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# The Larva and Advertisement Call of *Bokermannohyla ahenea* (Anura: Hylidae)

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**Abstract.** *Bokermannohyla ahenea* is endemic to the Serra da Bocaina, a portion of the Serra do Mar in the Atlantic Forest of Southeastern Brazil. Little information is currently available about this species. Herein, we describe the larval morphology of *B. ahenea,* including internal oral features, chondrocranium, and hyobranchial apparatus, along with its advertisement call and natural history notes. This is the first description of the chondrocranium and hyobranchial apparatus for a member of the genus *Bokermannohyla.* The larval external morphology of *B. ahenea* is similar to those of other species of the *B. circumdata* group, but it can be distinguished from those of other species of the genus by its oral apparatus. The advertisement call of *B. ahenea* is complex with many numbers of notes. Also, spectral and temporal parameters of the advertisement call can be used to distinguish *B. ahenea* from its congeners.

**Keywords.** Bioacoustics; Brazilian Atlantic Forest; Chondrocranium; Larval morphology; Serra da Bocaina National Park.

## INTRODUCTION

The genus *Bokermannohyla* Faivovich et al., 2005 was erected to accommodate the species formerly assigned to the *Hyla circumdata, H. claresignata, H. martinsi,* and *H. pseudopseudis* species groups (Faivovich et al., 2005). Currently, 32 species are assigned to this genus (Frost, 2018), divided into four groups: *B. circumdata, B. claresignata, B. martinsi,* and *B. pseudopseudis* (Faivovich et al., 2005, 2009). The monophyly of the *B. circumdata* group is currently based on molecular data, pending a comprehensive morphological study (Faivovich et al., 2009). In their analysis, Faivovich et al. (2009) found a close relationship among the genera *Aplastodiscus* Lutz, 1950, *Bokermannohyla, Hyloscirtus* Peters, 1882, *Boana* Gray, 1825 (as *Hypsiboas*), and *Myersiohyla* Faivovich et al., 2005 placing them in the tribe Cophomantini Faivovich et al., 2005. The diagnosis of Cophomantini (*sensu* Faivovich et al., 2005) included three larval character states: the increase in the number of labial tooth rows, a ventral oral disc, and complete marginal papillae. Furthermore, they also pointed out that the taxonomic distribution of at least two other larval character states within this tribe deserves further scrutiny: the presence of an anteromedial loop in the prenarial arena in the buccal roof of the oral cavity and the presence of fleshy projections of variable shape at the inner margins of nostrils of larvae (Faivovich et al., 2005). However, a comprehensive set of morphological characters is still lacking for most taxa included in Cophomantini.

The same topology of Faivovich et al. (2005) with small differences in node support was found in further studies (e.g., Pyron and Wiens, 2011; Pyron, 2014; Duellman et al., 2016), but other authors took strikingly different nomenclatural decisions. For example, among other changes, Duellman et al. (2016) elevated Cophomantini to the subfamily rank. This nomenclatural decision has been followed by Frost (2018). In a recent paper, Faivovich et al. (2018) continued treating Cophomantini as a tribe, arguing that Duellman et al. (2016) did not provide any commentary in support of their view. Nonetheless, the phylogenetic hypotheses available only included 6 of the 32 species currently assigned to *Bokermannohyla,* demonstrating the large Darwinian shortfall for Neotropical taxa that impairs comparative studies (Hortal et al., 2015).

Similarly, data on the advertisement call of some species within this tribe are lacking. Although not widely used in anuran phylogenetic analysis (e.g., Sullivan et al., 1996), the advertisement call is an important taxonomic

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tool to distinguish closely related species (Martins and Jim, 2003). The advertisement call of 23 species of *Bokermmanohyla* have been described (approximately 68%), which facilitates the use of acoustic traits to differentiate closely related species (e.g., Carvalho et al., 2013). However, the evolution of advertisement call traits within this genus have never been studied.

*Bokermannohyla ahenea* has been assigned to the *B. circumdata* species group, which currently comprehends 18 species (Frost, 2018). This species is only known from its type locality in the Serra da Bocaina, southeastern Brazil, and further information on natural history is lacking. Additionally, regarding its conservation status, this species is classified as Data Deficient according to IUCN (Napoli, 2006) and the Brazilian Red List of endangered species (Brasil, 2014). This status means that habitat use, occurrence pattern, and temporal and spatial variation in abundance of this species are poorly known. The endemism and absence of information about populational trends of *B. ahenea* (Napoli, 2006) emphasize the importance of obtaining these data in the field. Herein, we describe the external morphology, internal oral features, chondrocranium, and hyobranchial apparatus of the larva of *B. ahenea* based on specimens from the type locality. We also describe the advertisement call and provide novel natural history data, including calling site, larval diet, temporal distribution, and habitat use for both adults and larvae.

## MATERIALS AND METHODS

### Study area

We carried out field work in the Serra da Bocaina National Park, São José do Barreiro, São Paulo, southeastern Brazil (22°45′5″S, 44°37′7″W, DATUM = SAD69; 1,550 m above sea level). The vegetation is typical of the Atlantic Rain Forest, with patches of highland grasslands. Samplings were conducted at 1,300–1,600 m in natural highland grasslands and high montane rainforest. A thorough description of the study area and a map showing the sampling sites is available elsewhere (Garey et al., 2014).

### Sampling

We surveyed 16 sites, including ponds, marshes, and forest rivulets monthly between April 2008 and February 2010. Samplings were carried out both during the day for tadpoles and at night for adults. Larvae of *Bokermannohyla ahenea* were collected with hand dipnets by walking around the entire margin of water bodies. We surveyed the same breeding sites for calling males (Scott Jr. and Woodward, 1994). We walked around each breeding site to quantify the number of calling males and species composition. Larvae were fixed and preserved in 10% formalin in the field. We fixed adults in 10% formalin and preserved them in 70% ethanol. Voucher specimens are deposited in the Coleção DZSJRP-Amphibia, Departamento de Zoologia e Botânica, São José do Rio Preto, and in the Coleção Célio F.B. Haddad (CFBH), Departamento de Zoologia, Rio Claro, both in the Universidade Estadual Paulista, in the state of São Paulo, Brazil (see Appendix). Voucher of the advertisement call is deposited in Fonoteca Neotropical Jacques Vielliard.

### Description of the larva

The description of the external morphology is based on 13 larvae in stages 36–38 (Gosner, 1960) collected in the field. To confirm identification, larvae were reared in plastic vials in the laboratory with a mixture of water from the sampling sites and tap water, at room temperature, and under daylight regime. Larvae fed on commercial fish food and algae from the pond where they were collected. We compared tadpoles and newly metamorphosed individuals in stages 44–46 (DZSJRP 13920, 13947, 13949–50, 13955–7) with adults of *B. ahenea* (DZSJRP 12124–7) from the same locality. We followed Altig and McDiarmid (1999) for the total length (TOL), body length (BL), tail length (TL), tail musculature height (TMH), and oral disc diameter (OD) measurements. Additionally, we took the following measurements: maximum dorsal fin height (DFH, the maximum height of dorsal fin), maximum ventral fin height (VMH, the maximum height of the ventral fin), maximum nostril diameter (ND, the greatest diameter of the nostril), maximum spiracle length (SL, the longer border of the spiracle), maximum spiracle width (SW, the greatest portion of the spiracle width), maximum spiracle opening width (SOW, the widest diameter of the spiracle opening), interocular distance (IOD, the distance between the internal margin of the eyes), and internarial distance (IND, the distance between the internal margins of the nostrils), tail musculature width (TMW, the widest portion of the tail musculature), maximum body width (BW, the widest portion of the body), maximum body height (BH, the highest portion of the body), eye–snout distance (ESD, the distance between the anterior edge of the eye and the tip of the snout), nostril–snout distance (NSD, the distance between the anterior edge of the nostril and the tip of the snout), and eye diameter (ED, the greatest diameter of the eye). We took these measurements using a stereomicroscope (Leica MZ75) coupled to an ocular grid, except for TOL, which we measured with handheld digital calipers to the nearest 0.01 mm. We followed Lannoo (1987) to describe the lateral line system and Altig and McDiarmid (1999) for external morphology terminology.



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For the description of internal oral morphology, we dissected five larvae in stages 28–38. Terminology follows Wassersug (1976). Specimens were prepared for scanning electron microscopy following the protocol of Provete (2016). For the description of chondrocranial morphology, we cleared and stained three specimens, one in stage 31 and two in 37 following Taylor and Van Dyke (1985). Terminology follows Haas (2003). Additional scanning electron microscopy images of the larval external morphology, chondrocranium, and internal oral features are available at MorphoBank (O'Leary and Kaufman, 2012), Project 2441 (http://doi.org/10.7934/P2441).

The diet of larvae collected in the field was analyzed following Rossa-Feres et al. (2004). Briefly, we took a sample of the first centimeter of the gut of five larvae in stages 35–38 collected in January 2009 and identified algae to genus according to Bicudo and Menezes (2006). We did not quantify detritus or other fine organic matter ingested.

### Advertisement call

We recorded vocalizations with a Marantz PMD222 coupled to a semi-directional Sennheiser K6 + ME 66 microphone. We recorded the advertisement call of six male *Bokermannohyla ahenea* (21 ± 24 calls per individual) at a minimum distance of 50 cm (FNJV 37788). Calls were digitized and analyzed with Raven Pro 1.4 (Bioacoustics Research Program, 2011), with sampling frequency of 44.1 kHz, 16 bits of resolution, and mono channel. Frequency measurements were made with Fast Fourier Transformation with 512 points, 90% overlap, and Hamming windows. Sound was analyzed with 50% brightness and 50% contrast. Audiospectrogram and sonogram were prepared using seewave R package (Sueur et al., 2008). Air temperature was measured with a mercury thermometer to the nearest 0.5°C.

We measured 11 call parameters, of which three were spectral—maximum frequency (Hz), minimum frequency (Hz), and dominant frequency (Hz)—and eight were temporal—call length (s), number of notes per call, note length (s), pulse number per call, pulse number per note, interval between notes (s), call rate (calls/min), and pulse rate (pulses/s). The definition of advertisement call, pulse, and note followed Toledo and Haddad (2005). Measurements followed Cocroft and Ryan (1995). We considered the number of pulses as a temporal variable because it was correlated with call duration. Data are presented as mean ± SD (range, sample size). To test for differences between notes, we used Student's *t*-test. Residuals were tested for normality and variance homogeneity.

## RESULTS

### External larval morphology

In Gosner larval stage 37, body ovoid in dorsal view (with the anterior region narrower than the posterior region), depressed in lateral view (BH/BW = 0.75–0.78 in stage 37 [*n* = 9]; Table 1; Fig. 1A–B). Snout rounded in

**Table 1.** Measurements of larvae of *Bokermannohyla ahenea* in stages 36–38. Data are in millimeters and presented as mean ± SD (range). See text for abbreviations.

| | Stage (*n*) | | |
|---|---|---|---|
| | **36 (2)** | **37 (9)** | **38 (2)** |
| TOL | 45.30 ± 2.72 (47.22–43.38) | 40.83 ± 1.54 (37.85–43.76) | 40.08 ± 2.76 (38.12–42.03) |
| BL | 15.76 ± 0.79 (15.2–16.32) | 14.67 ± 0.38 (14.4–15.36) | 14.72 ± 0.75 (14.4–15.04) |
| TL | 29.54 ± 1.92 (28.18–30.9) | 26.16 ± 1.40 (23.45–28.56) | 26.16 ± 1.40 (23.72–26.99) |
| BW | 9.92 ± 0.23 (9.76–10.08) | 10.06 ± 0.40 (9.6–10.72) | 10.16 ± 0.57 (9.76–10.56) |
| TMW | 4.48 ± 0.00 | 4.16 ± 0.29 (3.84–4.48) | 4.48 ± 0.00 |
| BH | 7.52 ± 0.23 (7.36–7.68) | 7.98 ± 0.33 (7.2–8.32) | 8.24 ± 0.79 (7.68–8.8) |
| DFH | 2.55 ± 0.21 (2.4–2.7) | 2.21 ± 0.24 (2–2.7) | 2.20 ± 0.28 (2–2.4) |
| VFH | 2.00 ± 0.00 | 1.79 ± 0.15 (1.7–2.1) | 1.65 ± 0.21 (1.5–1.8) |
| TMH | 4.72 ± 0.11(4.64–4.8) | 4.66 ± 0.17 (4.48–4.8) | 4.40 ± 0.57 (4–4.8) |
| IOD | 3.09 ± 0.31 (2.88–3.31) | 2.75 ± 0.15 (2.63–2.94) | 2.72 ± 0.13 (2.63–2.81) |
| IND | 2.78 ± 0.04 (2.75–2.81) | 2.71 ± 0.06 (2.63–2.81) | 2.63 ± 0.00 |
| ESD | 3.52 ± 0.00 | 3.59 ± 0.23 (3.36–4) | 3.36 ± 0.23 (3.2–3.52) |
| NSD | 1.76 ± 0.00 | 1.83 ± 0.20 (1.6–2.24) | 1.76 ± 0.00 |
| END | 1.76 ± 0.00 | 1.76 ± 0.13 (1.6-2.08) | 1.6 ± 0.16 (1.44-1.76) |
| ED | 1.45 ± 0.07 (1.4–1.5) | 1.68 ± 0.16 (1.3–1.8) | 1.70 ± 0.00 |
| ND | 0.37 ± 0.03 (0.35–0.39) | 0.41 ± 0.04 (0.35–0.47) | 0.37 ± 0.03 (0.35–0.39) |
| SL | 1.18 ± 0.22 (1.03–1.34) | 1.46 ± 0.41 (0.95–1.97) | 1.78 ± 0.61 (1.34–2.21) |
| SW | 1.25 ± 0.07 (1.2–1.3) | 1.28 ± 0.22 (0.8–1.5) | 1.30 ± 0.14 (1.2–1.4) |
| SOW | 0.47 ± 0.04 (0.44–0.5) | 0.56 ± 0.09 (0.44–0.75) | 0.56 ± 0.00 |
| OD | 3.03 ± 0.22 (2.88–3.19) | 3.07 ± 0.18 (2.88–3.38) | 3.25 ± 0.44 (2.94–3.56) |



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dorsal and lateral views. Eyes dorsal, oriented dorsolaterally. Nostrils elliptical with a small fleshy projection on inner marginal rim, positioned dorsally, located almost equidistant between eye and snout (NSD/END = 0.91–1.4 in stage 37 [*n* = 9]), directed dorsolaterally. Intestine visible, centered, arranged spirally. Spiracle single, sinistral, aperture directed posteriorly, inner wall attached to the body. Vent tube dextral, slightly longer than wide (length/width = 1.14, in stage 37 [*n* = 9]), inner wall attached to ventral fin. All lateral lines evident in preserved specimens; 38 neuromasts in dorsal line, 66 in middle body line, ca. 43 in fused supraorbital and infraorbital lines, 8 in posterior infraorbital, and 2 in posterior supraorbital. Ventral line with 40 neuromasts, interrupted at base of spiracle, descending to ventral region, continuing to spiracle opening and vent tube. Circular cumulus of stitches present on abdominal surface near base of vent tube. Angular lines surround venter, almost fused, with 24 neuromasts. Middle and dorsal lines fused on posterior third of tail. Medial line extending to tail tip, distance between stiches increasing on posterior third. Longitudinal oral line with 9 neuromasts, anterior oral line with 12 neuromasts. Anterior oral line initiating lateral to oral disc, ascending to near the nostrils, descending to ventral region, terminating in branchial region, comprising 16 neuromasts. A small ventrolateral stitch and a whitish set of stitches also present near end of ventral line (Fig. 1A). Tail long (TL/TOL = 0.62–0.65 in stage 37 [*n* = 9]). Dorsal fin originating at body-tail junction, its contour parallel to longitudinal axis of tail musculature. Maximum height of dorsal fin at posterior third of tail where tail muscle becomes thin. Ventral fin low, its contour parallel to longitudinal axis of tail musculature. Tail musculature wide in dorsal view (TMW/BW = 0.4–0.42 in stage 37 [*n* = 9]), high in lateral view (TMH/BH = 0.58–0.62 in stage 37 [*n* = 9]), gradually tapering towards pointed tail tip.

Oral disc ventral (OD/BW = 0.27–0.32 in stage 37 [*n* = 9]) with two posterior emarginations (Fig. 1C). Mar-

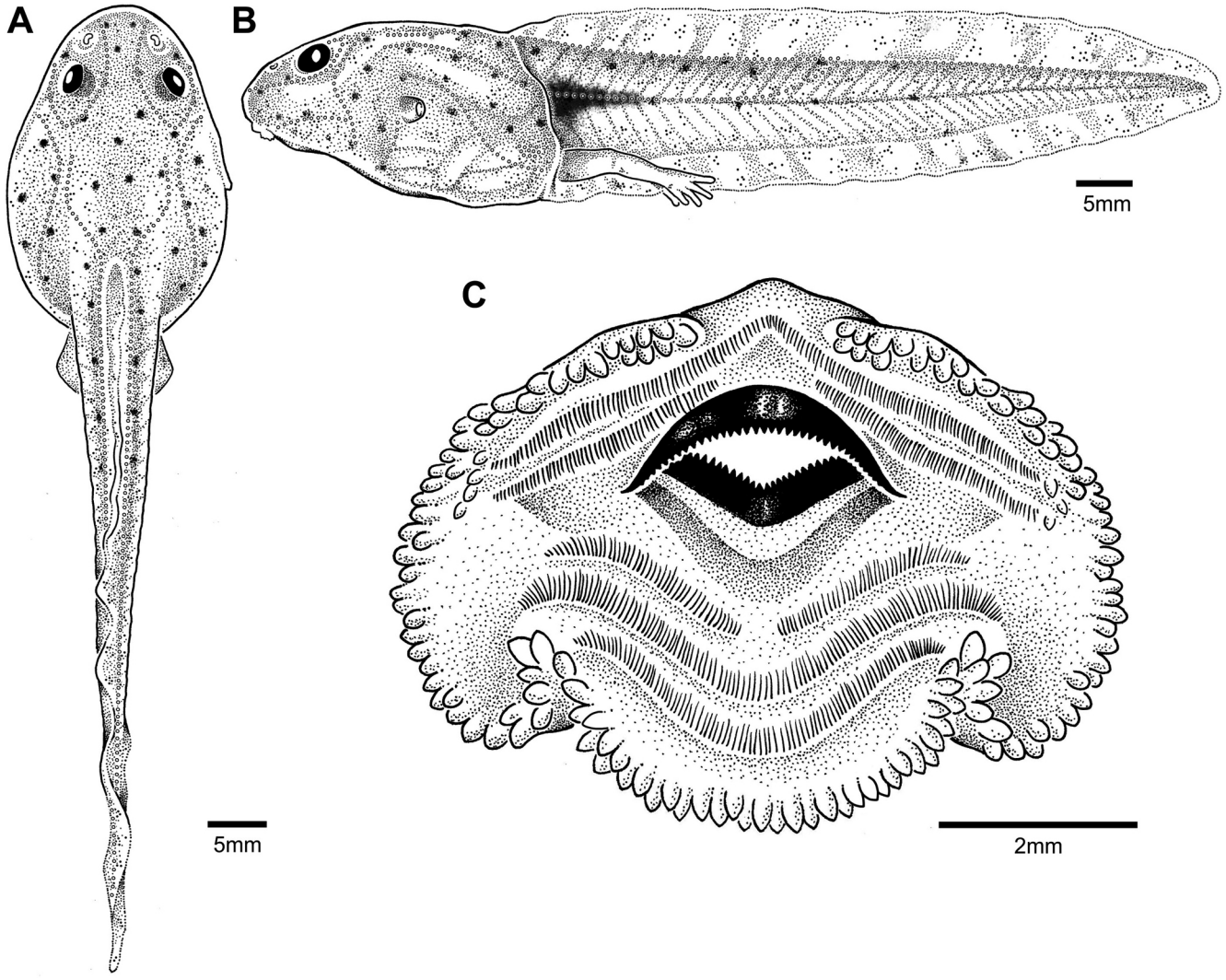



**Figure 1.** Larva of *Bokermannohyla ahenea* (DZSJRP 2496) in stage 37. **(A)** Dorsal and **(B)** lateral views, and **(C)** oral apparatus.



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ginal papillae conical, arranged in single row, alternating posteriorly and anteriorly, with a narrow anterior gap (about 12.3% of oral disc width). Papillae unpigmented, their density varying from 8–16 papillae per linear millimeter. Submarginal papillae present in some specimens (see Variation). Labial tooth row formula (LTRF) 2(2)/3(1), A-1 and A-2 with same length, P-2 slightly longer than P-1, P-3 slightly shorter than P-1 and P-2. Labial teeth slightly curved on outer edges, ca. 60 labial teeth/mm (estimated on A-1). Anterior jaw sheath arched, posterior jaw sheath V-shaped, both keratinized and finely serrated, ca. 34 serrations/mm on anterior jaw; serrations conical.

## Intraspecific variation

Submarginal papillae were present in 14 (8.5%) out of the 165 tadpoles analyzed, six (3.6%) had only one papilla laterally to P1, either on the left or right side, and only one tadpole had a row with nine submarginal papillae lateral to the posterior teeth rows. The remaining tadpoles had either two papillae on each side of P1 (1.8%), or anteriorly and posteriorly to the left side of P1 (1.2%), or six papillae on the left side of the posterior teeth rows. Most specimens of *Bokermannohyla ahenea* had abnormal asymmetric oral apparatus, such as dekeratinized mandibles and absent or fragmented teeth rows.

The inner wall of the spiracle varies from a slight ridge to completely free from body. This variation is independent of the developmental stage. The ratio between body height and body width varies ontogenetically, from 0.75–0.76 ($n$ = 2) in stage 36 to 0.79–0.83 in stage 38 ($n$ = 2). TL/TOL varies from 0.6–0.71 in stage 36 ($n$ = 2) and 0.62–0.64 in stage 38 ($n$ = 2). TMH/BH is 0.63 in stage 36 ($n$ = 2) and ranges from 0.52–0.55 in stage 38 ($n$ = 2). The ratio OD/BW varies from 0.29–0.33 in stage 36 ($n$ = 2) and from 0.30–0.34 in stage 38 ($n$ = 2).

## Larval coloration

Live larvae have a brown body with a light brown area around nostrils. The tip of the spiracle lacks pigmentation. The tail is orange. The dorsal margin of the tail musculature is reddish. The tail musculature has a pair of longitudinal dark brown stripes on the dorsal margin. There are many melanophores distributed longitudinally on the skin over the caudal musculature, with higher density on its first half. Also, some individuals present a dark mark over the axis between dorsal and ventral myomers on the anterior portion of the tail (Fig. 1B). The fins are transparent with a few small melanophores. The venter is light orange. The first third of the tail musculature has a dark bar between the upper and lower myomers that can be seen in lateral view (Fig. 1B). The iris is orange and the pupil is black. In formalin, the body turns yellowish and the tail musculature turns beige. The iris is black and pupil is white. Digital images of live larvae are available at MorphoBank (O'Leary and Kaufman, 2012), Project 2441 (http://doi.org/10.7934/P2441).

## Internal oral anatomy

Buccal floor hexagonal (Fig. 2A), wider than long. Two pairs of multiple-branching infralabial papillae: anterior pair small with four short projections, posterior pair large with several long projections. A pair of long, conical lingual papillae with pustulations at their base (Fig. 3A). Buccal floor arena (BFA) triangular, surrounded by ca. 35 conical papillae arranged in a V pattern, largest papillae bifurcated, positioned medially. Approximately 12 small papillae diverging obliquely and laterally from BFA. Approximately 10–14 small prepocket papillae, along with scattered pustulations. Approximately 120 pustulations on BFA, more concentrated posteriorly. Buccal pockets deep, oriented transversally, width twice length. Free velar surface broad with secretory pits arranged in parallel stripes between spiculae. Secretory pits absent on median notch. Posterior margin with three projections over filter cavities on each side. Spicular support distinct, spiculae thin and long. Median notch without projections, partially covering glottis, which is thick with broad lips.

Buccal roof rectangular (Fig. 2B), about 1.5 times longer than wide. Nostrils at 25% of distance from mouth to esophagus; median ridge at 40% of distance from mouth to esophagus (Fig. 2B). Prenarial arena with anteromedial loop forming inverted arch (Fig. 3B). Nostrils almost four times longer than wide. Elliptical vacuities anterior to nostrils distinct with a smooth concave bottom. Vacuities shallow. Anterior wall thick and serrated (Fig. 3B). Posterior wall thin with three thin papillae on each side. Nostrils oriented ca. 50° from transverse plane. Narial valve short. Two pairs of postnarial papillae, medial pair smaller than lateral pair. Median ridge triangular with three short papillae on margin. Lateral ridge papillae triangular with serrated margins. Buccal Roof Arena (BRA) rectangular, lacking papillae. Pustulations evenly distributed over BRA. Approximately 10 short, conical, lateral roof papillae, all similarly sized. Dorsal velum papillate, discontinuous at midline. Secretory pits small, distributed all along the dorsal velum but more concentrated anteriorly.

## Chondrocranium and hyobranchial apparatus

Neurocranium slightly longer than wide (width/length = 0.86), depressed (height/width = 0.33), greatest



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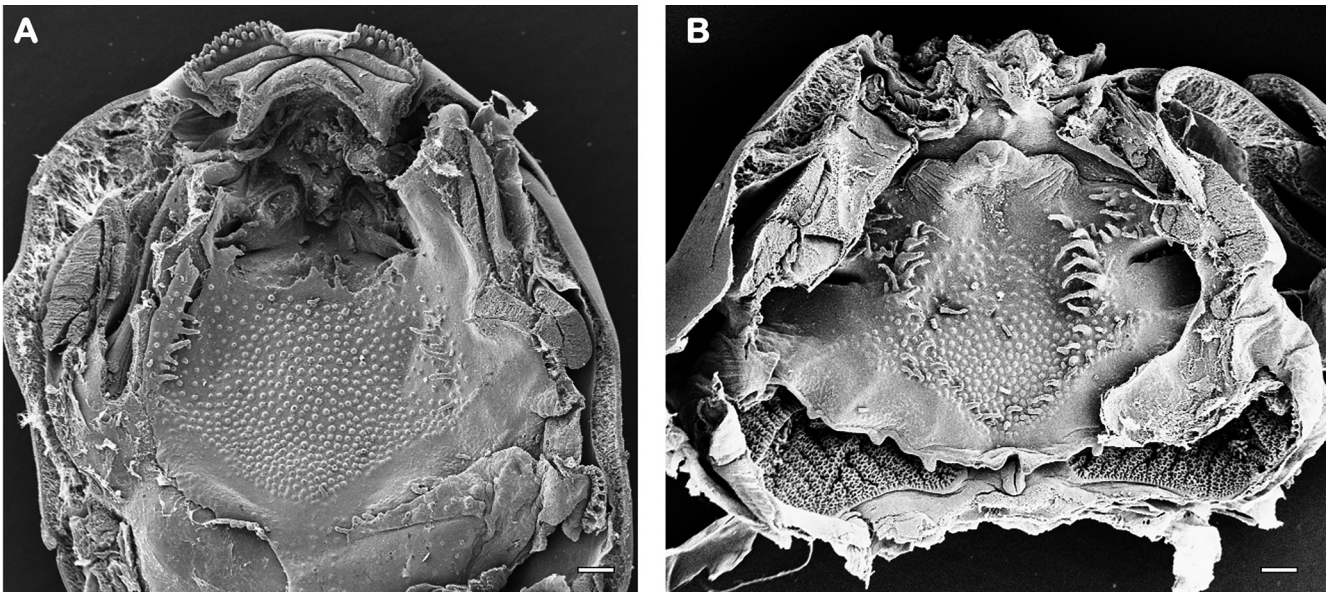



**Figure 2.** Internal oral features of larvae of *Bokermannohyla ahenea* in stage 28 (DZSJRP 1918.21). **(A)** Buccal roof and **(B)** buccal floor. Scale bars = 500 μm.

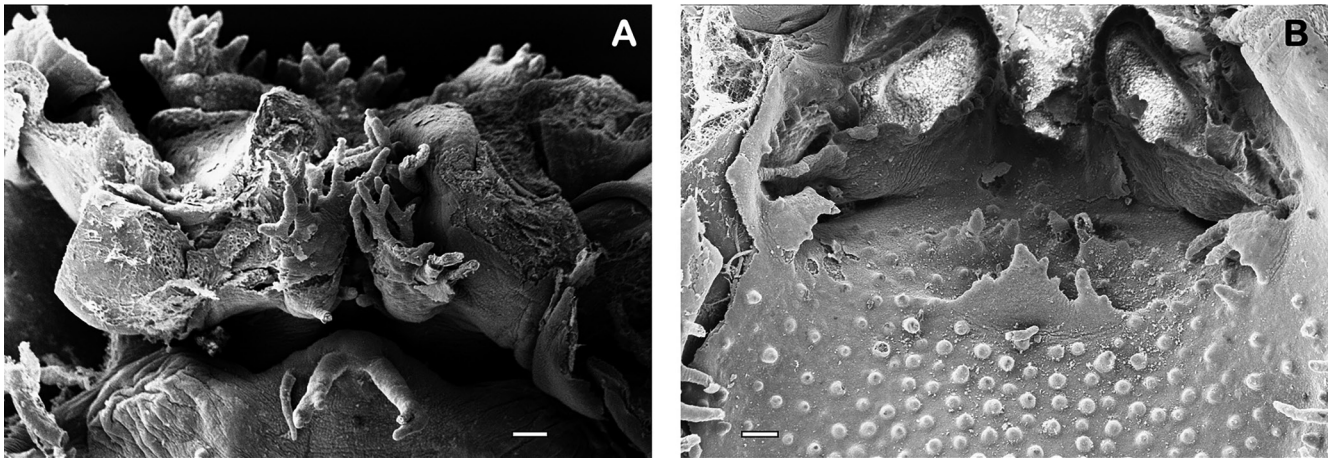



**Figure 3.** Details of the internal oral features of the *Bokermannohyla ahenea* in stage 28 (DZSJRP 1918.2). **(A)** Infralabial and lingual papillae in the buccal roof and **(B)** internal nostrils and median ridge in the buccal floor. Scale bars = 100 μm.

width at the posterior portion of the palatoquadrate. *Cartilago labialis superior* with V-shaped *pars corporis* articulating syndesmodically with *pars alaris* anteriorly, fused posteriorly (Fig. 4A). *Partes alaris* of *cartilago labialis superior* broad, slightly rounded ventrally, bearing distinct *processus posterior dorsalis* that tapers conically. Lower jaw composed of paired, syndesmodically connected *cartilago labialis inferior* and L-shaped *cartilagines Meckeli,* with a distinct, downcurved *processus retroarticularis*. *Cornua trabeculae* uniformly wide, relatively short (ca. 25% of neurocranium length), with ventrally curved tips; *septum nasi* present in *lamina orbitonasalis*. *Tectum nasi* slightly curved, wide. *Foramina olfactorium* present. *Cornua trabeculae* lack *processus lateralis*. *Cartilago orbitalis* is thin plate of cartilage surrounding rounded *cavum cranii*. *Cavum cranii* delimited posteriorly by *tectum parietale,* which is confluent and fused with *tectum synoticum* in tadpoles in stage 37. *Foramina carotica primaria* and *craneopalatina* posterolateral. Otic capsule diamond-shaped, ca. 23% of chondrocranial length. Each capsule with short, thin *processus anterolateralis* with elliptical *fenestra ovalis* ventral to otic capsule.

Palatoquadrate connected anteriorly to neurocranium by broad *commissura quadratocranialis* and posteriorly by thin *processus ascendens* with low attachment to neurocranium (Fig. 4B–C), immediately below *foramen oculomotorium* in posteroventral portion of otic capsules. *Pars articularis quadrati* articulated anteriorly with *cartilagines Meckeli*. *Processus antorbitalis* of *lamina orbitonasalis* short, broad. *Processus muscularis quadrati* triangular, broad. Tip of *processus muscularis quadrati* fastened to *processus antorbitalis* by ligamentous connection. Posteriorly, one *foramen jugulare* well defined. Notochordal canal closed anteriorly.



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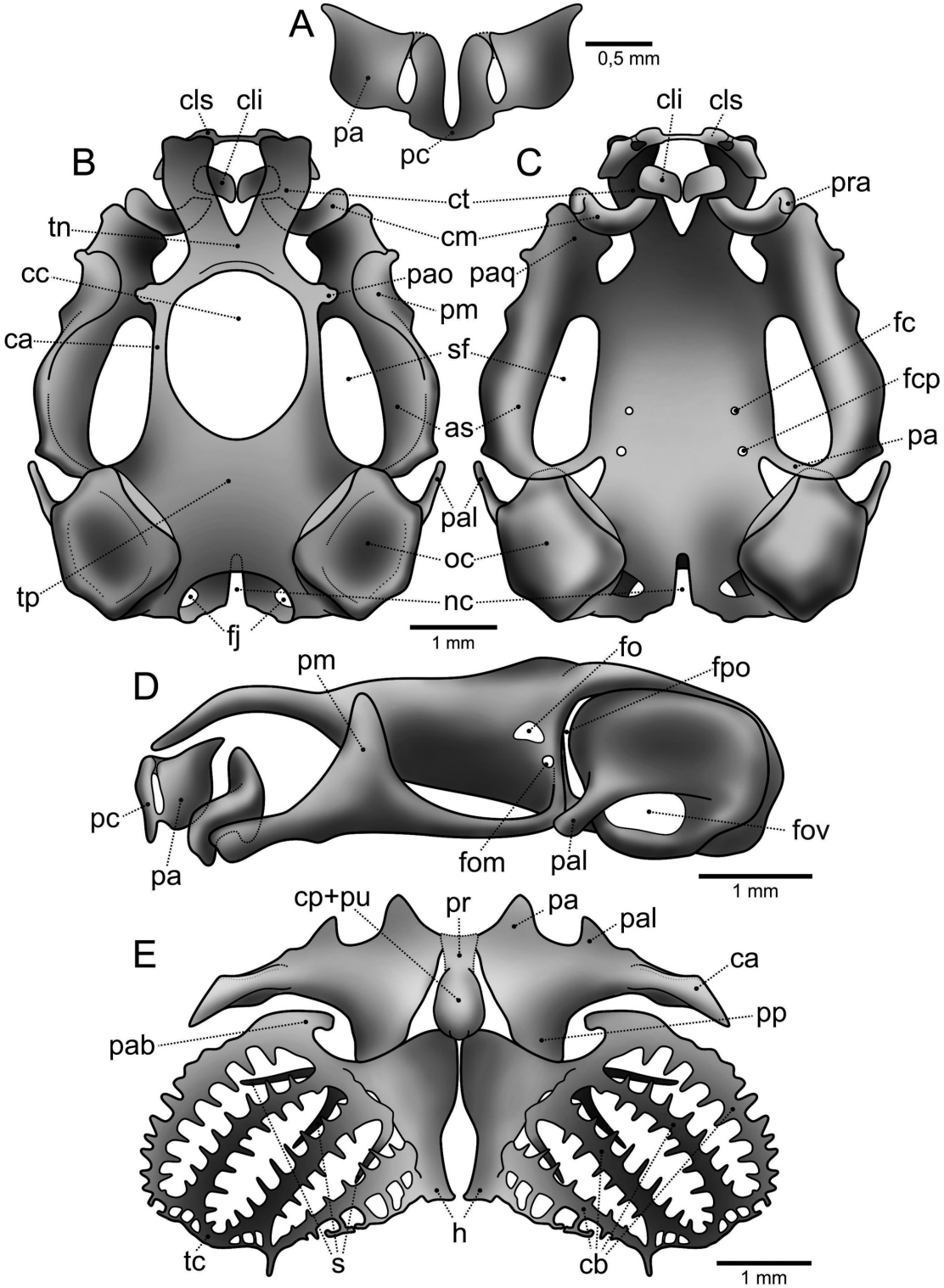



**Figure 4.** Larval chondrocranium of *Bokermannohyla ahenea* in stage 34 (DZSJRP 2494.1). **(A)** frontal view of the *cartilago labialis superior;* **(B)** dorsal, **(C)** ventral, and **(D)** lateral views of the chondrocranium; **(E)** ventral view of the hyobranchial apparatus. Legends in (B) and (C): as, *arcus subocularis;* cc, *cavum cranii;* cli, *cartilago labialis inferior;* cls, *cartilago labialis superior;* cm, *cartilago Meckeli;* ca, *cartilago orbitalis;* ct, *cornua trabeculae;* fc, *foramen craneopalatinum;* fcp, *foramen caroticum primarium;* fj, *foramen jugulare;* nc, notochordal canal; oc, otic capsule; pa, *processus ascendens;* pal, *processus anterolateralis hyalis;* pao, *processus antorbitalis;* paq, *processus articularis quadrati;* pm, *processus muscularis quadrati;* pra, *processus retroarticularis;* sf, *fenestra subocularis;* tn, *tectum nasi;* tp, *tectum parietale.* Legends in (D): fo, *foramen opticum;* fpo, *fissura prootica;* fom, *foramen oculomotorium;* fov, *fenestra ovalis;* pa, *pars alaris;* pc, *pars corporis;* pm, *processus muscularis;* pal, *processus anterolateralis hyalis.* Legends in (E): ca, *condylus articularis;* cb, *ceratobranchiales;* cp+cu, *copula posterior* and *processus urobranchialis;* h, *hypobranchiales;* pa, *processus anterior hyalis;* pab, *processus anterior branchialis;* pal, *processus anterolateralis hyalis;* pp, *processus posterior dorsalis;* pr, *pars reunens;* s, *spiculae;* tc, *commissura terminalis*.



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Hyobranchial skeleton composed of paired *ceratohyalia* articulated medially via a square *pars reuniens*, *planum hypobranchiale*, and four *ceratobranchialia* (Fig. 4D). *Basihyal* absent. *Ceratohyalia* with large *processus anterioris* and small *processus anterolateralis hyalis*. *Basibranchial* articulated ventrally with *planum hypobranchialis*, possessing tiny, pointed *processus urobranchialis*. *Ceratobranchialia* connected posteriorly by *commissurae terminales*. *Processus anterior branchialis* above *ceratobranchialis* I. Spiculae I–III present, associated with *ceratobranchialia* I–III.

**Advertisement call**

The advertisement call is composed of two types of multipulsed notes emitted sequentially (A and B; Fig. 5), usually varying from 3–4 notes per call. However, more than 10 notes are rarely emitted in a single call (5.24 ± 7.07, *n* = 32). Note A can be either multipulsed or not, while note B is always multipulsed. The maximum frequency of note A is 1,316.7–2,017.1 Hz (1,736.6 ± 156, *n* = 72), minimum frequency is 392.2–

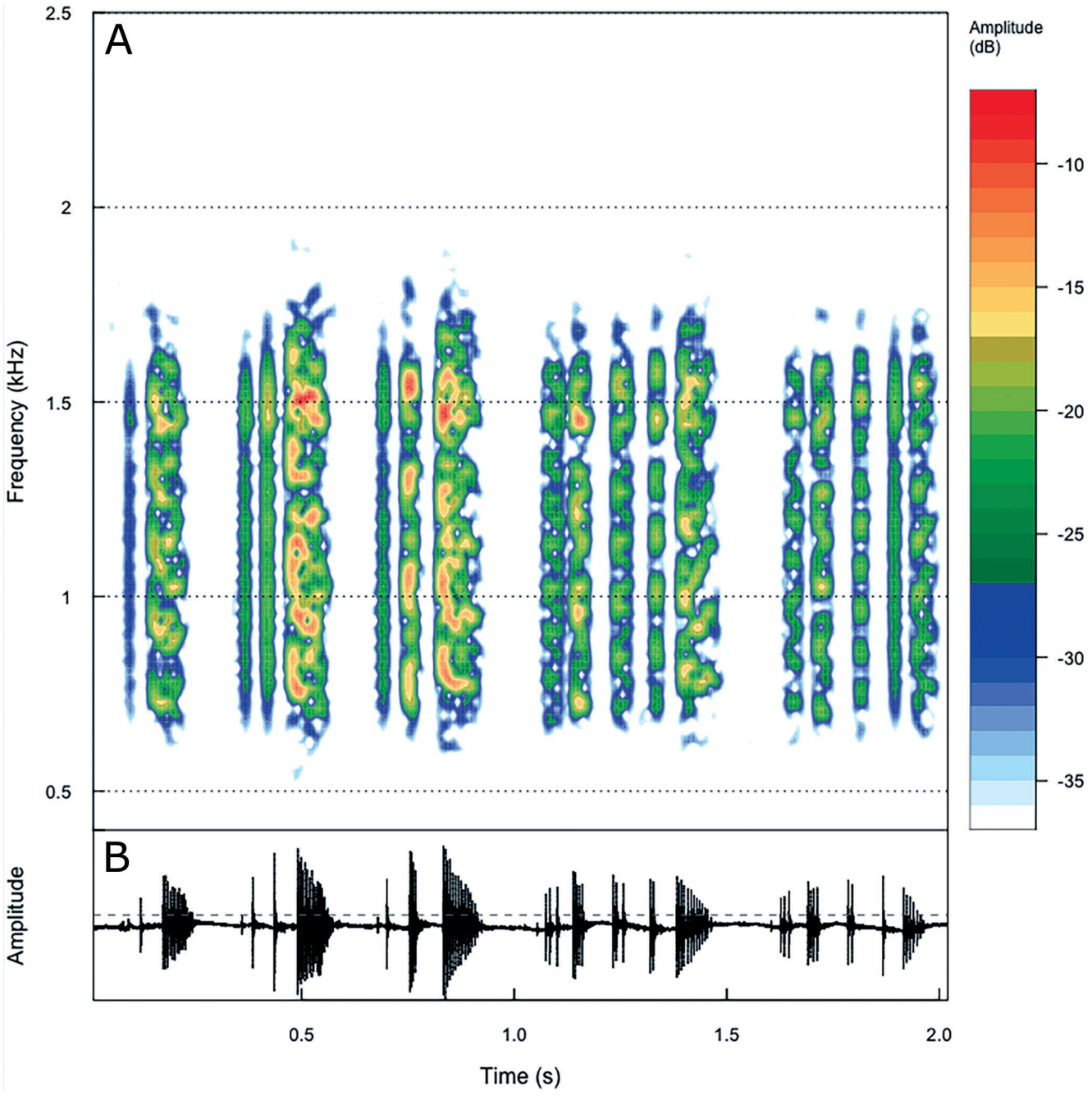



**Figure 5. (A)** Audiospectrogram and **(B)** oscillogram of the advertisement call of *Bokermannohyla ahenea* (CFBH 28797) recorded at the Serra da Bocaina National Park, São José do Barreiro, São Paulo, Brazil on August 20, 2008. Air temperature 13.5°C.



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889.1 Hz (668.6 ± 175.6, *n* = 72), and dominant frequency is 1,033.6–1,679.6 Hz (1,368.8 ± 214.1, *n* = 72). The duration of note A is 0.10–0.39 s (0.20 ± 0.07, *n* = 72), pulse number is 1–38 pulses/note (22.12 ± 5.40, *n* = 72), and pulse rate is 0.05–0.28 pulses/s (0.12 ± 0.04, *n* = 72). The maximum frequency of note B is 1,386.8–2,009.4 Hz (1,696.14 ± 143.27, *n* = 55), minimum frequency is 409–871.3 Hz (654.67 ± 178.86, *n* = 55), and dominant frequency is 861.3–1,636.5 Hz (1,360.92 ± 191.45, *n* = 55). The duration of note B is 0.20–0.78 s (0.42 ± 0.13, *n* = 55), pulse number is 11–44 pulses/note (25.98 ± 5.51, *n* = 55), and pulse rate is 0.04–0.11 pulses/s (0.07 ± 0.02, *n* = 55). Note A initially increases in pulse intensity and then stabilizes, whereas note B has a clear decrease in pulse intensity. Notes A and B do not differ in maximum ($t_{125}$ = 1.50; *P* = 0.13), minimum ($t_{125}$ = 0.44; *P* = 0.66), or dominant frequency ($t_{125}$ = 0.20; *P* = 0.84). However, note B is longer ($t_{125}$ = 12.21; *P* = 0.0001) and has a higher number of pulses ($t_{125}$ = 3.88; *P* = 0.0002) and lower pulse rate ($t_{125}$ = 9.54; *P* = 0.0001) than note A. Despite the overlapping in the raw data, the confidence intervals between notes A and B did not overlap because note A is commonly emitted with a lower number of pulses than note B.

In general, call duration is 0.15–6.83 s (1.68 ± 1.18, *n* = 32), with 56–263 pulses per call (95.09 ± 40.37, *n* = 32). Calls are usually composed of two or three A notes followed by one or more B notes, with the most frequent sequence being AAB, AABB, or AAAB. Note interval between AA is 0.12–0.22 s (0.18 ± 0.02, *n* = 40), between AB from 0.12–0.21 s (0.18 ± 0.02, *n* = 32), and between BB from 0.17–0.28 s (0.22 ± 0.03, *n* = 23). The note interval between BB is longer than AA and AB ($F_{2,92}$ = 22.21; *P* = 0.0001). Calls are emitted at a rate of 8.10–19.69 calls/minute (13.72 ± 3.64, *n* = 6).

## Natural history

Tadpoles occured year-round, mainly in shallow marshes with slow-flowing waters and in rivulets and narrow forest streams. Considering all sampled water bodies, the peak of tadpole abundance was in July (Fig. 6), but they were highly abundant year-round. Potential predators that co-occured with larvae nclude the heteropterans *Belostoma* sp., *Ranatra segrega* Montandon, 1905, *R. travassosi* De Carlo, 1950, *Notonecta polystolisma* Fieber, 1851, and *Sigara* sp., the coleopterans *Tropisternus* sp., *Megadytes* sp., *Cybister* sp., *Copelatus* sp., *Hydrocanthus* sp., and *Gyrinus* sp., and the odonates *Erythemis* sp. and *Aeshna* sp. Larvae of *Rhinella icterica* (Spix, 1824), *Aplastodiscus perviridis* Lutz, 1950, *Dendropsophus minutus* (Peters, 1872), *Scinax* sp. (aff. *duartei*), *S. hayii* (Barbour, 1909), *Boana bandeirantes* (Caramaschi and Cruz, 2013), *Leptodactylus furnarius* Sazima and Bokermann, 1978, *Physalaemus barrioi* Bokermann, 1967a, and *Proceratophrys melanopogon* (Miranda-Ribeiro, 1926) co-occured with larvae of *Bokermannohyla ahenea*. The bottoms of marshes and streams were often composed of clay, sand, and fine gravel. The most abundant items in the larval diet were Dynophyceae, *Trachelomonas,* and *Phormidium,* while fragments of arthropods, coarse particulate organic matter, fungi hyphae, algae of the genera *Cosmarium, Chlorococcum, Oedogonium, Oocystis, Lepocincles, Phacus,* and *Spirulina* were less abundant.

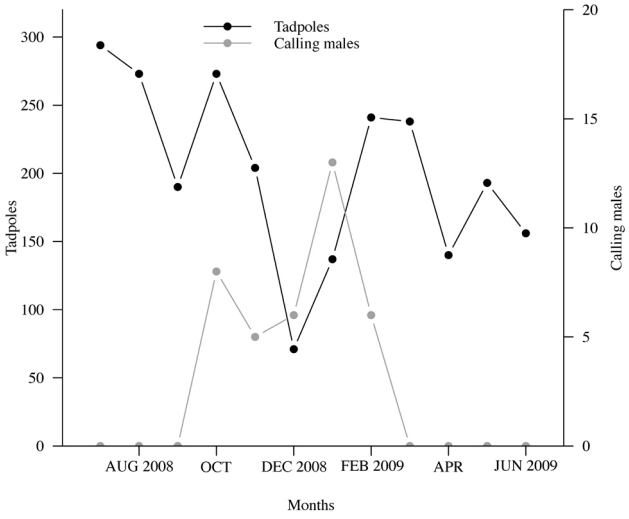



**Figure 6.** Temporal variation in the abundance of calling males and tadpoles of *Bokermannohyla ahenea* at the Serra da Bocaina National Park, São José do Barreiro, São Paulo, Brazil.

Males called while perched on herbaceous vegetation (height 156 ± 31 cm) at night along the margin of first and second order streams, mainly in forest fragments amidst highland grasslands above 1,500 m above sea level. Calling activity took place between November and February, and the peak of abundance was in January (Fig. 6). We found adults of *Bokermannohyla ahenea* at the type locality, Campo de Fruticultura (nowadays called Fazenda Ponte Alta), within the National Park. However, the species also occurs in other forest patches in private properties outside the Park. Adults of *Aplastodiscus perviridis, Physalaemus barrioi,* and *Scinax squalirostris* (Lutz, 1925) co-occurred with adults of *B. ahenea* during calling activity.

## DISCUSSION

The tadpoles of most species *Bokermannohyla* have been described (23 of 32 species, or 72%; Provete et al., 2012; Magalhães et al., 2015; Pezzuti et al., 2015). There is striking variation in larval morphology among species groups of the genus (Table 2). However, information about internal oral features is scarce, and their larval chondrocranium is unknown. Larvae of the genus *Bokermannohyla* are all exotrophic and occur in both lentic and lotic habitats. Most are benthic and, among those, species of the *B. claresignata* group belong to the suctorial guild



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**Table 2.** Main external morphological characteristics of known larvae of the genus *Bokermannohyla*. See text for abbreviations.

| Species | TOL/stage | BD | NS | NP | SO | SIW | TT | NMP | ALG | PLE | LTRF | HT | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *B. ahenea* (Napoli and Caramaschi, 2004) | 40.8 (37) | Ovoid | Elliptical with a small marginal rim | Dorsally | PO | Small and free | Pointed | 1A; 1P | Yes | Two folds | 2(2)/3(1) | Lentic and lotic | Present study |
| *B. alvarengai* (Bokermann, 1956) | 53 (40) | Ovoid | Elliptical | Dorsally | PD | ? | Rounded | 1A;2P | Yes | Two folds | 2(1,2)/5 | Lotic | Sazima and Bokermann, 1977 |
| *B. capra* Napoli and Pimenta, 2009 | 48.7 (34–37) | Elliptical | Elliptical with a small marginal rim | Dorsally | PO | ? | Rounded | 2A;2P | Yes | Two folds | 2(2)/4(1) | Lotic | Mercês et al., 2012 |
| *B. caramaschii* (Napoli, 2005) | 39.3 (29–33) | Ovoid or elliptical | Elliptical with marginal rim | Dorsally | PD | Fused | Pointed | 1A;1P | Yes | Three folds | 2(2)/4(1) | Lotic | Pezzuti et al., 2015 |
| *B. carvalhoi* (Peixoto, 1981) | 47 (31) | Elliptical | Elliptical with a small marginal rim | ? | PD | ? | Rounded | 1A;1P | Yes | Two folds | 2(2)/5(1) | Lotic | Peixoto, 1981 |
| *B. circumdata* (Cope, 1871) | 46.8 (36) | Elliptical | Elliptical with marginal rim | ? | PO | Small and free | Rounded | 2A; 2P | Yes | Two folds | 2(2)/3(1); 2(2)/4(1) | Lotic | Mongin and Carvalho-e-Silva, 2013 |
| *B. claresignata* (Lutz and Lutz, 1939) | 60 (?) | Elongated elliptical | Elliptical | ? | PO | ? | Rounded | 1A;1P | No | ? | 8/12 to 9/14 | Lotic | Lutz and Orton, 1946 |
| *B. clepsydra* (Lutz, 1925) | 57 (37) | Elliptical | ? | Dorsally | PO | ? | Pointed | 1A;1P | No | None | 7(7)/12-13(1); 8(8)/12-13(1) | Lotic | Bokermann, 1972 |
| *B. diamantina* Napoli and Juncá, 2006 | 46.5 (30–35) | Ovoid | Elliptical with marginal rim | Dorsally | PD | Fused | Pointed | 1A;1P | Yes | Three folds | 2(2)/3(1) | Lotic | Pezzuti et al., 2015 |
| *B. flavopicta* (Lutz, 1925) | 69.7 (36) | Elliptical | Reniform | Dorsolaterally | PD | Partially fused, free distal margin | Pointed | 1A;1P | Yes | Two folds | 2(2)/7(1) | Lotic | Magalhães et al., 2015 |
| *B. gouveai* (Peixoto and Cruz, 1992) | 38.7–52.5 (30–37) | Elliptical | Elliptical | ? | PD | Small and free | Pointed | 2A;1P | Yes | Two folds | 2(2)/3 | Lotic | Costa et al., 2010 |
| *B. hylax* (Heyer, 1985) | 34.2 (37) | Elongated elliptical | Reniform | Dorsolaterally | PO | Small and free | Pointed | 2A;1P | No | ? | 2(2)/4[1,2] | Lotic | Bertoluci et al., 2003 |
| *B. ibitiguara* (Cardoso, 1983) | 62 (35) | Elliptical | ? | ? | PD | ? | Pointed | 1A;1P | Yes | Two folds | 2(2)/4(1) | Lotic | Cardoso, 1983 |
| *B. ibitipoca* (Caramaschi and Feio, 1990) | 46.7 (35) | Elongated elliptical | Elliptical with a small marginal rim | Dorsally | PO | Fused into body | Pointed | 2A;2P | Yes | Two folds | 2(2)/4(1) | Lotic | Magalhães et al., 2012 |
| *B. itapoty* Lugli and Haddad, 2006b | 76.3 (37) | Elliptical | Elliptical | Dorsally | PD | ? | Pointed | 1A;1P | No | Two folds | 2(2)/6(1) | Lotic | Lugli and Haddad, 2006b |
| *B. lucianae* (Napoli and Pimenta, 2003) | 39.6 (25–36) | Elongated elliptical | Elliptical with marginal rim | Dorsally | PO | ? | Pointed | 2A;2P | Yes | Two folds | 2(2)/4(1) | Lotic | Mercês et al., 2015 |
| *B. luctuosa* (Pombal and Haddad, 1993) | 14.9 (25) | Ovoid | ? | Dorsally | PO | ? | Pointed | 1-2A;1-2P | Yes | ? | 2(2)/3(1) | Lentic | Pombal and Haddad, 1993 |
| *B. martinsi* (Bokermann, 1964) | 46.4 (25) | Elliptical | Elliptical with a marginal rim | Dorsally | PO | Fused into body | Rounded | 2A;2P | No | Two folds | 3(3)/5-6(1) | Lotic | Leite and Eterovick, 2010 |
| *B. nanuzae* (Bokermann and Sazima, 1973) | 65 (33–34) | Ovoid | ? | Dorsally | PO | ? | Pointed | 2A;2P | No | Two folds | 2(2)/5(1) | Lotic | Bokermann and Sazima, 1973 |
| *B. oxente* Lugli and Haddad, 2006a | 58.7 (37) | Elliptical | Elliptical | Dorsolaterally | PD | ? | Pointed | 1A;1P | Yes | Two folds | 2(2)/5(1) | Lotic | Lugli and Haddad, 2006a |
| *B. pseudopseudis* (Miranda-Ribeiro, 1937) | 62.5 (25) | Elliptical | Elliptical | Dorsally | PD | Free | Pointed | 1A;1P | No | Two folds | 2(2)/6(1) | Lotic | Eterovick and Brandão, 2001 |
| *B. saxicola* (Bokermann, 1964) | 30 (25) | Elliptical | Elliptical | Dorsally | PO | Free | Pointed or rounded | 1A;1P | No | Lateral folds | 2(2)-3(3)/6-8(1) | Lotic | Eterovick and Brandão, 2001 |
| *B. sazimai* (Cardoso and Andrade, 1982) | 60 (27) | Ovoid | Reniform | Dorsolaterally | PD | ? | Pointed | 1A;1P | Yes | Two folds | 2(2)/4(1) | Lotic | Cardoso and Andrade, 1982 |
| *B. vulcaniae* (Vasconcelos and Giaretta, 2005) | 33.6 (26–27) | Ovoid elongate | Elliptical | ? | PD | Fused into body | Pointed | 1A;2P | Yes | Three folds | 2(2)/3(1) | Lentic | Gaiga et al., 2013 |

(Altig and Johnston, 1989). The oral apparatus is ventral and lateroposteriorly emarginated, except for the *B. claresignata* group, in which it lacks emargination. The marginal papillae row can be either uni- or bisseriate and includes a short gap anteriorly in all larvae of all *Bokermannohyla* species except *B. hylax, B. clepsydra, B. claresignata, B. itapoty, B. martinsi, B. pseudopseudis,* and *B. saxicola,* which have a continuous row of marginal papillae (Table 2). In the *B. circumdata* group, *B. carvalhoi* and *B. capra* have a biseriate row of papillae on the anterior labium and uniseriate row on the posterior labium (Peixoto, 1981; Mercês et al., 2012). *Bokermannohyla ahenea* and *B. vulcaniae* share a uniseriate row of papillae on the anterior labium and alternated on the posterior one (this study; Gaiga et al., 2013). Submarginal papillae are rare in tadpoles of the genus (Pezzuti et al., 2015) but may occur in low density.

The other species of *Bokermannohyla* that occurred in the study area was *B. circumdata,* which was very rare and never found in the same stream where we collected *B. ahenea* tadpoles. Its tadpole (Mongin and Carvalho-e-Silva, 2013) can be differentiated from *B. ahenea* by its body shape in dorsal view, size of marginal rims of nostril, and number of marginal papillae. *Bokermannohyla circumdata* has an elliptical body, nostrils with large marginal rims, and two marginal papillae rows. Conversely, *B. ahenea* has an ovoid body, nostrils with small marginal rims, and one marginal papillae row, with alternated papillae.

The larva of *Bokermannohyla ahenea* can be readily distinguished from those of the *B. claresignata* species group (Lutz and Orton, 1946; Bokermann, 1972), which have a suctorial oral apparatus without emargination, LTRF 7(7)-8(8)/12-13(1), 9(9)/14(1), continuous marginal papillae, and submarginal papillae laterally on the anterior labium, some with labial teeth. Tadpoles of *B. martinsi* have LTRF 3(3)/5-6(1) and no submarginal papillae according to Leite and Eterovick (2010); however, in their drawing it is possible to see a few submarginal papillae in the lateral portion of the oral disc, as noted by Pezzuti et al. (2015). These characteristics easily distinguish them from *B. ahenea*. All larvae of the *B. pseudopseudis* species group are lotic, benthic, and their LTRF is typically 2(1,2)-3(3)/4(1)-5(1)-6(1)-7(1)-8(1) (Cardoso, 1983; Sazima and Bokermann, 1977; Eterovick and Brandão, 2001; Lugli and Haddad, 2006a, b; Magalhães et al., 2015), which is distinct from the 2(2)/3(1) labial teeth row formula of *B. ahenea*. The submarginal papillae of *B. pseudopseudis* species group are arranged either in 1–4 rows antero-laterally or only one row around the whole oral disc (Sazima and Bokermann, 1977; Eterovick and Brandão, 2001; Lugli and Haddad, 2006a, b; Magalhães et al., 2015), while those of *B. ahenea* are scattered and may or may not form a row.

In general, species of the *Bokermannohyla circumdata* group have a distinct lateral line system, as in *B. ahenea*. Some species of the *B. pseudopseudis* and *B. martinsi* groups also show an evident lateral line system (e.g., Lugli and Haddad, 2006a, b; Leite and Eterovick, 2010). The number and distribution of lateral lines vary among species groups. All lateral lines of *B. ahenea* are evident, as they are in *B. caramaschii, B. diamantina* (Pezzuti et al., 2015), and *B. oxente* (Lugli and Haddad, 2006a), whereas other species have fewer lines (e.g., *B. carvalhoi* and *B. ibitipoca*), and no lateral lines are visible in *B. luctuosa* (Pombal and Haddad, 1993). An interesting pattern is that tadpoles of *B. ahenea* have a pair of circular cumuli of neuromasts on the base of the vent tube. These cumuli occur also in *B. capra, B. caramaschii, B. carvalhoi, B. diamantina, B. lucianae, B. nanuzae, B. martinsi,* and *B. saxicola* (Mercês et al., 2015; Pezzuti et al., 2015, Walker et al., 2015) and in larvae of *Boana, Aplastodiscus* (Kolenc et al., 2008), and *Hyloscirtus* (Sánchez, 2010). It is important to assess the distribution of these cumuli of stitches in other genera to test if it is correlated with ecomorphological guilds (Kolenc et al., 2008), or even if there is a phylogenetic component in this characteristic, or if it is restricted to Cophomantini.

All known larvae of *Bokermannohyla* have 20–40 BFA papillae per side and 4–7 prepocket papillae; 2 lingual papillae (except *B. luctuosa,* which has 3); buccal pockets narrow, deep, and transversally oriented; ventral velum wide with irregular posterior margin, spicular support weak, distinct median notch; presence of vacuities anterior to nostrils; 2–3 postnarial papillae arranged in a Λ-pattern, with the antero-medial papilla larger than the others; median ridge triangular; and presence of lateral ridge papillae either as complex hand-like or with few, small secondary projections (d'Heursel and Haddad, 2007; Magalhães et al., 2015; Pezzuti et al., 2015). Most species of *Bokermannohyla* share a pair of large infralabial papillae anteriorly, with secondary, digitiform projections and another smaller posterior pair of conical papillae (d'Heursel and Haddad, 2007; this study). The tadpoles of *B. circumdata* (Mongin and Carvalho-e-Silva, 2013), *B. flavopicta, B. oxente* (Magalhães et al., 2015), and *B. caramaschii* (Pezzuti et al., 2015) are unique in having five, four, and three pairs of infralabial, multiple-branching papillae, respectively—more than the remaining species of the genus. Short papillae occur posteriorly to the BRA in *B. nanuzae* (d'Heursel and Haddad, 2007) and *B. diamantina* (Pezzuti et al., 2015) and are lacking in all species of the *B. pseudopseudis* group (d'Heursel and Haddad, 2007; Magalhães et al., 2015). The prenarial arena of species in the *B. pseudopseudis* group has an anteroposterior ridge (d'Heursel and Haddad, 2007), which is lacking in most larvae of the *B. circumdata* group. Instead, larvae of the *B. circumdata* group have 2–3 large papillae in that arena (d'Heursel and Haddad, 2007; Mongin and Carvalho-e-Silva, 2013; Pezzuti et al., 2015). However, the prenarial arena of *B. ahenea* has an anteromedial loop, making it more similar to species of the *B. pseudopseudis* group. However, this character seems to be very plastic (see Pezzuti et al., 2015) and deserves further investigation to distinguish between these two states.



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To our knowledge, this is the first description of the larval chondrocranium of a species of *Bokermannohyla*. Data on the larval chondrocranium for Cophomantini are scarce and available only for *Boana riojana* (Koslowsky, 1895) (Lavilla and Fabrezi, 1987), *B. lanciformis* (Cope, 1871) (de Sá, 1988), *B. semilineata* (Spix, 1824), *B. geographica* (Spix, 1824) (d'Heursel and de Sá, 1999), *B. raniceps* (Cope, 1862) (Alcalde and Rosset, 2003), and *B. rosenbergi* (Boulenger, 1898) (Haas, 1996; Vera Candioti, 2007). There are also few data available on certain character states of the chondrocranium of *Aplastodiscus perviridis* and *Boana cordobae* (Barrio, 1965) that were used to infer a phylogeny for Anura (Haas, 2003), and also *Hyloscirtus armatus* (Boulenger, 1902) (Haas and Richards, 1998), but without detailed illustrations and a comprehensive description. Thus, we could not readily compare the chondrocranial morphology of these species to that of *B. ahenea*. Within Cophomantini, the larvae of *Hyloscirtus* are rheophilous and have a highly modified chondrocranium. For example, in *H. armatus* the *pars corporea* and *alaris* of the *cartilago labialis superior* are fully fused and the *cornua trabeculae* are extended anteriorly and fused medially (Haas and Richards, 1998), whereas the *pars corporea* and *alaris* of the *cartilago labialis superior* are bound anteriorly syndesmodically and fused posteriorly and the *cornua trabeculae* of *B. ahenea* are longer and thinner. All these features are shared by other distantly related species with rheophilous larvae, such as *Ranoidea nannotis* (Andersson, 1916) (Haas and Richards, 1998), suggesting that these characteristics could be convergent.

The *processus anterolateralis* in *Bokermannohyla ahenea* is thin and short, similar to that of *Boana geographica* (d'Heursel and de Sá, 1999), *B. raniceps* (Alcalde and Rosset, 2003), and *B. rosenbergi* (Vera Candioti, 2007), whereas in *B. lanciformis* it is longer and broader (de Sá, 1988). However, the length of this process varies ontogenetically (de Sá, 1988). Additionally, the tectal roofing of *B. lanciformis* bears the *taenia tecti transversalis* and *medialis* projecting from *tectum synoticum* (de Sá, 1988), whereas a continuous *tectum parietale* is found in *B. ahenea,* like that of *B. geographica* and *B. semilineata* (d'Heursel and de Sá, 1999). The *tectum synoticum* of *Boana* is thinner than in *B. ahenea,* which covers about one third of the chondrocranium, but these cartilages also change throughout ontogeny (Haas, 2003). The *foramen opticum* of *B. ahenea* is also much smaller than that of *Boana* (Lavilla and Fabrezi, 1987; de Sá, 1988; d'Heursel and de Sá, 1999; Alcalde and Rosset, 2003; Vera Candioti, 2007). Like other hylids (Haas, 2003), the tip of the *processus muscularis quadrati* of *B. ahenea* is fastened to the *processus antorbitalis* by a thin ligamentous connection. The hyobranchial apparatus of *B. ahenea* is overall similar to that of most *Boana* species, except for the absence of the basihyal (also absent in *B. rosenbergi*) and the shape of the *processus anterior branchialis,* which is pointed in *B. ahenea,* but broader in *B. riojoana* or very reduced in *B. rosenbergi*. The *cartilago labialis superior* is fused posteriorly in *B. ahenea,* similarly to *B. lanciformis* (de Sá, 1988). This character state is uncommon in Cophomantini, since the *pars corporis* and *alaris* are not fused in most species. However, it is not known if there is an ontogenetic variation in this structure or how common it is in other genera within the tribe.

The advertisement calls of species of the genus *Bokermannohyla* have a wide variation, but most species (10 species, ca. 45%) have two types of multipulsed notes without harmonic structure (ca. 79%). However, sidebands cannot be ruled out, mainly in old descriptions. Approximately 50% of the species of the genus *Bokermannohyla* emit two or more notes per call. About 71% of the species have multipulsed calls. However, the remaining spectral and temporal parameters are extremely variable and further experimental studies are needed to test the function of multiple notes.

Spectral and temporal parameters of the advertisement call can be used to distinguish *Bokermannohyla ahenea* from its congeners (Table 3). For example, the presence of harmonics in the advertisement call is uncommon in *Bokermannohyla*. However, harmonics occur in the call of at least one species of each group (sensu Faivovich et al., 2005). Specifically, the advertisement call of *B. ahenea* differs from those of seven species (*B. circumdata, B. juiju* Favovich et al., 2009, *B. luctuosa, B. napolii* Carvalho et al., 2012, *B. pseudopseudis, B. sapiranga* Brandão et al., 2012, and *B. saxicola*) by the absence of a harmonic structure (Eterovick and Brandão, 2001; Carvalho et al., 2012, 2013; Taucce et al., 2015). The call of *B. ahenea* can be readily distinguished from those of *B. carvalhoi, B. ibitiguara, B. ibitipoca, B. nanuzae,* and *B. sazimai* by the lower dominant frequency (Napoli and Caramaschi, 2004; Carvalho et al., 2012; Nali and Prado, 2014; Walker et al., 2015), which is greater than that of *B. diamantina, B. hylax, B. luctuosa, B. napolii, B. pseudopseudis,* and *B. sapiranga* (Napoli and Caramaschi, 2004; Napoli and Juncá, 2006; Carvalho et al., 2012, 2013). Yet, the advertisement call of *B. ahenea* differs from those of *B. capra, B. carvalhoi, B. diamantina, B. hylax, B. itapoty, B. juiju, B. pseudopseudis, B. sapiranga,* and *B. saxicola* by the higher number of note types per call (Eterovick and Brandão, 2001; Lugli and Haddad, 2006b; Napoli and Juncá, 2006; Carvalho et al., 2012, 2013; Taucce et al., 2015), and from that of *B. capra* by the lower number of note types per call (Napoli and Pimenta, 2009). The call of *B. ahenea* differs from that of *B. flavopicta* by pulse presence (Rocha et al., 2016) and is different from those of *B. astartea* (Bokermann, 1967b), *B. lucianae, B. martinsi,* and *B. vulcaniae* by the higher number of pulses per call (Heyer et al., 1990; Napoli and Pimenta, 2003; Gaiga et al., 2013; Pinheiro et al., 2014). Finally, it differs from the advertisement calls of *B. astartea, B. flavopicta,* and *B. oxente* by its longer note duration (Heyer et al., 1990; Lugli and Haddad, 2006a; Rocha et al., 2016).



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**Table 3.** Call features of members of the genus *Bokermannohyla*. Cdur = call duration (s); Knot = kinds of note; Nnot = number of notes per call; Ndur = note duration (ms); Nhar = number of harmonics; Npuls = pulses per call; Prat = pulse rate (pulse/s); Fdom = dominant frequency (Hz).

| | Cdur | Knot | Nnot | Ndur | Nhar | Npuls | Prat | Fdom | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *B. ahenea* | 1.68 ± 1.18 (0.15–6.83) | 2 | 5.24 ± 7.07 (3–44) | 205 ± 68 (95–391)/ 424 ± 131 (201–782) | - | 95.09 ± 40.37 (56–263) | 57.84 ± 10.24 (38.52–88.08) | 1,368.27 ± 214.15 (1,033.6–1,679.6)/ 1,360.92 ± 191.45 (861.3–1,636.5) | Present study |
| *B. astartea* | (0.35–0.95) | ? | ? | (20–120) | - | (2–20) | (100–400) | (800–2,400) | Heyer et al., 1990 |
| *B. capra** | 0.42 ± 0.08 (0.24–0.85) | 4 | ? | ? | ? | 67.68 ± 14.13 (30–110) | 152.68 ± 28.97 (88.27–260.50) | 1,960 ± 220 (820–2,490) | Napoli and Pimenta, 2009 |
| *B. carvalhoi* | 0.32 ± 0.01 (0.26–0.54) | 1 | 2 ± 0.1 (1–3) | 98.3 ± 6.4 (64–147) | - | 13.5 ± 0.5 (7–22) | - | 1,740 ± 120 (1,500–2,060) | Carvalho et al., 2012 |
| *B. circumdata* | 0.50 ± 0.06 (0.24–0.54) | 1 | 1 | - | 4–5 | - | - | 540 ± 40 (520–610)/ 1,050 ± 50 (980–1,080)/ 1,460 ± 030 (1,450–1,550)*** | Carvalho et al., 2012 |
| *B. diamantina* | 1.16 ± 0.29 (0.63–1.85) | 1 | (2–4) | (140–400) | - | 48.08 ± 23.16 (21–110) | ? | 400 ± 30 (390–560) | Napoli and Juncá, 2006 |
| *B. flavopicta* | 67.7 ± 194. (56–111) | ? | 220.3 ± 57.5 (182–336) | 34 ± 8 (14–63) | - | - | - | (1,200–1,700) | Rocha et al., 2016 |
| *B. hylax* | 0.52 ± 0.05 (0.36–0.69) | 1 | 1 | - | - | ? | ? | 2,000 ± 180 (1,500–2,440) | Carvalho et al., 2012 |
| *B. ibitiguara*** | ? | 2 | 6 ± 4 (1–17) | 800 ± 170 (440–152) | - | ? | 25 ± 7 (9–46) | 2,024 ± 205 (1,378–2,842) | Nali and Prado, 2014 |
| *B. ibitipoca* | (0.13–0.36) | 2 | (1–4) | (40–120) | - | ? | ? | (400–600)/ (1,700–1,900) | Napoli and Caramaschi, 2004 |
| *B. itapoty* | 17.2 ± 14.2 (7–50.7) | 1 | 28.5 ± 20.8 (16–79) | 31 ± 7.6 (15–53) | - | ? | ? | ? | Lugli and Haddad, 2006b |
| *B. juiju* | 0.06 ± 0.01 (0.05–0.07) | 1 | 1 | - | 3 | - | - | (903–2,268) | Taucce et al., 2015 |
| *B. lucianae* | (0.16–7.64) | 2 | (1–11) | 210 ± 40 (160–280)/ 330 ± 30 (260–370) | - | 17.85 ± 3.07 (15–23)/ 38.7 ± 3.43 (33–44) | ? | (1,250–2,590)/ (1,250–2,710) | Napoli and Pimenta, 2003 |
| *B. luctuosa* | 0.61 ± 0.05 (0.55–0.71) | 2 | ? | 57.2 ± 20.3 (23–93)/ 440.6 ± 46.6 (371–526) | 0/5–6 | - | - | 570 ± 90 (490–650)/ 880 ± 40 (820–900) | Carvalho et al., 2012 |
| *B. martinsi* | ? | 2 | ? | 103 ± 20 (49–129)/ 586 ± 140 (350–809) | - | 23.9 ± 1.97 (20–28)/ 22.3 ± 2.69 (18–27) | ? | (964–2,078) | Pinheiro et al., 2014 |
| *B. nanuzae* | 0.36 ± 0.03 (0.31–0.50) | 2 | ? | 149.3 ± 21.7 (95–229)/ 132.5 ± 1.2 (111–185) | - | 10 ± 0.4 (5–17)/ 24.6 ± 1.1 (19–28) | ? | 2,470 ± 0.60 (2,250–2,630)/ 2,470 ± 0.60 (2,250–2,630) | Carvalho et al., 2012 |
| *B. napolii* | 0.62 ± 0.07 (0.46–0.81) | 2 | ? | 93.4 ± 15.6 (53–156)/ 399.5 ± 77.4 (242–550) | (5–6)/(5–6) | - | - | 430 ± 70 (390–560)/ 510 ± 60 (470–650) | Carvalho et al., 2012 |
| *B. pseudopseudis* | 2.82 ± 0.56 (2.12–3.65) | 1 | 15.2 ± 1.9 (12–18) | 98.8 ± 7.5 (80–122) | Up to 12 | - | - | 559.6 ± 62.3 (469–656) | Carvalho et al., 2013 |
| *B. oxente* | 2.8 ± 1.5 (1.2–7.2) | ? | 10–60 | 33.5 ± 8.6 (20.5–57.6)/ 26.1 ± 3.4 (17.4–36.8) | - | - | - | ? | Lugli and Haddad, 2006a |
| *B. sapiranga* | (0.41–1.25) | 1 | (3–8) | 91.5 ± 6.7 (77–102) | Up to 12 | - | - | (516–797) | Carvalho et al., 2013 |
| *B. saxicola* | (3–6) | 1 | 20–25 | 22–441 | Up to 3 | - | - | ? | Eterovick and Brandão, 2001 |
| *B. sazimai* | 0.66 ± 0.10 (0.48–0.89) | 2 | ? | 656.7 ± 97.8 (476–892)/ 100.9 ± 28.6 (80–165) | - | 26.7 ± 4.6 (13–36) | ? | 2,470 ± 90 (2,240–2,580)/ 2,450 ± 120 (2,240–2,580) | Carvalho et al., 2012 |
| *B. vulcaniae* | 0.7 ± 0.01 (0.5–0.8) | 2 | ? | ? | - | 4.5 ± 0.5/ 10 ± 1.6 | ? | 1,140 ± 214.5 (880–1,350) | Gaiga et al., 2013 |

*Acoustic parameters of call type A, which is the most frequently emitted one according to Napoli et al. (2009).
**Acoustic parameters of call composed by only long notes according to Nali and Prado (2014).
***Dominant frequency of each harmonics.

The advertisement call of *Bokermannohyla ahenea* comprises more than one type of note, but the social function of the different types of note is unknown. For example, the advertisement call of *B. ibitiguara* has two parts: one with a territorial function and the other used to attract females (Nali and Prado, 2014). This is possibly also the case for *B. ahenea*. In general, species of the genus *Bokermannohyla* have a complex advertisement call, and future studies should assess whether different notes have different functions.

Our results provide valuable data for future studies on bioacoustics and phylogenetic comparative studies to investigate the evolution of call features. The information provided about larvae of *Bokermannohyla* is also key to support taxonomic, phylogenetic (e.g., Haas, 2003), and ecological studies (e.g., Strauβ et al., 2010). Our results can certainly help in the taxonomy of the genus, since *Bokermannohyla* still lacks diagnostic morphological characters. For example, the same whitish structure at the base of vent tube has been recorded in *Boana* and also seems to be present not only in *B. ahenea*, but in other members of *Bokermannohyla* from either lentic or lotic habitats. However, its function is not clearly understood and deserves further studies.

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## APPENDIX

### Specimens examined

*Bokermannohyla ahenea:* BRAZIL: **São Paulo:** São José do Barreiro, Parque Nacional da Serra da Bocaina, DZSJRP-Amphibia Tadpoles 1918.2; 1984.1; 2493.1–2495.1; DZSJRP-Amphibia-adults 12124, 12126, 13920, 13947, 13949–50, 13955–57; CFBH 28796–77, 28824.



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