

Description of the Tadpole of *Bokermannohyla martinsi* (Anura: Hylidae), Morphological and Ecological Comparison with Related *Bokermannohyla* Tadpoles

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ABSTRACT.—The *Bokermannohyla martinsi* species group includes two species, *B. martinsi* and *B. langei*. *Bokermannohyla martinsi* is found mainly in rocky permanent streams, associated with gallery forests in the highlands of the southernmost portion of the Espinhaço Mountain Range, Brazil. Its tadpoles have robust, oval/ovoid in lateral and dorsal views, black bodies, and a muscular tail. External morphology, color in life and in preservative, and detailed morphometric data are presented, as well as natural history notes for the species. Diagnostic characteristics that help distinguish *B. martinsi* tadpoles from other species within the *B. circumdata*, *B. pseudopseudis*, *B. alvarengai*, and *B. claresignata* groups are as follows: labial tooth row formula, absence of a median gap on the anterior row of marginal papillae, and black coloration of the body and tail. Data on microhabitat use available for five species of *Bokermannohyla* indicate that their tadpoles have broad niches, being able to exploit many types of microhabitats (e.g., substrate type, depth, current, and vegetation presence or absence) throughout the year within the streams where they occur. Regardless of the available microhabitats in the sampling sites, tadpoles showed high niche overlap, rendering their differentiation based on microhabitat use unlikely.

The taxonomic position of *Bokermannohyla martinsi* has been controversial since its original description, when it was related to *Bokermannohyla circumdata* (Bokermann, 1964). The *B. martinsi* species group (then named *Hyla martinsi* species group) was first mentioned by Bokermann (1965) when he described *Bokermannohyla langei* and suggested that it should form a distinct group with *B. martinsi*. Caramaschi and Feio (1990) included *B. martinsi* in the *B. circumdata* species group (then *Hyla circumdata* species group) and by implication, also *B. langei*. Excluded formally from the *B. circumdata* group by Caramaschi et al. (2001), *B. martinsi* and *B. langei* were the only species within the *B. circumdata* group that share the development of the humeral crest into a hook-like projection and bifid prepollex (Bokermann, 1965) as distinctive features, and they were reallocated in the *B. martinsi* group (Caramaschi et al., 2001).

Faivovich et al. (2005) proposed the genus *Bokermannohyla*, to include all species previously allocated in the *Hyla circumdata*, *H. martinsi*, and *H. pseudopseudis* groups, plus tentatively the

H. claresignata group and *H. alvarengai*. Later, Lugli and Haddad (2006b) proposed the *B. alvarengai* group to allocate *B. alvarengai* and *B. itapoty*.

The *B. martinsi* group shows a discontinuous distribution throughout south-southeastern Brazil: *B. martinsi* occurs in the southernmost portion of the Espinhaço Mountain Range, state of Minas Gerais (Bokermann, 1964; Leite et al., 2008), and *B. langei* occurs in the state of Paraná (Bokermann, 1965).

Bokermannohyla martinsi is a medium-sized treefrog (males reaching 64 mm snout-vent length) found mainly in rocky streams, associated with gallery forests, surrounded by mountain meadows called “campos rupestres” (Bokermann, 1964; Leite et al., 2008). For a characterization of the “campo rupestre” vegetation, see Giulietti et al. (1987) and Giulietti and Pirani (1988). For a characterization of the Serra do Espinhaço Mountain Range anurofauna, see Leite et al. (2008).

To date, no tadpoles of the *B. martinsi* group have been described. Here, we describe the external morphology of *B. martinsi* tadpoles and compare it with all 15 *Bokermannohyla* species that have tadpoles formally described. We also provide data on natural history and analyze niche breadth and overlap among tadpoles of five *Bokermannohyla* species for which we could obtain data on microhabitat use (including microhabitat features and month of use): *B.*

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alvarengai, *B. ibitiguara*, *B. nanuzae*, *B. martinsi*, and *B. saxicola*. We were interested in studying to what extent these tadpoles show differential use of microhabitats, in which case spatial/temporal patterns of microhabitat use could aid in species differentiation when in sympatry. Ecological and morphological diversity among anuran larvae can be captured in the composite of microhabitats and morphotypes described by Altig and McDiarmid (1999). Although a study found no significant phylogenetic signal in microhabitat use by tadpoles in southeastern Brazil (Eterovick et al., 2010b), ecological niches occupied by different species could be linked to diversified morphological adaptations and contribute to species characterization and identification. This would be possible if species showed distinct ecological niches with low overlap. Tadpoles of several species in streams in southeastern Brazil may have broad niches and be very plastic regarding microhabitat use, but some species are more restricted in their preferences (Eterovick and Barros, 2003). Both *B. saxicola* (Eterovick and Barros, 2003) and *B. ibitiguara* (Eterovick et al., 2010a) presented intermediate niche breadths compared with other co-occurring species at sites in southeastern Brazil, whereas *B. alvarengai* had a relatively broad niche (Eterovick and Barros, 2003). However, even if tadpoles present broad niches, they can still show low overlap with co-occurring species (see Eterovick and Barros, 2003). Because tadpole identification is a hard task and not a great deal of morphological variation is available or sufficiently understood for species identification (Altig and McDiarmid, 1999), it is important to search for other features that could aid to species identification in tadpoles, for example, ecological features.

MATERIALS AND METHODS

Tadpole Collection and Description.—We used dipnets to collect tadpoles of *B. martinsi* in a backwater of a high-altitude mountain stream, surrounded by semideciduous gallery forest, at Serra da Moeda (20°06'04.7"S, 43°59'19.2"W; 1,436 m above sea level [a.s.l.]; Datum WGS 84), Municipality of Brumadinho, Minas Gerais state, Brazil, on 7 February 2008. We reared some tadpoles through metamorphosis to confirm species identity. We killed tadpoles in 5% benzocaine and then fixed and preserved them in 10% formalin. Tadpoles were deposited in the DZSJRP Collection, Department of Zoology and Botany, Universidade Estadual Paulista, São Paulo state, Brazil (series DZSJRP 1346.1. Serra da Calçada, Brumadinho, MG, 27/02/2008, 20°06'04.7"S, 43°59'19.2"W; 1,436 m a.s.l.,

T. Pezzuti and C. Rievers). External morphology descriptions were based on 30 tadpoles in stage 25 (sensu Gosner, 1960). Measurements and terminology followed Altig and McDiarmid (1999). We took measurements with digital calipers (total, body, and tail lengths) or under a stereomicroscope with an ocular micrometer (other measurements) to the nearest 0.01 mm. We obtained data about morphological features of known tadpoles of the genus *Bokermannohyla* from their original descriptions or other taxonomic accounts: *B. carvalhoi* and *B. circumdata* in Peixoto (1981); *B. feioi* (Napoli and Caramaschi, 2004); *B. hylax* in Bertoluci et al. (2003); *B. luctuosa* (Pombal and Haddad, 1993); *B. nanuzae* (Bokermann and Sazima, 1973); *B. sazimai* (Cardoso and Andrade, 1983); *B. claresignata* in Lutz and Orton (1946); *B. clepsydra* in Bokermann (1972); *B. ibitiguara* (Cardoso, 1983); *B. oxente* in Lugli and Haddad (2006a); *B. pseudo-pseudis* and *B. saxicola* in Eterovick and Brandão (2001); *B. alvarengai* in Sazima and Bokermann (1977); and *B. itapoty* in Lugli and Haddad (2006b).

Tadpole Comparison Based on Microhabitat Use.—We used data on tadpole microhabitat use from previous studies (e.g., Eterovick and Barros, 2003; Eterovick and Barata, 2006; Eterovick et al., 2010b) for *Bokermannohyla alvarengai* and *B. saxicola* from Serra do Cipó (19°12'–19°20'S, 43°30'–43°40'W, 1,000–1,485 m a.s.l.); *B. nanuzae* and *B. martinsi*, from the Reserva Particular do Patrimônio Natural (RPPN) Santuário do Caraça (20°05'S, 43°29'W, 850–2,070 m a.s.l.); and *B. ibitiguara*, from the Parque Nacional da Serra da Canastra (20°10'S, 46°30'W, 900–1,496 m a.s.l.), all in Minas Gerais state (Table 1; for a map showing the location of the study sites, see Eterovick et al., 2010b). We identified these tadpoles based on comparisons with the original descriptions and rearing of individuals in the laboratory to confirm tadpole identity whenever necessary. At the three sites, temporary and permanent streams were searched for tadpoles through at least 1 yr, with samplings equally distributed between rainy and dry seasons, to study their spatial and temporal distribution and factors affecting community structure (Table 1; for details, see Eterovick and Barros, 2003; Eterovick and Barata, 2006; Eterovick et al., 2010a). Data collection included the record of specific features of tadpole location and position when detected, before any disturbance caused by the observer that could result in tadpole movement. Variables recorded included a total of six variables: one quantitative variable (depth [in centimeters], measured with a metric tape), four binary variables—presence (1) or absence (0) of aquatic vegetation and current, rocky (0) or silty

TABLE 1. Numbers of records of tadpoles of five *Bokermannohyla* species using 24 microhabitat types at three localities in Minas Gerais state, southeastern Brazil, percentage of correct classifications according to the discriminant analysis and PIE diversity index standardized for the smallest sample size ($N = 18$). nv = without vegetation, v = with vegetation, nc = without current, c = with current.

Species:	<i>B. alvarengai</i>	<i>B. ibitiguara</i>	<i>B. nanuzae</i>	<i>B. martinsi</i>	<i>B. saxicola</i>
Site:	Serra do Cipó	Parque Nacional da Serra da Canastra	RPPN Santuário do Caraça	RPPN Santuário do Caraça	Serra do Cipó
Sampled streams:	Four temporary	Six permanent	Four permanent	Seven permanent	Four permanent, one temporary
Sampling periods:	Nov 1998–Feb 2000*	Apr, Jun, Nov, Dec 2005	Apr 2003–Oct 2004	Apr 2003–Oct 2004	Nov 1998–Feb 2000 ¹
Microhabitat types used					
Shallow, rocky, nv, nc	2	8	4	45	18
Shallow, rocky, nv, c	0	0	7	7	5
Shallow, rocky, v, nc	4	4	1	0	2
Shallow, rocky, v, c	0	0	0	1	0
Shallow, silty, nv, nc	2	1	6	19	5
Shallow, silty, nv, c	0	0	9	12	0
Shallow, silty, v, nc	0	15	0	3	0
Shallow, silty, v, c	0	0	0	8	0
Median, rocky, nv, nc	1	53	4	41	9
Median, rocky, nv, c	0	0	5	23	0
Median, rocky, v, nc	7	0	2	2	1
Median, rocky, v, c	0	0	0	25	0
Median, silty, nv, nc	0	6	6	35	0
Median, silty, nv, c	0	0	5	25	0
Median, silty, v, nc	0	3	0	0	0
Median, silty, v, c	0	0	0	8	0
Deep, rocky, nv, nc	1	46	4	16	14
Deep, rocky, nv, c	0	0	0	23	0
Deep, rocky, v, nc	1	0	0	0	1
Deep, rocky, v, c	0	0	0	1	0
Deep, silty, nv, nc	0	1	0	28	0
Deep, silty, nv, c	0	0	0	17	0
Deep, silty, v, nc	0	1	0	7	0
Deep, silty, v, c	0	0	0	7	0
Total	18	138	53	353	55
Classification success (% correct)	67	28	55	48	54
Spatial niche breadth (PIE, $N = 18$)	0.810	0.727	0.908	0.927	0.800

¹ At the Serra do Cipó, tadpoles were sampled monthly during the rainy season and every 2 months during the dry season.

(1) substrate, tadpole positioning on the bottom (0) or at midwater (1)—and a categorical variable related to month of occurrence (numbered from 0 to 11 starting at the beginning of the rainy season at all sites [October]). We used these data to perform a Discriminant Analysis (Klecka, 1980; McGarigal et al., 2000) to show whether variables related to microhabitat use could aid in species differentiation and identification of tadpoles of *Bokermannohyla*.

We estimated niche breadth for each of these five species of *Bokermannohyla* to investigate whether they differ in microhabitat use and we also estimated niche overlap among each species pair, testing whether they differ more or less than expected by chance in microhabitat use. For these analyses, we classified microhab-

itats into 24 types based on the possible combinations of their measured features. Depth was divided in three classes: 0–15 cm (shallow), >15–30 cm (median), and >30 cm (deep) (Table 1). We did not use tadpole position in the water column because we found most tadpoles were on the bottom.

To investigate whether specialization in the use of microhabitats differed among species of *Bokermannohyla*, we estimated niche breadth for each species using Hurlbert’s diversity index (PIE), which is unbiased by sample size (Gotelli and Entsminger, 2005):

$$PIE = (N/N - 1) \left(1 - \sum P_i^2 \right)$$

where P_i represents the proportional use of microhabitat i by a species based on total

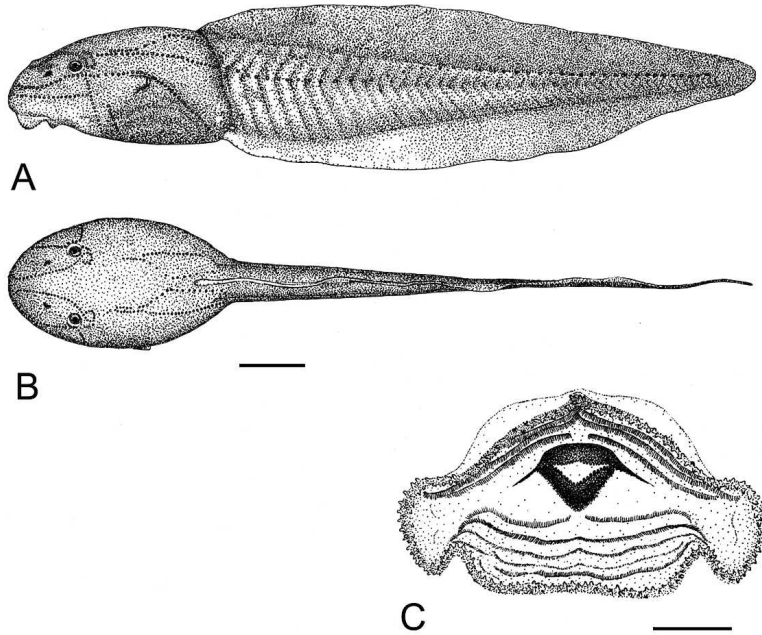


FIG. 1. Tadpole of *Bokermannohyla martinsi* at stage 25 (Gosner, 1960). (A) Lateral view and (B) dorsal view (scale bar = 5 mm). (C) Oral disc (scale bar = 1 mm). DZSJRP 1346.1.

numbers of its microhabitat use records (N). We built rarefaction curves with 1,000 simulations (Gotelli and Entsminger, 2005) to estimate each species' niche breadth with a sample size equal to that of *B. alvarengai* ($N = 18$), the species with the least data, to compare niche breadths without the possible influence of sample size.

To investigate whether niche overlap between species pairs within *Bokermannohyla* is smaller or larger than expected by chance, we used Pianka's (1973) overlap index (O_{jk}) with retained niche breadth and reshuffled zero states (RA3 randomization algorithm) in the software EcoSim (Gotelli and Entsminger, 2005). The expected value of niche overlap was given by the mean value of 1,000 simulations. By estimating "niche overlap," we simply intended to obtain a measurement of the amount of overlap that exists in these tadpoles' microhabitat preferences, because not all of these species are expected to co-occur. However, some of them co-occur at sites in southeastern Brazil, for example, *B. nanuzae* and *B. martinsi* at the RPPN Santuário do Caraça (Afonso and Eterovick, 2007); *B. nanuzae* and *B. saxicola* at the Serra do Cipó (Eterovick, 2003); and *B. martinsi* and *B. saxicola* at Jaboticatubas (Pacheco, pers. comm.), although in this last case it is not known whether tadpoles co-occur in the same streams. Except for *B. alvarengai*, which prefers to breed in temporary streams (Eterovick and Sazima, 2004) tadpoles of all the remaining species usually occur in

permanent streams. However, tadpoles of *B. saxicola* and *B. alvarengai* have already been recorded co-occurring in a temporary stream at Serra do Cipó, southeastern Brazil (Eterovick and Sazima, 2000). In these and other instances when tadpoles of two or more species of the genus *Bokermannohyla* co-occur, differential patterns of microhabitat use, once detected, would aid in species identification.

RESULTS

DESCRIPTION OF THE TADPOLE

Bokermannohyla martinsi

External Morphology.—Body depressed, oval in dorsal view and ovoid in lateral view (Fig. 1A,B). Body length approximately 36% total length, body width approximately 72% body length, and body height approximately 62% body length (Table 2). Snout oval in dorsal and rounded in lateral view. Eyes dorsally positioned, dorsolaterally directed, interorbital distance approximately 56% body width (Table 2). Nares elliptical, positioned dorsally, opening anterolaterally, with a small projection on the inner rim. Spiracle sinistral, directed posteriorly, opening at the end of the middle third of the body, right above the lateral midline, inner wall attached with body. Vent tube short, dextral, associated to the ventral fin, with ventral wall slightly longer than dorsal. Oral disc (Fig. 1C) emarginated and ventral;

TABLE 2. Measurements (in mm) of the tadpoles of *Bokermannohyla martinsi* (DZSJRP 1346.1).

Measurement	Stage 25 (N = 30)		
	Mean	SD	Range
Total length	46.36	11.32	23.81–59.93
Body length	16.61	3.92	8.79–21.18
Tail length	29.74	7.51	15.00–39.56
Maximum tail height	11.84	3.20	5.80–16.34
Tail muscle height	6.24	1.97	2.46–9.52
Dorsal fin height	4.17	1.14	2.07–6.02
Ventral fin height	3.25	0.93	1.33–4.60
Interorbital distance	6.64	1.49	3.13–8.75
Eye diameter	1.57	0.31	0.88–2.00
Eye–nostril distance	2.62	0.56	1.38–3.63
Eye–snout distance	5.12	1.15	2.50–6.50
Internostril distance	3.95	0.71	2.25–4.88
Nostril–snout distance	2.81	0.59	1.50–4.25
Maximum body width	11.88	3.14	6.01–15.97
Maximum tail width	3.76	1.26	1.71–5.78
Maximum body height	10.25	2.62	4.81–13.44
Oral disc diameter	4.96	1.00	2.88–6.25

row of conical marginal papillae biserialated without dorsal or ventral gaps. Labial tooth row formula 3(3)/5–6(1); A3 interrupted medially by a relatively short gap; medial gap of P1 very short; (if present) P6 frequently broken. Short lateral tooth rows present, varying in number and size among individuals. Upper jaw sheath arch-shaped and lower jaw sheath V-shaped; both jaws finely serrate and dark (Fig. 1C). Caudal musculature strong, higher than dorsal and ventral fins at the tail anterior third. Dorsal fin with convex margin, emerging at the body-tail junction at a slow to medium slope; ventral fin with convex margin, emerging at the body-tail junction. Lateral line system easily visible (Fig. 1B).

Color in Life.—Body entirely black in ventral and lateral views (Fig. 2). Spiracle black pigmented. Vent tube translucent, lightly pigmented with dark and golden tiny spots. Tail black, in dorsal view, with a brownish median, longitudinal stripe on the dorsal fin anterior fourth. In lateral view, tail muscle black. Fins black.

Color in 10% Formaldehyde.—Coloration is very similar to that of living tadpoles, with black coloration becoming shaded. The dorsal brownish median longitudinal stripe on the tail tends to disappear.

Variation.—Individuals, in lateral view, can show a body shape ovoid instead of oval. Some tadpoles, including large tadpoles, but especially those with smaller sizes, can be lighter colored, tending to grayish. In lateral view, they can show some nonpigmented patches on the tail muscles and fins gathering mostly on its proximal ventral region. The dorsal brownish median longitudinal stripe on the tail is also less frequent in smaller larvae.

Differential Diagnosis.—The tadpole of *B. langei* is not known; therefore, no comparison among larvae within the *B. martinsi* species group is possible to date. The tadpoles of *B. martinsi* can be promptly distinguished from the known tadpoles of the *B. circumdata* group by having more labial tooth rows on the anterior labium (three in *B. martinsi* and two in the *B. circumdata* group). The third labial tooth row on the anterior labium also distinguishes *B. martinsi* from *B. ibitiguara*, which has a labial tooth row formula (LTRF) 2(2)/4(1) and from *B. oxente* and *B. alvarengai*, both with LTRF 2(2)/5(1). The LTRF distinguishes *B. martinsi* tadpole from the tadpoles of *B. claresignata* group, which present at least seven and 11 labial tooth rows on the anterior and posterior labia, respectively.

The absence of a median gap on the anterior row of marginal papillae distinguishes the tadpole of *B. martinsi* from those of *B. carvalhoi*, *B. circumdata*, *B. luctuosa*, *B. sazimai*, *B. ibitiguara*, and *B. oxente*, which present this character.

The plain black life coloration of body and tail distinguishes *B. martinsi* from most of *Bokermannohyla* tadpoles. Except for *B. nanuzae*, *B. ibitiguara*, and *B. feioi*, which also show a dark brownish to blackish coloration, all other *Bokermannohyla* tadpoles described to date show lighter, spotted color patterns, or both.

Natural History Notes.—At Serra da Moeda (20°06'04.7"S, 43°59'19.2"W; 1,436 m a.s.l.), adult males were seen calling from October 2003 to April 2004 on streamside vegetation, 0.5–1.8 m above the water level, or from rock crevices in permanent streams, usually close to waterfalls. This relatively long period of calling activity also was observed for populations at the RPPN Santuário do Caraça (Canelas and Bertoluci,

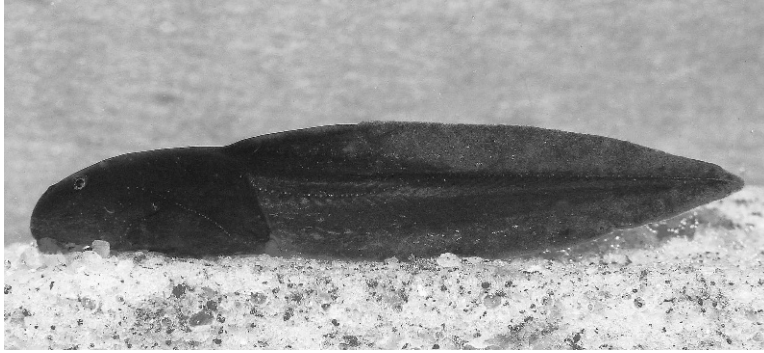


FIG. 2. Lateral view of tadpole of *Bokermannohyla martinsi* in life at stage 25 (Gosner, 1960). DZSJRP 1346.1.

2007). Adult males often present scars on their dorsal surface, due to fights when they use their large bifid prepollex spines to attack an opponent (F. S. F. Leite, pers. obs.). When caught, they also use their prepollex spines against the collectors' hands. During the day, adults were also found resting on leaves and on rocky cliffs, when they acquire a more cryptic coloration, as their white spots turn lighter and give them an aspect that resembles lichens on rocks. Five adults were seen several times, during the day, resting together, side by side on a quartzitic wall by a waterfall, without any protection from sunlight (F. S. F. Leite, pers. obs.).

Eggs of *B. martinsi* were not found. Tadpoles were found on the bottom of rocky pools formed by backwaters of permanent streams surrounded by gallery forests. Tadpoles are nocturnal, when they can be found grazing on the rocky bottom. When disturbed, they promptly escape through fast short movements. During the day, they can be found under rocks, dead leaves, or on root clusters on the stream bed. At the RPPN Santuário do Caraça (20°07'21"S, 43°27'56"W, 1,213 m a.s.l.), tadpoles occurred in high concentrations in permanent streams surrounded by forest, being found active and exposed during day and night. Despite collections being made in different months, tadpoles were only found in stage 25, in which they showed great total length variation (Table 2), suggesting a relatively long duration of this stage and that most growth occurs before stage 26.

MICROHABITAT USE BY *BOKERMANNOHYLA* SPECIES

Tadpoles of *Bokermannohyla alvarengai* were recorded up to 5 months after the onset of the rains, at depths from 8 to 42 cm, mostly on rocky substrates with vegetation and never in the current. Tadpoles of *B. ibitiguara* were recorded year-round, at depths from 5 to 80 cm, on rocky or silty substrates without current and with or without vegetation. Tad-

poles of *B. nanuzae* were recorded year-round, at depths from 2 to 40 cm, on rocky or silty substrates with or without current and usually without vegetation. Tadpoles of *B. martinsi* were recorded year-round, at depths from 0.5 to 100 cm, on both substrate types with or without current and vegetation. Tadpoles of *B. saxicola* were recorded year-round, at depths from 6 to 93 cm, mostly on rocky substrates without vegetation or current. Almost all tadpoles were recorded on the bottom, except for one of 138 individuals of *B. ibitiguara* and 10 of 353 individuals of *B. martinsi*.

The discriminant analysis was efficient in summarizing the available information in the first three axes of discriminant space (Wilks's Lambda = 0.570; $df = 24$; $P < 0.0005$). The first axis explained 79% of total variation in tadpole distribution within streams and was mostly related to current. The second axis explained an additional 13% of variation and was related to aquatic vegetation. The third axis explained additional 7.5% of the variation and was related to depth (Table 3). Nevertheless, species could not be recognized as distinct groups (Fig. 3), which is reflected in the low classification success of individuals to species based on their microhabitat use (Table 1). General classification success was only 39% after Jackknife correction, varying from 28 to 67% for particular species (Table 1).

Although the five studied species of *Bokermannohyla* differed in niche breadth ($P < 0.05$), all of them had intermediate to broad niches (PIE = 0.727–0.927; Table 1). The PIE values estimated with all data available for each species were identical to those obtained through rarefaction for a sample size of 18 records for *B. martinsi* and *B. nanuzae* and almost the same for *B. ibitiguara* (PIE = 0.728, $N = 138$) and *B. saxicola* (PIE = 0.797, $N = 55$). Niche overlaps between species pairs varied from $O_{jk} = 0.210$ for *B. alvarengai* and *B. ibitiguara* to $O_{jk} = 0.686$ for *B. saxicola* and *B. ibitiguara*. Overall niche

TABLE 3. Canonical discriminant functions standardized by within variances for the three axes derived by the discriminant analysis, with axes eigenvalues and cumulative proportion of total dispersion. The variables that contributed the most to each axis are shown in bold.

Variable	Axis 1	Axis 2	Axis 3
Depth	0.233	0.176	0.847
Vegetation	0.365	0.929	0.051
Current	-0.855	-0.041	0.019
Substrate	0.343	0.150	-0.506
Position	-0.064	0.087	0.284
Month	0.451	-0.482	0.176
Eigenvalues	0.531	0.087	0.050
Cumulative proportion of total dispersion	0.790	0.920	0.995

overlap among species was higher than expected by chance (observed $O_{jk} = 0.451$, expected $O_{jk} = 0.268$, $P = 0.001$).

DISCUSSION

We did not find any external morphological feature which could be recognized as a unique feature of the *B. martinsi* species group. Eter-

ovick and Brandão (2001) characterized the larvae of species in the *B. pseudopseudis* group on the basis of the presence of short, lateral irregular tooth rows and having more tooth rows (between six and eight rows on the posterior labium) in their oral discs than those in the *B. circumdata* group. Nevertheless, Faivovich et al. (2005) observed that the tadpoles of *B. ibitiguara*, included in this group by Caramaschi

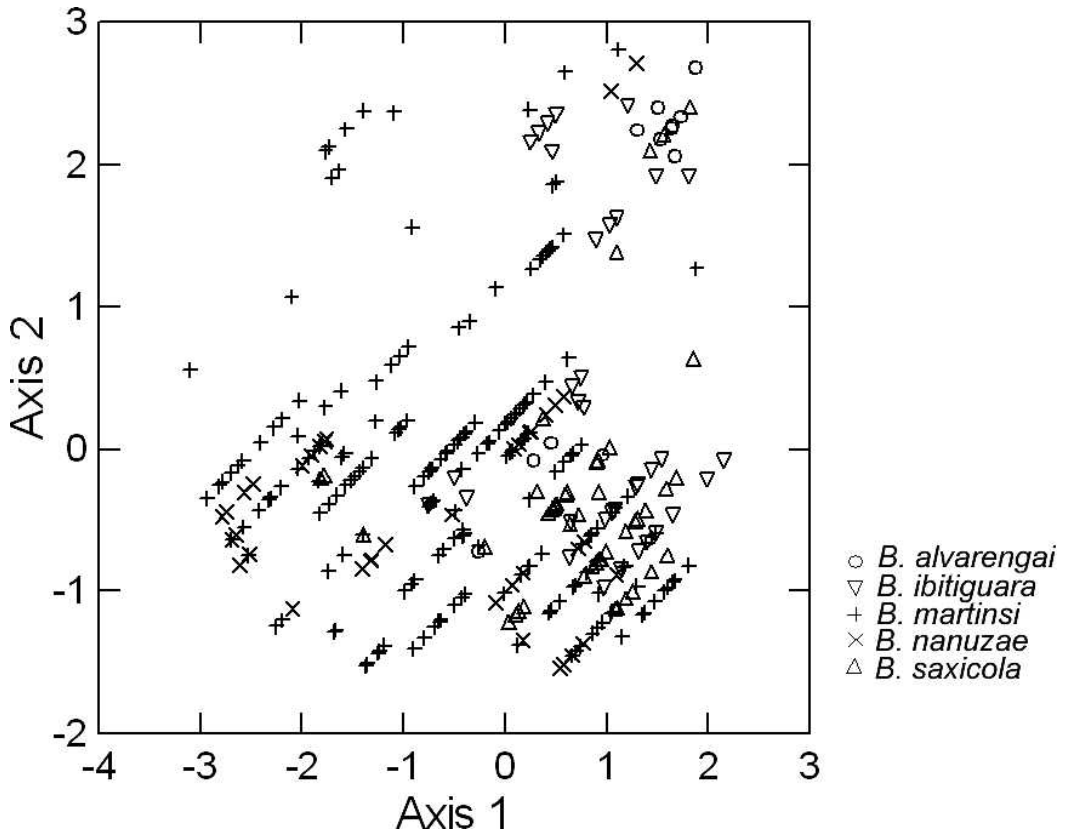


FIG. 3. Representation of the first two axes of the discriminant space explaining the variation in microhabitat use by tadpoles of five *Bokermannohyla* species at three different sites in Minas Gerais state, southeastern Brazil.

et al. (2001), has a LTRF of 2(2)/4(1) (Cardoso, 1983) and seems to lack the short, lateral irregular tooth rows. The tadpole of *B. oxente*, also included in the *B. pseudopseudis* group by Lugli and Haddad (2006a), has a LTRF of 2(2)/5(1), but has the short, lateral irregular tooth rows. The tadpole of *B. martinsi* also presents these lateral irregular tooth rows, reinforcing that this feature is not useful for characterizing the *B. pseudopseudis* group.

Except in the case of the likely monophyletic *B. claresignata* group, which is easily recognized by having distinct larval oral features as enlarged oral disc and large number of labial tooth rows, tadpole external morphology might not be an informative source for diagnosing *Bokermannohyla* species groups (sensu Faivovich et al., 2005). Nevertheless, tadpole external morphology has been shown to be a good tool for diagnosing species within the *Bokermannohyla* genus.

The pattern of development observed for *B. martinsi*, with most growth occurring during stage 25 (sensu Gosner, 1960), also was described for *B. saxicola* and *B. pseudopseudis* (Eterovick and Brandão, 2001), *B. hylax* (Bertolucci et al., 2003), and *B. nanuzae* (Bokermann and Sazima, 1973). This development/growth pattern seems to be common within *Bokermannohyla* tadpoles, which are permanent streams dwellers, excepted *B. alvarengai*, which is known to develop in temporary streams (Sazima and Bokermann, 1977). A similar pattern also was recorded for *Hypsiboas faber*, for which 90% of larval growth occurred during stage 25. The long developmental period of this species was considered as an adaptation to permanent ponds (Martins, 1993).

The species of *Bokermannohyla* for which data on microhabitat use were available represent four (*B. alvarengai*, *B. circumdata*, *B. pseudopseudis*, and *B. martinsi* groups) of the five different groups recognized for the genus (sensu Faivovich et al., 2005; Lugli and Haddad, 2006b). Only the *B. claresignata* group was not represented. Just two of these five species belong to the same group (*B. saxicola* and *B. ibitiguara*, in the *B. pseudopseudis* group).

Month of occurrence was not a useful variable to classify tadpoles of species of *Bokermannohyla*, probably because most species could be recorded year-round, except for *B. alvarengai* at Serra do Cipó. Position in the water column did not aid in species classification, because almost all tadpoles remained on the bottom, which is probably a conservative feature for most species of *Bokermannohyla*, whose tadpoles belong to the exotroph, lotic, benthic ecomorphological guild (sensu Altig and McDiarmid, 1999). Tadpoles of the *B. claresignata* group could be considered

exotroph, lotic, suctorial (sensu Altig and McDiarmid, 1999), but they were not included in the analysis.

Although ecomorphological guilds are related to microhabitat use by tadpoles (Altig and McDiarmid, 1999), within a guild, tadpoles can still show variation in many aspects of microhabitats they use, regarding depth, current, and vegetation presence or absence, as shown here for *Bokermannohyla* tadpoles. The variation, however, is not useful in distinguishing among species or groups, because tadpoles have broad niches and show considerable niche overlap. Differences in microhabitat use can reflect specific adaptations, interactions, or microhabitat availabilities at the sites where tadpoles were sampled. Nevertheless, the largest niche overlaps were not observed between species from the same locality, indicating that it is not just a consequence of microhabitat availability. Tadpoles may respond to a combination of environmental features (e.g., Eterovick and Barata, 2006); interactions with other species, such as predators (e.g., Kopp et al., 2006); and specific preferences (e.g., Eterovick and Barata, 2006) when choosing microhabitats. Differences among the study sites could contribute to differential microhabitat use caused by local factors such as co-occurring species and structural features of the habitats. However, even considering that these additional sources of variation could lead to greater niche differentiation, "niche overlap" was still larger than expected by chance among the studied species. Nevertheless, these results cannot be interpreted as indicative of microhabitat use being a conservative ecological feature in the group, because convergence among tadpoles of different species may lead to even higher levels of similarity among unrelated species (Eterovick et al., 2010b). Although it is of little use for species differentiation, ecological information can be useful to improve knowledge about species of *Bokermannohyla* and aid in their conservation.

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