prenasal in *Rhinella fernandezae* raised the question whether it is an autapomorphy of the species or a possible synapomorphy for the *R. granulosa* species group, pending its discovery in other species of the clade. It may have not been noticed or accidentally removed (including by authors that have previously studied *R. fernandezae*) owing to damage of skulls during the process of skin removal either for double cleared-and stained or for dry skull preparations.

The presence of a prenasal, along with a very developed anterior end of the septomaxilla and bony ornamentation (exostosis and skin co-ossification) surely must be related to the fossorial habits of *Rhinella fernandezae*. Adult *R. fernandezae* live in burrows that they dig themselves; whereas this habit might reduce water loss

and provide protection against predators and fires (Gallardo, 1957). According to Gallardo (1957), *R. fernandezae* is highly sedentary and spends most of the time in its burrow, leaving only to feed or breed. The suite of skull features described herein is used by these toads to close the openings of their burrows (phragmotic behaviour); presumably, this behaviour along with the noxious secretions of the dorsal skin glands protects the toads from predators (Gallardo, 1957; Huertas and Vallejos, 1988).

5. Conclusions

The present study explored the nature of the “prenasal” or “rostral” bones of the *Rhinella granulosa* species group by describing the ontogenetic development and adult osteology of *R. fernandezae*. The “prenasal” or “rostral” bones are actually part of the enlarged and exposed anterior ends of the septomaxillae. The unpaired prenasal bone at the anterior end of the snout of *R. fernandezae* has not been described for other bufonids. Its position, origin, and shape indicated the bone represented a homologue of the prenasal described for some casque-headed hylids.

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Appendix A.

Rhinella fernandezae. MLPA 5384: 23 larvae (stages 25–28, 35–40, 42–45) from Los Porteños–La Plata–Buenos Aires province–Argentina; **MLPA5769**: two 18 mm SVL froglets from Punta Lara–Ensenada–Buenos Aires province–Argentina; **MLPA5772**: one 18 mm SVL froglet from Punta Lara; **MLPA5770**: two 25 mm SVL froglets from Punta Lara; **MLPA5771**: two 30 mm SVL froglets from Punta Lara; **MLPA5773, 5774, 5775**: three 40 mm, 45 mm, and 47 mm adults from Punta Lara.

Rhinella arenarum. MLPA5776: 34 larvae (stages 36–38, 41–43, 45–46) from La Plata–Buenos Aires province–Argentina; **MLPA5777**: two 15 mm SVL froglets from unknown locality; **MLPA5780**: two SVL 13 mm and 15 mm froglets from Dique Ameghino–Chubut province–Argentina; **MLPA5778**: one 18 mm SVL froglet from Punta Lara; **MLPA178**: one 28 mm SVL froglet from Neuquén province–Argentina; **MLPA5779**: two 30 mm SVL froglets from Punta Lara; **MLPA179, 181, and 182**: three 30 mm SVL froglets from Neuquén province; **MLPA5732**: one 90 mm SVL female from Estancia “El Rosario”–Chascomús–Buenos Aires province–Argentina; **MLPA5731**: one 90 mm SVL male from Estancia “El Rosario”.

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