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VARIATION IN MEMBERS OF THE *CENTROLENELLA EURYGNATHA* COMPLEX (AMPHIBIA: CENTROLENIDAE) FROM SERRA DO MAR AND SERRA DA MANTIQUEIRA, BRASIL

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ABSTRACT

The patterns of variation for 21 characters used in the systematics of the Centrolenella eurygnatha *complex are analyzed. The results indicate that a single, geographically variable species is found in the Serra do Mar and Serra da Mantiqueira in the states of Minas Gerais, Rio de Janeiro, and São Paulo. Consequently, the following names are synonymized with* C. eurygnatha: bokermanni, delicatissima, divaricans, *and* surda. *Systematic and zoogeographic implications are discussed.*

Taylor and Cochran (1953) were the last workers to review the centrolenid frogs of southeast Brasil. They apparently had 23 previously unreported specimens at their disposal, forming two groups. There is some confusion regarding the allocation of names to these two groups. In the introduction to their paper, Taylor and Cochran indicated that of the new material at hand they recognized 6 species of a short headed group and 4 species of a spatulate headed group. In the species descriptions, 5 species are described as short headed and 5 as spatulate headed. Upon re-examination of their material, I believe that the correct allocation is 5 and 5, namely: Short-headed, *C. bokermanni, delicatissima, divaricans, eurygnatha, surda;* spatulate-headed, *C. albotunica, dubia, lutzorum, petropolitana, vanzolinii.* The short-headed, or *C. eurygnatha* complex, was represented by 16 specimens in Taylor and Cochran's (1953) study. With so few specimens available at that time, no absolute decision could be reached regarding whether some distinctive features were species specific or represented individual variation. Another problem concerning the distinctive features was the generally poor condition of their specimens. Their frequent use of the term, "indifferently preserved", is, if anything, an understatement. Based on Dr. Taylor's experience with Mexican and Middle American centrolenids, the distinctive features Taylor and Cochran observed were considered to represent species differences.

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Materials are now adequate to describe intra- and inter-population variation of the characters Taylor and Cochran (1953) used to diagnose members of the *Centrolenella eurygnatha* complex. Hopefully, description of the variation in this larger sample will provide a new starting point for further studies.

Materials and Methods

Samples of from 9 to 60 adult males are available from 6 localities in either the Serra do Mar or Serra da Mantiqueira regions. Each series from a given locality represents a single species. Data were taken on each of these specimens for the characters Taylor and Cochran (1953) used to diagnose their forms. The analysis of these characters of the males from these 6 localities provides the basis for describing the intra- and inter-population variation of members of the *C. eurygnatha* complex. Available data on colors in life, mating call, specimens from other localities and female specimens are incorporated into the male data based analysis.

The six localities arranged by major geographical features and number of specimens (all in MZUSP and USNM) are:

Serra do Mar

Serra do Mar

1. Boracéia, São Paulo, 23° 38′ S, 45° 50′ W, N = 60.

Serra da Bocaina

2. Serra da Bocaina, probably Lutz Fazenda, São Paulo, 22° 46′ S, 44° 35′ W, N = 14.
3. Fazenda do Veado, São Paulo, 22° 49′ S, 44° 39′ W, N = 9.

Serra da Mantiqueira

4. Cidade Azul, São Paulo, 22° 51′ S, 45° 44′ W, N = 22.
5. Brejo da Lapa, Itatiaia, Minas Gerais, 22° 22′ S, 44° 44′ W, N = 10.
6. Macieiras, Itatiaia, Rio de Janeiro, 22° 25′ S, 44° 38′ W, N = 9.

The statistical analysis used is the one way analysis of variance program for the Texas Instruments SR 52 calculator.

Museum abbreviations used are MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil) and USNM (National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A.).

Mating calls were recorded on a Uher CR 134 cassette recorder and analyzed with a Kay Sonagraph 6061 B, Hewlett Packard 7402A strip chart recorder, and a B & K 2121 frequency analyzer.

Character Variation

Choanae

Taylor and Cochran (1953) used the shape and relative position of the choanae to differentiate certain species within their spatulate

head group. They found no variation within the short-headed group. There are no obvious differences in size, shape, or relative position of choanae in the present sample. All choanae are moderate sized, oval, near the anterior roof of the mouth.

Tympanum

Tympani on both sides of the head of each individual were categorized into 5 arbitrary states: (1) distinct, (2) only lower edge distinct, (3) covered with skin, but visible, (4) covered with skin, indistinctly visible, (5) hidden. The frequency distributions of states among the six major samples are presented in Table 1. Two conclusions may be drawn from the data of Table 1: (1) All states are represented in the sample represented by the greatest number of individuals, (2) The distinctiveness of the tympanum is different in each of the samples.

Some of the differences observed among the samples are likely due to differences of preservation. For example, the Bocaina and Fazenda do Veado samples are geographically close in the same coastal mountain system. The Bocaina samples is represented by specimens collected in the 1930's and the specimens are poorly preserved. The Fazenda do Veado sample is based on recently collected specimens in a good state of preservation. In these cases, the diferences among the last three tympanum categories are likely due to state of preservation.

About 30% of the individuals comprising the data of Table 1 had different tympanum states on either side of the head. The distinctiveness of the tympanum is thus variable within individuals, within populations, and among populations. With the extent of within individual and within population variation noted, confused by different states of preservation, it is impossible at this time to understand the degree and significance of the inter-populational variation.

The states recorded for the female specimens give no indication of sexual dimorphism in distinctiveness of the tympanum.

Eye Tunic

The eye tunic of almost all specimens examined is silvery-white. All of the specimens collected in the last five years have white eye tunics. Aside from type material (discussed later) the only specimens with a dark eye tunic are single specimens from Campos do Jordão (MZUSP 10091) and Eugênio Lefevre (MZUSP 14000). Two specimens from Bocaina (USNM 96560-61) have pale silver tunics, intermediate between the dark and silvery-white tunic conditions. All of the specimens with dark or pale silver tunics are very faded. It appears as though the silver-white pigment of the tunic is the last light pigment to fade. The dark tunic condition is interpreted as an artifact of preservation in members of the *C. eurygnatha* complex.

Head-Body Constriction

There is a constriction between the head and the body in all of the specimens examined. I interpret the variation exhibited as due to differences of preservation.

Ventral Texture

Taylor and Cochran (1953) used ventral texture to distinguish among some members of their spatulate headed complex. They recorded all members of the *eurygnatha* complex as having granular venters. All specimens examined in this study also have granular venters.

Anal Decoration

All recently collected material demonstrates a granular seat patch demarcated by a white color. Three conditions are found in the older material: (1) an evident granular white seat patch, (2) a granular seat patch without white pigment, and (3) no trace of pigment or a granular seat patch in some of the poorly preserved specimens. If the femur was preserved at a right angle or an acute angle towards the head, the lateral edges of the seat patch are not strikingly differentiated from the thigh. If the femur was preserved with the hind leg in a relatively straight line behind the body, the lateral edges of the seat patch are produced into distinct ridges.

Heel Decoration

In many of the recently collected specimens the heel is weakly granular and weakly white pigmented. This is probably the condition in life for all members of this complex. The faint white color and weak granular condition are apparently easily lost or obscured in preservation. The weak granules are evident in some of the older specimens, but in none of older material is any white pigment left.

Outer Tarsal Fold

As for the preceding character, the apparent condition in life for all specimens of this complex is a weak outer tarsal fold weakly outlined with white pigment. This condition is seen in many of the recently collected specimens. The outer tarsal fold is weakly developed at best, likely accounting for its apparent absence in most of the older specimens which are not particularly well preserved. The white pigment apparently fades rapidly in preservative.

Dorsal Pattern

The usual condition of the dorsal pattern is a rather uniform scattering of the purple pigment cells over the back with a heavy concentration of pigment cells on the upper eyelid (Table 2). Two of the specimens from Macieiras are distinctive in having a slightly blotchy pattern approaching the reticulate dorsal pattern characteristic of members of the spatulate-headed species group. The two most extreme Macieiras specimens are the end of a continuum from a uniform pattern and are not discretely different from the other specimens. The purple pigment cells were visible in all but two of the non-type specimens examined.

The females at hand have the same dorsal patterns exhibited by the males.

Nostril Position

Taylor and Cochran (1953) used nostril position in diagnosing members of the spatulate headed group, noting that the nostril was closer to the tip of the snout than the orbit in all members of the *eurygnatha* complex. Using an ocular micrometer, the distances were recorded for all specimens examined in this study. The larger sample demonstrates the same condition that Taylor and Cochran reported (1953). The nostril — tip of snout distance is usually about ½ the nostril — orbit distance for both sexes.

Hand and Foot Web

Webbing formulae (Savage and Heyer, 1967) were recorded for a single hand and foot for each specimen. Summary formulae (Figures 1 and 2) indicate broad overlap in extent of web among all populations. The degree of variation seen is similar to that found in a study of hylid frogs (Savage and Heyer, 1969). Most samples have the same range of variation and nearly the same modal formulae. The single exception is the Boracéia sample, in which individuals have slightly more hand webbing than individuals from the other samples.

The webbing formulae of the available females all fall within the range of variation exhibited by the males.

Size

Size characteristics of the six geographic samples of males show some overlap (Table 3). Statistically, the samples are not the same ($F_{5, 118} = 17.15$, $P < .001$). Looking at the data of Table 3, the Brejo da Lapa sample is the most distinctive. When this sample is deleted from analysis, the remaining samples still differ statistically ($F_{4, 109} = 5.88$, $P < .001$). The samples from the Serra do Mar do not differ statistically ($F_{2, 80} = 0.74$, $P > .05$). The samples from the Serra da Mantiqueira differ statistically ($F_{2, 80} = 12.84$, $P < .001$). The Macieiras and Cidade Azul samples do not differ statistically ($F_{1, 29} = 0.002$, $P > .05$).

Five females are in the same size range exhibited by males. Two females measure 24.0, slightly exceeding the maximum size recorded for males, suggesting the possibility of sexual dimorphism in size.

Body Proportions

Because of the statistical difference in size among the population samples, proportions, rather than straight measurement values, are used. All proportions use the length of the variable divided by the snout-vent length.

Head Width — The differences among head widths in the six samples are small (Table 4) but statistically significant ($F_{5, 117} = 3.14$, $.01 < P < .05$). There is a statistically significant difference

between the Serra do Mar and Serra da Mantiqueira group samples ($F_{1, 121} = 14.66$, $P < .001$). There is no statistical difference within the Serra do Mar samples ($F_{2, 79} = 0.66$, $P > .05$) or Serra da Mantiqueira samples ($F_{2, 38} = 0.11$, $P > .05$). Female head width proportions fall within the range demonstrated by males.

Head Length — The mean head length proportions of the six samples all fall within one standard deviation of each other (Table 4), but are statistically different ($F_{5, 117} = 7.42$, $P < .001$). If the population with the shortest heads (Brejo da Lapa) is deleted from analysis, the remaining five samples still differ statistically ($F_{4, 108} = 4.05$, $P < .01$). When the Serra do Mar samples are statistically compared to the Serra da Mantiqueira samples, the results are statistically significant ($F_{1, 121} = 24.2$, $P < .001$). The Serra do Mar samples do not statistically differ among themselves ($F_{2, 79} = 2.23$, $P > .05$), but the Serra da Mantiqueira samples do differ statistically ($F_{2, 38} = 3.45$, $.01 < P < .05$). The Brejo da Lapa sample is distinctive among the Serra da Mantiqueira samples ($F_{1, 29} = 0.09$, $P > .05$, for Macieiras and Cidade Azul samples). Female head length proportions all fall within the range exhibited by males and do not appear to be distinctive.

Femur — The femur proportion means for each of the samples all fall within one standard deviation of each other (Table 4), but the six samples differ statistically ($F_{5, 118} = 4.73$, $P < .001$). When the most distinctive sample is deleted (Boracéia) the other five samples do not differ statistically ($F_{4, 59} = 0.98$, $P > .05$). Female femur proportions fall within the range exhibited by males.

Tibia — The mean tibia proportions of each sample fall within one standard deviation of all other samples (Table 4), but the samples differ statistically ($F_{5, 118} = 10.53$, $P < .001$). The Serra do Mar samples differ from the Serra da Mantiqueira samples ($F_{1, 122} = 29.70$, $P < .001$). The Serra do Mar samples differ statistically among themselves ($F_{2, 80} = 6.08$, $P < .005$) — the Boracéia sample is the distinctive one ($F_{1, 21} = 0.02$, $P > .05$ for Bocaina and Fazenda do Veado). The Serra da Mantiqueira samples differ statistically among themselves ($F_{2, 38} = 3.59$, $P < .05$) — the Brejo da Lapa sample is distinctive ($F_{1, 29} = 0.27$, $P > .05$ for Macieiras and Cidade Azul). Female tibial proportions fall within the range of values exhibited by the males.

Femur plus Tibia — One of the diagnostic characters used by Taylor and Cochran (1953) was the position of the "heel" (distal end of the tibia) relative to the eye or tip of snout when the leg was adpressed to the body. The adpressing of the limb in this manner often results in broken bones in well preserved material and the degree of adpression is dependent on the state of preservation. For these reasons, I have combined the femur and tibial lengths in determining the leg proportion to approximate the character used by Taylor and Cochran (1953). Measurement errors are compounded, but using the measurements is likely as accurate as adpressing the limbs.

The mean femur plus tibia proportions all fall within one standard deviation of each other (Table 4), but the samples differ statistically ($F_{5, 118} = 8.49$, $P < .001$). When the most distinctive sample is omitted from analysis (Boracéia), the remaining samples

do not differ statistically ($F_{4, 59} = 1.81$, $P > .05$). The differentiation pattern is the same as that for the femur proportions. All female ratios fall within the values exhibited by males.

Foot — Mean foot proportions are similar for the 6 samples (Table 4) and do not significantly differ statistically ($F_{5, 118} = 1.91$, $P > .05$). Female foot proportions fall within the range of values exhibited by males.

Color in Life

Color notes and photographs are available for individuals from Boracéia, Fazenda do Veado, and Brejo da Lapa. All specimens were leaf green dorsally. The limbs had small white dots. The belly was transparent. A white shearth covered the heart, liver, and digestive tract.

The only difference noted in color was the iris color. The Boracéia specimen had a silver-green iris, the Brejo da Lapa and Fazenda do Veado specimens had silver-bronze irises.

Mating Call

Calls are available from Boracéia, Brejo da Lapa, and Fazenda do Veado. In all calls, a call group is defined by 1-5 calls, each call composed of 1-8 distinctive pulses (Figure 3). Within each call, the frequency of each pulse increases perceptibly (Figure 3).

The frequency ranges are: Boracéia, 4000-4500 hz at 18.6° C air temperature; Fazenda do Veado, 4100-4300 hz at 18-20° C air temperature; Brejo da Lapa, 3700-4000 hz at 15-17° C air temperature.

The calls are pulsatile; the pattern of pulsation is complex (Figure 4). Duration of individual high intensity pulses ranges from 0.01 to 0.03 s.

Data are too few to determine whether the differences in calls (Figures 3 and 4) represent individual or geographic variation. The calls are clearly of the same type. Although the variation probably has a geographic component, the differences are here interpreted as not being indicative of species level differentiation.

Geographic Variation

The pattern of variation for characters which vary among populations (for which data are available on all specimens) correlates well with geography (Figures 5 and 6). The greatest differences are between the Serra do Mar and Serra da Mantiqueira samples. Within the Serra do Mar samples, the Boracéia sample is distinctive from the other two samples. The Bocaina and Fazenda do Veado samples are geographically very close to each other and do not differ from each other. Within the Serra da Mantiqueira samples, the Brejo da Lapa sample is distinctive from the other samples. Macieiras and Brejo da Lapa are geographically close; Macieiras is on the east face of the Serra da Mantiqueira, Brejo da Lapa is from a west facing slope of the Serra da Mantiqueira.

The data on life color and mating call is consistent with the pattern described by morphological features (Figure 6).

Taxonomic Conclusions

There is consistent geographic variation in the samples analyzed, but a glance at the data (Tables 1-4, Figures 1-2) indicates that variation is not discrete. The variation is in degree, not kind, which I interpret to be at a population level and not at the species level. The six samples analyzed represent a single, geographically variable, species.

Taylor and Cochran (1953) described 5 species of the *C. eurygnatha* complex from the Serra do Mar and Serra da Mantiqueira, 4 as new. The results of this study indicate that there is but a single species involved, for which the oldest name is *eurygnatha*. For each species described as new by Taylor and Cochran, the diagnostic characters are listed and discussed below. The diagnostic characters are taken from their key and diagnoses and include only those characters used to distinguish each species from the other species of the *C. eurygnatha* complex (the order is that of Taylor and Cochran's descriptions).

C. surda

1. Eyeball with dark tunic
2. Tympanum hidden or concealed
3. Prominent anal pads
4. Distinct heel ridge
5. Heel to eye
6. Vestigial finger web

Characters 1 and 3 are artifacts of preservation (the legs of the types extend more or less straight back from the body in the specimens; figure 1 of Taylor and Cochran is idealized). Character 2 is indicative of individual or population variation and not diagnostic at the specific level. Character 4 is also an artifact of preservation; the tibia and tarsus of both specimens are preserved in an extended manner, producing the fold of skin. Character 5 is difficult to evaluate due to the posteriorly extended position of the legs. Measurements are difficult to make on such preparations. The femur plus tibia lengths are 94% snout-vent length for both types, lower than any other values recorded. The limbs do not visually appear shorter in the types than in other specimens. The measured shortness of the limb, either by measurement of elements or adpression is likely caused by the preserved position of the limbs. The hand web formula for both type specimens is I N II N III $3^- - 2\ ½$ IV, which is similar to the modal hand web for several populations (Figure 1).

C. delicatissima

1. Flesh of body very white with scattering of lavender pigment
2. Eye tunic black

3. Tympanum visible, directed laterad
4. Heel to beyond tip of snout
5. Outer fingers ¼ webbed

Characters 1 and 2 are artifacts of preservation. Character 3 is indicative of individual or population variation. The femur plus tibia is 106% snout-vent length, not different from other individuals (Table 4). The hand webbing formula is I N II T III 2 2/3 — 2 1/3 IV and is not different from the formula of other individuals (Figure 1).

C. bokermanni

1. Diminutive
2. Eye tunic dark
3. Tympanum covered
4. Neck not constricted
5. Pair of swellings behind vent, widely separated
6. Heel to between eye and nostril
7. Finger web vestigial
8. First finger much shorter than second
9. Skull transparent

Taylor and Cochran (1953) listed the snout-vent length of the holotype as 20.4 mm; I measure 19.7 mm, the difference due to the poor state of the specimen. Most of the other females examined fall into this size range. Character 2 is an artifact of preservation. Character 3 is variable within individuals and populations and is not diagnostic at the species level. Character 4 differs from all other specimens examined. The difference is one of degree, however and may be due to state of preservation. Character 5 is a normal expression of the seat patch. The femur plus tibia length (Character 6) is 99% the snout-vent length, which is relatively short, but this value is matched by individuals from most of the six samples. The finger web formula is I N II N III 3 — 2 2/3 IV, a formula shared by individuals from all six samples except the Boracéia sample. Character 8 is matched by other individuals and is a difference of degree, not kind. Taylor and Cochran (1953) indicated that the transparency of the skull could be due to an artifact of preservation. This is almost certainly the case. All of the MZUSP amphibians bearing low museum numbers are strongly sun-bleached; the holotype of *C. bokermanni* is one of these sun-bleached specimens. Thus, of all the characters listed, only the head-neck constriction character is diagnostic. I do not think the difference is of a magnitude to indicate species differentiation.

C. divaricans

1. Tympanum covered, outline partly visible
2. Eye tunic dark
3. No anal decoration
4. Heel to front edge of eye
5. Toes 3/5 to 3/4 webbed

Character 1 is variable within individuals and populations and is not diagnostic at the species level. Characters 2 and 3 are artifacts

of preservation. The femur plus tibia is 96% the snout-vent length, a low value, matched by only one non-type specimen. The leg does not appear visually shorter than legs of other specimens. The leg length is at the low end of the continuum and not discretely different from leg lengths of the other specimens examined. The foot webbing formula (specimen brittle and web can not be located accurately on inner side of second digit) is I 2 — ? II 1 ½ — 2 ½ III 1 ½ — 3 IV 3 — 2⁻ V; the webbing is not diagnostic from the webbing recorded in the 6 samples (Figure 2).

The synonymy for members of the *C. eurygnatha* complex from Serra do Mar and Serra da Mantiqueira is:

Centrolenella eurygnatha (A. Lutz)

Hyla eurygnatha A. Lutz, 1925: 137. Type-locality, Serra da Bocaina, Brasil. Syntypes, Museu Nacional, Rio de Janeiro, 973-975.

Cochranella surda Taylor and Cochran, 1953: 1630, Fig. 1. Type-locality, Passa Quatro, Minas Gerais, Brasil. Holotype, USNM 96916, female.

Cochranella delicatissima Taylor and Cochran, 1953: 1640. Type-locality, Angra dos Reis, Rio de Janeiro, Brasil. Holotype, USNM 96481, male.

Cochranella bokermanni Taylor and Cochran, 1953: 1641. Type-locality, Itatiaia, Rio de Janeiro, Brasil. Holotype, MZUSP 328, female.

Cochranella divaricans Taylor and Cochran, 1953: 1643. Type-locality, Serra da Bocaina, Brasil (locality clarified by Bokermann, 1966, as Fazenda do Bonito, Serra da Bocaina, São José do Barreiro, São Paulo, Brasil). Holotype, USNM 96562, male.

Centrolenella eurygnatha: B. Lutz, 1947: 243. First association of *eurygnatha* with *Centrolenella*.

Other available specimens of *C. eurygnatha* examined in this study are from the following localities. Guanabara; Rio de Janeiro, USNM 165127; Rio de Janeiro: Tijuca, MZUSP 20891-94; São Paulo: Campos do Jordão, MZUSP 10091, Eugênio Lefevre, MZUSP, 14000, USNM field 5371.

Systematic and Zoogeographic Implications

Taylor and Cochran provisionally treated two taxa as distinct: *C. parvula* (Boulenger, 1894) and *C. uranoscopa* (Müller, 1924), both from the state of Santa Catarina. Until fresh material is studied from Santa Catarina, detailed examination of the types is premature. It is possible that one or both of these names is synonymous with *Centrolenella eurygnatha* in which case either name would have priority over *eurygnatha*.

Two general conclusions can be drawn at this point: (1) The species diversity of centrolenids is significantly lower in southeast Brasil than previously recognized; (2) Regional differentiation has occurred within the species *Centrolenella eurygnatha*.

The kind of regional variation seen is the same kind as apparently occurs at the species level in some other groups of frogs, such

as the *Hyla rubra* complex. This suggests that (1) The major units of elevational relief within the Atlantic forest system have served as evolutionary centers of differentiation for the indigenous frog fauna; (2) The isolation of each unit of elevational relief from each other took place during relatively more xeric times when the wet forests were restricted to higher elevations; (3) The pattern of expansion and contraction of the wet forest units has been cyclic; and (4) The species level of differentiation correlates with an early cycle, the within-species level of differentiation correlates with a later cycle, suggesting that (5) centrolenids are relatively recent invaders of the Atlantic forest system in the Serra do Mar and Serra da Mantiqueira regions. Whether these patterns and hypotheses are valid depends on detailed analysis of distribution and differentiation patterns of several more exemplary frog groups.

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Boraceia

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  N    N     2+      2
I N II T III 2 1/2 - 2+    IV
  T    T     3-      2 2/3
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Bocaina

```
       N     2 1/2   2+
I N II N III 2 2/3 - 2 1/2 IV
       T     3       2 2/3
```

Fazenda do Veado

```
       N     2 1/2   2+
I N II T III 3-    - 2 1/2 IV
       T     3       2 2/3
```

Brejo da Lapa

```
  N    N     2 2/3   2+
I N II T III 3-    - 2 1/2 IV
  T    T     3       3-
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Macieiras

```
       N     2 2/3
I N II T III 3-    - 2 1/2 IV
       T     3
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Cidade Azul

```
  N    N     3-      2 1/2
I N II N III 3-    - 2 1/2 IV
  T    T     3       3-
```

Figure 1. Hand webbing formulae for males from six localities. Top row of each formula minimum web formula, middle row modal formula, bottom row maximum formula. Formulae follow Savage and Heyer (1967) with the following modifications: N = no web, T = trace of web.

Boraceia

	1^+	2		1^-		2^+		1^+		2 1/3		2 1/4	1^+	
I	2^-	- 2^+	II	1 1/2	-	2 1/2	III	1 1/2	-	3^-	IV	2 2/3	- 1 1/2	V
	2^+	3^-		2^-		3		2^-		3		3	2^-	

Bocaina

	2^-	2^+		1 1/2		2 1/2		1 1/2		3^-		2 2/3	1 2/3	
I	2	- 2 1/2	II	1 1/2	-	2 1/2	III	1 2/3	-	3^-	IV	3^-	- 2^-	V
	2^+	3		2		3^-		2^-		3		3	2	

Fazenda do Veado

	2	2 1/2		1 1/2		2 1/2		1 1/2		2 1/2		2 1/2	1 1/2	
I	2	- 2 1/2	II	1 1/2	-	2 1/2	III	1 1/2	-	3^-	IV	3^-	- 2^-	V
	2	3^-		2^-		3^-		1 2/3		3		3	2^-	

Brejo da Lapa

	2^-	2^+		1 1/2		2^+		1 1/2		2 1/2		2 2/3	1 1/2	
I	2	- 2 1/2	II	1 1/2	-	2 2/3	III	1 2/3	-	3^-	IV	3	- 1 1/2	V
	2^+	3^+		1 2/3		3^-		2^-		3		3	2	

Macieiras

	2^-	2^+		1^+		2^+		1^+		2 1/2		3^-	1 1/2	
I	2	- 2 1/2	II	1 1/2	-	2 1/2	III	1 1/2	-	3^-	IV	3^-	- 1 2/3	V
	2	3		1 2/3		3		2		3^+		3^+	2	

Cidade Azul

	2^-	2^+		1 1/3		2 1/2		1 1/2		2 2/3		2 2/3	1 2/3	
I	2	- 3^-	II	1 1/2	-	3	III	1 1/2	-	3^-	IV	3	- 2^-	V
	2	3^+		2^-		3		2^-		3^+		3^+	2	

Figure 2. Foot webbing formulae for males from six localities. Top row of each formula minimum web formula, middle row modal formula, bottom row maximum formula. Formulae follow Savage and Heyer (1967).

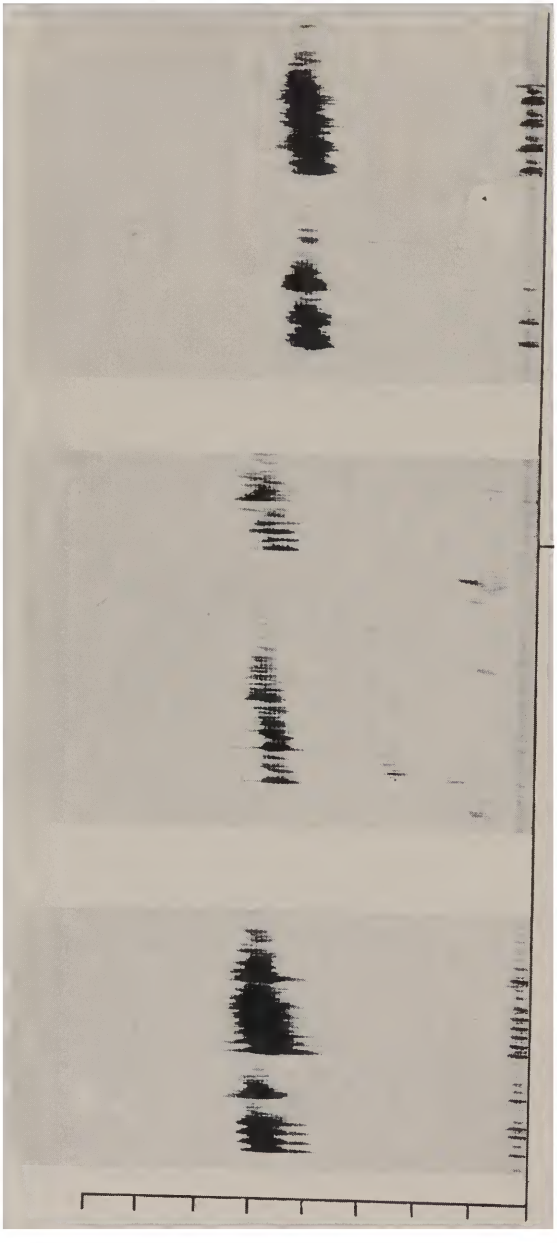

Figure 3. Wide band (300 hz filter) sonagrams of male calls. Mark on horizontal axis indicates 1 second. Marks on vertical axis at 1000 hz intervals. Left — call of specimen USNM field 4291 from Boracéia recorded at an air temperature of 18.6° C. Middle — call of specimen USNM field 4909 from Fazenda do Veado recorded at an air temperature of 19-20° C. Right — call of specimen USNM field 5315 from Brejo da Lapa recorded at an air temperature of 15-17° C.

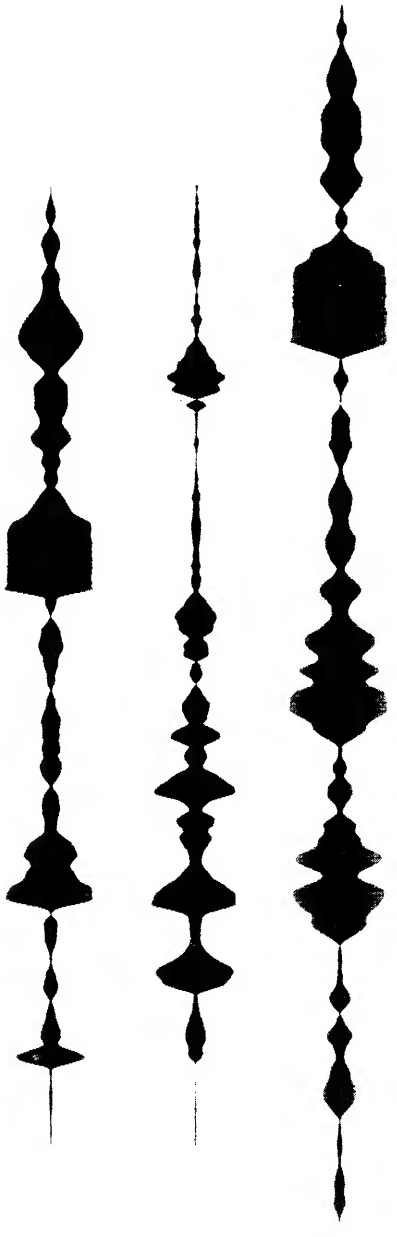

Figure 4. Filtered strip chart oscillographic records of male calls. Line equals 0.01 second. Due to background noise, each call filtered at 1% bandpass; top and middle calls filtered at 4500 hz, lower call filtered at 4150 hz. Top — call of specimen USNM field 4291 from Boracéia recorded at an air temperature of 18.6° C. Middle — call of specimen USNM field 4909 from Fazenda do Veado recorded at an air temperature of 19-20° C. Bottom — call of specimen USNM field 5315 from Erejo da Lapa recorded at an air temperature of 15-17° C.

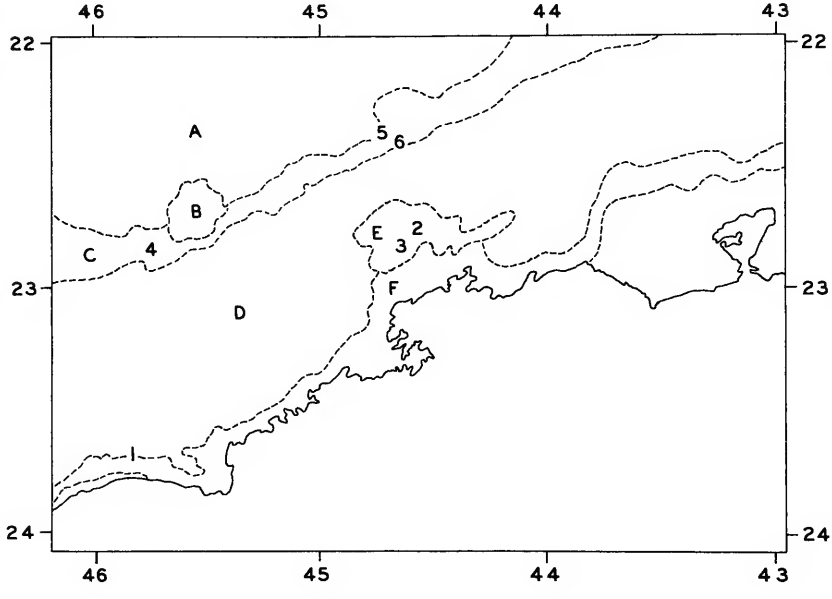

Figure 5. Morphological areas of southeast Brasil and localities of six major collections of *Centrolenella*. A = Sul-Mineiro Planalto, B = Campos do Jordão Planalto, C = Serra da Mantiqueira, D = Paraíba Valley, E = Serra da Bocaina Planalto, F = Serra do Mar. 1 = Boracéia, 2 = Bocaina, Lutz Fazenda, 3 = Fazenda do Veado, 4 = Cidade Azul, 5 = Brejo da Lapa, 6 = Macieiras.

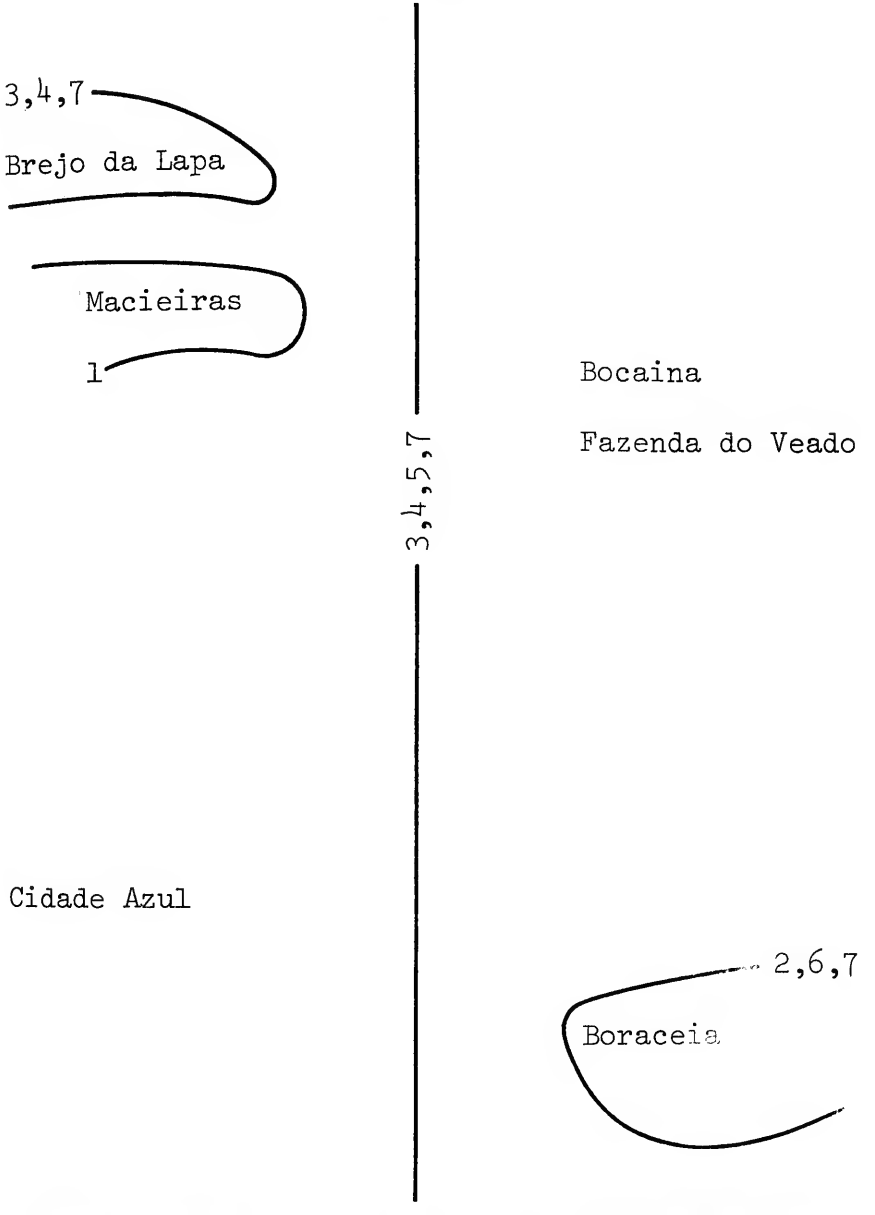

Figure 6. Variation among samples of males from six localities. Names of sample sites arranged in relative geographic position (see Figure 5). Lines indicate differences among samples. Numbers refer to characters: 1 = dorsal pattern, 2 = hand webbing, 3 = snout-vent length, 4 = head length, 5 = head width, 6 = femur, 7 = tibia. Also see text.

Table 1. Frequency distribution of tympanum states among six geographic samples of males. Tympanum states recorded from both sides of head. D = tympanum distinct, L = only lower edge for tympanum distinct, C = tympanum covered with skin, but visible, I = tympanum covered with skin, indistinctly visible, H = tympanum hidden.

	Boracéia	Brejo da Lapa	Macieiras	Cidade Azul	Bocaina	Fazenda do Veado
D	0.04	0.10	0.00	0.00	0.00	0.00
L	0.16	0.55	0.00	0.09	0.04	0.00
C	0.30	0.30	0.50	0.43	0.04	0.44
I	0.26	0.00	0.39	0.27	0.04	0.11
H	0.24	0.05	0.11	0.20	0.89	0.44

Table 2. Frequency distribution of dorsal pattern states among six geographic samples of males. U = rather uniform scattering of purple pigment, M = mostly uniform scattering of purple pigment cells with some bare spots, S = slightly blotchy pattern due to clumping of pigment cells.

	Boracéia	Brejo da Lapa	Macieiras	Cidade Azul	Bocaina	Fazenda do Veado
U	0.76	0.90	0.67	0.73	0.50	0.78
M	0.24	0.10	0.11	0.27	0.50	0.22
S	0.00	0.00	0.22	0.00	0.00	0.00

Table 3. Size statistics for six geographic samples of males.

	Minimum	Maximum	Mean	Standard Deviation
Boracéia	18.4	21.7	20.0	0.7
Brejo da Lapa	20.9	23.6	22.4	0.6
Macieiras	19.7	21.9	20.8	0.6
Cidade Azul	19.7	23.6	20.8	0.8
Bocaina	17.9	20.8	19.7	0.6
Fazenda do Veado	19.2	20.6	20.1	0.3

Table 4. Body proportions relative to snout-vent length for six geographic samples of males. Mean proportions expressed as percentages plus or minus one standard deviation.

	Head Width	Head Length	Femur	Tibia	Femur plus Tibia	Foot
Boracéia	36 ± 1	34 ± 1	53 ± 3	56 ± 2	109 ± 5	45 ± 2
Bocaina	36 ± 1	33 ± 2	51 ± 2	54 ± 1	105 ± 2	45 ± 2
Fazenda do Veado	36 ± 2	33 ± 1	52 ± 2	54 ± 2	106 ± 2	46 ± 2
Brejo da Lapa	35 ± 1	32 ± 1	50 ± 1	52 ± 2	102 ± 2	46 ± 2
Macieiras	35 ± 2	33 ± 2	51 ± 2	53 ± 1	104 ± 3	44 ± 2
Cidade Azul	35 ± 1	33 ± 1	51 ± 2	54 ± 2	105 ± 5	45 ± 2