

DIFFERENTIATION IN THE GENERA *ENYALIUS* AND *STROBILURUS* (IGUANIDAE): IMPLICATIONS FOR PLEISTOCENE CLIMATIC CHANGES IN EASTERN BRAZIL

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ABSTRACT

Geographic variations in meristic and morphometric characters are examined to delimit the taxa of the forest-restricted genus Enyalius in eastern Brazil. Eight taxa are recognized. Phenetic affinities among these are described by multiple discriminant analysis and Wagner networks based on separate morphological data sets. A phylogeny is proposed, and a sequence of allopatric differentiations is hypothesized. The locations of refugia of the Brazilian Atlantic forest during drier climatic periods are hypothesized from present variation in vegetation and precipitation: Santa Catarina refuge, around Baías de Paranaguá and São Francisco and adjacent slopes of Serra do Mar; São Paulo refuge, Serra do Mar between Paranapiacaba and São Sebastião; Bocaina refuge, around Baía da Ilha Grande; Mantiqueira refuge, on Serra da Mantiqueira; Órgãos refuge, on Serra dos Órgãos; Southern Espírito Santo refuge, in the mountains south of Rio Doce; Northern Espírito Santo refuge, on the coastal plain north of Rio Doce; Salvador refuge, around Baía de Todos os Santos; Pernambuco refuge, along coast of northern Alagoas and southern Pernambuco; Upper Rio Doce refuge, near the headwaters in Minas Gerais. Locations of the hypothesized refugia are compared with the geographical separation in Enyalius proposed to have preceded differentiation. Differentiation in Enyalius is most interpretable with reference to past forest refugia separated by corridors of open vegetation. Geographic variation in Strobilurus torquatus in northeastern Brazil requires similar conclusions.

INTRODUCTION

The humid lowland tropical forests of the world are separated into four major geographic units: the Amazon Basin and parts of Central America, coastal eastern Brazil, equatorial Africa, and southeastern Asia. For the first and third of these exists increasingly compelling evidence, both geological and biological, that Quaternary periods of drier climate caused the replacement of humid forests by open formations over large areas with continuous retention of forest biotas only in locally more humid refugia that were largely separated from each other (Moreau, 1966; Vanzolini and Williams, 1970; Haffer, 1974). For coastal eastern Brazil (= the Atlantic forest) there is considerable geological evidence of Quaternary climatic cycles (Tricart, 1959; Bigarella, 1971), but until now no search has been made for biological evidence of such fluctuations in this region. This paper presents such evidence from the genera *Enyalius* and

Strobilurus. The argument is straightforward. In species or species groups whose present-day distribution extends throughout an expanse of humid forest, the existence of geographic differentiation with zones of intergradation or simply allopatric replacement indicates probable past geographic separation of the taxa, presumably by occupation of different refugia. The critical assumption, that strong differentiation normally occurs only during cessation of gene flow, is supported by a large body of evidence (Mayr, 1963; Metter and Pauken, 1969; Ballinger and Tinkle, 1972; Jackson, 1973). Given this assumption, patterns of differentiation in tropical forest biotas can supplement geological evidence of Quaternary climatic changes (Vanzolini and Williams, 1970; Haffer, 1974; Brown, et al., 1974).

The genera *Enyalius* and *Strobilurus* were chosen as highly appropriate material because (1) they are ecologically restricted to closed-canopy forest (with the interesting exception of *E. bilineatus*), (2) their known range in the Atlantic forest is extensive, and (3) being lizards, they provide an abundance of quantifiable characters. Etheridge (1968 a and b) cursorily reviewed these genera based on material in European and North American museums, but

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because he did not examine material from Brazilian museums nor have adequate locality data for many specimens, he considered his work as characterizations of the genera rather than as definitive revisions.

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ABBREVIATIONS USED IN THE TEXT ARE:

- AMNH - American Museum of Natural History, New York
- BM - British Museum (Natural History)
- CAS - California Academy of Sciences, San Francisco
- DEUFP - Departamento de Ecologia da Universidade Federal de Pernambuco, Recife.
- FMNH - Field Museum of Natural History, Chicago
- IBUEC - Instituto de Biologia da Universidade Estadual de Campinas, São Paulo
- ICBUFV - Instituto de Ciências Biológicas da Universidade Federal de Viçosa, Minas Gerais
- MCN - Museu Rio-Grandense de Ciências Naturais, Porto Alegre
- MCZ - Museum of Comparative Zoology, Cambridge, Massachusetts
- MEPDIR - Museu da Empresa de Turismo de Pernambuco, Parque Dois Irmãos, Recife
- MNRJ - Museu Nacional, Rio de Janeiro
- MP - Muséum National d'Histoire Naturelle, Paris
- MVZ - Museum of Vertebrate Zoology, University of California at Berkeley
- MZUSP - Museu de Zoologia da Universidade de São Paulo
- NMW - Naturhistorisches Museum, Wien
- RMNH - Rijksmuseum van Natuurlijke Historie, Leiden
- UFP - Departamento de Zoologia, Universidade Federal do Paraná
- UFRRJ - Universidade Federal Rural do Rio de Janeiro
- UMMZ - University of Michigan Museum of Zoology
- USNM - United States National Museum, Washington
- ZIM - Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg
- ZMC - Zoologiske Museum, Copenhagen

METHODS

A. Recognition of Taxonomic Units

1. Explanation of Approach

The criteria employed in this study for recognition of evolutionary units above the popula-

tion level were the traditional ones: concordant geographic variation in several independent characters and strict sympatry of phenetically distinct forms. Had the sample sizes been considerably larger for most localities, an economical method for obtaining a summarization of the most important geographic variation would have been multiple discriminant analysis. However, the fact that the average sample size per locality per sex was less than three would have required reducing the geographic precision (by lumping samples) in order to obtain meaningful basic statistics for the multiple discriminant analysis. Instead, in both genera variation was treated separately for each character by plotting sample means on a map of eastern Brazil. Because of the small sample sizes, establishing presence or absence of sexual dimorphism in each sample was impossible, and hence the sexes were treated separately. The most rigorous method for comparison of single morphometric characters between samples in animals with continuous growth is by regression analysis (e.g. Vanzolini and Williams, 1970), but again small sample sizes make the use of this method here pointless. Hence I employ the hoary ratio method for morphometric characters although recognizing its shortcomings (Jackson, 1973).

A preliminary keying of the *Enyalius* in the Museu de Zoologia da Universidade de São Paulo using Etheridge (1968b) convinced me that *E. bilineatus* is a well-defined taxon relatively divergent from the remainder of the genus. For this reason, geographic variation in *bilineatus* was examined separately. However, the other species recognized by Etheridge are phenetically much more similar, and it was evident that two distinct entities were included under one of Etheridge's nominal species. Therefore, I plotted character variation in eastern Brazil for the rest of the genus together.

2. Localities

As alluded to above, the sample sizes and degree of geographic coverage in this study do not attain the standards of recent studies of geographic variation in temperate lizards (Kerfoot, 1968; Ballinger and Tinkle, 1972; Jackson, 1973). The problem is most serious for northeastern Brazil and is partly due to the lack of natural history museums in this region. My collecting efforts ameliorated but did not solve the problem because *Enyalius* species (except perhaps *bilineatus*) apparently have very low

population densities. Therefore, the use of some museum material with inexact locality data was deemed worthwhile. My acceptance or rejection of dubious locality records as well as delimitation of inexact locality data are justified below.

MHNP 6816 (A and B) – These are the syntypes of *brasiliensis* and have the locality data “Santa Catarina”. At the time of collection (1822) “Santa Catarina” referred primarily to the island rather than to the interior of the present-day state. Collection occurred during a trans-world natural history expedition aboard the French ship *La Coquille*. According to Lesson (1828), the ship made its first and only Brazilian landfall at present-day Florianópolis on Ilha de Santa Catarina. Collections were made on the island and nearby mainland during 16-29 October; then the ship sailed for temperate South America. Thus there is no reason to restrict the type locality to the isld of Santa Catarina and the nearby continent.

RMNH 4966 – This specimen is assumed to have come from near Teresópolis, Santa Catarina, because the same collector deposited similar material in the British Museum from this locality.

MCZ 6315 – This specimen is assumed to have come from near Blumenau, Santa Catarina, because the collector (A. Müller) was a resident there (Papavero, 1973).

USNM 40214-15 – These specimens are assumed to have come from Hansa, Santa Catarina, because the same collector supplied similar material to the British Museum and the Museu de Zoologia da USP from this locality.

RM without numbers – These specimens are assumed to have come from near Porto Real, Rio de Janeiro, because the collector deposited similar material in the British Museum from this locality.

BM1893.9.30.1 – The museum records give only “Colônia Alpina, Teresópolis” without designation of the state. Etheridge (1968b) assumed the Teresópolis in question to be that of Santa Catarina. However, it is clear that the correct locality is Teresópolis, Rio de Janeiro, since he collector (Goeldi) made his home at the nearby Colônia Alpina in the early 1890's (Papavero, 1973).

ZIM 2546 (6 and 7) – Museum records give the locality as “Santa Leopoldina, Brasilien”. Etheridge (1968b) assumed this referred to Leopoldina, Minas Gerais. As far as I can determine, Leopoldina, Minas Gerais, was always cal-

led simply this, never Santa Leopoldina. Santa Leopoldina, Espírito Santo, has had this name since its founding by German settlers in 1887. The collector had a German surname (Schlüter) and the specimens were deposited in a German museum. I conclude that the correct locality is Santa Leopoldina, Espírito Santo.

MHNP 2373, and 6815 — Etheridge (1968b) felt that the locality Cayenne might be in error. Because recent field work has failed to confirm the presence of *Enyalis* in Cayenne (J. Lescure, *in litt.*; M. S. Hoogmoed, pers. comm.), these old MP records probably should be considered erroneous.

MHNP 2374 — The locality for this specimen collected by Castelnau is given only as “Bahia”. Between 1843-47 he traveled through south-east, central and northern Brazil but never entered Bahia. In the late 1840’s Castelnau returned to Brazil as the French consul in Salvador, Bahia. There is no evidence that he traveled widely during his term there as he was occupied both with official duties and writing an account of his South American travels (Papavero, 1971). In common usage of the time, “Bahia” was more employed to designate the city now called Salvador than for the surrounding province. I assume this specimen was collected near the city of Salvador.

BM 1861.2.2.3.3 — The locality is given as “Bahia”. Dr. Otto Wucherer, the collector, lived around the Bahia de Todos os Santos in the towns of Nazaré, Cachoeira and Salvador from 1843 until his death (Coni, 1967). As a practicing physician, he probably did not travel extensively in his zoological collecting. The locality is assumed to be near Salvador.

BM 1869.11.3.7. and 8. — The specimens, one the type of *bibronii*, have locality data only as “Bahia”. No information about travels or residence of the collector allow further delimitation.

RMNH 3061 and 3058 — These specimens are the types of Spix’s *Lophyrus margaritaceus* and *Lophyrus albomaxillaris*, respectively; and they correspond to his illustrations (Spix, 1825). According to Papavero (1971), Spix collected between Salvador and Ilhéus in coastal Bahia, so I assume these specimens to be from this region.

BM 1923.22.4.38. — The locality “Montevideo, Uruguay” is considered erroneous because of the absence of the required habitat (tropical

evergreen forest) in the area. I was not able to examine ZMH 10081 supposedly from Buenos Aires, but the record seems equal improbable ecologically.

AMNH 108 — This is the putative type of Wied’s *catenatus*, but for reasons detailed later I do not believe it to be the specimen upon which the description was based. Hence the specimen is lacking locality data and was not utilized in the study of geographic variation.

ICBUFV without numbers — These specimens without locality labels are part of an old collection at the Universidade Federal de Viçosa, Minas Gerais. Dr. João Moojen de Oliveira informed me that they were collected near Araponga about 50 km north of Viçosa. I accepted this record.

In a few instances, geographically close localities were lumped: Piassaguera, São Paulo, with Cubatão; Rio Grande, São Paulo, with Paranaícabá; Humboldt, Santa Catarina, with Corupá do Sul; Pedro de Toledo, São Paulo, with Musácea; Guarujá and Praia Grande, São Paulo, with Santos. A number of separate localities in the old state of Guanabara were combined to form a single Guanabara sample.

There follows a list of all localities for *Enyalis* samples except *bilineatus* with code numbers that correspond to the map of Figure 1. On the maps, localities enclosed in a square are referred only to a state, more exact placement being impossible. The following abbreviations for states names are used in the list and throughout the paper: RS, Rio Grande do Sul; SC, Santa Catarina; PR, Paraná; SP, São Paulo; MG, Minas Gerais; GO, Goiás; RJ, Rio de Janeiro; ES, Espírito Santo; BA, Bahia; AL, Alagoas; PE, Pernambuco.

1. Rio Grande do Sul
2. Porto Alegre, RS
3. Colônia de São Pedro, RS
4. Torres, RS
5. Santa Catarina
6. Lauro Müller, SC
7. Teresópolis (Palhoça), SC
8. Ilha de Santa Catarina, SC
9. Blumenau, SC
10. Nova Brêmen (Ibirama), SC
11. Dona Ema, SC
12. Jaraguá do Sul, SC
13. Hansa, SC
14. Joinville, SC
15. Corupá do Sul (old name Humboldt), SC
16. São Bento do Sul, SC

17. Porto União da Vitória, PR
 18. Paulo Frontin, PR
 19. Irati, PR
 20. Caiobá, PR
 21. Morretes, PR
 22. Antonina, PR
 23. Barigui, PR
 24. Marumbi, PR
 25. Rio Ipiranga (Sete Barras), SP
 26. Iguape, SP
 27. Juquiá, SP
 28. Pedro de Toledo, SP
 29. Ana Dias, SP
 30. Peçuíbe, SP
 31. Itanhaém, SP
 32. Santos, SP
 33. Evangelista de Souza, SP
 34. Cubatão, SP
 35. Paranapiacaba, SP
 36. Salto de Itu, SP
 37. São João Novo, SP
 38. Quilombo, SP
 39. São Paulo and suburbs, SP
 40. Poá, SP
 41. Bom Jesus, SP
 42. Boracéia, SP
 43. Ubatuba, SP
 44. Ilha de São Sebastião, SP
 45. Ilha dos Búzios, SP
 46. Ilha Vitória, SP
 47. Paranapuã, SP
 48. Garça, SP
 49. Serra Azul, SP
 50. Serra Negra, SP
 51. Machado, MG
 52. Piquete, SP
 53. Parati, RJ
 54. Serra da Bocaina, SP
 55. Itatiaia, RJ
 56. Porto Real, RJ
 57. Rio Claro, RJ
 58. Mangaratiba, RJ
 59. Ilha Grande, RJ
 60. Paulo de Frontin, RJ
 61. Tijuca and Corcovado, RJ
 62. Suburbs of Rio de Janeiro, RJ
 63. Petrópolis, RJ
 64. Teresópolis, RJ
 65. Rio de Janeiro
 66. Madalena, RJ
 67. Macaé, RJ
 68. Goiás, GO
 69. Rio das Almas, GO
 70. Veadeiros, GO
 71. Araponga (50 km N. Viçosa), MG
 72. Espírito Santo
 73. Alfredo Chaves, ES
 74. Araguaia, ES
 75. Border between ES and MG
 76. Santa Leopoldina, ES
 77. Santa Teresa, ES
 78. São João de Petrópolis, ES
 79. Itá (Colatina), ES
 80. Reserva Sooretama (Linhares), ES
 81. Conceição da Barra, ES
 82. Itaúnas (Conceição da Barra), ES
 83. Mucuri, BA
 84. Itamaraju, BA
 85. Minas Gerais
 86. Montezuma (Monte Azul), MG
 87. Itapetinga, BA
 88. Poritaguá, BA
 89. Ilhéus, BA
 90. Salvador, BA
 91. Bahia
 92. Garanhuns, PE
 93. Água Preta, PE
 94. Palmares, PE
 95. Rio Formoso, PE
 96. Recife, PE
 97. Igarapu, PE
 98. Agua Azul (Vicência), PE
- The list immediately below gives localities for *Enyalius bilineatus* with code numbers that correspond to the map in Figure 2.
1. Conservatório, RJ
 2. Rio Preto, border between RJ and MG
 3. Benjamin Constant, MG
 4. Madalena, RJ
 5. Muriaé, MG
 6. Sereno, MG
 7. Antônio Carlos, MG
 8. Juiz de Fora, MG
 9. Viçosa, MG
 10. Santa Teresa, ES
 11. Mariana, MG
 12. Ouro Preto, MG
 13. Serra do Caraça, Santa Bárbara, MG
 14. Pampulha, MG
 15. Lagoa Santa, MG
- The list immediately below gives localities for *Strobilurus torquatus* with code numbers that correspond to the map in Figure 3.
1. Santa Cruz, ES
 2. Linhares, ES
 3. Ilhéus, BA

4. Itabuna, BA
5. São Miguel dos Campos, AL
6. Itamaracá, PE
7. Agua Azul, PE

3. Definition of Characters in *Enyalius*

Thirty-seven meristic, morphometric and qualitative characters were examined in *Enyalius*. They are defined as follows: 1) topography of subdigital lamellae, smooth = 1, intermediate = 2, keeled = 3; 2) curvature of the canthal ridge, straight = 1, intermediate = 2, curved medianly behind nasal = 3; 3) topography of ventral scales, smooth = 1, intermediate = 2, keeled = 3; 4) topography of enlarged supraoculars, smooth = 1, intermediate = 2, keeled = 3; 5) total vertebral scales counted along midline from hind margin of thigh to interparietal, including any small scales which separate the enlarged vertebral scales; 6) enlarged vertebral scales counted along midline from hind margin of thigh to interparietal; 7) paravertebral scales counted two or three scale rows lateral of midline from hind margin of thigh to interparietal; 8) one half of midbody scales counted from ventral midline to enlarged vertebral row; 9) right supraorbital semicircle counted from intersection of semicircle with imaginary line extending posteriorly from arc between the superciliaries and the lateralmost supraocular scale adjacent to the superciliary-canthal ridge; 10) minimum scale count between the supraorbital semicircles; 11) minimum scale count between the interparietal and either supraorbital semicircle; 12) minimum scale count between rostral scale and point of closest contact between the supraorbital semicircles; 13) right superciliaries counted to but not including the posteriormost canthal; 14) subocular series counted from the imaginary line that begins the supraorbital semicircle to the canthal row; 15) minimum count of loreal series from upper labials to the preocular; 16) upper labials (enlarged scales only); 17) lower labials (enlarged scales only); 18) minimum count of gular series from mental to and including the anteriormost row of scales in gular fold; 19) subdigital lamellae of second hind toe (most proximal scale included was the last one that flexes with the digit); 20) subdigital lamellae of fourth hind toe; 21) subdigital lamellae of first front toe; 22) subdigital lamellae of fourth front toe; 23) infratibials counted along ventro-lateral edge of right leg from the scale row at the base of the fifth

toe to a point even with junction of large and small scales on ventral side of thigh under knee; 24) sum of number of dorsal scales in the first, third and seventh caudal segments; 25) sum of number of ventral scales in the first, third and seventh caudal segments; 26) sum of the scales on the right halves of the second and fourth caudal segments; 27) percent of scales on right halves of second and fourth caudal segments that are not aligned with other scales; 28) percent of scales on right halves of second and fourth caudal segments that are aligned in pairs or trios; 29) percent of scales on right halves of second and fourth caudal segments that are aligned in quartets or quintets; 30) percent of scales on right halves of second and fourth caudal segments that are aligned in sextets; 31) tail length as a percent of snout-vent length; 32) thigh length as a percent of snout-vent length; 33) shank length as a percent of snout-vent length; 34) distance from posterior edge of nasal scale to tip of snout as a percent of distance from anterior corner of orbit to tip of snout; 35) distance between nares as a percent of maximum distance across head between the lateral edges of the superciliaries; 36) maximum distance across head between the lateral edges of the superciliaries as a percent of snout-vent length; 37) topography of infratibials, smooth = 1, intermediate = 2, keeled = 3.

4. Definition of Characters Examined in *Strobilurus*

Twenty-three meristic, qualitative and color pattern characters were examined in *Strobilurus torquatus*. They were defined as follows: 1) dorsal scales counted along midline from first small scale at hind margin of thigh to interparietal; 2) one half of midbody scales; 3) ventral scales counted from vent to gular fold; 4) gular scales from mental to gular fold; 5) subdigital lamellae of second hind toe; 6) subdigital lamellae of fourth hind toe; 7) subdigital lamellae of first front toe; 8) subdigital lamellae of fourth front toe; 9) infratibials counted from base of fifth toe to knee; 10) sum of upper labials; 11) sum of lower labials; 12) maximum scale count between nasals; 13) sum of superciliaries counted to exclude one postnasal and two canthals on each side; 14) sum of supraorbital semicircles; 15) total number of scales on snout in area bounded by interparietal, supraorbitals, postnasals, canthals, nasals and rostral; 16) sum of lorilabials; 17) total number of

scales in loreal region bounded posteriorly by elongate subocular, dorsally by subocular series, anteriorly by nasals-postnasals-canthals and ventrally by lorilabials; 18) degree of middorsal mucronation; none = 0, moderate = 1, strong = 2; 19) enlarged scales on ventral side of thigh; 20) width of posteriormost dark collar at midline as percent of snout-vent length; 21) dark reticulation on throat; absent = 0, present = 1; 22) number of dark collars behind eyes; 23) median anterior extension on second dark collar; absent = 0, present = 1.

B. Phylogenetic Relationships of Taxonomic Entities in *Enyalius*

1. Phylogenetic Methods

After the major phenetic units of *Enyalius* in eastern Brazil were recognized, phylogenetic hypotheses were advanced. These were arrived at by clustering the OTU's (operational taxonomic units) according to phenetic affinity through use of two clustering techniques, multiple discriminant analysis and Wagner trees (see Lynch and Wake, 1975, for discussion). Clustering of OTU's by different techniques on the same data base is desirable to confirm the robustness of the data, but does not provide independent measures of phenetic affinity. Such independent measures can come only from applying clustering methods to different data sets. In the present study the meristic-morphometric characters used initially to delimit the OTU's provided one data set for phenetic clustering. For a second data set, 400 individuals were scored according to 20 color pattern characters; descriptions of these characters are given below. In addition, osteological data from the cranium were taken from 1 to 3 specimens of each OTU to allow clustering by a third data set; the osteological characters are described below.

The multiple discriminant analysis was done using the BMD 07M program (Dixon, 1968). This clustering technique was applied only to the meristic-morphometric and osteological data sets. It could not be used on the color characters because these data were in the form of frequency of occurrence in each OTU, and hence there was no within-OTU variance.

Wagner Trees were calculated for all three data sets. Characters were not weighted and were standardized to the range 0 to 1. In order that the Wagner Trees be rooted and thus be phylogenetic hypotheses rather than merely

phenograms (Farris, 1970), one of the OTU's had to be designated the hypothetical ancestor. The choice was made by considering both zoogeography and the distribution of several qualitative characters among genera closely-related to *Enyalius*.

2. Definition of Characters Examined

Three independent data sets were used to estimate phylogenetic relationships in *Enyalius*. The first set consisted of the thirty-seven meristic, morphometric and qualitative characters whose geographic variation was examined to delimit the taxonomic entities. Clustering of all individuals examined was deemed unworkable, so instead samples representative of each OTU were obtained and clustered. Where possible, a local sample furnished this representative sample, but in several taxa small sample sizes necessitated lumping individuals from several localities. Only females were utilized. The localities and specimens used to generate the representative sample were as follows: *iheringii*, Greater São Paulo, SP, MZUSP 696, 3124, 3126-27, 3140-41, 4254, 4280, 36665, 40757 and IBUEC without number; *perditus*, Teresópolis, RJ, MNRJ 3449, 3450 (2 specimens), 3451-53, MZUSP 12281; *brasiliensis brasiliensis*, Guanabara, RJ, CAS 96876, MNRJ1609, 3457, 3459, 3461, MZUSP 2532, 3232, 3234, 4258, 10247; *brasiliensis boulengeri*, Santa Teresa, ES, MNRJ 1611, 1618 (3 specimens), MZUSP 8825, 39519, 39531-32, 39534, 39537, 39541; *catenatus catenatus*, Salvador, BA, BM.1861.2.23.3, MHNP 2374, Rio Formosa, PE, MCNR-4727, Recife, PE, MCN R-4725, Água Azul, PE, MZUSP 23086; *catenatus pictus*, Sooretama, ES, MCZ 82873, Itaúnas, ES, MZUSP 39539, Itamaraju, BA, MZUSP 30748; *catenatus bibronii*, Montezuma, MG, MZUSP 10115, Bahia, BM.1869.11.3.8, Garanhuns, PE, MCN R-4728; *bilineatus*, Santa Teresa, ES, MZUSP 17456, 39526, Viçosa, MG, MNRJ 1604 (2 specimens), MVZ 14931. Table 1 presents means of meristic, morphometric and qualitative characters of the *Enyalius* taxa of eastern Brazil based on these representative samples.

Twenty color pattern characters were examined in *Enyalius*. Individuals were scored for presence or absence of each character, and frequencies of occurrence were calculated for each OTU. These characters were defined as follows; 1) middorsum unicolored; 2) middorsum with dark longitudinal triangles; 3) middorsum with

dark diamonds; 4) middorsum with two rows of dark triangles offset along the midline; 5) middorsum with two rows of dark trapezoids offset along the midline; 6) middorsum with dark elongated ovals; 7) middorsum with two rows of dark elongated half-ovals offset along the midline; 8) middorsum with dark transverse rectangles; 9) sides with dark blotches; 10) paravertebral area with full length light stripes; 11) paravertebral area with light stripes only anteriorly; 12) paravertebral area with series of light spots; 13) paravertebral stripes wide; 14) labials with extensive light area; 15) post-orbital region with black-bordered stripe; 16) belly with lateral dark stripes; 17) throat with lateral dark stripes; 18) ventral side of legs with dark stripes; 19) belly with narrow dark midventral stripe; 20) belly spotted.

Eleven osteological characters provided data used to estimate phylogeny: 1) distance from snout to anterior edge of orbit as percent of skull length; 2) qualitative score for anterior angle between mandible and retroarticular process of mandible; $90^\circ = 1$, $70^\circ = 2$, $45^\circ = 3$; 3) width of squasomal at center as percent of squasomal length; 4) maximum anterior-posterior distance of splenial as percent of maximum dorso-ventral distance of splenial; 5) topography of posterior half of premaxilla; smooth = 1, slightly rugose = 2, rugose = 3; 6) minimum width at center of premaxilla as percent of premaxilla length; 7) distance between pterygoids at level of lateral junction of palatines and pterygoids as percent of skull length; 8) distance of anterior border of basioccipital as percent of distance of lateral border of basioccipital; 9) length of anterior processes of nasal as percent of skull length; 10) length of posterior maxillary process of palatine as percent of skull length; 11) distance *between* anterior point of pterygoids *and* lateral junction between pterygoid and palatine, as percent of width of pterygoid at level of junction between pterygoid and palatine.

RESULTS

A. Geographic Variation in *Enyalius bilineatus*

Specimens of *Enyalius bilineatus* were available from 15 localities. The range of variation of each character was divided into seven equal classes, and for each character (for each sex) a

map was prepared on which each locality was plotted according to the class to which it belonged. These maps were compared to identify regions of concordant geographic variation. The pattern of geographic variation is almost invariably mosaic without any clear region differentiation (Figs. 4 and 5). The only outstanding trend was that certain peripheral populations often have extreme values, e. g. Santa Teresa, ES, and Lagoa Santa, MG.

B. Geographic Variation in the *Enyalius catenatus* Complex

1. Keeling on Subdigital Lamellae (Fig. 6)

Males. All but four samples from SP, PR, SC, and RS have unkeeled subdigital lamellae. Three of the exceptions are from SC: sample 5 shows traces of keeling; sample 8 has completely keeled lamellae; and sample 14 shows nearly an intermediate degree of keeling [1.8.]. Sample 37 from SP has traces of keeling.

From RJ samples have either unkeeled lamellae (53, 56, 57, 60, 63, 67), completely keeled lamellae (55, 59, 61, 66), or a mixture of character states. Sample 64 has both states without intermediates. Sample 65 has both the unkeeled state and one individual with an intermediate degree of keeling [2]. Sample 62 has both the keeled state and one individual with intermediate keeling [2].

Sample 68 from GO has strongly keeled scales [2.5]. From southeastern MG and southern ES all samples have completely keeled lamellae. From northern ES, BA, and PE all samples have unkeeled lamellae, as does the unlocated MG sample (85).

Females. From RS north through SP most samples have unkeeled lamellae, but several samples from northern SC and PR have traces of keeling (5, 10, 12, 13, 18, 23) or slight keeling (14, 15, 24). In RJ samples are either unkeeled (53, 56, 63, 65, 67) or completely keeled (57, 58, 59, 61, 62) except for sample 64 in which both character states occur. At 53 one individual shows traces of keeling. In southeastern MG and southern ES all samples have complete keeling. From northern ES north to PE all samples have unkeeled lamellae. In GO locality 69 has unkeeled lamellae and 70 has completely keeled lamellae.

Summary

Combining the pattern of both sexes, was seen that the distribution of complete keeling is considerably disjunct. The center of complete keeling is RJ and southern ES, but three samples are widely separated: Ilha Santa Catarina (8), GO (68, 70). Unkeeled lamellae are separated into northern and southern geographic distributions, the hiatus occurring in southern ES. In the northern samples no individuals exhibit even traces of keeling, but in certain southern samples from SC and PR exist individuals with lamellae that are partially keeled. This fact suggests that the northern and southern unkeeled lamellae are not monophyletically derived. That keeled and unkeeled lamellae are sympatric at locality 64 suggests existence of either two species or polymorphism there.

2. Curvature of Canthal Ridge (Fig. 7)

Males. The pattern is essentially a division into southern samples (RS to RJ) that have straight canthal ridges and northern samples (northern ES to PE) that have markedly curved canthal ridges. In the intermediate region of southern ES and southeastern MG samples have either straight ridges (75, 79) or ridges that are partially curved (71, 77). Sample 68 from GO is of the southern type.

Females. The southern samples (RS to RJ) have straight canthal ridges, whereas northern samples (northern ES to PE) have a markedly curved canthal ridge. Canthal ridges of the intervening southern ES – southeastern MG samples vary from slightly curved (72, 73, 75) to a degree of curvature that is clearly intermediate (71, 74, 76, 77, 78). In GO are both straight (70) and curved canthal ridges (69).

Summary

Samples from RJ south have straight or, rarely, very slightly curved canthal ridges. Samples from northern ES north have strongly curved canthal ridges. Geographically intermediate samples are either phenetically intermediate or with straight canthal ridges. Two GO samples have straight ridges, and one has the curved condition.

3. Keeling of Ventral Scales (Fig. 8)

Males. Samples from southern ES southward and from Ilhéus, BA (89) northward all have strongly keeled scales. Samples from northern ES (80, 81, 82) and extreme southern BA (83), as well as the unlocated MG sample, have smooth central scales. No sample shows intermediacy on the southern border of the region of smooth ventrals, but a sample from southern BA (88) and an unlocated BA sample (91) are intermediate in degree of keeling and thus suggest intergradation in this character along the northern border of the region of smooth ventrals. Sample 68 from GO has keeled ventrals.

Females. Samples from southern ES southward have strongly keeled ventral scales. In northern ES and the panhandle of BA ventrals are smooth, again without evidence of intergradation with populations in southern ES. Three other more separated localities have smooth ventrals: 86, well inland near the MG – BA border; 91, an unlocated BA sample; 92 from the most inland locality in the northeast. Otherwise, northward from sample 87 and 89 ventrals are keeled. The slightly weaker keels on ventrals of sample 89 provide the only indication of intergradation with populations in the panhandle of BA. Samples from GO have keeled ventrals.

Summary

In all samples south of the Rio Doce, ES, ventrals are keeled, as does that from GO. In northern ES and the panhandle of BA, all samples have smooth ventrals. Smooth ventrals also characterize two more inland samples north of the Rio Doce (86, 92) and two unlocated samples (85, 91). Coastal samples from PE and northern and central BA have keeled ventrals. There is weak evidence of intergradation between these populations and those of the panhandle with smooth ventrals.

4. Keeling Supraoculars

Males. From southern ES southward all samples have keeled supraoculars, although there is some variation in degree. The region of strongest keeling is in SP and RJ. Farther south in PR, SC and RS some samples show less keeling. Samples from northern ES and southern BA have smooth supraoculars, as does sample 68 from

GO. The samples from PE have moderate keels on the supraoculars.

Females. All samples north to ES have keeled enlarged supraoculars but the keeling is less pronounced from the city of São Paulo southward. Samples from northern ES and extreme southern BA, as well as isolated inland samples 69, 86, and 92, have smooth supraoculars. The coastal PE samples have strongly keeled supraoculars. The intermediacy of samples 89 and 90 suggest intergradation in this character.

Summary

Again the Rio Doce marks a break in the distribution of the character states. South of it the enlarged supraoculars are keeled, most strongly in RJ and eastern SP, less strongly in southern SP, PR, SC, and RS. Between the Rio Doce and Rio Jequitinhonha supraoculars are smooth. In coastal PE supraoculars are keeled. There is probably intergradation between the PE keeled condition and the northern ES smooth condition, as evidenced by intermediacy of samples 89 and 90. Several interior samples have smooth supraoculars (68, 69, 85, 86, 92).

5. Vertebral Scales

Males. From RS to southern SP values are low [<80] except for 5 and 8 with intermediate values and 25 with a high value. From the city of São Paulo to the SP – RJ border values are generally less than 80 in monomorphic samples; in dimorphic samples (34, 35, 39, 42) the taxon with the lower value has counts (80 while that with the high value has counts >90). In RJ monomorphic populations show considerable variation from <70 to >90 . The dimorphic sample at 53 has character states similar to those of dimorphic samples in SP. The dimorphic sample 64 shows a magnitude of difference similar to other such samples but both means are elevated. In southern ES samples have moderate values [78-87]. The northern ES, southern BA, and unlocated MG samples have the highest values [91-96]. North of Rio Jequitinhonha to PE mean values are again lower [<90] but the variation among these samples appears to be mosaic.

Females. From RJ – SP border southward values are generally low [<80] in monomorphic samples; exceptions are a pocket of higher va-

lues in the interior of PR (17, 18, 19) and several localities in SP (33, 43, 48, 49, 52). In the dimorphic samples in eastern SP the minimum difference is 6 (39) and the maximum is 22 (42). In RJ and southern ES values are intermediate in monomorphic samples except for 67 [106]. Differences in dimorphic samples 53 and 64 are of the same degree of magnitude as in the dimorphic SP samples. In northern ES are two samples with high values. Farther north along the coast the values range from low (84) to high (96) but most are intermediate. The two inland northeastern samples (86 and 92) have low values. Values of the GO samples are intermediate.

Summary

The lowest monomorphic samples are found from SP south. The highest monomorphic samples are found in northern ES and extreme southern BA. Monomorphic samples in RJ and southern ES have intermediate values. Samples from southern BA to PE are variable without any clear pattern. Dimorphic samples are found only in SP and RJ. In these the difference in the character states ranges from 7 – 32% of the value of the lower character state ($\bar{x} = 20\%$).

6. Enlarged Vertebral Scales

Males. Low counts are evident in two areas: southern ES – southeastern MG and from SP south, with exception of samples 8, 12 and 21 with intermediate values. In the second region the dimorphic samples have taxa both low [<53] and intermediate-high [>54] counts. The samples from RJ, including the dimorphic samples, show intermediate values. Samples north of the Rio Doce have intermediate to high values but show no pattern.

Females. Low values are predominant from RS to eastern SP, except for the dimorphic samples that have both low and intermediate values. In central SP and southern MG values are intermediate-high. In extreme eastern SP (43, 52) and RJ values are also intermediate-high. The samples from southern ES – southeastern MG have low values. From northern ES to PE values are intermediate to high, as are the GO samples.

Summary

There are two regions with low values: southern ES and from eastern SP south to RS. In RJ

and from the Rio Doce north values are intermediate or high. The dimorphic samples from SP have both low values characteristic of the southern region and intermediate values similar to those of RJ.

7. Paravertebral Scales (Fig. 9)

Males. Excluding the dimorphic samples, values are uniformly low from eastern SP to RS except for samples 8 and 23 which have intermediate values. The dimorphic samples of SP and Parati (34, 35, 39, 42, 53) have one taxon with low values typical of southern samples and another with intermediate or high values. Values in RJ, extreme eastern SP (43, 52, 54), western SP (47, 48) and GO are intermediate or high. The two dimorphic RJ samples (62, 64) have one taxon with intermediate values and the other with high values. Southern ES samples (71, 75, 77, 79) have very similar intermediate values. North of the Rio Doce all samples have intermediate values, but those of northern ES and BA are consistently higher than those of PE.

Females. The description for males also applies to the females except that the samples north of the Rio Doce are not so clearly separable into northern ES – BA and PE entities. The low values of samples 86, 91, 92, and 98 are of note.

Summary

Low values characterize almost all monomorphic samples, and one taxon of the dimorphic samples, from eastern SP south to RS. The exceptions are 8 and 23, which have intermediate values. The second taxon of the dimorphic SP samples has high-intermediate values similar to most samples from western SP, extreme eastern SP, GO, and RJ. Southern ES samples have a narrow range of intermediate values. Values of northern ES and BA samples are intermediate, but generally higher than intermediate values of PE. The several inland northeastern samples have values anomalously low for the region.

8. Midbody Scales

Males. Except in samples 8 and 23, and in one taxon of the dimorphic samples, values are low from RS north to eastern SP. In these exceptions, values are intermediate to high. Inter-

mediate-high values are also found in GO, western SP, extreme eastern SP (43, 52), and in most RJ samples. Samples from southern ES have low-intermediate values. Northern ES and southern BA samples intermediate to high values, whereas values in PE are low-intermediate. Intervening BA samples (89, 91) suggest intergradation between these two regions.

Females. The same pattern is evident in the females. The northeastern inland samples (86, 92) have low values.

Summary

Except for samples 8 and 23, low values are the rule in monomorphic samples from RS north to eastern SP. In dimorphic samples, one taxon has similar low values whereas the second has high or high-intermediate values. High or intermediate values are found in western SP (47, 48), extreme eastern SP (43, 53), RJ and GO. The degree of difference between the two taxa of RJ dimorphic samples (62, 64) is less than differences in SP dimorphic samples. Values from southern ES – southeastern MG are intermediate and markedly uniform. Values in northern ES – southern BA are high to intermediate but, through gradual transition at Ilhéus (89) and Salvador (90), intergrade with the low-intermediate values in PE. The northeastern inland samples again have anomalously low values.

9. Right Supraorbital Semicircle

Males. From eastern SP south to RS monomorphic samples have low to intermediate values, except for sample 8 with a high value. The lower values are concentrated in RS and SC. The dimorphic samples have one taxon with intermediate values and the other with intermediate to high values. Samples from GO, western SP, extreme eastern SP, and RJ have high to intermediate values. Values from ES and southern BA are intermediate, whereas those from PE tend to be high.

Females. Values from RS to eastern SP are low to intermediate; within this region values increase clinally to the north. The dimorphic SP samples are composed of one taxon with intermediate values and the second with high or high-intermediate values. Values from western SP, southern MG, GO, and RJ are intermediate to high. The taxa within the RJ dimorphic sam-

ples (62, 64) differ little in this character. From ES to PE the values are intermediate without any marked geographic pattern. The inland MG sample 86 and the unlocated BA sample 91 have anomalously low values.

Summary

In monomorphic samples from eastern SP south to RS values are low to intermediate. There appears to exist a cline with values decreasing toward the south. A conspicuous exception is the high value of sample 8. The lower value of the dimorphic SP samples is similar to that of the southern region, and the higher value is close to those of RJ, extreme eastern SP, western SP and GO. From ES north along the coast a wide range of intermediate to high values are found without any clear pattern. Samples 86, 91 and 92 have unusually low values for the northeast.

10. Minimum Number of Scales Between Supraorbital Semicircles

Males. There are two regions of high or high-intermediate values: RS — SC and southern ES — southeastern MG. Intermediate values are predominant from PR (except for the low value of sample 23) to RJ; however, some samples, both monomorphic and dimorphic, in RJ have low values. Values are low in northern ES and BA and are consistently higher in PE.

Females. In southern ES and from eastern SP south to RS values are intermediate to high. In the SP dimorphic samples the two taxa have high-intermediate and low-intermediate values respectively. In RJ values vary from low to low-intermediate. Northern ES has low values, but from southern BA north values are low-intermediate. Samples from GO have low-intermediate values.

Summary

Values of monomorphic samples are consistently highest from eastern SP to RJ and in southern ES. In SP dimorphic samples, the taxa either have similar values, or one is high-intermediate while the second is low-intermediate. In northern ES values are markedly low and intergrade through BA to low-intermediate values in PE. GO samples have low-intermediate values.

11. Minimum Number of Scales Between Interparietal and Supraorbital Semicircles

Males. From RS north to RJ values are intermediate to low, the lower values tending to concentrate in the south. In dimorphic SP samples, taxa are either similar or one taxon has values similar to southern samples while the other has values more common in RJ. Values are consistently highest in southeastern MG — southern ES, ranging from high to intermediate. In northern ES — southern BA values are low-intermediate, whereas in PE they tend to be higher.

Females. Low to intermediate values are predominant from eastern SP to RS. The taxa of the dimorphic SP and RJ samples do not differ greatly. Samples from RJ have intermediate values, and no low values were observed there. Southern ES is a region of consistently higher values. Values in PE are high-intermediate.

Summary

Values are lowest from eastern SP south, while values in RJ, western SP and GO are intermediate to high-intermediate. Values are consistently highest in southern ES. Northern ES and southern BA have low-intermediate values that intergrade near Salvador with the high-intermediate values of PE.

12. Number of Scales Between Interorbital Midpoint and Rostral

Males. Excepting samples 8, 12, and 23, values in monomorphic samples, and in one taxon of the dimorphic samples, are intermediate to high-intermediate from RS to eastern SP. The other taxon of the SP dimorphic samples tends to low-intermediate values. Low to low-intermediate values predominate in RJ, western SP, and GO. Values in southern ES are intermediate. Those from northern ES north are low-intermediate.

Females. From eastern SP south values are typically intermediate to high-intermediate. In RJ values are more often intermediate. The SP and Parati (53) dimorphic samples have one taxon with values typical of the south and the second with values typical of RJ. Southern ES is homogeneous with high-intermediate characters. From the Rio Doce north values are patternlessly variable, except for the low values of

the inland northeastern samples (86, 92, 98, and perhaps 91).

Summary

Southern ES and the region from SP south to RS have the consistently highest values, usually intermediate to high-intermediate. Values in RJ and western SP tend to be lower, intermediate to low. The taxa of the dimorphic SP samples have values corresponding to those of the regions RS–SP and RJ. Values from Rio Doce northward are variable between low and high-intermediate and do not show a geographic pattern. Interior northeastern samples have markedly low values.

13. Right Supraciliaries

Males. From eastern SP south to RS all values are high to intermediate except for samples 8 and 23 and one taxon of the dimorphic samples, which have low-intermediate values. Values in western SP, extreme eastern SP, GO, and RJ are intermediate to low. Values in ES are intermediate and in BA are low-intermediate. Those of PE are intermediate and low.

Females. Values from eastern SP south are highest. Values in RJ and in one taxon of the dimorphic SP samples are low to low-intermediate. Values in southern ES are consistently intermediate. In northern ES – southern BA values tend to be higher than in PE.

Summary

RS to eastern SP, including one taxon of the dimorphic SP samples, is the region of highest values. In the other taxon of the dimorphic SP samples, and in RJ, values are intermediate to low. Southern ES has only intermediate values. Values in PE are mixed but tend to be lower than in northern ES – southern BA.

14. Subocular Series

Males. From RJ south there is considerable variation but generally values in RJ, extreme eastern SP, and in one taxon of the dimorphic SP samples are higher than in RS – eastern SP and in the other taxon of the SP dimorphic samples. Southern ES has intermediate values. Northern ES – southern BA has low values while northern BA and PE have intermediate values. The low value for sample 79 in the lowlands immediately south of Rio Doce suggest

possible intergradation between northern and southern ES taxa.

Females. The variation is mosaic except for the consistency of intermediate values in southern ES and of low to low-intermediate values in northern ES – southern BA.

Summary

Geographic patterns are not marked but RS to eastern SP has generally lower values than RJ; southern ES has consistently intermediate values; and there is a difference between northern ES – southern BA and central BA to PE.

15. Vertical Count Across Loreal Region

Males. Except for sample 8 and one taxon of the dimorphic SP samples, values are intermediate to low-intermediate from RS north to eastern SP. In western SP, RJ, and in the other taxon of the dimorphic SP samples values are high to high-intermediate. From northern ES north to PE values are low to low-intermediate. In southern ES values are intermediate except for sample 79 whose low value indicates possible intergradation with the taxon of northern ES.

Females. Values from RJ south are generally intermediate to low-intermediate, except for high-intermediate values in one taxon of the dimorphic SP samples. In southern ES values are intermediate to high-intermediate while in northern ES values are low; the low value of sample 78 might indicate some intergradation between northern and southern ES. Two northeastern samples (91 and 92) have unusually high values, but most PE and BA samples have values similar to those of northern ES.

Summary

Values from RS north to eastern SP tend to be slightly lower (intermediate to low-intermediate) than those of RJ, eastern SP, and one taxon of dimorphic SP samples (high-intermediate). Values from northern ES to PE are low. Values from southern ES are intermediate to high-intermediate and may intergrade with those of northern ES.

16. Enlarged Upper Labials (Fig. 10)

Males. Values from eastern SP to RS are high or high-intermediate except for samples 8 and 12 – 14 with intermediate values and 23 with a

low value. Values in RJ and extreme eastern SP are low to intermediate, as they are in one taxon of the dimorphic SP samples. From southern ES, north to PE values are high to intermediate.

Females. Except for a pocket of lower values in northern SC (9, 12-15), values from RS to eastern SP are high to high-intermediate. Values in the other taxon of the SP dimorphic samples are low-intermediate. Values in extreme eastern SP and RJ are intermediate. In southern ES values are similar to those of RS - eastern SP. Northern ES - southern BA have intermediate values, whereas values from central BA north are high to high-intermediate.

Summary

RJ and extreme eastern SP have generally intermediate values; low-intermediate values are characteristic of one taxon of the dimorphic SP samples. From eastern SP south values are generally high-intermediate except for an area in northern SC with values similar to those of RJ. Southern ES has intermediate to high-intermediate values. There is a weak tendency for differences between northern ES - southern BA and central BA-PE.

17. Enlarges Lower Labials

Males. From RS to eastern SP is a mosaic of high to intermediate values, except for one low value at locality 23. Values in RJ and in one taxon of the dimorphic SP localities are intermediate to low. From southern ES north values are intermediate to high with the northeastern values highest.

Females. From RS to eastern SP is a mosaic of high to intermediate values, including one taxon of the dimorphic SP localities. In RJ and eastern SP values are intermediate to low, including the second taxon of the dimorphic SP localities. Values in ES are intermediate. From BA northward values are high to intermediate.

Summary

RJ and one of the taxa of eastern SP have the lowest values, varying from low to intermediate. Both southern ES and the region from eastern SP to RS have slightly higher values that range from intermediate to high. Values from BA north are consistently the highest.

18. Gular Count (Fig. 11)

Males. From RS to eastern SP values are low to intermediate, except for locality 8 which has a high value. In ES, RJ, and in one taxon of the dimorphic SP samples values are high to intermediate. From BA north values are intermediate to low.

Females. Values from eastern SP south are low to intermediate, including those of one taxon of the dimorphic SP samples. The other taxon from eastern SP has higher values, as do both taxa in RJ. Values in southern ES are high to high-intermediate. Values in northern ES and BA intermediate, while PE shows a tendency for lower values. Samples from the interior northeast (86, 91 and 92) are consistently low.

Summary

The region from RS north to eastern SP is set off by consistently lower values. High to high-intermediate values characterize southern ES, RJ and one of the taxa of eastern SP. From northern ES northward values drop from high-intermediate to low.

19. Second Hind Toe Lamellae

Males. Values from RS to PR represent the complete spectrum. From SP to southern ES high to high-intermediate values predominate. In northern ES and southern BA values are low to low-intermediate. Farther north values are low.

Females. The pattern of variation for females is similar except that some high values are found in PE.

Summary

Values throughout the spectrum are found south of SP. In SP, RJ and northern ES values tend to be higher than intermediate. Southern ES has low values. Values in BA are high-intermediate while those in PE range from intermediate to high.

20. Fourth Hind Toe Lamellae

Males. Values are generally intermediate throughout. Low values occur sporadically in PE, in southern BA and in one of the taxa of the dimorphic SP sample.

Females. From PR south values are low to intermediate. In SP and RJ values tend to be high-intermediate. Values in southern ES are high. Values in BA are intermediate while those in PE are high-intermediate.

Summary

The variation is largely mosaic with intermediate values predominating. The only regions set off are southern ES, by high values in females, and PE, by high values in females and low values in males.

21. First Front Toe Lamellae

Males. Low values predominate from PR south. In SP and RJ values range from low to low-intermediate. Values in southern ES are high to low-intermediate. From northern ES north values are uniformly low.

Females. From RS to RJ the whole spectrum of values is present, although high-intermediate values predominate. In southern ES values are high-intermediate. In northern ES and southern BA values are consistently low. Northward, values range from low to low-intermediate.

Summary

The only well-defined region is that of northern ES and southern BA where both sexes show low values. The rest of BA and PE have low to low-intermediate values. Southern ES has high to intermediate values. From RJ south the variation is mosaic although the samples from RS, SC and PR show more homogeneity in having low values.

22. Fourth Front Toe Lamellae (Fig. 12)

Males. From RJ south is a mosaic of high to intermediate values. Values in southern ES are intermediate. From northern ES north all values are low.

Females. From RJ south the spectrum of values is found in a mosaic pattern. Values in southern ES are intermediate. North from northern ES values are low except for some low-intermediate values in PE.

Summary

There is a sharp separation at the Rio Doce. Low values are found from northern ES north,

and a spectrum dominated by high-intermediate values is found from southern ES south.

23. Infratibials

Males. From southern ES south values are low to high-intermediate with a tendency for lower values in PR and southern SC and in one taxon of the dimorphic SP samples. In northern ES and southern BA values are intermediate to high. Values in the rest of BA and PE are high-intermediate to high.

Females. From southern ES south is a mosaic of low to intermediate values. From northern ES north values are intermediate to high, except for several localities (86, 92, 98) that have low values.

Summary

The Rio Doce divides the samples clearly into two groups: to the south is a region of low to intermediate values, while to the north values are high to intermediate. The only exception is a series of low values for interior north-eastern localities.

24. Sum of Dorsal Scales on Three Caudal Segments (Fig. 13)

Males. From SP south values range from low to intermediate. In RJ values tend to be intermediate to high. In southern ES and adjacent MG values are invariably low. From northern ES and southern BA values are high to intermediate to low.

Females. From RS north to eastern SP values are low to low-intermediate. Values in eastern SP and RJ vary from intermediate to high. Southern ES has low values. From northern ES north values are high to intermediate except for low values at interior localities (86, 87, 92, 98).

Summary

The most distinctive set of localities is that of southern ES which has low values. North from ES values range from intermediate to high except for several interior localities with low values. High values are common in RJ, but south of there the variation is a mosaic of low to intermediate values.

25. Sum of Ventral Scales on
Three Caudal Segments (Fig. 14)

Males. From RS to eastern SP variation is a mosaic of high to intermediate values. In RJ values are low to intermediate. Southern ES and adjacent MG low values. In northern ES and BA values are intermediate. PE has low to intermediate values.

Females. Values from RS to eastern SP are high to intermediate. There is a tendency for values in PR and SC to be higher than those in SP. Values from RJ and from one taxon of the dimorphic SP samples are low to intermediate. From southern ES north values are mostly low with some intermediate values.

Summary

Values from eastern SP south are consistently the highest. One taxon from eastern SP and the samples from RJ have intermediate values. Southern ES and PE have low values. In BA and northern ES values are intermediate in males and low in females.

26. Sum of Scales on Halves of
Two Caudal Segments (Fig. 15)

Males. From RS to PR values range from low to intermediate except for localities 8 and 14 which have high-intermediate values. Values from SP to southern ES are a mosaic of low to high-intermediate. In northern ES and southern BA values range from intermediate to high. In the rest of BA and PE values are intermediate.

Females. From PR south values are low to intermediate except for a high-intermediate value at 12. In SP and RJ values range throughout the spectrum although intermediate values predominate. There are high values in northern SP. Values in southern ES are low to intermediate. From northern ES north values are low to intermediate along the coast with higher values in the interior (86, 87, 91, 92).

Summary

The region from PR south has relatively low values, as does southern ES. Values in SP and RJ include the whole spectrum, but intermediate and high-intermediate values predominate. From northern ES north, values tend to be intermediate along the coast with higher values for interior localities.

27. Percent of Unaligned Caudal Scales

Males. Values are high to high-intermediate from RS north to SP including one taxon of the dimorphic samples from eastern SP. An exception is locality 8 which has a low value. Values in RJ are low to low-intermediate. From southern ES north values are low.

Females. From RS to SP values are high and high-intermediate. In RJ and in one of the taxa of the dimorphic SP samples values are low. From southern BA to southern ES values range from low to low-intermediate. The rest of BA and PE have low values.

Summary

Values are high to high-intermediate from RS to SP, including one taxon of the dimorphic SP samples. In RJ, southern ES and the other taxon of the dimorphic samples from SP, values are low to low-intermediate. From northern ES north values are low.

28. Percent of Aligned Pairs
and Trios Among Caudal Scales

Males. The variation occurs in a mosaic pattern except that values in RJ are high-intermediate and values in southern ES are intermediate.

Females. Variation is mosaic except that values in southern ES are consistently intermediate to high-intermediate.

Summary

Values in southern ES are intermediate to high-intermediate. Otherwise the variation shows only a geographic mosaic.

29. Percent of Aligned Quartets
and Quintets Among Caudal Scales

Males. Low values are found from RJ to SP, including one of the taxa of dimorphic SP samples. An exceptionally high value occurs at locality 8. Otherwise the variation is mosaic with intermediate and high-intermediate values predominating.

Females. Low values are found from RJ to SP, including one of the taxa of the dimorphic SP samples, except for a few intermediate values in central coastal SP. Elsewhere variation is

mosaic dominated by high to intermediate values.

Summary

Values are low from SP south, and in one taxon of the dimorphic SP samples. Values elsewhere show little concordance with geography and generally range from intermediate to high.

30. Percent of Aligned Sextets Among Caudal Scales (Fig. 16)

Males. From SP south values are uniformly low except for one taxon of the dimorphic SP samples and locality 8, which have intermediate values. Values in RJ and southern ES are intermediate. Values in northern ES and BA tend to be high. In PE values are intermediate to low.

Females. Values from RS to SP are low except for intermediate values in one taxon of the dimorphic SP samples. RJ is dominated by intermediate values. Values in southern ES are consistently low-intermediate. Values in northern ES and BA are predominately intermediate. PE shows a variety of values including some low ones.

Summary

Values from SP south are consistently low except for locality 8. Values in RJ and in the second taxon of the dimorphic SP samples tend to be intermediate. Southern ES has low-intermediate values. The consistently highest values occur in northern ES and in BA. Values in PE are variable.

31. Tail Length (Fig. 17)

Males. Values from SP south are high to high-intermediate with some intermediate values. In RJ values are high to high-intermediate. Values in southern ES are low to low-intermediate. In northern ES values are intermediate. Values are high in BA and PE.

Females. From RS to RJ values vary from low-intermediate to high with intermediate values predominating. Values in southern ES are low. From BA north values range from intermediate to high-intermediate.

Summary

The most distinctive set of localities is that from southern ES and adjacent MG. It is cha-

racterized by low values. Values from RJ to RS, and from northern ES to PE, vary from low-intermediate to high but are mainly intermediate and high-intermediate.

32. Thigh Length

Males. From SP south, including one taxon of the dimorphic SP samples, values are low to low-intermediate except for high-intermediate values at 8 and 23. Values from southern BA to RJ are high-intermediate to low-intermediate with some high values in RJ. Values from PE to northern BA are high to high-intermediate.

Females. From SP south low to low-intermediate values are found. Between southern BA and eastern SP, including one taxon of the dimorphic SP samples, intermediate and low-intermediate values predominate. Values from northern BA to PE are high except for low values in some interior localities (86, 91, 92).

Summary

Values from RS to SP including one of the taxa of the dimorphic SP samples, are consistently the lowest, ranging from low to intermediate except for high-intermediate values at 8 and 23. Values from the other taxon of dimorphic SP samples, and from between RJ and southern BA range higher, tending to be intermediate to high-intermediate. The highest values are from northern BA and PE, but interior localities (86, 91 and 92) have low values.

33. Shank Length (Fig. 18)

Males. Values are low from RS to SP except for localities 8, 23 and 25. From southern BA to RJ, including one taxon of the dimorphic SP samples, values range from intermediate to high-intermediate. Values in northern BA and PE are high.

Females. Values south of SP are low. Values in RJ and southern ES are intermediate to low-intermediate. From northern ES to PE values are high to high-intermediate except interior localities (86, 91 and 92) that are low-intermediate.

Summary

From SP south values are uniformly low except for 8. One taxon of the dimorphic SP samples and localities from RJ and southern ES are

intermediate. Values in northern ES and southern BA are high-intermediate and represent a transition between the regions to the north and south. Values in northern BA and PE are high, except low-intermediate values in interior localities.

34. Snout Length (Fig. 19)

Males. Values from SP south are generally high but with a cluster of high-intermediate values in PR and northern SC. In RJ and in one taxon of the dimorphic SP samples values are generally high-intermediate. Southern ES has intermediate values. From northern ES to PE values vary from intermediate to low but are primarily low-intermediate.

Females. RS and interior SC have high to high-intermediate values. Values in coastal PR and SC are uniformly high-intermediate. In SP values are high to high-intermediate. In RJ they are primarily high-intermediate. Values in southern ES vary from high-intermediate to intermediate. In northern ES and BA values are intermediate and low-intermediate. PE has low-intermediate to low values.

Summary

Values from SP south tend to be high, but a group of values in PR and coastal SC are consistently slightly lower. Values from RJ are generally intermediate to high-intermediate. In southern ES and adjacent MG values are generally intermediate. Values in northern ES and BA tend to be intermediate to low-intermediate. In PE values are low-intermediate to low.

35. Internares Distance

Males. Except for localities 8 and 12 the monomorphic samples from SP south and one taxon of the dimorphic SP samples have high-intermediate values. The other taxon of the dimorphic SP samples has intermediate or low-intermediate values. In RJ a spectrum of values is found but is dominated by intermediate and low-intermediate values. Values in southern ES are low to low-intermediate. From northern ES north values are low.

Females. From SP south values are primarily high-intermediate. In RJ and in one taxon of the dimorphic SP samples values are largely intermediate. Values are low to low-intermediate

in southern ES. From northern ES north values are low, with a few intermediate values present.

Summary

Monomorphic samples from SP south and one of the taxa of the dimorphic SP samples have values that range from high to intermediate but which are primarily high-intermediate. In the other taxon of the dimorphic SP samples and in RJ a spectrum is present, but intermediate and low-intermediate values predominate. In southern ES values are low to low-intermediate. Values north of the Rio Doce are primarily low.

36. Intersuperciliary Width

Males. The consistently lowest values are found from PR south and in central RJ. In SP and western RJ values range from low to low-intermediate. In southern ES values are intermediate. From northern ES north, values range through the spectrum but are primarily low-intermediate.

Females. Values in RJ and from PR south are low. SP is characterized by low to intermediate values. From southern ES north values are intermediate.

Summary

From RJ south values are low, except for SP and western RJ which have some intermediate and low-intermediate values. From southern ES north values vary erratically between low and high-intermediate, but values are predominantly intermediate and low-intermediate.

37. Keeling on Infratibials

Males. From southern ES south and from northern BA north values are uniformly high. In northern ES and southern BA values are low except for one intermediate value.

Females. The same pattern is found except that samples from the interior northeast (86, 91 and 92) and one sample from GO (69) also have low to intermediate values.

Summary

Values south of the Rio Doce are uniformly high. Between the Rio Doce and the Rio Jequitinhonha, values are low or intermediate. In the northeast values are high except that interior

samples have low or intermediate values. Values in GO are either high or intermediate.

C. Taxonomic Conclusions

The concordance patterns of the characters indicate the existence of seven phenetic entities above the population level in the *catenatus* complex in eastern Brazil (see Fig. 20). One of these is unnamed and the rest have available names at the species level. The unnamed form is syntopic with two forms, but the other six forms are apparently allopatric with respect to each other. The unnamed form clearly deserves specific status due to the high probability of reproductive isolation inferable from the phenetic gap in sympatry. Taxonomic treatment of the other forms is necessarily more arbitrary given the non-operationality of the biological species concept (Sokal and Crovello, 1970). Either to consider them races of a single polytypic species or to accord them all specific status would be to forgo use of these categories to express my judgment of phenetic similarities. The species-subspecies dichotomy is clearly too crude to adequately express degree of relationship even among so few as six forms, but feeling that it is worth employing, I have recognized three allopatric phenetic species (sensu Sokal and Crovello, 1970): one with three subspecies, one with two, and one without subspecies. Only in the case of the northern ES – southern BA and northern BA – PE forms does the evidence of intergradation strictly justify the subspecific category.

D. Species Accounts

Enyalius catenatus (Wied)

Holotype – The American Museum of Natural History has listed AMNH 108 as the holotype of *catenatus*. This specimen is clearly a member of an unnamed taxon of which all other specimens have been collected in southeastern Brazil. Wied (1825) gives the type locality as the sertão (= interior) of Bahia. Etheridge (1968b) concluded from location of the original description within the account of Wied's travels (Wied, 1821) that the type locality is near Cabeça de Boi, Bahia. I agree with this conclusion. The illustration in Wied (1825) shows several characteristics of the adult female

Bahia form: the middorsal dark area scalloped into elongated ovals, a dark post-orbital stripe that extends to the shoulder, several dark transverse bands on the head, light upper labials and lorilabials, a broken dark stripe along the lateral portion of the throat, and numerous small dark dots on the sides and limbs. Wied's (1825) description mentions two dark bands across the head, the dark dots, and a chain-shaped mid-dorsal stripe. The description and illustration correspond well with females of my Ilhéus, Bahia, sample. Therefore, I restrict the name *catenatus* to the species found from northern ES north to PE.

The holotype on which Wied's description was based is apparently lost. AMNH 108 is of another taxon to be described below and thus no longer has status as a type. C. W. Myers (*in litt.*) informed me that AMNH 108 was originally cataloged as *Enyalius rombifer* from "Brazil". The subsequent history of this specimen is best explained by quoting from Dr. Myers' letter:

"Types are not designated as such in Wied's catalogue. Someone subsequently decided that AMNH 108 was the type of *catenatus* and the catalogue was so marked. The original AMNH entry was *emended* by attempting to erase "*rombifer*" (which, however, is still legible under a magnifying lens) and superimposing the name "*catenatus*"; furthermore, *the same hand added "Bahia"* to the locality!

To sum things up, the specimen appears to be a *bona fide* Wied specimen (presumably his n^o 380) from Brazil, but our records give no supporting evidence that it came from Bahia. That catalogue emendation would seem to be based solely on someone's notion that the specimen is the type of *catenatus*."

Diagnosis. – 1) anterior portion of canthal ridge curved toward midline; anteriormost enlarged canthal scale does not closely approach hind edge of nasal scale; the enlarged canthals bridge only about half the distance between the superciliaries and nasal scale; 2) subdigital lamellae not keeled; 3) scales on tail aligned in dorso-ventral rows; 4) tail shorter than 2.4 times snout-vent length; 5) a row of enlarged vertebral scales present; 6) ventralmost subocular somewhat enlarged or not; 7) keel of preocular either medial or located posterior to midpoint of scale; 8) enlarged supraoculars smooth or keeled; 9) ventral scales keeled or smooth. The curved canthal ridge easily separates this species

from all other forms except certain individuals of *brasilensis boulengeri* from which it may be distinguished by the smooth subdigital lamellae.

Description. — See the subspecies.

Distribution. — From Sooretama, Linhares, ES, north along the coast to Água Azul, Vicência, PE. Isolated populations in northern MG, central GO, and the interior of BA and PE.

Remarks on Nomenclature — My examination of Spix's types of *Lophyrus margaritaceus* (RMNH 3061) and *L. albomaxillaris* (RMNH 3058) indicates that these names are junior synonyms of *catenatus*. These specimens compose two-thirds of the male sample 91. I also consider *Lophyrus rhombifer* Spix a junior synonym of *catenatus* because the illustration (Spix, 1825; Tab. XI) shows features restricted to *catenatus*: a dark post-orbital stripe that widens above the shoulder, dark crossbands on the head, and the narrow light undulating lines that border the mid-dorsal dark diamonds. Gray's *Ophyressa braziliensis* is a nomen dubium.

Boulenger (1885b) based his concept of *catenatus* both on *catenatus* (sensu stricto) material from BA and on *brasilensis* material from RJ. Etheridge (1968b) included under the name *catenatus* both *catenatus* (sensu stricto) material from BA and PE and material of the unnamed taxon from RJ and SP; he was probably misled by the erroneous designation of AMNH 108 as the holotype of *catenatus*.

Enyalius catenatus catenatus (Wied)

Agama catenata Wied, 1821: 247 (type-locality: "Sertong der Capitania da Bahia").

Lophyrus rhombifer Spix, 1825:9.

Lophyrus margaritaceus Spix, 1825: 10.

Lophyrus albomaxillaris Spix, 1825: 11.

Ophyressa catenata; Fitzinger, 1826: 48.

Ophyressa margaritaceus; Fitzinger, 1826: 48.

Uraniscodon rhombifer; Kaup, 1826: 90.

Uraniscodon margaritaceus; Kaup, 1826: 90.

Uraniscodon (Ophyressa) catenata; Kaup, 1827: 612.

Uraniscodon (Ophyressa) margaritacea; Kaup, 1827: 612.

Enyalius (Agama) catenata; Wagler, 1830: 150.

Enyalius (Lophyrus) margaritaceus; Wagler, 1830: 150.

Oph. (Xiphurus) margaritaceus; Gray, 1831: 40.

Oph. (Xiphurus) rhombifer; Gray, 1831: 40.

Hypsibatus (Enyalius) catenatus; Fitzinger, 1843: 57.

Enyalius catenatus (part); Etheridge, 1968b: 244.

Holotype. — As indicated above, the holotype is apparently lost. Assuming that a the type locality is near Cabeça de Boi, Jaguaquara, Bahia, the name *catenatus* applies to the northern subspecies since the locality is at the southern edge of the range of this taxon.

Diagnosis. — This subspecies is distinguished from the others by the following characteristics: 1) enlarged supraoculars keeled; 2) enlarged supraoculars much smaller than scales of the supraorbital series; 3) ventral scales keeled; 4) infratibials strongly keeled; 5) infratibials longer than wide; 6) none of suboculars enlarged; 7) keel of the preocular medially located; 8) midbody scale count greater than 120; 9) shank/snout-vent length ratio greater than .34.

Description. — Maximum snout-vent length for males is 101 mm, for females 117 mm. The pattern is sexually dimorphic. In preservative males are normally unicolorous; the color varies from light tan to purplish-brown. Other species of *Enyalius* with this color in preservative are green in life. The illustration of *Lophyrus margaritaceus* (Spix, 1825; Tab. XII) indicated that live males of this race are green. Infrequently, males have traces of middorsal blotches. Ventral ground color is light, probably white or cream in life. The belly is immaculate, but there is a pair of lateral broad dark stripes on the throat; these are frequently joined anteriorly to form a horseshoe. Ventral surfaces of hind limbs are either immaculate or with dark blotches.

Females in preservative have a dorsal ground color of tan or brown. There are two dark crossbands over the eyes and sometimes the snout is dark dorsally also. Mid-dorsally may be a series of dark ellipses or rounded diamonds, or in some individuals there is a dark mid-dorsal stripe (Fig. 21A). Others are intermediate in having a dark mid-dorsal stripe that is partially scalloped into ellipses. Some individuals have well-defined paravertebral stripes, but others have only an area generally lighter surrounding the dark mid-dorsal marks. Such a lighter area usually follows the contours of the dark marks, narrowing in the intervals between them. The dorsal surfaces of the hind legs and the sides of the body

are often covered irregularly with small dark dots. There are 8-14 dark bars or blotches dorsally on the tail. There is a dark, black-bordered post-orbital stripe that widens over the shoulder; however, instead of terminating there as usual in the other races, the stripe merges with the dark ground color of the sides. The upper labials, lorilabials, suboculars, throat and other ventral surfaces are cream or grey. On the lateral parts of the throat are two broad dark irregular stripes, frequently joined anteriorly. These stripes sometimes continue posteriorly down the belly. In other individuals the stripes are represented only by disconnected dark mottling laterally on the belly. Ventrally the hind legs are mottled with brown; sometimes the mottling on the thighs forms irregular stripes. The sexual dimorphism of pattern appears to occur in juveniles. See Table 1 for meristic and morphometric data.

Distribution. — *Enyalius c. catenatus* is distributed near the coast from Água Azul and Igarapu, PE, south to near Ilhéus, BA. The Ilhéus population shows influences of *pictus*. Although there is not sufficient material to know for sure, I suspect that the whole region between Rio Jequitinhonha and Ilhéus is one of gradual intergradation between *catenatus* and *pictus*. A specimen from Rio das Almas, GO, appears to be an intergrade between *catenatus* and *pictus*; it occurs at the same latitude as the zone of intergradation in BA but more than 900 km to the west.

Remarks on Nomenclature. — Spix's (1825) types of *Lophyrus margaritaceus* and *Lophyrus albomaxillaris* are clearly of this subspecies. This is consistent with the fact that Spix's collecting in coastal Bahia did not extend south of Ilhéus (Papavero, 1971).

Enyalius catenatus pictus (Wied)

Agama picta Wied, 1825: 125 (type-locality: "Morro d'Arara am Flusse Mucuri").

Ecpymotes pictus; Fitzinger, 1826: 49.

Uraniscodon picta; Kaup, 1826: 91.

Uraniscodon (Pneustes) picta; Kaup, 1827: 612.

Hypsibatus picta; Wagler, 1830: 150.

Ophyressa pictus; Gray, 1831: 40.

Calotes pictus; Schinz, 1835: 86.

Uperanodon pictum; Duméril and Bibron, 1837: 251.

Hypsibatus (Uperanodon) pictus; Fitzinger, 1843: 48.

Uraniscodom pictum; Gray, 1845: 223.

Enyalius zonatus Wettstein, 1926: 1.

Enyalius pictus; Etheridge, 1968b: 240.

Holotype — According to Etheridge (1968b) Wied's holotype is lost. Etheridge designated NMW 13894 from "Muriti dist." as the neotype of *Agama picta*. This specimen is a member of the taxon found in northern Espírito Santo and southern Bahia, and corresponds well with Wied's (1825) illustration of *Agama picta*.

Diagnosis. — This subspecies is distinguished from others of the species by the following characters: 1) enlarged supraoculars not keeled; 2) enlarged supraoculars as large as or larger than scales of the supraorbital series; 3) ventral scales smooth; 4) infratibials smooth or with weak keels; 5) infratibials wider than long; 6) one of the suboculars enlarged or not; 7) keel of preocular medially located; 8) midbody scale count greater than 140; 9) shank/snout-vent length ratio greater than .30.

Description. — Maximum snout-vent length 111 mm for males, 117 mm for females. There is apparently sexual dimorphism in color pattern. Pattern of adult males in preservative is as follows: Ground color of dorsal body, limbs, and head is tan or grey. On the body are five wide dark crossbands with undulating edges (Fig. 21C). The first band above the front limbs is the widest and the darkest, being dark brown. The succeeding bands are progressively narrower and lighter brown. There are 8 or 9 brown crossbands on the tail. Sometimes the ground color between the first and second crossbands is white. The limbs are barred with brown. The ventral ground color is tan-grey and generally immaculate except for two series of dark reticulations that form two dark stripes on the lateral portions of the throat. Pattern of two adult females (MCZ 82873 and MZUSP 39539) in preservative is as follows: Ground color light brown to grey, with the mid-dorsal area being lighter. Within the light mid-dorsal stripe is a series of 5 to 7 elongated dark ellipses (Fig. 21B). There are paravertebral stripes. There are one or two crossbands over the eyes. A black-bordered dark stripe extends from behind the eye to above the shoulder, being wider posteriorly. The upper labials, lorilabials, throat and other ventral surfaces are white to grey. Dark reticulations form an ill-defined broad stripe on either side of the throat and, more

ill-defined still, on the sides of the belly (Fig. 22A). Ventral surfaces of the hind legs are mottled with light brown. The pattern of juveniles is similar to that of these adult females. A third female (MZUSP 30748) has light paravertebral stripes and a dark immaculate mid-dorsal stripe. Females have 8-12 dark bars on the tail. Etheridge (1968b) states that both sexes have the pattern here described for males, but all four *pictus* males I examined have the crossbanded pattern and none of the three females have it. See Table 1 for meristic and morphometric data.

Distribution. — *Enyalius c. pictus* occurs on the coastal plain of northern Espírito Santo and extreme southern Bahia, from Sooretama, Linhares, ES, north at least to Itamaraju, BA. What form of *Enyalius* occurs in the Serra dos Aimorés to the west is not known, but a specimen of this race from MG without further precision indicates its presence to the west. *Enyalius c. pictus* apparently intergrades with *E. c. catenatus* over a wide region centered on Ilhéus, BA.

Enyalius catenatus bibronii (Boulenger)

Enyalius bibronii Boulenger, 1885b: 119 (type-locality: Bahia)

Enyalius bibronii; Etheridge, 1968b: 242.

Holotype. — BMNH 69.11.3.8 from "Bahia".

Diagnosis. — This subspecies is distinguished from the others of the species by the following combination of characters: 1) enlarged supraoculars not keeled; 2) enlarged supraoculars slightly smaller than scales of supraorbital series; 3) ventral scales smooth; 4) infratibials smooth or weakly keeled; 5) infratibials wider than long; 6) one of the suboculars usually larger than the others; 7) keel of the preocular is near the posterior-dorsal edge; 8) midbody scale count less than 120; 9) shank/snout-vent ratio less than .30.

Description. — The males are not known. Snout-vent length of the largest female is 118 mm. The pattern of females in preservative is as follows: Ground color grey or grey-brown. Five to 8 light brown spots or bars mark the dorsal midline of the body (Fig. 23A). There are 17 to 20 narrow dark bars on the tail. Instead of continuous paravertebral stripes, there is a line of

small white spots on either side of the dorsum. The spots in each line occur in pairs that are tangent to, or invade, the sides of each transverse dark spot or bar. These white spots sometimes cut the transverse bar into separate mid-dorsal and lateral dark spots. There is a dark brown post-orbital stripe that is wider above the shoulder. Ventral ground color is white to cream. There are 3 to 4 broad solid longitudinal stripes on the throat and 3 on the belly; they vary from faint to quite dark (Fig. 22B). One or 2 solid dark stripes run down the ventral surfaces of the thigh and shank. Table 1 gives meristic and morphometric comparisons with other taxa.

Distribution. — *Enyalius c. bibronii* is known from only two localities, both unusually inland: Montezuma, MG and Garanhuns, PE. I predict that this will be the form typically found in relict forests of arid interior northeastern Brazil.

Enyalius bilineatus Duméril and Bibron

Enyalius bilineatus Duméril and Bibron, 1837: 234 (type-locality: "Brésil").

Hypsibatus (Dryophilus) bilineatus; Fitzinger, 1843: 57.

Enyalius fitzingeri; Boulenger, 1885b: 121.

Enyalius bilineatus; Etheridge, 1968b: 237.

Holotype. — MHNP 6817 from "Brésil".

Diagnosis. — The following combination of characters distinguishes this species from all others in the genus: 1) canthal ridge straight; or, if slightly curved, anteriormost enlarged canthal bridge the distance nearly to hind nasal scale; the enlarged canthals bridge the distance between the superciliaries and nasal scale by much more than half; 2) subdigital lamellae not keeled; 3) scales on tail not aligned in dorso-ventral rows; 4) tail longer than 2.4 times snout-vent length; 5) a row of enlarged vertebral scales present; 6) the ventralmost subocular is usually considerably large than other scales in the subocular series; 7) preocular has strong keel on posterior-dorsal margin; 8) enlarged supraoculars and other dorsal head scales flat and unkeeled; 9) ventral scales strongly keeled.

Description. — Maximum snout-vent length 82 mm for males, 92 mm for females. The color in preservative is as follows: the dorsal surface

of the head is light-brown. The ground color of the dorsal body and limbs is lighter tan or grey. On either side is a dark-brown post-orbital stripe that extends to above the front leg; its shape varies from that of an exclamation point, wider at the shoulder, to L-shaped with the shorter arm directed ventrally above the shoulder (Fig. 23B and C). The post-orbital stripe is edged narrowly in black; along its entire ventral border is a narrow white or cream line, and along the posterior half of the dorsal border is a white or cream stripe that continues posteriorly to form a paravertebral stripe when these are present. Mid-dorsally there is usually a series of 5-7 dark-brown spots that vary in shape from squares to diamonds to ovals. Some individuals have a solid mid-dorsal stripe. Laterally there is usually a series of transverse dark-brown spots. These may be perpendicular or diagonal to the body axis and vary in shape from oval to elliptical to triangular. When paravertebral stripes are present, the mid-dorsal and lateral spots are separated, but when stripes are lacking the spots of the two series may touch or partially fuse. The upper labials, lorilabials, suboculars, lower labials, and throat are white. The belly and ventral limb surfaces are white or light-grey. On the throat is usually a pair of lateral grey-tan stripes that continue down the belly to the vent (Fig. 22C). A narrower medial stripe is often present on the belly from the gular fold to vent. Longitudinal grey-tan stripes are often present on the ventral surface of the thigh and sometimes continue down the shank. There is no noticeable sexual dimorphism nor ontogenetic change in color pattern. See Table 1 for meristic and morphometric data.

Distribution. — The known distribution is in southeastern MG, western RJ, and central-western ES. All records are in a triangle defined by Belo Horizonte, MG; Rio Preto, RJ; and Santa Teresa, ES.

Enyalius iheringii Boulenger

Enyalius iheringii Boulenger, 1885a: 192.

Syntypes. — BM 1946.8.9.3-4 from "Rio Grande do Sul".

Diagnosis. — 1) canthal ridge straight; or if slightly curved, anteriormost enlarged canthal scale extends to or nearly to hind edge of nasal scale; the enlarged canthals bridge the distance

between superciliaries and nasal scale by much more than half; 2) subdigital lamellae unkeeled or those of hind feet weakly-keeled; 3) scales on tail not aligned in dorso-ventral rows; 4) tail shorter than 2.4 times snout-vent length; 5) a row of enlarged vertebral scales present; 6) ventralmost subocular not enlarged; 7) keel of pre-ocular medial; 8) enlarged supraoculars keeled; 9) ventral scales keeled.

Description. — Maximum snout-vent length 115 mm for males, 124 mm for females. The pattern is sexually dimorphic. In life males are medium green dorsally. In preservative the dorsal ground color is brown or purplish-brown. Males are usually unicolor but occasionally they have small faint dark spots, partially bordered in cream, mid-dorsally. Dorsally the limbs may be either uniform ground color or crossed by cream bands. The tail is irregularly banded in cream. Ventral ground color varies from cream to light-brown. A narrow dark mid-ventral stripe is frequently present, especially on the chest.

In live females, the dorsal ground color is light to medium leaf green or olive green. When dark marks are present, these vary from dark green to dark brown. The paravertebral stripes are cream or white. The female pattern is variable (Fig. 24). In preservative the dorsal ground color is tan or brown. Usually broad light paravertebral stripes extend unbroken from near the tympanum to the tail base. The mid-dorsal area between the stripes may be uniform ground color or may include a series of dark irregular round diamonds or triangles, principally on the posterior two-thirds; the anterior third is usually uniform, slightly darker than ground color of head, and extends forward to form a Y- or bell-shaped area on the occiput. Less commonly, paravertebral stripes are absent; in these individuals the mid-dorsal dark rounded diamonds and triangles are larger and consistently white-bordered. The sides are usually crossed by narrow irregular diagonal white-cream bands, especially posteriorly. The limbs are banded dorsally by irregular dark bands and/or narrow light bands. The tail has a lighter ground color and is irregularly blotched dorsally. There is usually a cream bar from the orbit posteriorly to the corner of the mouth. The venter is cream, either immaculate or lightly reticulated in brown; a narrow mid-ventral brown stripe may be present. In females, the pattern of juveniles is essentially that of adults. Small juvenile males may have mid-dorsal dark marks

that are presumably lost with age. See Table 1 for meristic and morphometric comparisons with other taxa.

Distribution. — From the southernmost extreme of the Atlantic tropical forest between Porto Alegre and Torres, RS, north in a continuous distribution to Bom Jesus (mun. Jacaré), SP and Parati, RJ. Inland *iheringii* reaches Porto União da Vitória and Irati, PR, and Salto de Itu, SP. An inland record near Serra Azul, SP, needs confirmation. The species is found on Ilhas São Sebastião, Búzios, and Vitória off the northeast coast of SP.

Enyalius perditus sp. nov.

Enyalius catenatus (part); Etheridge, 1968b: 244.

Holotype. — MZUSP 42685, a small adult female from Estação Biológica de Boracéia, Município de Salesópolis, Estado de São Paulo, Brazil.

Paratypes. — Brazil. *São Paulo*; Estação Biológica de Boracéia, MZUSP 2319, 2323, 8252, 8380, 10272, 38381; Saco da Ribeira, Ubatuba, MZUSP 38382, 39550; Paranapiacaba, MZUSP 584, 3123, 3136, 7692, 10375-6, 11463-4; Cantareira, MZUSP 578, 590; Paranapuã, MZUSP 8266. *Rio de Janeiro*; Porto Real, BM 1887.12.29.1-2; Teresópolis, MZUSP 12281, BM 1893.9.30.1; Sacra Família do Tinguá, MZUSP 36926; Petrópolis, MCZ 7320; Macaé, MZUSP 592-3, 709, 3147.

Etymology. — From the Latin *perditus*, meaning lost, in reference to the previous taxonomic confusion of this species with *catenatus*.

Diagnosis. — 1) canthal ridge straight; or if slightly curved, anteriormost enlarged canthal scale extends to or nearly to hind edge of nasal scale; the enlarged canthals bridge the distance between the superciliaries and nasal scale by much more than half; 2) subdigital lamellae not keeled; 3) scales on tail aligned in dorso-ventral rows; 4) tail shorter than 2.4 times the snout-vent length; 5) a row of enlarged vertebral scales present; 6) ventralmost subocular not enlarged; 7) keel of preocular medial; 8) enlarged supraoculars keeled; 9) ventral scales keeled. This species is distinguished from the superficially similar *catenatus catenatus* by its straight canthal ridge. Although *perditus* sometimes has a narrow post-orbital stripe, it is never black-

-bordered nor as broad as that of *catenatus*. Dark lateral stripes on the throat and belly are absent in *perditus* but usually present in *c. catenatus*. In females and juveniles, a nearly immaculate white area on the suboculars, lorilabials, and upper labials is absent in *perditus* but present in *c. catenatus*.

Description of Holotype. — Female, snout-vent length 70.5 mm; tail 139 mm; subdigital lamellae unkeeled; canthal ridge straight; ventral scales keeled; enlarged supraoculars keeled; 95 vertebral scales between interparietal and hind margin of thigh; 51 enlarged vertebral scales; 206 paravertebral scales between interparietal and hind margin of thigh; 153 scales around midbody; 19 scales in right supraorbital semicircle; minimum of 3 scales between center of supraorbital semicircle; minimum of 4 scales between interparietal and supraorbital semicircle; 16 scales on head between rostral and mid-point between eyes; 11 right supraciliary scales; 23 scales in right subocular series; minimum of 10 scales in loreal region between preocular and upper labials; 11 right upper labials; 10 right lower labials; 49 scales between mental and gular fold; 15 subdigital lamellae on second hind toe; 32 subdigital lamellae on fourth hind toe; 10 subdigital lamellae on first front toe; 21 subdigital lamellae on fourth front toe; 24 infratibials between base of fifth hind toe and ventral side of knee; scales of tail aligned in dorso-ventral rows; 37% of the scales are in rows of six or more aligned scales; hind thigh is 33.3% of snout-vent length; hind shank is 32.3% of snout-vent length; distance between snout and posterior edge of nasal scale is 54.8% of distance between snout and anterior edge of orbit; distance between nares is 39.5% of widest distance between supraciliaries over the eyes; widest distance between supraciliaries over the eyes is 16.2% of snout-vent length.

Color in life: The dorsal ground color of the body is a very light greenish-brown; that of the head is a slightly greener brown. On the head a medium-brown band crosses the anterior half of the eyes; and a small light brown triangle is centered in the remaining area of ground color on the snout. On the sides of the head the ground color is a very pale green; it extends dorsally on the occiput and neck and continues posteriorly on the body to form an ill-defined area of lighter color mid-dorsally. On the occiput is a rough transverse rectangle of light greenish-brown ground color that is continuous

with the ground color of the head anteriorly but bounded laterally and posteriorly by the pale green. On the neck is a rounded, irregular diamond also of the dorsal ground color of the head. In the pale green anterior and posterior to this diamond are elongated rust-colored patches. Starting over the shoulders is a series of seven rounded dark brown diamonds narrowly outlined in pale green mid-dorsally on the body. The first two are symmetrical across the midline, but the other five are asymmetric in that the lateral halves are displaced slightly anterior-posteriorly. The fourth on the right and the last on the left lack corresponding halves and so are actually triangles. The asymmetry of the diamonds creates the effect of a dark brown zig-zag dorsal stripe on the posterior two-thirds of the body. Dorsally on the tail are 14 irregular equidistant dark brown blotches. A rusty wash on the vertebral crest superimposes a diffuse narrow mid-dorsal stripe over the dark brown diamonds. On the sides are several small dark brown spots. The front limbs are irregularly spotted by light brown. The dorsal surface of each thigh and shank has a dark brown transverse bar; also on the shank are one or two smaller brown spots, and similar ones occur on the hind feet. All the digits are banded by light brown. The side of the head has three greenish-brown bars radiating from the orbit: one continues dorsally across the head, another extends ventrally to the lower labials, and the third runs posteriorly to the antero-ventral edge of the tympanum. A short, narrow dark brown stripe extends posteriorly from the postero-dorsal corner of the tympanum. The upper and lower labials are speckled with brown. The ventral ground color is cream flecked with pale yellow. The throat is finely reticulate with grey-brown. The chest is lightly speckled with grey-brown, but the belly has somewhat larger spots of dark brown laterally. There is a very narrow mid-ventral grey-brown stripe on the chest. The underside of the limbs are finely reticulated and speckled with grey-brown and brown. The underside of the tail is banded by 18 brown blotches.

Description. — Maximum snout-vent length of males is 90 mm, for females 105 mm. The pattern is sexually dimorphic. The males are unicolored. In life they are leaf green dorsally. In preservative they are tan to purplish-brown dorsally, sometimes with darker irregular spots on the hind legs. The tail is crossed by ill-defin-

ed darker bands. Ventrally, the males are usually cream to light tan, either immaculate or with irregular fine brown spots or reticulations; reticulations are best developed on the hind legs. There is sometimes a very narrow dark mid-ventral stripe, but there are never lateral stripes on the throat or on the belly. Some males have a light brown throat.

Females in preservative have a ground color of brown, tan, or light grey. In one third of the individuals, the head is unmarked dorsally; in the rest one or two dark bands cross the head over the eyes, as in juveniles. Usually, paravertebral stripes are absent, but when present are narrow. The mid-dorsal region is lighter than the general ground color. Within the light mid-dorsal area on the body is a series of 6-8 brown marks (Fig. 25A). These are normally diamond-shaped with the lateral corners roundly truncated. Frequently, the more posterior diamonds do not have their two lateral halves in line; this gives the impression of a zig-zag dark stripe. Neither the entire diamonds nor the homologous halves of the divided diamonds touch adjacent ones. One brown band crosses the mid-thigh and one or two cross the shank. Ventral ground color is white to tan. Fine brown spotting or reticulation occurs on the throat and belly and grosser reticulation on the limbs. There is often a very narrow brown stripe mid-ventrally from the posterior throat to the vent (Fig. 26A). There is usually a narrow ill-defined postorbital stripe *without* a black border. The upper labials below the eye frequently have a dark brown spot; in some individuals two more dark spots occur on the anterior upper labials. In the absence of dark marks on the upper labials, these have the same ground color as the head and are never white. One live juvenile female had a pattern like adult females but in tones of brown. Small juvenile males also have mid-dorsal spots, but these contrast less with the ground color than in females. The unicolor pattern appears in larger juvenile males. See Table 1 for meristic and morphometric data.

Distribution. — From Macaé, RJ, west to Paranapuã and Garça in western SP and southwest at least to the vicinity of the city of São Paulo. One specimen (MZUSP 3145) has locality data as Barigui near Curitiba, PR, and Etheridge (1968b) cites as "*catenatus*" a specimen from near Curitiba (Natur Museum Senckenberg, Frankfurt, 36217) that I was unable to examine. Thus *perditus* may occur in eastern PR, but

this needs to be confirmed. I have shown Etheridge's citation of Teresópolis, SC (BM 1893.9.30.1) to be in error and to apply to Teresópolis, RJ, well within the range of *perditus*.

Remarks on Nomenclature. — As explained in the section on *catenatus*, the putative type of *catenatus*, AMNH 108, is not of that species as defined by Wied's (1825) description and illustration. AMNH 108 is a specimen of *perditus*. That no specimens of *perditus* are known from north of RJ is further evidence that AMNH 108 is not Wied's type of *catenatus* since the type locality is specified as the interior of Bahia. Wied passed through part of *perditus*' range between the city of Rio de Janeiro and Cabo Frio (Bokermann, 1957), and AMNH 108 was probably collected in this region.

Enyalius brasiliensis (Lesson)

Syntypes. — MHNP 6816 (2 specimens) from "Sainte-Catherine du Brésil".

Diagnosis. — 1) canthal ridge straight; or, if slightly curved, the enlarged canthals bridge the distance between the superciliaries and nasal scale by more than half; 2) subdigital lamellae keeled; 3) scales on tail aligned in dorso-ventral rows; 4) tail shorter than 2.4 times snout-vent length; 5) a row of enlarged vertebral scales present; 6) ventralmost subocular not enlarged; 7) keel of preocular medial; 8) enlarged supraoculars keeled; 9) ventral scales keeled.

Description. — See the subspecies.

Distribution. — The known range is from Itatiaia and Ilha Grande, RJ, northeast to the south side of the Rio Doce, ES. Isolated populations occur near Veadeiros, GO and on Ilha de Santa Catarina, SC.

Enyalius brasiliensis brasiliensis (Lesson)

Lophyrus brasiliensis Lesson, 1828: 32.

Enyalius rhombifer; Duméril and Bibron, 1837: 231.

Enyalius brasiliensis; Etheridge, 1968b: 248.

Syntypes. — MHNP 6816 (2 specimens) from "Sainte-Catherine du Brésil".

Diagnosis. — This subspecies differs from the other by the following characters: 1) tail longer than 2.00 times snout-vent length in males and longer than 1.85 times snout-vent length in females; 2) usually more than 50 enlarged scales in vertebral series; 3) usually more than 192 paravertebral scales between interparietal and hind margin of thigh in males and more than 205 paravertebral scales in females; 4) usually more than 67 scales in one half of midbody count (from mid-dorsal line to mid-ventral line) of males and more than 69 in females; 5) ratio of nares width to maximum superciliary width usually greater than .34 in males and greater than .36 in females; 6) enlarged canthals either reach or closely approach the level of the hind edge of the nasal scale.

Description. — Maximum snout-vent length 96 mm for males, 109 mm for females. The pattern is sexually dimorphic. Males in preservative are unicolor tan or brown dorsally. Small juveniles have faint darker mid-dorsal diamonds, but in larger juveniles the pattern is uniform. The irregular dark bands on the tail are very faint. Venter is white to light grey except for the throat which may be darker grey or tan. The venter is either immaculate or sparsely reticulated with brown, especially on the hind legs. There is frequently a very thin brown mid-ventral stripe on the belly and posterior throat.

Dorsal ground color of females in preservative is tan, grey, or brown, often being lighter mid-dorsally. Half of the individuals have 1-2 dark bands between the eyes. About half complete white or cream paravertebral stripes from tympanum to tail base, infrequently speckled with brown; the width of the stripes varies considerably among individuals from nearly as wide as in *iheringii* to narrow ones as in *perditus*. The other half either lack stripes completely or have them only on the anterior half of the body. In unstriped individuals the mid-dorsal series of dark marks is in the form of 5-6 rounded diamonds (Fig. 25B). In striped individuals, there is a tendency for the lateral halves of the diamonds to be displaced antero-posteriorly, so that they form a dark zig-zag mid-dorsal stripe. In either case, the dark marks often have a very narrow white border. The dark bars on the thigh and shank are relatively large and elongate. In some adults the side of the head is uniform, but others have 1-2 dark bars radiating dorsally from the eye and 3 ventrally; when present the post-orbital stripe is faint, narrow,

and unbordered. The white or cream venter is either immaculate or lightly reticulated in brown. There is often a broken fine brown mid-ventral stripe from posterior throat to vent. See Table 1 for meristic and morphometric data.

Distribution. — The core range is in Estado do Rio de Janeiro from Itatiaia and Ilha Grande northeast to Santa Maria Madalena. Isolated populations apparently occur on Ilha de Santa Catarina, SC, and in Goiás.

Enyalius brasiliensis boulengeri (Etheridge)

Enyalius boulengeri Etheridge, 1968b: 250.

Holotype. — ZMH 1338 from Espírito Santo, Brazil.

Diagnosis. — This subspecies is distinguished from the other by the following characters: 1) tail shorter than 1.88 times snout-vent length in males and shorter than 1.85 times snout-vent length in females; 2) usually less than 50 enlarged scales in vertebral series; 3) usually less than 192 paravertebral scales between interparietal and hind margin of thigh in males and less than 205 paravertebral scales in females; 4) usually less than 67 scales in one half of midbody count of males and less than 69 in females; 5) ratio of internares width to maximum superciliary width usually less than .34 in males and less than .36 in females; 6) enlarged canthals extend more than half distance between the supraciliaries and hind edge of the nasal scale, but do not closely approach the nasal scale.

Description. — Maximum snout-vent length 94 mm for males, 119 mm for females. At least in degree the pattern is sexually dimorphic, females having the pattern more vividly developed. Males are grey-green or olive-green in life. In preservative the ground color of head and dorsum is brown. Some males are unicolored dorsally, but there are usually two broad light paravertebral stripes on the anterior third of the body; often they are broken into several short light stripes or spots; more rarely they extend unbroken but less well-defined further posteriorly on the body. The mid-dorsal area may be of the ground color or slightly lighter with ill-defined dark diamonds or rectangles. The tail has 11-14 irregular bands dorsally. Venter is cream or white, either immaculate or sparsely

speckled with brown; there is sometimes a partial fine brown mid-ventral stripe on the belly.

Females are tan, light brown, or olive in life. In preservative the dorsal ground color is tan, brown, or grey. There are two extremes of female pattern. In one dorsum is unicolored except that the mid-dorsal ground color is slightly lighter and contains faint irregular dark diamonds, triangles, or rectangles. In the other there are broad but broken, wavy-edged white or cream paravertebral stripes, sometimes speckled lightly in brown (Fig. 25C). These may extend to the tail or only slightly past the shoulder. Mid-dorsally may be a relatively straight dark stripe or a zig-zag one formed by half-ellipses alternating on either side of the midline. Elements of the two patterns are sometimes found mixed. The dark marks on the thigh and shank are relatively small and rounded. The cream or white venter is immaculate or peppered by small brown spots. A partial brown mid-ventral stripe is sometimes present. In most adults the side of the head is uniformly brown, but some retain traces of two or three dark bars radiating dorsally and ventrally from the orbit. One of these forms a faint narrow postorbital stripe that is not black-bordered. See Table 1 for meristic and morphometric data.

Distribution. — Known distribution is in the mountains of southern ES from Alfredo Chaves north to São João de Petrópolis (Mun. Santa Teresa) and Itá (Mun. Colatina). The occurrence near Viçosa, MG, needs to be confirmed.

A KEY TO THE FORMS OF *ENYALIUS*

- 1a. A vertebral crest of enlarged conical or semi-conical scales absent. *leechi*
- 1b. A vertebral crest of enlarged conical or semi-conical scales present 2
- 2a. Anterior portion of canthal ridge curved toward midline; anteriormost canthal scale does not closely approach hind edge of nasal scale; the enlarged canthals bridge only about half the distance between the supraciliaries and nasal scale; subdigital lamellae not keeled 3
- 2b. Canthal ridge straight; or, if slightly curved, anteriormost canthal scale extends to or nearly to hind edge of nasal scale; the enlarged canthals bridge the distance between the supraciliaries and nasal

scale by more than half; subdigital lamellae keeled or smooth

5

3a. Enlarged supraoculars keeled; ventral scales keeled; infratibials strongly keeled; infratibials longer than wide . . . *catenatus*

3b. Enlarged supraoculars not keeled; ventral scales smooth; infratibials smooth or weakly keeled; infratibials wider than long

4

4a. Keel of preocular medial; midbody scale count greater than 140; shank/snout-vent length ratio greater than .30 *catenatus pictus*

4b. Keel of preocular near posterior-dorsal edge; midbody scale count less than 120; shank/snout-vent length ratio less than .30 . . . *catenatus bibronii*

5a. Tail longer than 2.4 times snout-vent length; ventralmost subocular usually enlarged; keel of preocular near posterior-dorsal edge; supraoculars smooth *bilineatus*

5b. Tail shorter than 2.4 times snout-vent length; ventralmost subocular not greatly enlarged; keel of preocular medial; supraoculars keeled

6

6a. Scales of tail not aligned in dorso-ventral rows; less than 170 paravertebral scales between interparietal and hind margin of thigh *iheringii*

6b. Scales of tail aligned in dorso-ventral rows; more than 170 paravertebral scales between interparietal and hind margin of thigh

7

7a. Subdigital lamellae not keeled *perditus*

7b. Subdigital lamellae keeled

8

8a. Tail longer than 2.00 times snout-vent length in males and longer than 1.85 times snout-vent length in females; at midbody usually more than 67 scales from mid-dorsal to mid-ventral line in males and more than 69 in females *brasiliensis brasiliensis*

8b. Tail shorter than 1.88 times snout-vent length in males and shorter than 1.85 times snout-vent length in females; at midbody usually less than 67 scales from mid-dorsal to mid-ventral line in males and less than 69 in females . . . *brasiliensis boulengeri*

E. Phylogeny of *Enyalius*

1. Multiple Discriminant Analysis

Table 1 presents the mean values of the representative samples for the meristic-morphometric characters. Table 2 gives the standardized discriminant coefficients for the first three discriminant axes. The importance of any variable in determining the placement of OTU's along a discriminant axis can be judged by the relative size of the standardized coefficient for that variable. The OTU's are plotted on the first two discriminant axes in Fig. 27. The K₁ axis is associated with 61.2% of the inter-OTU variation; the K₂ axis accounts for 24.2% so that Fig. 27 summarizes 85.4% of inter-OTU variation. The third discriminant axis adds 7.3% to the cumulative variation accounted for.

K₁ separates *catenatus pictus* and *catenatus bibronii* from the rest of the OTU's. Within these remaining OTU's are three subgroups: *brasiliensis brasiliensis* and *brasiliensis boulengeri* occupying the center of the K₁ axis; *perditus* and *catenatus catenatus* very close together slightly higher on K₁; and *iheringii* and *bilineatus* having the most positive values on K₁. K₁ is largely a contrast between OTU's with aligned scales on the tail and those without aligned caudal scales. OTU's with high values for characters 28, 29 and 30 and low values for character 27 will fall more toward the negative end of K₁ than will OTU's with low values for characters 28-30 and high values for character 27. Several other characters influence placement on K₁ less strongly. A large number of paravertebral scales (character 7) contributes to a negative position on K₁. More vertebral scales (character 5), more scales between the supraorbital semicircles (character 10), more lamellae on the fourth hind toe (character 20), greater internares width (character 35) and greater width across the head (character 36) all contribute to a positive position on K₁.

The K₂ axis functions to separate further the three groups on the positive end of K₁; *brasiliensis brasiliensis* and *brasiliensis boulengeri* have the most negative locations; *perditus* and *catenatus catenatus* are again close together and intermediate; *iheringii* and *bilineatus* have positive values on K₂. The differential weighting of characters 27-30 influences this placement. In addition, greater internares width (character 35) and more lamellae on the fourth hind toe (character 20) contribute to positive placement

on K_2 . More paravertebral scales (character 7) and longer shanks (character 33) yield more negative K_2 values.

Mean values for the osteological characters are found in Table 3, and standardized discriminant coefficients for the first three discriminant axes are given in Table 4. Figure 28 shows the placement of the OTU's on the first two discriminant axes. The first discriminant axis contains 91.1% of the inter-OTU variation; the second axis contributes an additional 7.2% to the cumulative variation accounted for.

K_1 separates the OTU's into three clusters: *catenatus* *c. bibronii* and *c. pictus* form one cluster; *iheringii*, *brasiliensis brasiliensis* and *b. boulengeri* form another cluster; and *perditus* alone forms a third. A position roughly intermediate between the first and second clusters is occupied by *bilineatus*. OTU's with narrow anterior angles between the mandible and the retro-articular process (character 2), rugose premaxillae (character 5) and long posterior maxillary processes of the palatine (character 10) have high values on K_1 . OTU's with low values on K_1 are characterized by less separation between the pterygoids (character 7), wider anterior border of the basioccipital (character 8), longer anterior processes of the nasals (character 9) and longer and narrower anterior processes of the pterygoid (character 11).

The contribution of K_2 is to separate *bilineatus* and *catenatus bibronii* from the other OTU's. High values for characters 2, 7 and 11, as well as a wide squasomal (character 3), cause placement to be positive on K_2 . A longer snout (character 1) and a more square basioccipital (character 8) bring about more negative location on K_2 .

2. Wagner Trees

In calculating Wagner Trees, one alternative is to construct a hypothetical taxon to function as the ancestor of the radiation being studied. Because such a procedure would entail numerous assumptions about characters whose directions of evolution are not well-understood, I considered it the more conservative alternative to designate an extant taxon as "ancestral", meaning that, of the extant taxa, it is believed to be nearest the base of the radiation.

Enyalius brasiliensis brasiliensis is the ancestor hypothesized for calculation of the Wagner Trees. This decision was based primarily on the correspondence between *brasiliensis* and primi-

tive iguanid genera in regard to certain qualitative characters. *Enyalioides*, *Hoplocercus* and *Morunasaurus* are considered to be near the base of the iguanid radiation, and *Enyalius* is believed to be an early product of the anoline branch (Etheridge, unpublished phylogeny, 1971). Representatives of the three primitive genera were surveyed and found to have a) straight canthal ridges, b) keeled subdigital lamellae, c) keeled (1) or smooth (2) ventrals, d) keeled (2) or smooth (1) supraoculars, e) caudal scales aligned in rows, and f) usually a vertebral crest. The taxon in *Enyalius* that best fits this combination of characters is *E. brasiliensis brasiliensis*. A secondary rationale supporting this choice is the apparently relict distribution of the taxon. Besides the core range in Estado do Rio de Janeiro, outlying populations apparently exist in Goiás and Ilha de Santa Catarina. Relict distributions are often associated with evolutionary antiquity.

The data bases for meristic-morphometric, osteological and color character sets are given in Tables 1, 3 and 5 respectively. Tables 6, 7 and present the distance matrices from which the Wagner Trees were calculated according to the algorithm of Farris (1970). The Wagner Trees are illustrated in Figures 29, 30 and 31. Pleasingly, they show considerable similarity. In all three, *perditus* differs least from *brasiliensis brasiliensis*. The OTU next most similar to *b. brasiliensis* is either *b. boulengeri* or *iheringii*. In both the color-based (Fig. 31) and the cranium-based (Fig. 30) phylogenies, there are two relatively distinct groups: a basal one composed of *b. brasiliensis*, *perditus*, *b. boulengeri* and *iheringii*; and a derived group composed of *c. catenatus*, *c. pictus*, *c. bibronii* and *bilineatus*. The OTU of the latter group that forms the bridge the former is always *c. catenatus*. Within the latter group, *bilineatus* and *c. bibronii* are more derived than is *c. pictus*. The meristic-morphometric based phylogeny (Fig. 29) differs in that one OTU, *bilineatus*, is shifted from the derived group to the basal group, and in that *iheringii* is somewhat more removed from the basal group.

It is noteworthy that multiple discriminant analysis and Wagner algorithm generate similar clustering patterns when applied to the same data set. These data sets appear to be robust.

This phylogenetic analysis did not include the genus' remaining taxon, *Enyalius leechi* (Boulenger, 1885b), because only two specimens were available to me and because this

Amazonian form is extralimital to the question of differentiation in the Atlantic forest. Definitive phylogenetic placement of *E. leechi* should await the accumulation of more material. However, examination of meristic-morphometric characters in the two specimens of *E. leechi* leads me to conclude that the closest extant relative of this taxon is *E. brasiliensis*. This conclusion is indicated by the following characters in *E. leechi*: straight canthal ridge; keeled subdigital lamellae, ventral scales, supraoculars and infratibials; high paravertebral scale count; high subocular series count; high gular count; aligned caudal scales; and relatively short tail. The presence of a vicariant form in the Amazon valley supports the contention that *E. brasiliensis* is near the basal stock of Atlantic forest *Enyalius*.

F. Ecological Observations on *Enyalius*

During the collection of material for this study, some data were obtained on perch niche and thermal niche of several *Enyalius* taxa. Most of the observations are mine, but some were obtained from other collectors. Vanzolini (1972), referring to the *catenatus* complex as a whole, stated that perch niche spans the forest understory from the ground up to 5 m on tree trunks. My data confirm his characterization.

The perch niche observations follow, by individual, for five taxa. *Enyalius c. catenatus*: on a fallen log; on the limb of a shrub; in a small shrub 2 m above the ground; on a tree trunk 3 m above the ground; low on a tree trunk (Vanzolini, 1974). *Enyalius brasiliensis boulengeri*: on the ground; on the ground; on a tree trunk 100 cm in diameter $1/2$ m above the ground; on the limb of a small tree $1\frac{1}{2}$ m above the ground; on a tree trunk 2 m above the ground; on a tree trunk. *Enyalius iheringii*: on the ground; on a tree trunk 20 cm in diameter $1\frac{1}{2}$ m above the ground; on a tree trunk 30 cm in diameter $1\frac{1}{2}$ m above the ground; on a trunk 3 cm in diameter 1 m above the ground; in a shrub $1\frac{1}{2}$ m above the ground; on the surface of a *Heliconia* leaf 1 m above the ground. *Enyalius perditus*: on a small fallen limb 2 cm above the ground; on a trunk 1 cm in diameter $1\frac{1}{2}$ m above the ground. *Enyalius bilineatus*: on a fallen limb 8 cm above the ground; on the ground crossing a dirt road; on the ground; on the ground; on the ground in a cafezal. All of these lizards inhabited shady old growth forest, except for the *bilineatus*. Near Santa Teresa,

ES, *bilineatus* were never seen in mature forest but were relatively common in young second growth (capoeira suja), especially that dominated by bracken fern, and in coffee plantations. One large series was collected when *bilineatus* were fleeing a burning cafezal. *Enyalius bilineatus* was probably not present in the mountains of Espírito Santo prior the European colonization that provided expanses of second growth vegetation. Invasion of the highlands near Santa Teresa probably occurred through the Vale de Canaã from the dry forests near the ES – MG border.

Although limited, these data show that Atlantic forest *Enyalius* taxa, excluding *bilineatus*, have similar perch niches. Such similarity indicates that the largely allopatric distributions result from inability for niche partitioning. The similarity also suggests that differentiation was not driven by adaptation to new foraging niches, and hence the differentiation is more likely to have required cessation of gene flow.

Cloacal and air temperatures were taken by Schultheis Quick-reading Thermometer at capture of several active *Enyalius*. Although too limited to analyze quantitatively, the data suggest that these taxa are thermally passive, as might be expected of denizens of mature forest understory: *E. iheringii* female, $T_a = 25.4^{\circ}\text{C}$, $T_b = 24.8^{\circ}\text{C}$; *E. iheringii* female, $T_a = 25.0^{\circ}\text{C}$, $T_b = 24.1^{\circ}\text{C}$; *E. iheringii* female, $T_a = 26.0^{\circ}\text{C}$, $T_b = 27.1^{\circ}\text{C}$; *E. iheringii* male, $T_a = 24.2^{\circ}\text{C}$, $T_b = 26.6^{\circ}\text{C}$; *E. perditus* juvenile, $T_a = 26.0^{\circ}\text{C}$, $T_b = 26.2^{\circ}\text{C}$; *E. perditus* male, $T_a = 25.2^{\circ}\text{C}$, $T_b = 26.0^{\circ}\text{C}$; *E. b. boulengeri* female, $T_a = 18.5^{\circ}\text{C}$, $T_b = 18.6^{\circ}\text{C}$; *E. b. boulengeri* female, $T_a = 23.4^{\circ}\text{C}$, $T_b = 23.8^{\circ}\text{C}$.

G. Character Displacement in Body Size.

The only pair of *Enyalius* taxa that are syntopic are *E. iheringii* and *E. perditus*. They occur together at Parati in southwestern Estado do Rio de Janeiro, and at the following localities in the extreme eastern part of Estado de São Paulo: Cubatão, Paranapiacaba, city of São Paulo, Boracéia, Ubatuba and Ilha de São Sebastião. For each sex in each taxon, snout-vent length was compared between a sympatric sample, composed of individuals from these localities, and an allopatric sample composed of individuals from several localities. For *iheringii* the allopatric sample was from Rio Grande do Sul, Santa Catarina and Paraná; individuals from

western Estado de São Paulo were excluded because of uncertainty whether allopatric is universal in this region. The allopatric sample for *perditus* came from northern Estado de São Paulo and from Estado do Rio de Janeiro: Paranaçuã, SP; Garça, SP; Piquete, SP; Porto Real, RJ; Rio Claro, RJ; Petrópolis, RJ; Teresópolis, RJ; and Macaé, RJ. Only individuals larger than 70.0 mm snout-vent length were included in the samples. Sample means were compared by two-tailed t-tests assuming inequality of variances.

Body size is smaller in the aggregate sympatric samples in both sexes of both species, but only in the females is the difference statistically significant. The mean body size of adult female *iheringii* in sympatry is only 95.0 mm (N = 22), whereas in allopatry the mean is 103.1 mm (N = 64) ($p < .01$). Sympatric female *perditus* have a mean body size of 81.6 mm (N = 11), but allopatric female *perditus* average 91.0 mm (N = 13) ($p < .005$). The sympatric male *iheringii* have a mean body size of 90.0 mm (N = 23); the allopatric male *iheringii* have a mean of 94.5) mm (N = 12) ($p > .2$). Sympatric male *perditus* average 75.9 mm (N = 11), while allopatric male *perditus* have a mean of 78.6 mm (N = 12) ($.1 < p < .2$).

Convergence towards reduced body size in sympatry may result from a small degree of difference in perch niche between the taxa. Schoener (1970) has shown that such situations should favor smaller body size in both competitors as an adaptation to exploiting the lower end of the prey size spectrum where prey biomass is concentrated.

H. Geographic Variation in *Strobilurus torquatus*

Specimens of *Strobilurus* were available from only seven localities. These fell into three geographic sets: Espírito Santo (ES), Bahia (BA) and Pernambuco-Alagoas (PE). Such a limited number of localities is clearly inadequate to plumb geographic variation in *Strobilurus*, and these results are presented only because they provide for the northeastern coast an independent test of the forest-contraction hypothesis. Means of the meristic-morphometric characters across the three regions are given in Table 9.

The samples represent three regions, hence seven patterns of geographic variation are possible: 1) mosaic variation, 2) ES samples different from BA and PE samples which do not differ much from each other, 3) PE samples different

from BA and ES samples which do not differ much from each other, 4) BA samples different from ES and PE samples which do not differ much from each other, 5) ES samples different from BA samples with PE samples intermediate, 6) PE samples different from BA samples with ES samples intermediate, and 7) ES samples different from PE samples with BA localities intermediate. Three of these patterns would support the hypothesis of differentiation in refugia: 2, 3 and 7. Because the samples were too small to permit statistical comparison among them, I compared them qualitatively by dividing the range of variation in each character into six equal classes and scoring each sample on this scale. Such qualitative comparison allowed each character (for each sex) to be designated as showing one of the above seven patterns of geographic variation. The results are presented in Table 10.

Mosaic variation in some characters neither supports nor refutes the hypothesis of differentiation among the regions, and this pattern is thus ignored. The null hypothesis of no difference in frequency among the remaining patterns is rejected ($p < .005$). The remaining six patterns can be divided into those in which one region is intermediate between the others (5, 6 and 7), and into those where no intermediacy occurs (2, 3 and 4). Within both subsets the null hypothesis of no difference in frequency among the patterns can be rejected. For the subset 5, 6 and 7, $p < .01$; for the subset 2, 3 and 4, $p < .025$. The most common pattern is for the *Strobilurus* from BA northward to be similar but different than *Strobilurus* from ES (Fig. 32). When one region is intermediate, it is most often BA (Figs. 33 and 34). The overall tendency can be summarized as differentiation between ES and PE *Strobilurus* with BA *Strobilurus* intermediate but most closely allied to PE samples.

Figure 26B illustrates the pattern of nuchal markings typical of *Strobilurus torquatus* from Espírito Santo. The nuchal pattern of Pernambuco *Strobilurus* is shown in Figure 26C.

DISCUSSION

A. Introduction

The ultimate objective of this study has been to ascertain whether differentiation in *Enyalis*

and *Strobilurus* is consistent with extensive climatically-induced vegetation changes in eastern Brazil. One approach would be to determine the evolutionary course of differentiation and then to search for barriers and refugia in the needed localities. A more honest method would try to separate the process of hypothesizing phylogeny from that of hypothesizing refugia. I have tried to follow this latter methodology. The hypotheses for differentiation and for climatic change were generated as nearly as was possible independently; they are presented separately below and then they are combined and compared for consistency.

B. The Paleoclimatological Evidence

It has become generally accepted that high-latitude Pleistocene glacial episodes were accompanied by drier climates at low latitudes (Bonatti and Gartner, 1973; Parmenter and Folger, 1974), and a good case has been made for world-wide synchrony of tropical glacial aridity (Williams, 1975). Haffer (1974) and Vanzolini and Williams (1970) review evidence of Pleistocene aridity in northern South America.

Few geomorphological investigations into Pleistocene climatic cycles have been made in eastern Brazil. These studies have provided evidence of alternating wet-dry cycles but have not been extensive enough to pinpoint locations of continuously humid climate. Ab'Saber (1970) showed the presence of inselbergs, indicators of past arid climate, slightly inland from Salvador, Bahia. Bigarella (1971) gives evidence of late Pleistocene aridity by correlating deposits of large erosional material, covered by lighter present-day sediment, with C14-dated wood fragments. He also correlated high fluvial terraces that were caused by heavy rain on a sparsely-vegetated landscape, and buried dunes with wood dated by the radiocarbon method. He shows that during the past 40,000 years there have been several dry periods in São Paulo and Santa Catarina. Tricart (1959) believes that during the Pleistocene the arid zone in northeastern Brazil expanded slightly to cover the inner margin of the present forest zone, but that the forests were not obliterated. For southeastern Brazil, he discusses evidence that climatic variations were more extreme and that semi-arid conditions affected the whole of the present cerrado and forest regions. Pleistocene deposits in southeastern Brazil are of coarse gravel, sand and loam unlike the organic argilla-

ceous deposits of present-day floodplains. Semi-arid depositional fans can be seen around Guanabara Bay. Ravines formed by mechanical erosion are found from Ilhéus to southern São Paulo. Geomorphological evidence exists for 3 or 4 wet-dry cycles. Tricart (1959) is forceful in stating that dry climates in southeastern Brazil were widespread *or even universal*. The theory of allopatric differentiation finds widespread aridity comforting for separation of populations. Universal aridity in southeastern Brazil is clearly untenable, however. Obviously, forest biotas must have survived in refugia; otherwise the large radiation of forest-restricted forms would not exist, e. g. the grypiscine frog genera of the family Leptodactylidae (Heyer, 1975).

C. Hypothetical Climatic and Vegetational Changes

Since eastern Brazil has not yet been sufficiently surveyed by geologists to use geomorphological evidence to determine where forest cover was continuously present during the Pleistocene, I have used maps of present-day aridity (Figs. 35 and 36) and vegetation (Fig. 37) as the next best indicators of where tropical forests were most likely to have persisted and where open formations were most likely to have invaded areas presently forested.

The probability that certain of the hypothesized refugia (Fig. 38) existed is high. The Santa Catarina refuge (1 in Fig. 38) would have been constituted by sizeable tracts of lowland forest around Baías de Paranaguá and São Francisco and by montane forest on the Serra do Mar in Santa Catarina. These receive heavy rains from adiabatic cooling of air moving landward from the Atlantic Ocean. The São Paulo refuge (2) would have been composed of a tract of lowland forest around Santos backed by montane forest. The wall-like section of the Serra do Mar between Paranapiacaba and São Sebastião interacts with sea winds to generate the highest rainfall in Brazil. The Bocaina refuge (3) would have been the result of rainfall around the Baía da Ilha Grande topographically induced by the Serra da Bocaina. The Mantiqueira refuge (4) would have been composed of montane forest able to survive on the Serra da Mantiqueira because of the lower temperatures and higher rainfall and fog there. For the same reasons a Serra dos Órgãos refuge (5) is postulated. A montane Espírito Santo refuge (6) is indicated by montane forest found in southern Espírito

Santo (Fig. 37). Most maps of aridity or pluviosity do not show the region to be especially humid but this appears to be due to insufficiently detailed mapping. For example, rainfall at Reserva Nova Lombardia, Santa Teresa, is more than half again greater (Ruschi, 1950) and at Guiomar twice as great (Simões, 1951) as indicated by contours of Map 44 in Atlas Climatológico do Brasil (1969). My observations in southern Espírito Santo suggest that the forest on the seaward face of the mountains is nearly as moist as that of more southern refugia.

Another refuge would have been constituted by lowland wet forest of the coastal plain of northern Espírito Santo and extreme southern Bahia (7). As shown by Figs. 35 and 36, this region is relatively humid. Perhaps as important for retention of forest cover during dry periods is its inclusion of the delta of the Rio Doce. Blocked by levee formation of the Rio Doce, a number of streams in the delta lack exits to the sea and instead form lakes and associated swamps. Also, during glacial sea level regressions, the area of this refuge would have been enormously augmented. From Rio de Janeiro north the 100 m depth contour generally lies 10-40 km offshore, but between Rio Doce and Rio Jequitinhonha the continental platform abruptly widens, with the 100 m contour 50-250 km offshore. The land uncovered between the latitudes of Caravelas, BA, and Linhares, ES, by a 100 m drop in sea level would have had an area roughly equal to the state of Espírito Santo. The existence of a refuge along the Pernambuco coast (8) is indicated both by the present humid climate and by geological evidence. Studying Pleistocene erosional patterns, Tricart (1959) concluded that, although the arid zone in Pernambuco expanded slightly several times to cover the inner edge of the present forest belt, the forest was not obliterated. Humid conditions along the central-eastern border of Goiás (9) suggest that forest may have continuously occupied this area.

The two other areas shown in black in Fig. 38 are perhaps less certain to have functioned as large-scale refugia. One is the region of the upper Rio Doce between Barbacena, Ponte Nova and Viçosa, Minas Gerais (10). Figs. 35 and 36 show the region to be more humid than usual for the interior but Hueck (1972a) did not recognize a more pluvial vegetation there. The second area is the vicinity of Salvador, Bahia, and the region immediately to the south

(11). This region is highly humid now (Figs. 35 and 36), but the wet forest belt is very narrow and to the west one rapidly passes into tropical deciduous forest (*mata de cipó*) and *caatinga*. Further, Tricart (1959) concluded from micro-erosion by salt crystals, from landward migration of dunes, from reduced latosol depth and from erosional patterns that near Itabuna, Ilhéus and Salvador the climate was recently drier, though it probably still supported forest.

It is equally important to explain the basis of the location of hypothesized expansions of open formations. An expansion of cerrado between the Santa Catarina and São Paulo refugia probably occurred along the upper Rio Parapanema and Rio Ribeira do Iguape. This area is the most arid in southeastern Brazil (Figs. 35 and 36), and extensive cerrados exist near Itapetinga, SP, one of the closest present approaches of cerrados to the coast (Fig. 37). The cerrado expansion between the São Paulo and Bocaina refugia is hypothesized because of the prong of aridity that approaches the coast near Ubatuba, SP (Fig. 36). Islands of cerrado extend in a wide band from Rio Grande to near São Paulo and São José dos Campos; this last is the cerrado presently nearest the coast. An expansion along upper valley of the Rio Paraíba between the Mantiqueira, Bocaina and Serra dos Órgãos refugia is hypothesized because of the relative aridity there in the rain shadow of the Serra do Mar (Hueck, 1972b).

The invasion of northern Estado do Rio de Janeiro along the lower valley of the Rio Paraíba seems likely both due to the more arid climate (Figs. 35 and 36) and the proximity of cerrado south of Belo Horizonte and northwest of Juiz de Fora, MG. I hypothesized a cerrado invasion of extreme southern Espírito Santo southwest of the montane Espírito Santo refuge because of the relative aridity there. This aridity is due to a weak rain shadow of the coastal side of the mountains and to the penetration of the valley of Rio Itapemirim through southern Espírito Santo. Because of the low relief, rainfall in this valley is little greater than 1000 mm (Simões, 1951). A narrow separation of the montane and lowland Espírito Santo refugia probably occurred along the south side of the Rio Doce between Colatina and Santa Cruz. The upper two-thirds of the valley of Rio Doce in Espírito Santo receives less than 1000 mm of rain: (Simões, 1951; Ruschi, 1950). Near Baixo Guandu exist areas of a lush version of *caatinga* (*caatinga suja*) (Ruschi, 1950).

The hypothesized expansions of cerrado immediately north and south of Rio Jequitinhonha are based on displacement of aridity isophenes toward the coast near 16°S. In total rainfall, differences between this latitude and areas immediately north and south in Bahia are not great (Map 44; Atlas Climatológico do Brasil, 1969), but the number of rainy days on the coast at 16°S is almost half that at 14°S or at 17°S. Cerrado most closely approaches the northeastern coast near Rio Jequitinhonha. A coastward expansion of caatinga south of Salvador is a possibility mainly because of the proximity of caatinga to the coast there, although the coastal plain itself is presently humid. Expansions of caatinga toward the coast of Sergipe and northern Bahia are hypothesized with greater confidence because of the sharp southeastern displacement of aridity isophenes (Figs. 35 and 36). Such expansions surely isolated the Pernambuco refuge.

D. Hypothetical Phylogeny

Inasmuch as the phylogenies proposed from the three data sets differ somewhat, a single phylogenetic scheme must be tentatively adopted before comparison can be made with the hypothesis of the preceding section.

For several reasons, I believe the phylogeny generated from the osteological data (Fig. 30) most accurately represents the evolutionary relationships in *Enyalius*. First, I think that *bilineatus* arising as a derivative of an *iheringii*-like ancestor in Fig. 29 is a reflection of convergence between the two taxa. *E. bilineatus* is probably derived from *c. bibronii* or *c. pictus* as suggested by Figs. 30 and 31. Ecologically, *bilineatus* is the most different of the taxa, and consequently it could be expected to show large phenetic differences from its ancestors. I believe several of these differences are understandable as adaptations to its open habitat and cursorial locomotion. The reduced number of dorsal scales (character 7) and the keeling on the ventrals (character 3) and infratibials (character 37) are modifications that are probable in a sunnier habitat where heat is a greater problem (Soule and Kerfoot, 1973; Regal, 1975). I suggest that in *bilineatus* the direction of evolution of these traits was reversed from the direction followed in *c. bibronii* and *c. pictus*, approached again the condition typical of the rest of the taxa, and finally surpassed that condition. In *bilineatus* the ventrals are more heavily keel-

ed and the dorsal scales are fewer than in any other taxon.

The tail of *bilineatus* is much longer than in the other taxa. It seems to function as a counterweight to the body that allows bipedal locomotion on the hind legs during escape behavior. No other members of the genus were observed running bipedally. Given this function of the tail, the evolution of non-aligned caudal scales appears understandable as a means of strengthening an attenuated tail that is probably under added mechanical stress during high speed running. In this character *bilineatus* is suggested to be convergent on *iheringii*, whose tail largely lacks aligned scales. These characters that represent adaptations to open vegetation are primarily responsible for placing *bilineatus* closer to *iheringii* than to the races of *catenatus* in regard to the meristic-morphometric data set. If they were ignored, *bilineatus* would be nearer to *c. bibronii* than to *iheringii*. In certain characters of head scalation (9, 10 and 12) *bilineatus* is very similar to *c. bibronii*.

Another reason that I prefer the phylogeny of Fig. 30 over that of Fig. 29 is that it places the origin of *iheringii* farther from that of *catenatus* and its derivatives. The arrangement in Fig. 29 hypothesizes a monophyletic origin of smooth subdigital lamellae. I believe that this trait arose at least twice in *Enyalius*, probably three times. It arose in the stock ancestral to the *catenatus* taxa. It arose again in *perditus*, and once again in *iheringii*. That the origin of smooth lamellae in *iheringii* was separate, and probably more recent, than that in the ancestral *catenatus* stock is shown by the presence of vestigial keels in some *iheringii* populations (12, 13, 14 and 15). A similar case of vestigial traits in the subdigital lamellae of *Anolis annectens* has been described by Williams (1974). Populations 12-15 are closer to *brasiliensis brasiliensis* in some other traits than is usual for *iheringii*.

Finally, the phylogenies of Figs. 30 and 31 are very similar; hence, even if equal importance is given to all three phylogenies, the weight of the evidence favors a phylogeny similar to Fig. 30 by a two-to-one ratio. This phylogeny is then accepted as the most probably correct.

E. Hypothetical History of Differentiation

In the interest of readability, the model is described in positive terms; nevertheless it is advanced as a hypothesis.

A form of *Enyalius* similar to *E. brasiliensis* was the ancestral taxon of the genus. It existed early enough to colonize both the Amazonian and Atlantic wet forests before they became separated by xeric-adapted vegetation; it persists on the fringes of the Amazonian region in Goiás, as well as in southeastern Brazil. In an extralimital speciation event, it probably gave rise to *E. leechi* of the Amazonian forest. Immediately after the initial colonization of the eastern Brazilian forest, the *brasiliensis*-like ancestor was widespread and geographically homogeneous.

The first dry period would have isolated several portions of this extensive population by interposition of drier, more open vegetation in the regions indicated by the arrows in Fig. 38. Certainly *Enyalius* could not have persisted in a locale after forest was replaced with caatinga or cerrado. Yet the assumption of complete conversion to cerrado or caatinga in the hypothesized breaks in the Atlantic forest is probably unnecessary to the belief that they functioned as barriers to wet forest fauna. These are indisputably drier corridors now, and moderate reduction in rainfall would convert their vegetation at least to deciduous forest. Whether such a change would eliminate any given wet forest species depends upon its ecology. I believe that no species of *Enyalius* except *bilineatus* would persist in dry, open deciduous forest, not only because of physiological problems of body temperature and desiccation but because of competition. As shown above, *Enyalius* are inhabitants of the forest floor and low understory. Most iguanids that perch low in the understory obtain food primarily on the ground, using perches on plants more as lookout sites than as locations of prey capture. As a ground-feeder preying on arthropods, *Enyalius* would likely be subject to competition from similarly-sized *Ameiva* and *Tropidurus* in sparse forests with sunny understories. These typically heliothermic, ground-feeding genera are absent from Atlantic wet forests except where the forest are disturbed by man, and so are not naturally syntopic with *Enyalius* now. That *Enyalius* could persist together with the normally dense populations of *Ameiva* and *Tropidurus* in a deciduous forest is doubtful.

One of the *brasiliensis*-like populations isolated either in the São Paulo, Bocaina or Serra dos Órgãos refugia gave rise to *perditus*. There is little evidence that would allow probability ranking of these refugia, but the São Paulo refu-

ge is recommended by the fact that it is outside the present range of *b. brasiliensis*. Whatever the refuge in which *perditus* differentiated, *b. brasiliensis* was preserved in one or both of the other refugia mentioned.

The same or another dry period cut gene flow between *brasiliensis* in the Santa Catarina refuge and those farther north, and thus allowed evolution of *iheringii* in this refuge. This case provides as clear non-fossil evidence for the process of geographic speciation as one could expect. First, *iheringii* is closely related to *b. brasiliensis* (Figs. 30 and 31). It can be assumed to be derived from rather than ancestral to *brasiliensis* because of the relict distribution of the latter and the derived character states of the former (non-aligned tail scalation, smooth subdigital lamellae, lower paravertebral count). Second, *b. brasiliensis* apparently exists within the hypothesized generative refuge of *iheringii*, but in a geographic situation that makes understandable its continued existence near the presumably competitively-superior derivative form: on an island, Ilha de Santa Catarina, protected from competition by the derived form except during glacial epochs. Third, several populations of *iheringii* (e. g. Joinville) in the heart of the putative refuge possess some *brasiliensis*-like traits (e. g. partial keeling of subdigital lamellae). When the wet forest again spread north from the Santa Catarina refuge, the new form *iheringii* expanded its range north to include eastern SP. When later dry periods broke gene flow between the SC and SP refugia, the *iheringii* populations isolated in these refugia differentiated slightly. The northward range expansion brought *iheringii* into sympatry with *perditus* in extreme eastern SP. Competition from *iheringii* favored smaller body size in sympatric *perditus*. The character displacement of body size in *perditus* that allowed syntopic coexistence with *iheringii* could have facilitated a subsequent range expansion by *perditus* north-eastward into sympatry with *b. brasiliensis*.

During an early dry episode the northern section of *b. brasiliensis* became isolated by the dry corridor along the lower Rio Paraíba. In one of the refugia north of this barrier, *b. boulengeri* was derived from the *b. brasiliensis*-like stock. Upon the renewal of contact among the refugia, *boulengeri* spread from its point of origin and competitively replaced the *brasiliensis*-like form north of the Rio Paraíba.

The next dry cycle isolated the *boulengeri* populations. One of the isolates north of the

montane ES refuge underwent relatively radical differentiation to become an entity near *c. catenatus*. It evolved smooth subdigital lamellae and a curved canthal ridge, though the latter trait had been foreshadowed in *b. bouleengeri*. Again the following humid period allowed the new form to extend its range through the Atlantic forest north of the Rio Doce.

The two coastal races of *catenatus* differentiated during one or more of the subsequent xeric periods when the continuous coastal population was fragmented into the lowland ES refuge, the Salvador refuge and the PE refuge. The uniform male coloration and keeling on the supraoculars, ventrals and infratibials suggest that *catenatus catenatus* is closer to the basal curved-canthal stock than is *c. pictus*. Possible rupture of gene flow between the *c. catenatus* in the Salvador and Pernambuco refugia did not result in strong differentiation between these populations. The curved-canthal form isolated in the lowland Espírito Santo refuge gave rise to *c. pictus*. When the coastal wet forest expanded again in the northeast, a zone of secondary intergradation developed between *c. catenatus* and *c. pictus* near Rio Jequitinhonha. The intergrade individual from Goiás indicates that this intergrade zone spread westward during a pluvial period!

Enyalius catenatus bibronii was derived from *c. pictus*, possibly during a pluvial period in adaptation to semi-deciduous forests of the inland northeast. This differentiation may have occurred through ecological, rather than large-scale geographic, isolation. During pluvial periods, *c. bibronii* became widespread in the expanded semi-deciduous interior forests from Minas Gerais to Pernambuco, possibly along the gallery forest of the Rio São Francisco. As the climate deteriorated later, *c. bibronii* was restricted to relict inland forests of the northeast.

One of these relict forests in Minas Gerais, possibly the Upper Rio Doce refugia, that was occupied by *c. bibronii* gradually became drier and more open such that selection favored the evolution of a more cursorial version of *Enyalius*, i. e. *bilineatus*. The selective forces probably included: 1) greater need for site change to control body temperature in a more insolated habitat; 2) greater need for site change during foraging due to probably lower insect biomass in a drier habitat (Janzen and Schoener, 1968); the smaller body size of *bilineatus* is what would be expected of a form with a reduced resource base (Schoener, 1969); 3) the increas-

ed visibility to predators caused by more frequent site change could have reinforced evolution of cursorial ability. Thus *bilineatus* seems an excellent example of evolution of a vicariant species in a refuge with a changing ecology (sensu Vanzolini).

Differentiation in *Strobilurus torquatus* supports the idea that the northern half of the Atlantic forest was fragmented into a Pernambuco refuge and a northern Espírito Santo refuge, although the variation could as well be interpreted as clinal. Populations of *S. torquatus* in the putative refugia are differentiated, while those of southern BA are intermediate.

F. Other Biological Evidence

Several systematic and biogeographic studies of other organisms are pertinent to the question of Pleistocene vegetational changes. Soderstrom and Calderón (1974) found that the Atlantic forest from northern Espírito Santo to Pernambuco contains a higher proportion of primitive herbaceous bambusoid grasses than to either the southeastern Atlantic forest or the Amazonian forest. More rapid differentiation in the southeastern portion of the Atlantic forest is consistent with Tricart's (1959) conclusion that this region underwent more extreme drying than the coastal northeast.

Two patterns of geographic variation in *Lepidactylus* (now in *Adenomera*, Heyer, 1975) in southeastern Brazil described by Heyer (1973) may be the result of differentiation in refugia. *Adenomera bokermanni* has a distinct color form in Paraná that is different from the São Paulo-Rio de Janeiro form. Separation of *A. bokermanni* populations into Santa Catarina and more northerly refugia by the dry corridor along the valley of Rio Ribeira do Iguape (Fig. 38) may have facilitated the differentiation. In *A. marmorata* the Santa Catarina population has one pattern of stripes whereas the Rio de Janeiro population has another, the São Paulo population being transitional. Again, the geographic variation suggests isolation of *Adenomera* populations in the Santa Catarina refuge, the São Paulo refuge and in one of the refugia in the state of Rio de Janeiro.

Langenheim et al. (1973) provide an example of a vicariant species, *Hymenaea eriogyne*, that apparently adapted *in situ* to progressively more arid forest in the way I suggest *E. bilineatus* did. This leguminous tree is restricted to caatinga, but its seedling morphology points to an

Amazonian origin. It apparently stayed in northern Bahia – southern Ceará and adapted to the aridity as forest gave way to caatinga.

Finally, the fascinating differentiation of *Mabuya* on the littoral of São Paulo that was elucidated by Rebouças-Spieker (1974) seems worth reconsidering in the context of climatic change. She demonstrated the differentiation of an entity, *Mabuya caissara*, along that part of the coast between Bertioga and Ubatuba. The *Mabuya* putatively ancestral to *M. caissara* are distributed coastally both north and south of the derivative form and on the small continental islands of the region. *Mabuya caissara* inhabits grass clumps, but the ancestral form lives in ground bromeliads. Rebouças-Spieker (1974) hypothesized that *M. caissara* “recently differentiated from an ancestral homogeneous population that occupied a continuous coastal plain in the last glacial.” She felt that differentiation occurred parapatrically during post-glacial time in response to physiographic changes caused by marine ingression. I would suggest, however, that the parapatric differentiation occurred earlier, during a glacial period when the section of coast immediately south of Ubatuba was more arid than at present (Fig. 38). Drier climate may have reduced the abundance of ground bromeliads relative to grass and thus favored a microhabitat shift in local *Mabuya* that led to morphological differentiation. That the small islands retained the ancestral *Mabuya* could be because, as disarticulated hills during lowered glacial sea level, they maintained a locally moister climate. Such a hypothesis of causation in no way conflicts with the demonstrated parapatric differentiation.

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Enyalius catenatus catenatus

Pernambuco: Água Azul (Vicência), MZUSP 23086; Água Preta, MEPDIR without number; Igarapu, BM 1888.4.18.5; Palmares, MCN R-4726; Recife, DEUF 659, MCN R-4725, MNRJ 1934; Rio Formoso, MCN R-4727.

Enyalius catenatus catenatus X *pictus*

Bahia: Ilhéus, MNRJ 1610, 3462-75, 3477; Itapeitinga, IBUEC without number; Poritaguá, MZUSP; *Goiás*: Rio das Almas, MZUSP 915.

Enyalius catenatus bibronii

Pernambuco: Garanhuns, MCN R-4728; *Bahia*: no further data, BM 1869.11.3.8; *Minas Gerais*: Montezuma, MZUSP 10115.

Enyalius catenatus pictus

Espírito Santo: no further data, MZUSP 8826; Conceição da Barra, MZUSP 42917; Itaúnas (Conceição da Barra), MZUSP 39539-40; Sooretama (Linhares), MCZ 82873, UFRRJ without number; *Minas Gerais*: no further data, MZUSP 704.

Enyalius iheringii

Rio de Janeiro: Parati, MNRJ 1607 (part), MNRJ 3445; *São Paulo*: Ana Dias, MZUSP 4242-48, 6862; Bom Jesus (Jacareí), MZUSP 6863; Cantareira (São Paulo), MZUSP 4278-80; Cubatão, MZUSP 417; Estação Biológica de Boracéia (Salesópolis), MZUSP 2315, 2318, 2322, 2533, 10270, 10273, 13593, 23575, 40608; Fazenda Água de Santa Rosa (Serra de Bocaina), MZUSP 756; Fazenda Olho d'Água (Serra Azul), MZUSP 2317; Guarujá, MZUSP 1056; Iguape, MZUSP 19549, NMW 12957; Ilha dos Búzios, MZUSP 11206-07; Ilha de São Sebastião, MZUSP 3121, 3728; Ilha Vitória, MZUSP 10820; Itanhaém, MZUSP 595; 8 km N. Juquiá, UMMZ 108629; Musácea, MZUSP 4253; Osasco, AMNH 74964, MZUSP 5397; Parana-piacaba, MZUSP 376, 588-89, 3148-49, 10374; Pedro de Toledo, MZUSP 4251; Peruíbe, MZUSP 42693, 42695, 42701, 42706, 42713-15, 42718, 42760; Piasaguera (Cubatão), MZUSP 3142-43, 11888; Poá, MZUSP 4275; Praia Grande, MZUSP 4269; Quilombo (Indaiatuba), MZUSP 14429; Rio dos Campos (São Vicente), MZUSP 6864; between Salesópolis and Mogi das Cruzes, MZUSP 2316; Salto de Itu, MZUSP 4281; Santo Amaro (São Paulo), MZUSP 273, 3120, 3124, 3126-27, 4254, 11951, 36665; Santos, MZUSP 4268, 4274, NMW 12959, 12963; São Bernardo do Campo, MZUSP 10136; São Paulo, IBUEC without number, MZUSP 696, 2320-21, 2534, 3140-41, 29612, 36112;

APPENDIX

1. Specimens examined

Enyalius bilineatus

Espírito Santo: Santa Teresa, MZUSP 17455-56, MZUSP 39520-27; *Minas Gerais*: Antônio Carlos, MCZ 84034; Benjamin Constant, MZUSP 5367; Juiz de Fora, MZUSP 42778; Mariana, MZUSP 546, 594, 719, 12302; Lagoa Santa, ZMC R37701-03; Ouro Preto, MZUSP 5631; Pampulha, MZUSP 29698; Muriaé, MNRJ 1612; Sereno, MZUSP 3729; Serra do Caraça (Santa Bárbara), MZUSP 8216; Viçosa, MNRJ 1604, MVZ 14931; *Rio de Janeiro*: Conservatório, MZUSP 5366; Madalena, MNRJ 1601; Rio Preto, MZUSP 10410.

Enyalius brasiliensis brasiliensis

Goiás: no further data, MCZ 4251; Veadeiros, MNRJ 3446; *Rio de Janeiro*: no further data, MP 6814; Ilha Grande, MNRJ 3456; Itatiaia, MZUSP 2662; Madalena, MNRJ 1608; Mangaratiba, AMNH 62143; Represa do Ribeirão de Lajes (Piraf), UFRRJ without number; Rio de Janeiro, CAS 15135-36, 16101, 96876, MNRJ 1609, 1613, 1616, 3457, 3459, 3460-61, MP 02-368, MZUSP 2531, 3232-34, 4257-58, 7756, 10247, 10251, 10259, UFRRJ without number, UMMZ 108627; Teresópolis, MNRJ 3458, USNM 98603; *Santa Catarina*: Ilha de Santa Catarina, MP 6816 (A and B). *Cayenne*: MP 2373, 6815.

Enyalius brasiliensis boulengeri

Espírito Santo: no further data, MZUSP 429; on border with Minas Gerais, ZIM 2205; Alfredo Chaves, MCZ 79025; Araguaia, MZUSP 4276; Itá (Colatina) MZUSP 4277; Santa Leopoldina, ZIM 2546; Santa Teresa, MNRJ 1611, 1618, MZUSP 8825, 17452-54,

UMMZ 108628; 15 km NE Sete Barras, MZUSP 8387; Taboão da Serra, MZUSP 40759; Saco da Ribeira (Ubatuba), MZUSP 42916; *Paraná*: Antonina, MZUSP 39516; Caiobá, MZUSP 3146; Irati, MZUSP 4243; Marumbi, MZUSP 39513-14; Morretes, MZUSP 4256, 39518; Paulo Frontim (Mallet), MZUSP 4260; Porto União da Vitória, MZUSP 4244, 4249-50; *Santa Catarina*: no further data, BM 1888.4.23.1-2, MNRJ 3454-55; Blumenau, MCZ 6315, MP 98-330; MZUSP 760, 769, 3150, NMW 12958, 14947; Corupá do Sul, MZUSP 4252; Dona Ema, MZUSP 39515; Hansa, BM 1928.11.5.109-113, MZUSP 427-28, 431, 596, 4261, USNM 40214-15; Humboldt (Corupá do Sul), MNRJ 1619; Jaraguá do Sul, MZUSP 39517, NMW 12964; Joinville, FMNH 11388-89, 11622-23, MNRJ 1615, NMW 12961 (1-7), ZIM 4536; Lauro Müller, MZUSP 21466; Nova Brêmen (Ibirama), NMW 12967; São Bento do Sul, MZUSP 4270-73; Teresópolis (Palhoça), BM 1888.9.21.2-3, RMNH 4966; *Rio Grande do Sul*: no further data, BM 1946.8.9.3-4, MCN R2651, MZUSP 265, NMW 14077; Colonia de São Pedro (Torres), MCN R0790, MZUSP 38380; Porto Alegre, ZMC R37699; 5 km W. Torres, MZUSP 39549; *Southern Brazil*: no further data, ZMC R37695-98, R37700.

Enyalius perditus

Rio de Janeiro: no further data, MCZ 3717, 3722, MNRJ 1606, ZMC R37694; Macaé, MZUSP 592; Para-

ti, MNRJ 1607 (part), 1815; Porto Real, BM 1887.12.29.1-2, RMNH without numbers; Petrópolis, MCZ 7320, MNRJ 1605; Rio Claro, MZUSP 4259; Sacra Família do Tinguá (Paulo de Frontim), MZUSP 36926; Serra de Macaé, MZUSP 593, 709, 3147; Teresópolis, BM 1893.9.30.1, MNRJ 1614, 3448-53, MZUSP 2281; *Minas Gerais*: Machado, MZUSP 4255; *São Paulo*: Cantareira (São Paulo), MZUSP 578, 590; Estação Biológica de Boracéia (Salesópolis), MZUSP 2319, 2323, 8252, 8380, 10272, 38381, 42685; Garcia, MZUSP 4266-67; Ilha de São Sebastião, MZUSP 285, 585, 3122, 10296; Osasco, MZUSP 250; Paranaíacaba, MZUSP 584, 3123, 3136, 7692, 10375, 11463-64; Paranapuã, MZUSP 8266; Piassaguera (Cubatão), MZUSP 697; Piquete, MZUSP 587, 3137-39; Saco da Ribeira (Ubatuba), MZUSP 38382, 39550; São Paulo, MNRJ 3447, MZUSP 835, 3125, 13594; Serra Negra, MZUSP 4265; Ubatuba, IBUEC without number; *Paraná*: Barigui, MZUSP 3145.

Strobilurus torquatus

Pernambuco: Água Azul, MCZ 133243, MZUSP 23072, 23075, 23078, 23081-82, 23087, 23094; Itamaracá, MZUSP 21481; *Alagoas*: São Miguel dos Campos, MCZ 59275; *Bahia*: Ilhéus, MNRJ 3441-42, MZUSP 423; Itabuna, MZUSP 29626; *Espírito Santo*: Linhares, MZUSP 30747, 39581; Santa Cruz (Araucruz), MZUSP 36715-16.

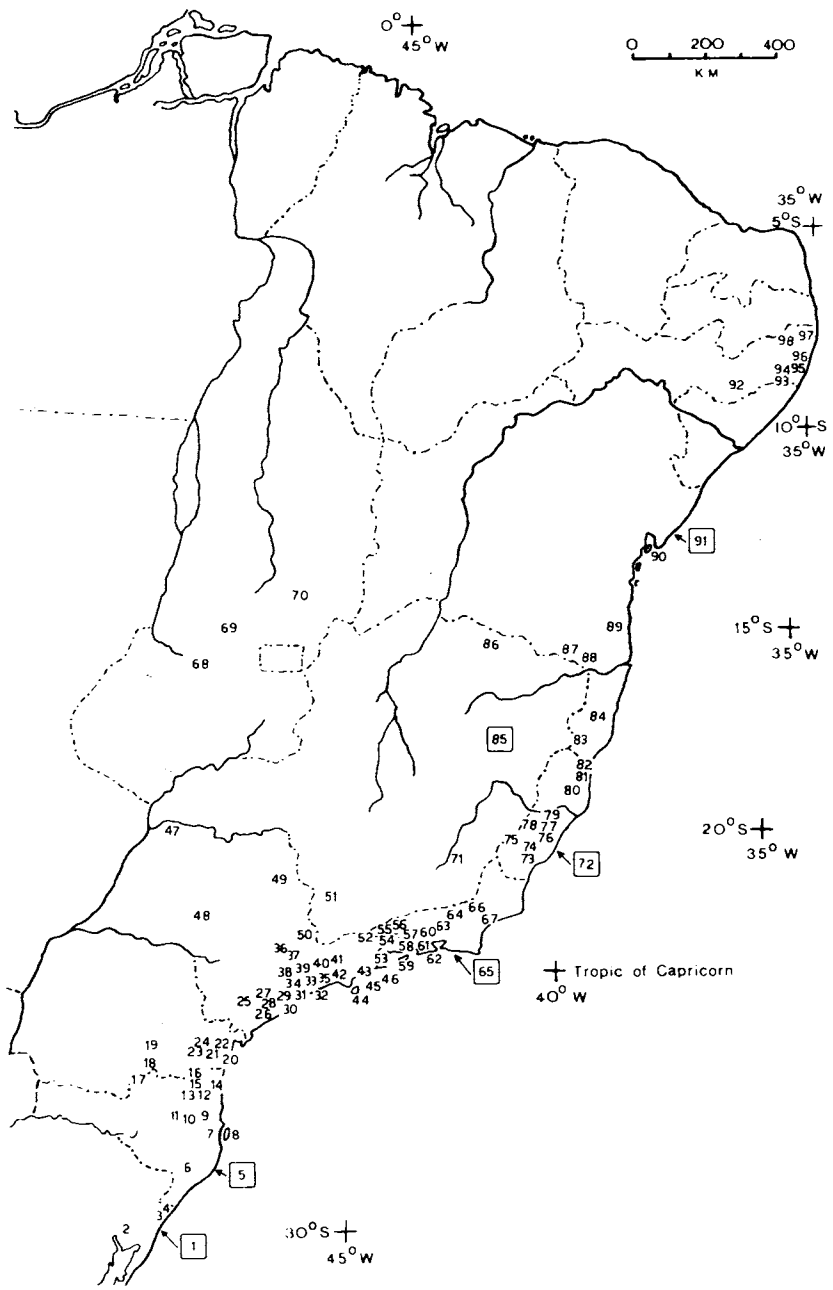


Figure 1. Localities from which *Enyalius* (except *E. bilineatus*) were examined. Text lists place names. Samples that could be located only by state are enclosed in a square.

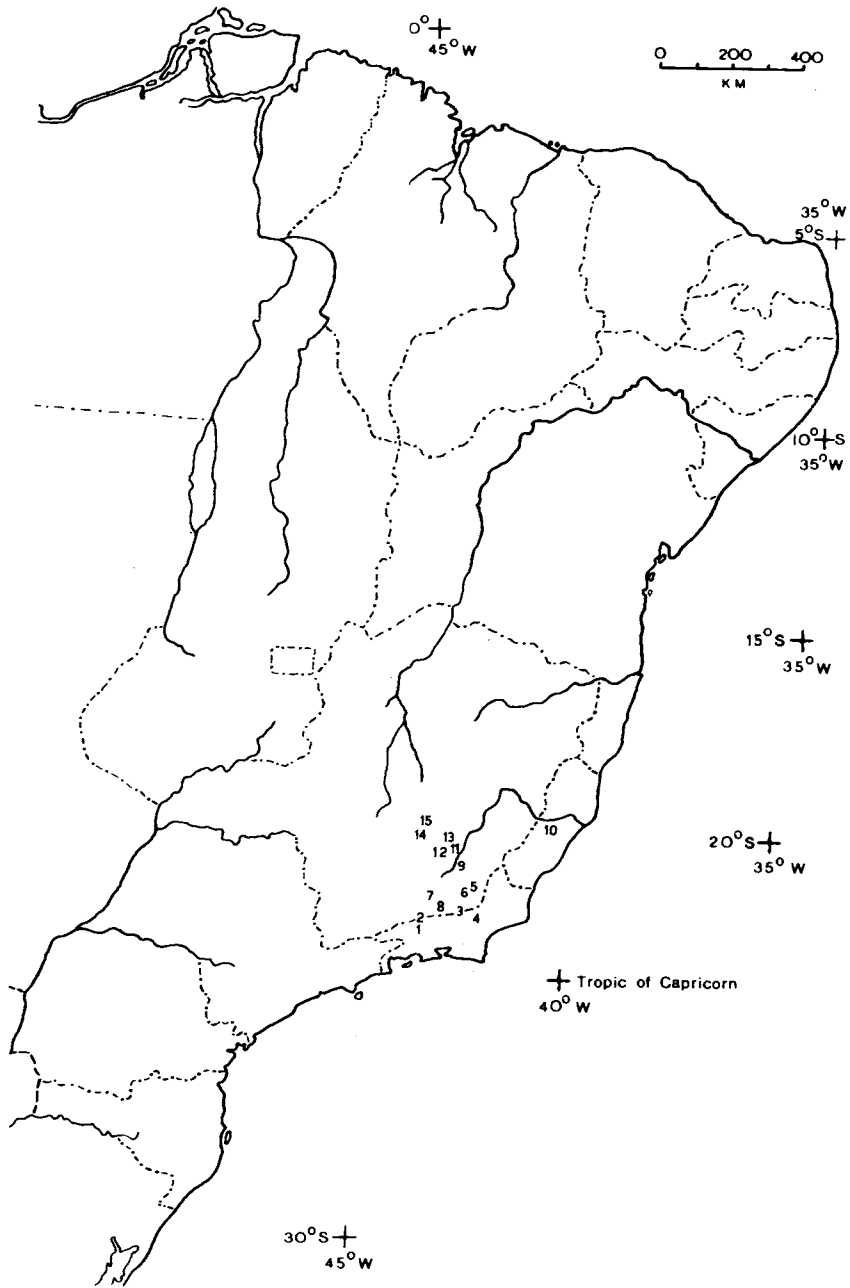


Figure 2. Localities from which *Enyalius bilineatus* were examined.

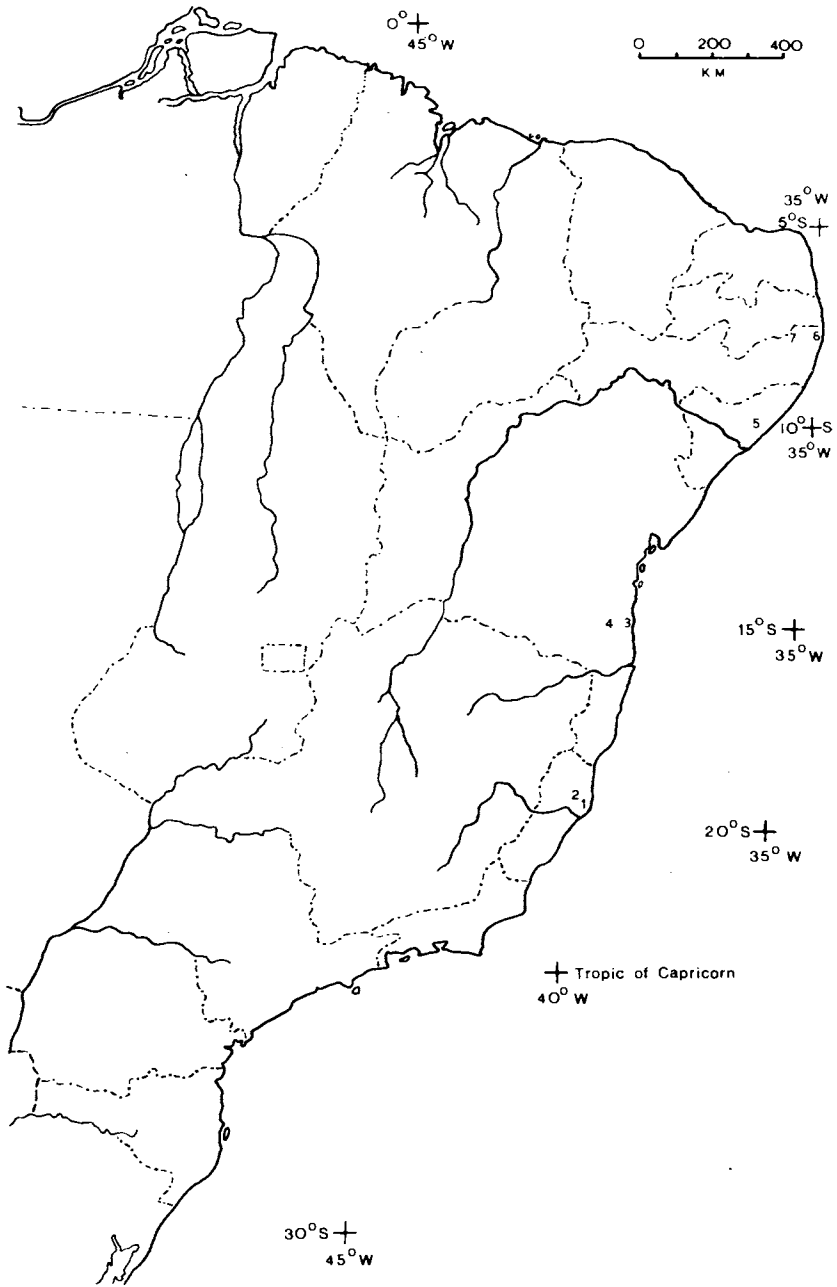


Figure 3. Localities from which *Strobilurus torquatus* were examined.

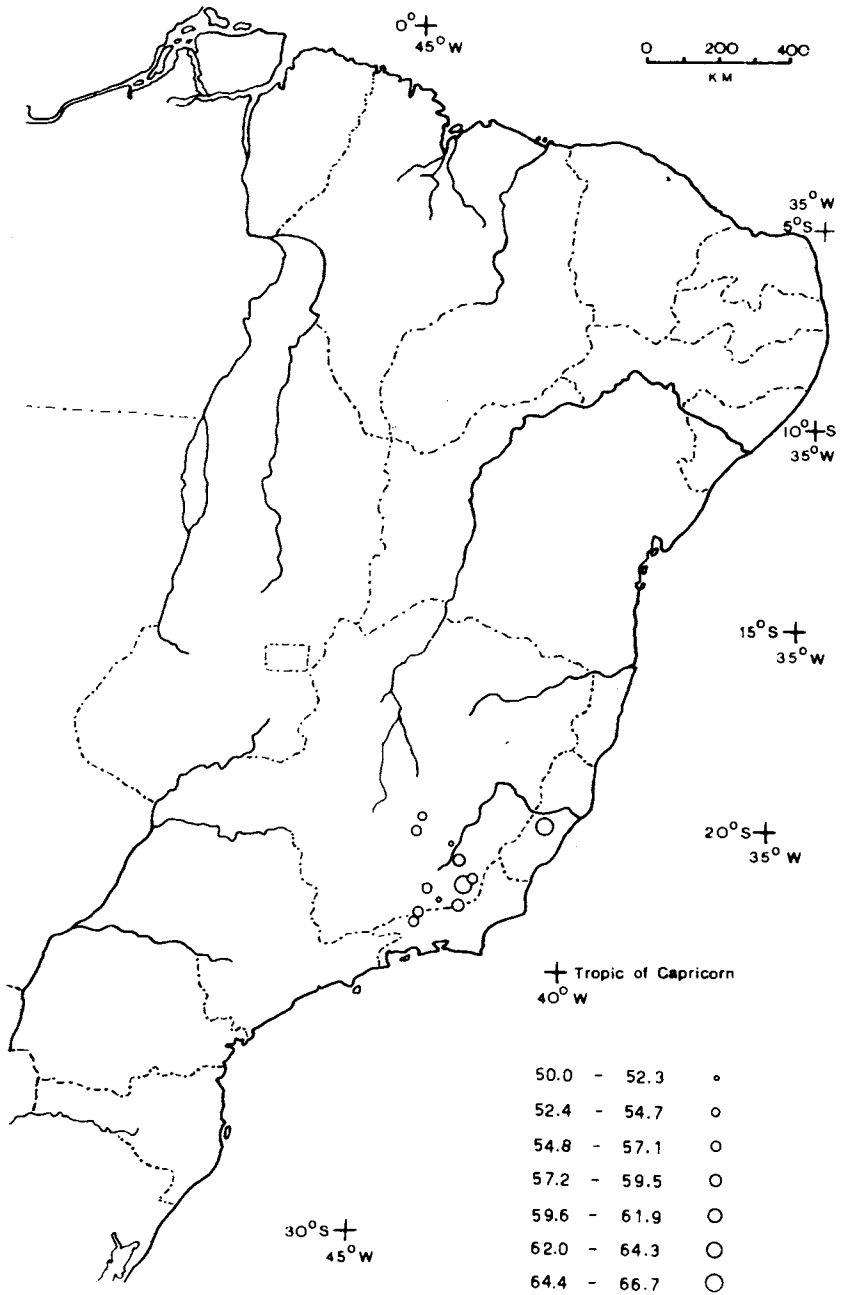


Figure 4. Geographic variation in number of enlarged vertebral scales in *E. bilineatus*.

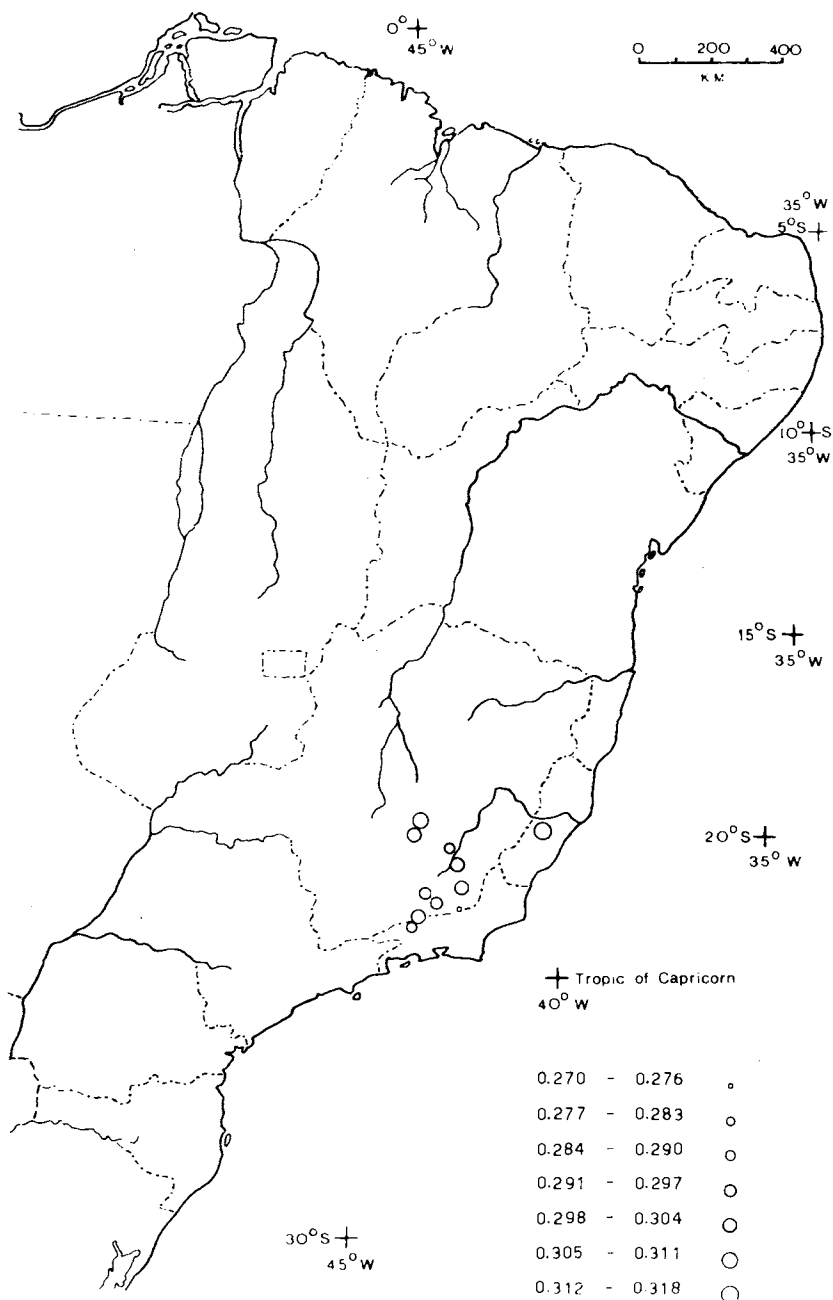


Figure 5. Geographic variation in thigh length/body length in *E. bilineatus*.

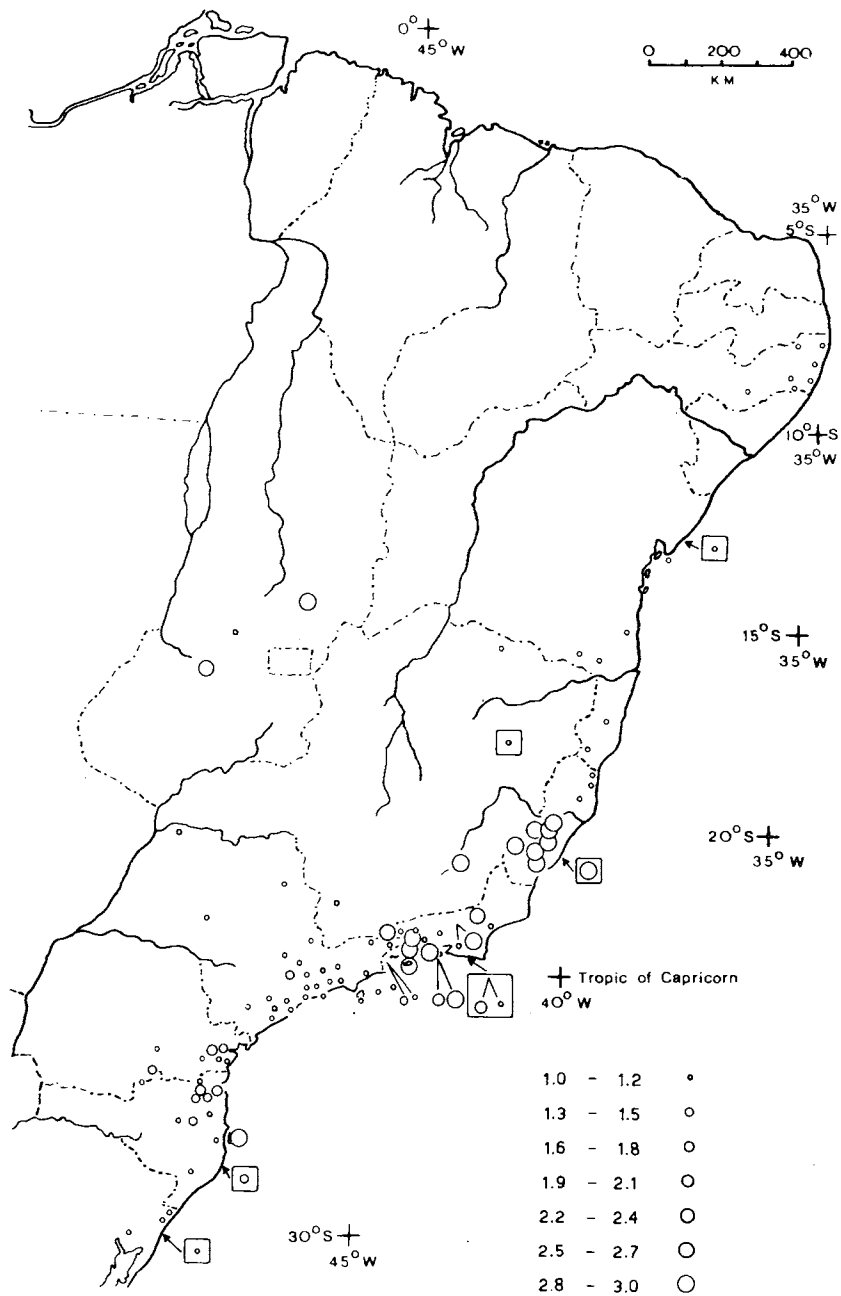


Figure 6. Geographic variation in degree of keeling of subdigital lamellae in *Enyalius* (except *E. bilineatus*).

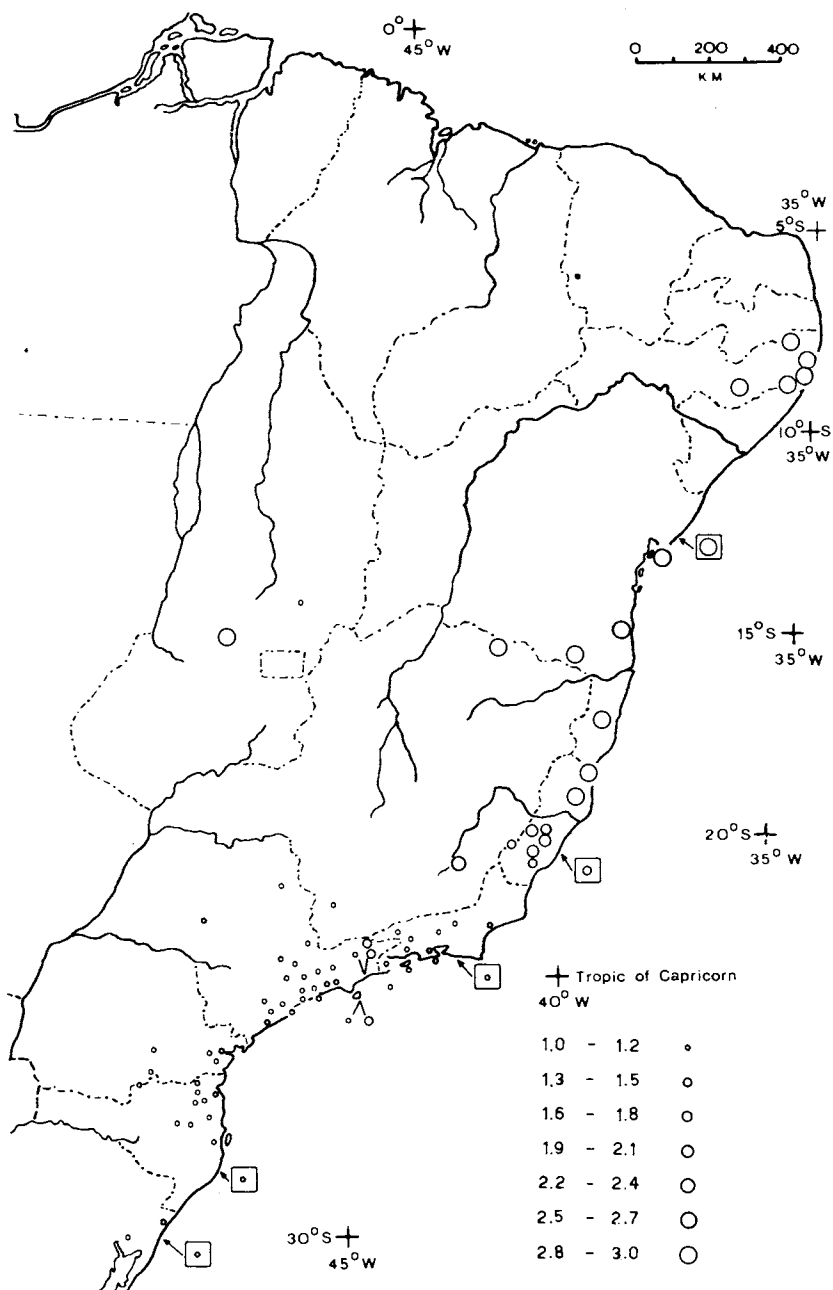


Figure 7. Geographic variation in degree of curvature of canthal ridge in female *Enyalius* (except *E. bilineatus*).

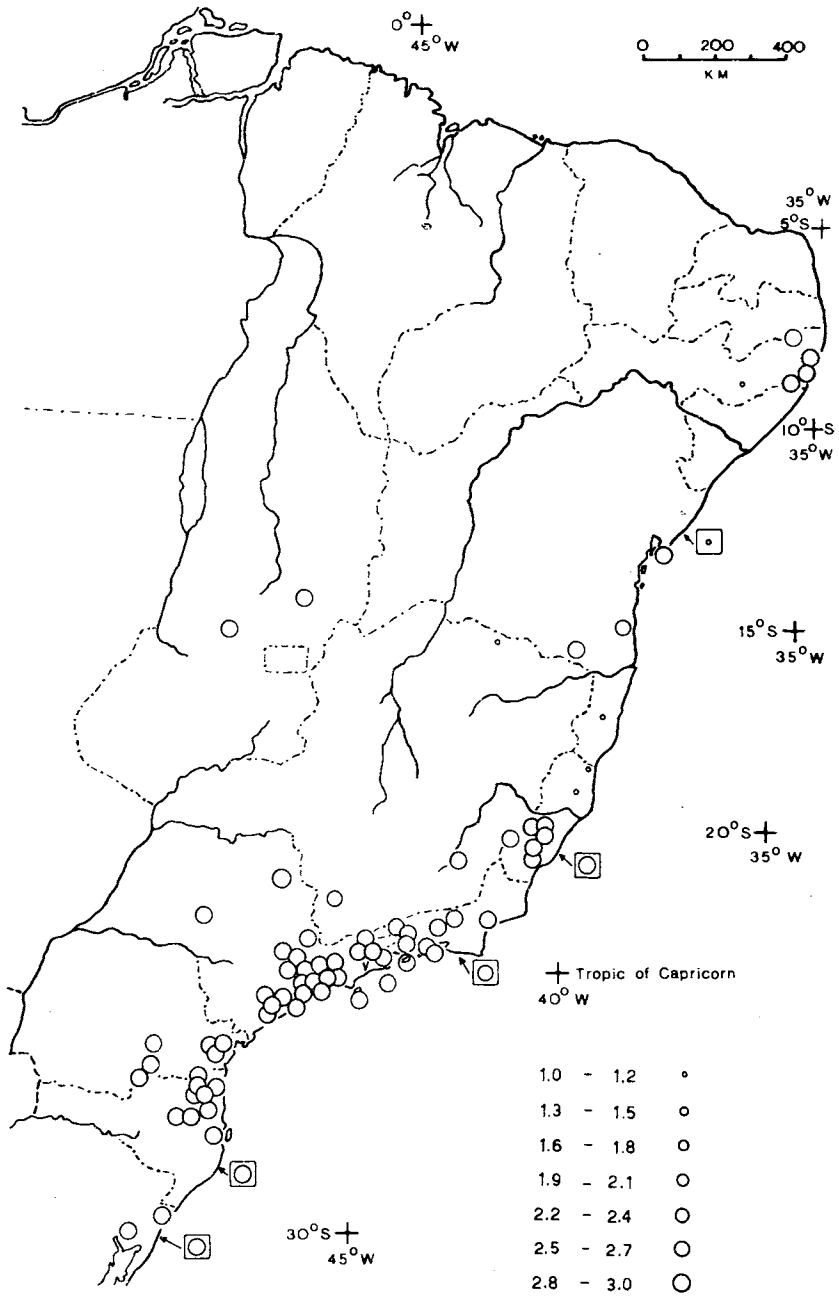


Figure 8. Geographic variation in degree of keeling of ventral scales in female *Erythrinus* (except *E. bilineatus*).

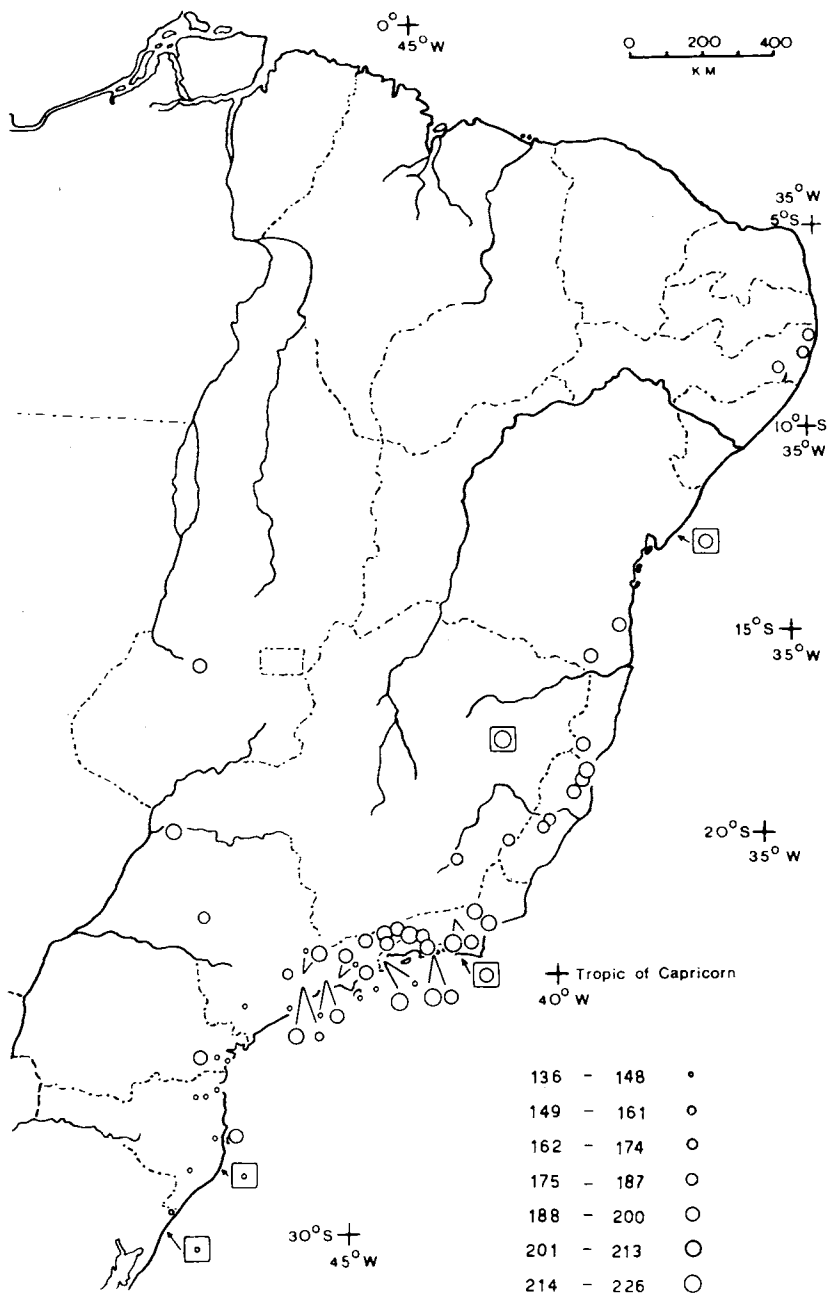


Figure 9. Geographic variation in number of paravertebral scales in male *Enyalius* (except *E. bilineatus*).

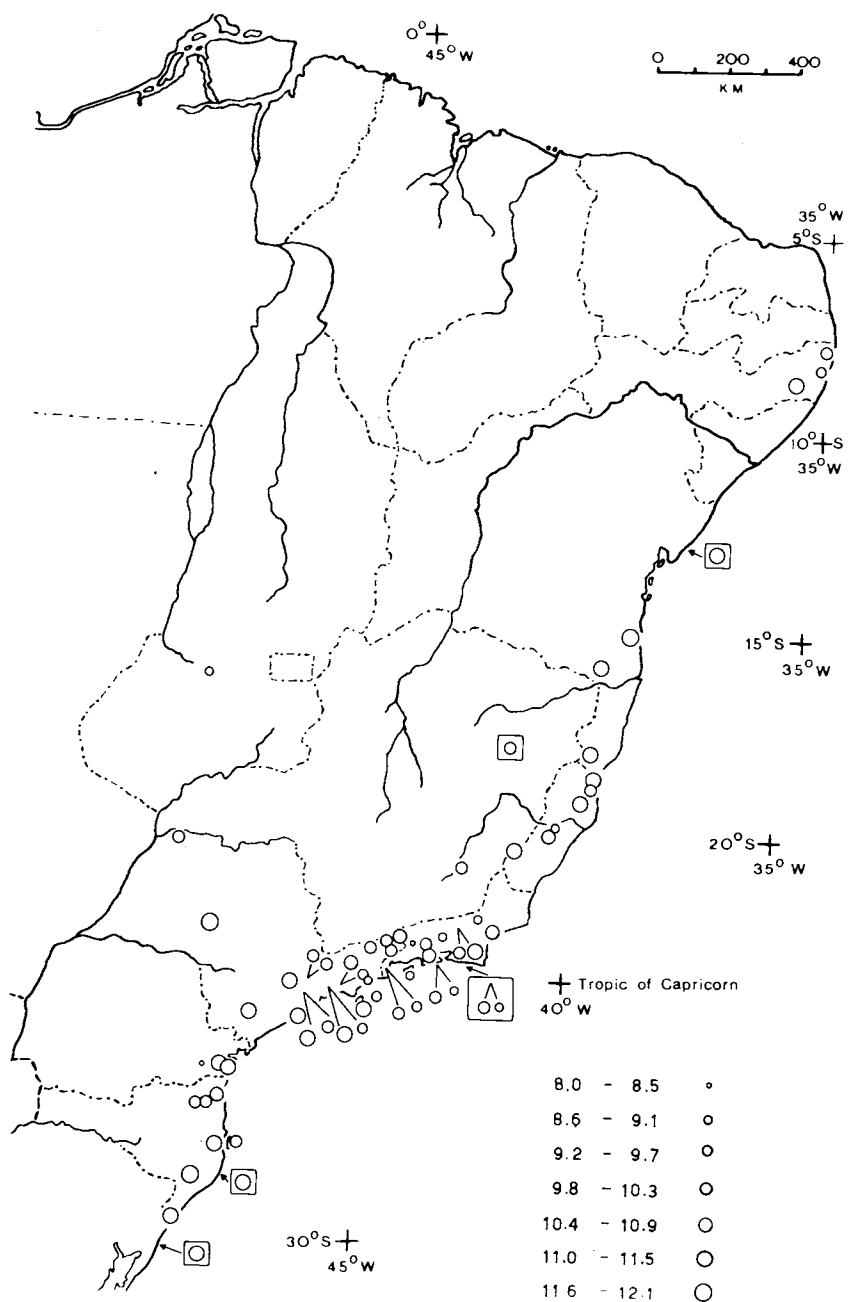


Figure 10. Geographic variation in number of enlarged upper labials in male *Enyalius* (except *E. bilineatus*).

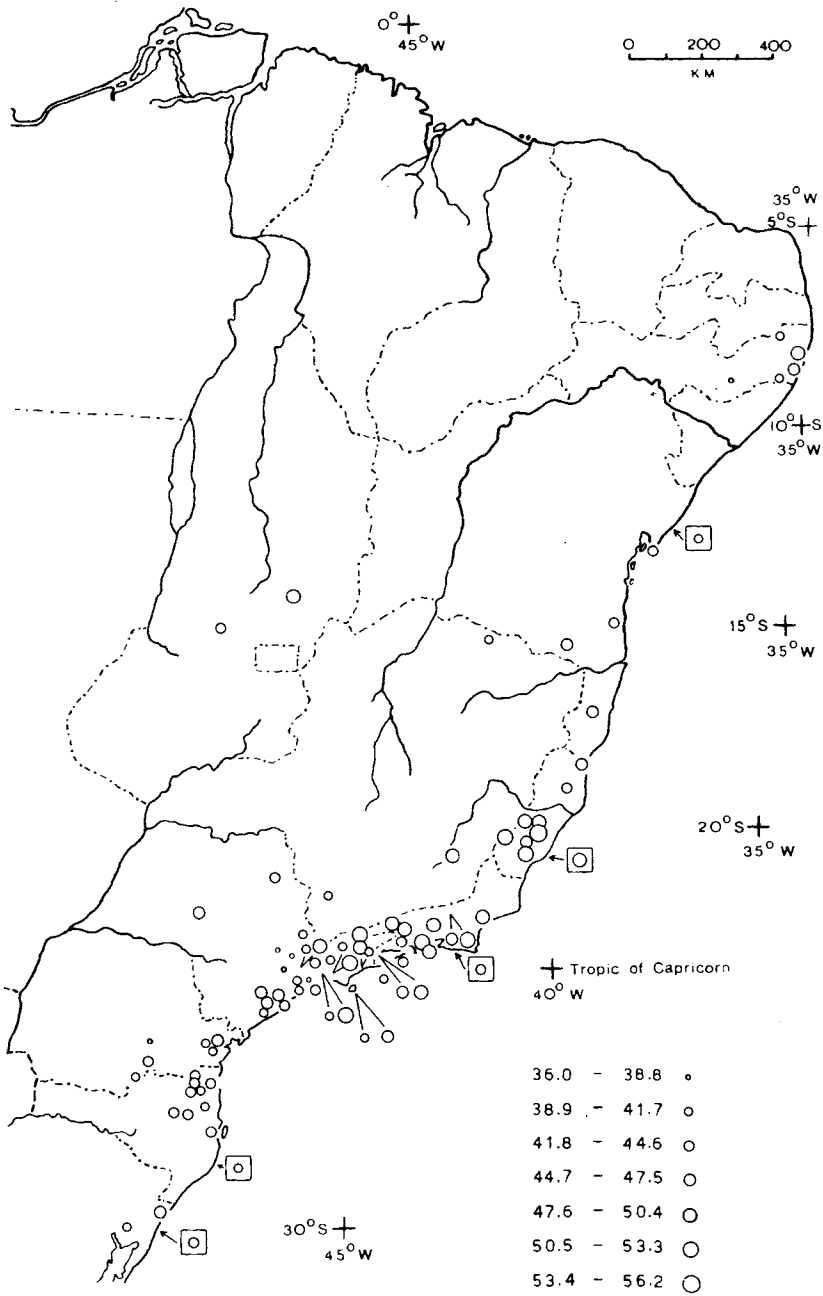


Figure 11. Geographic variation in number of gular scales in female *Enyalius* (except *E. bilineatus*).

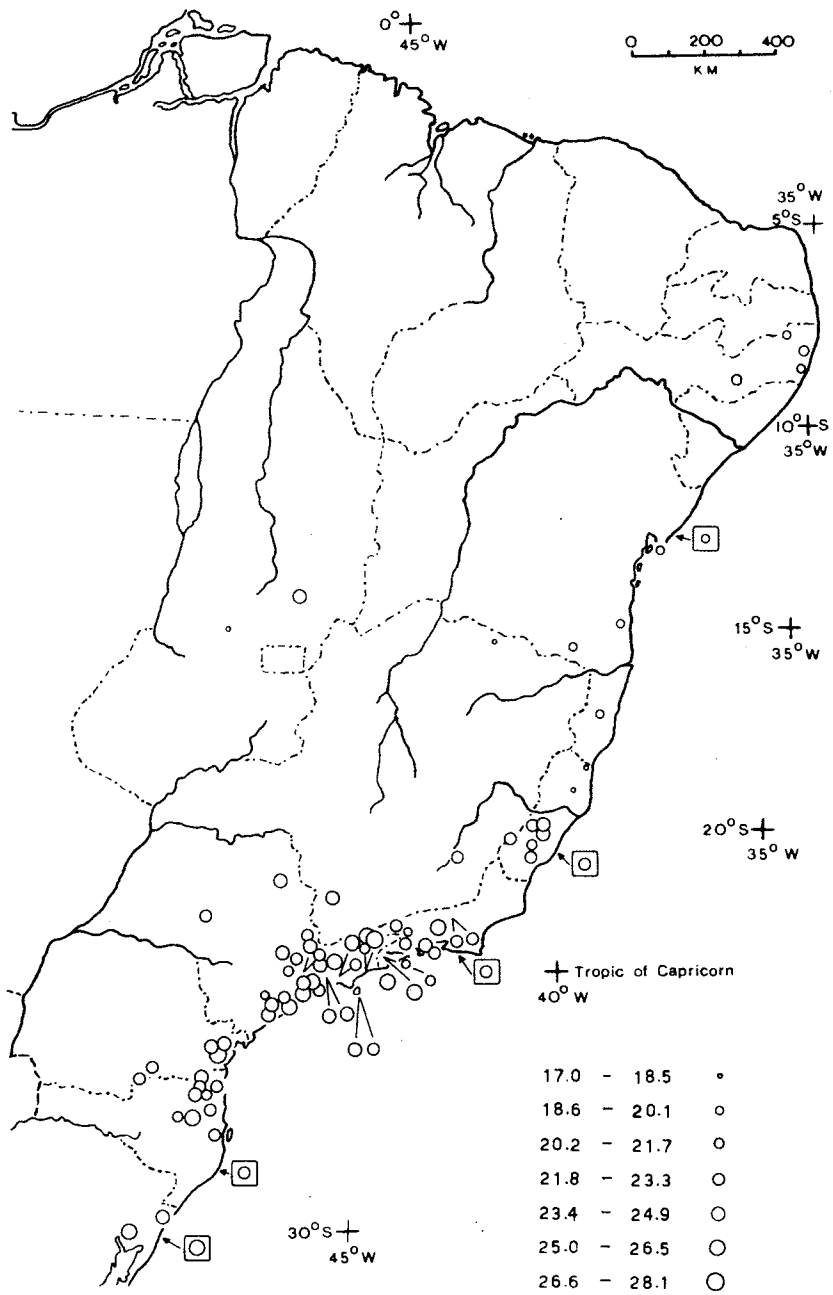


Figure 12. Geographic variation in number of subdigital lamellae on fourth front toe in female *Enyalius* (except *E. bilineatus*).

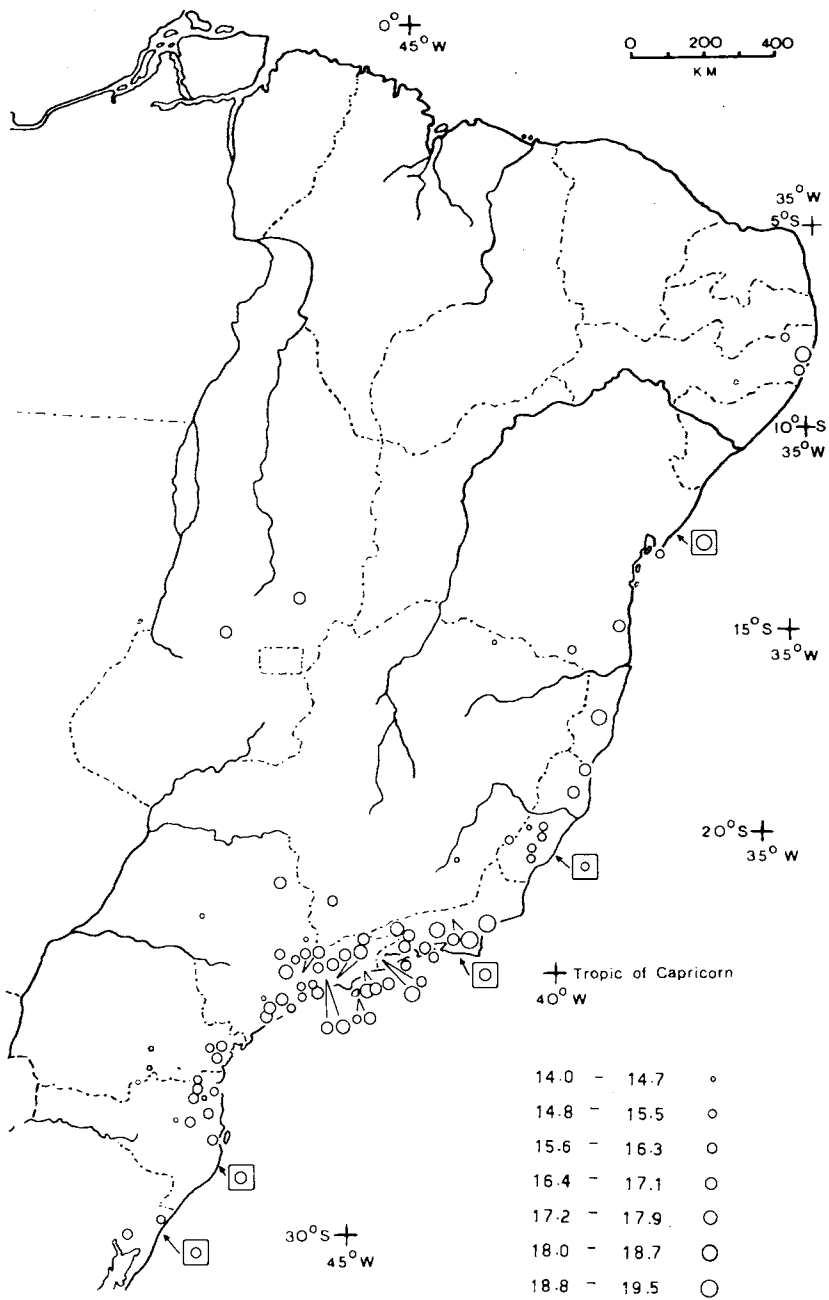


Figure 13. Geographic variation in number of dorsal scales on three caudal segments in female *Enyalius* (except *E. bilineatus*).

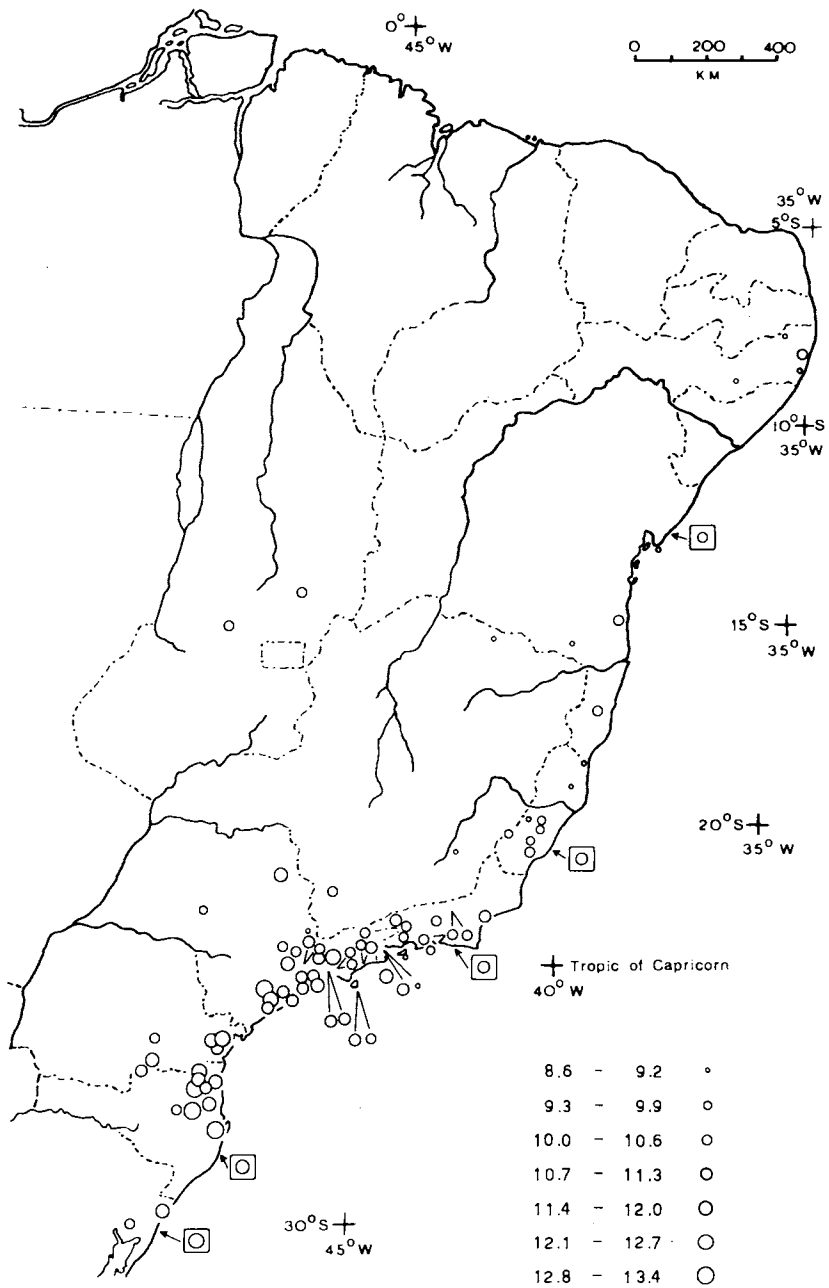


Figure 14. Geographic variation in number of ventral scales on three caudal segments in female *Enyalius* (except *E. bilineatus*).

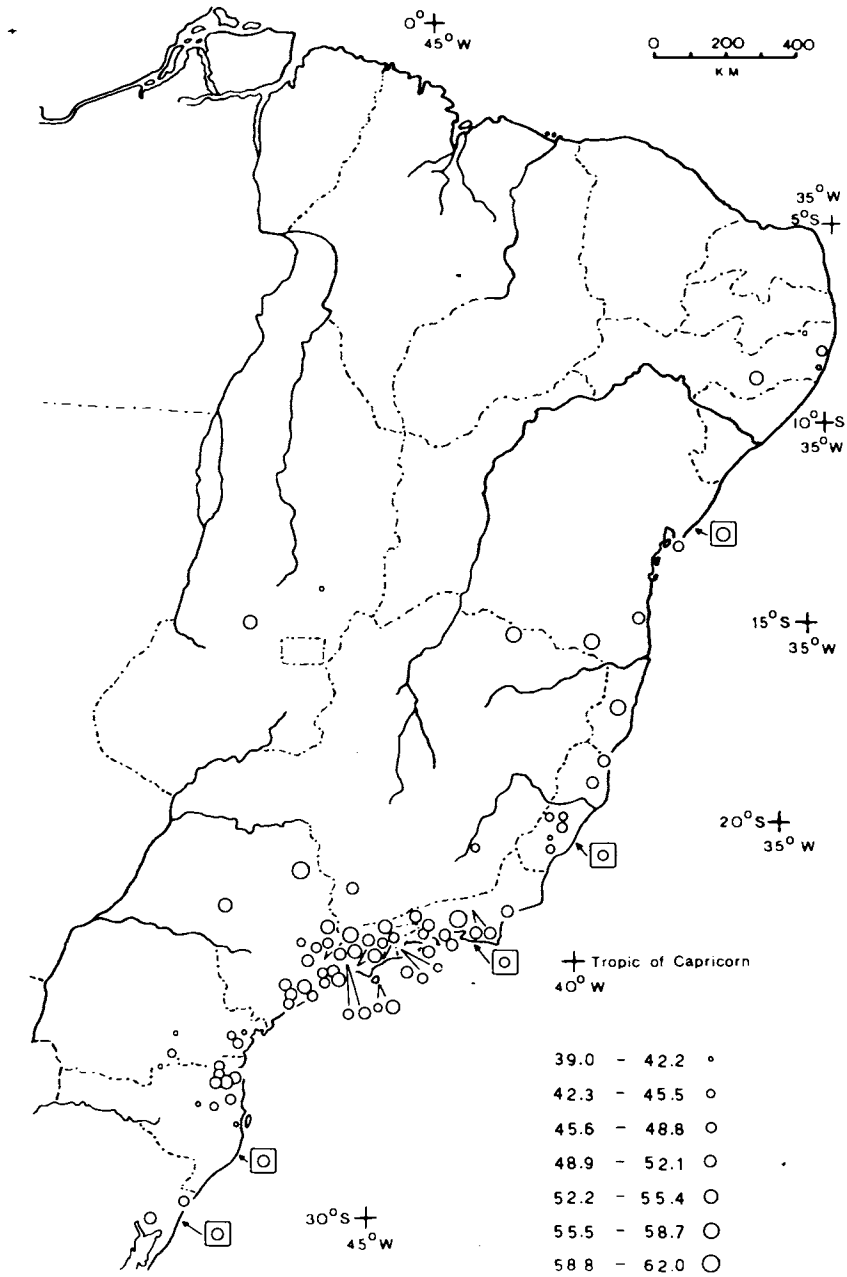


Figure 15. Geographic variation in number of scales on halves of two caudal segments in female *Enyalius* (except *E. bilineatus*).

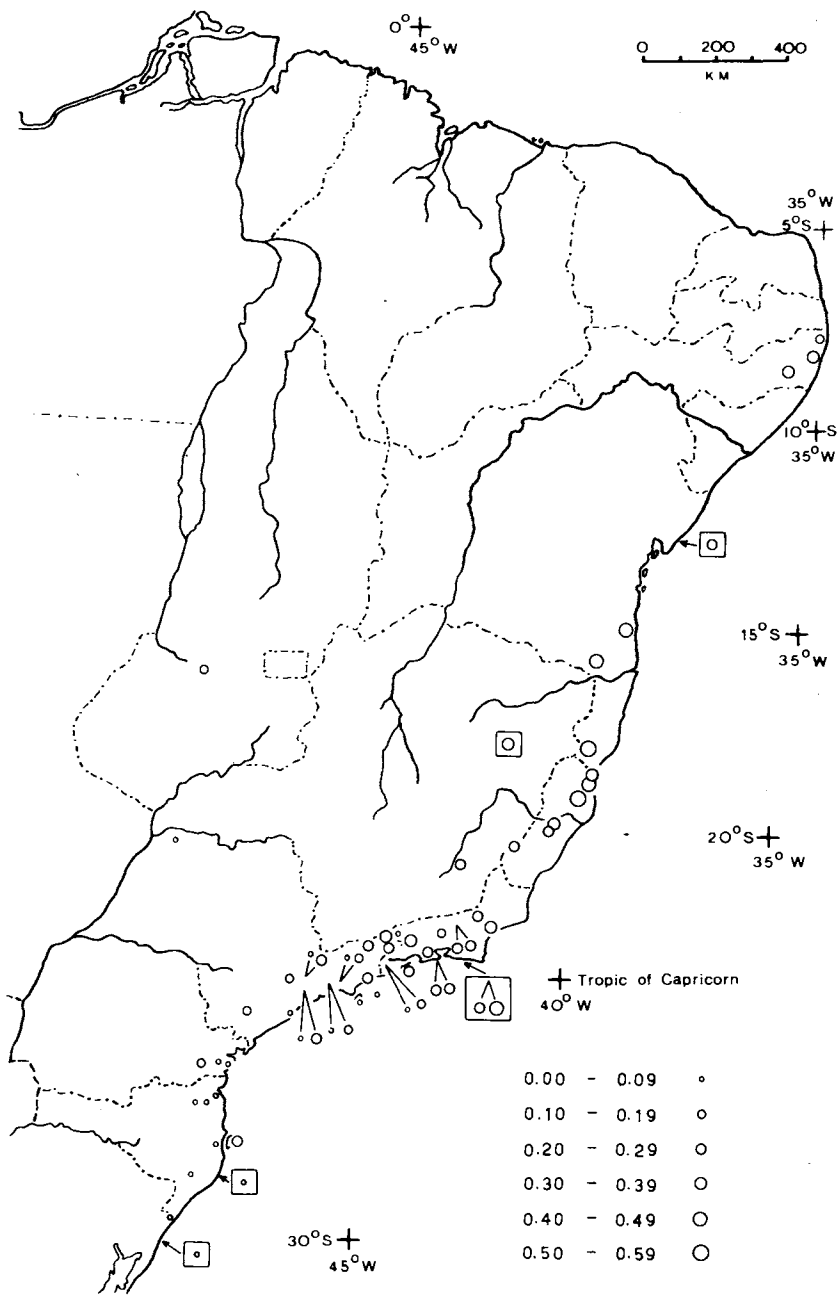


Figure 16. Geographic variation in percent of aligned sextets among caudal scales in male *Enyalius* (except *E. bilineatus*).

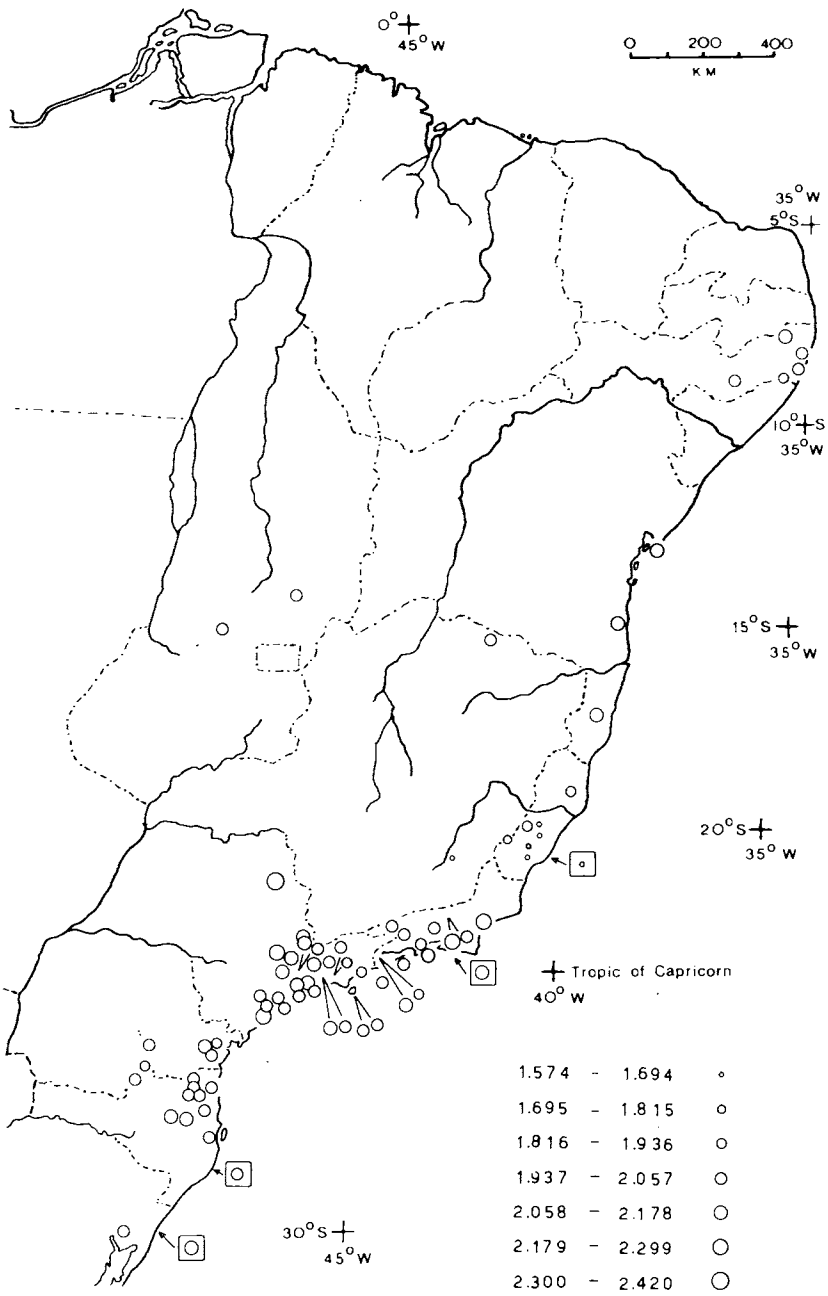


Figure 17. Geographic variation in tail length/body length in female *Enyalius* (except *E. bilineatus*).

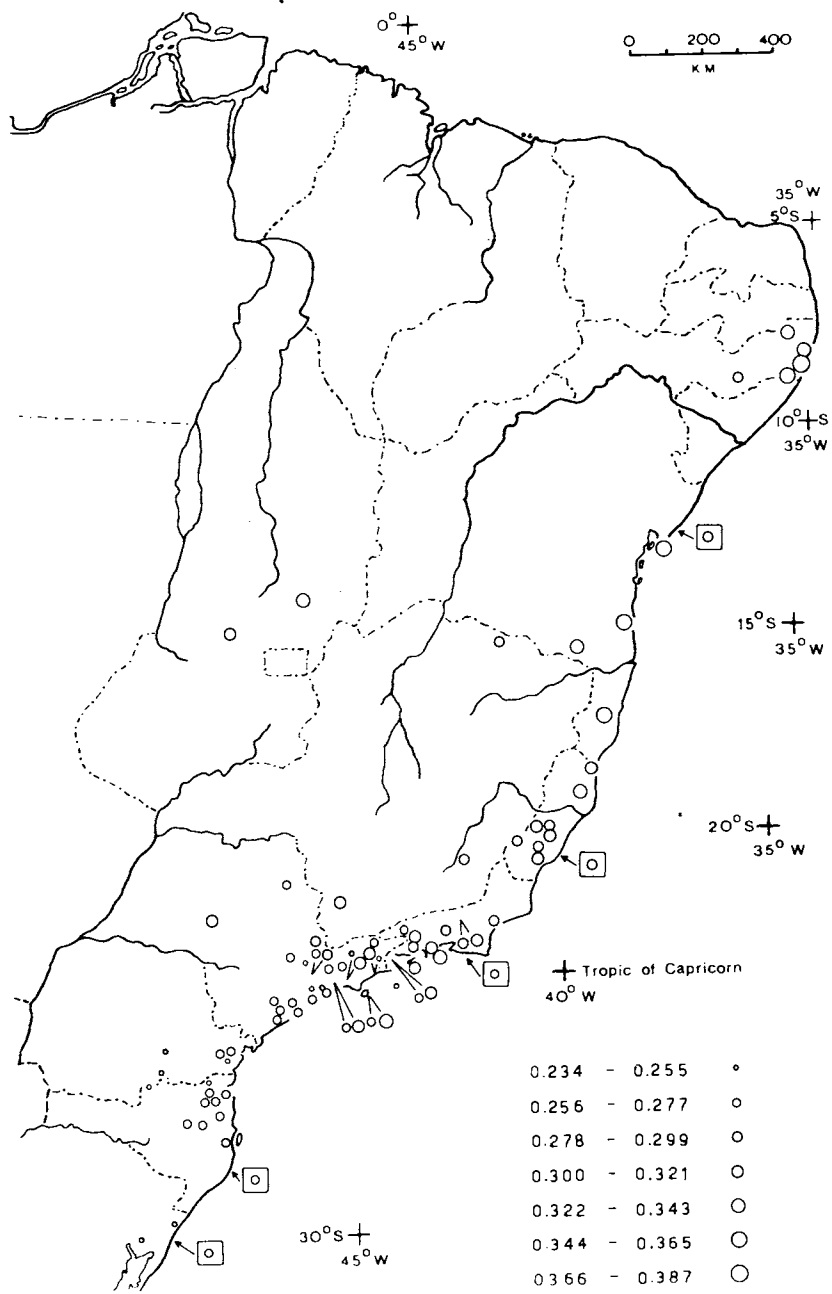


Figure 18. Geographic variation in shank length/body length in female *Enyalius* (except *E. bilineatus*).

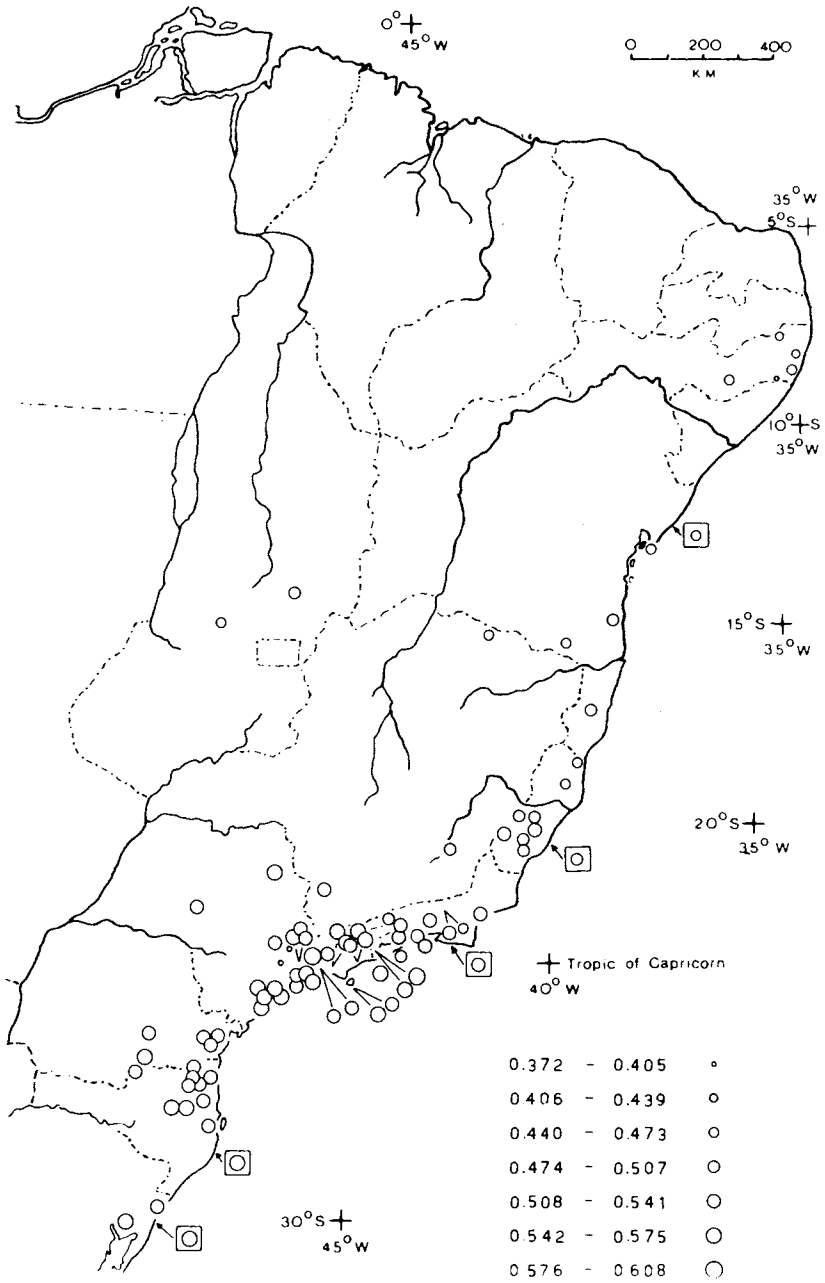


Figure 19. Geographic variation in rostral-nasal distance/rostral-orbit distance in female *Enyalius* (except *E. bilineatus*).

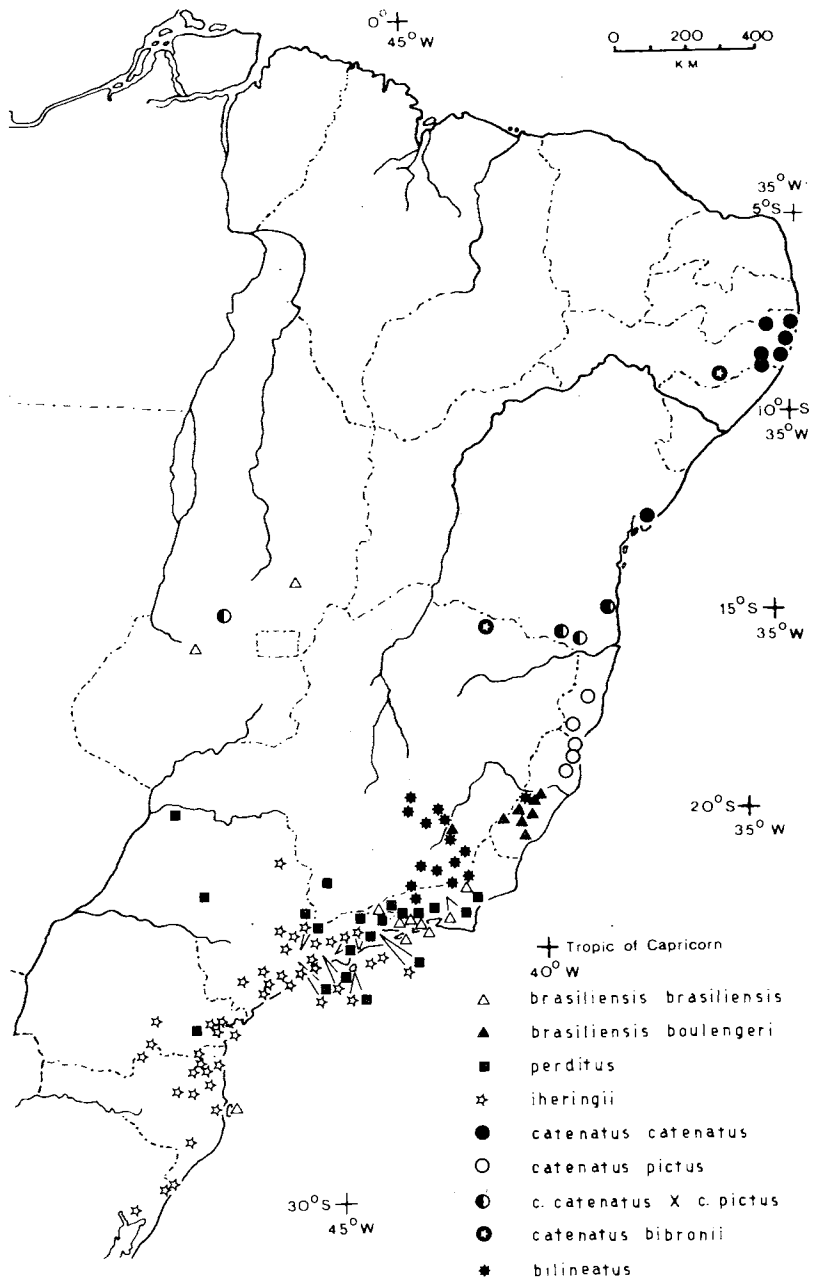


Figure 20. Distribution of *Enyalius* taxa in eastern South America.

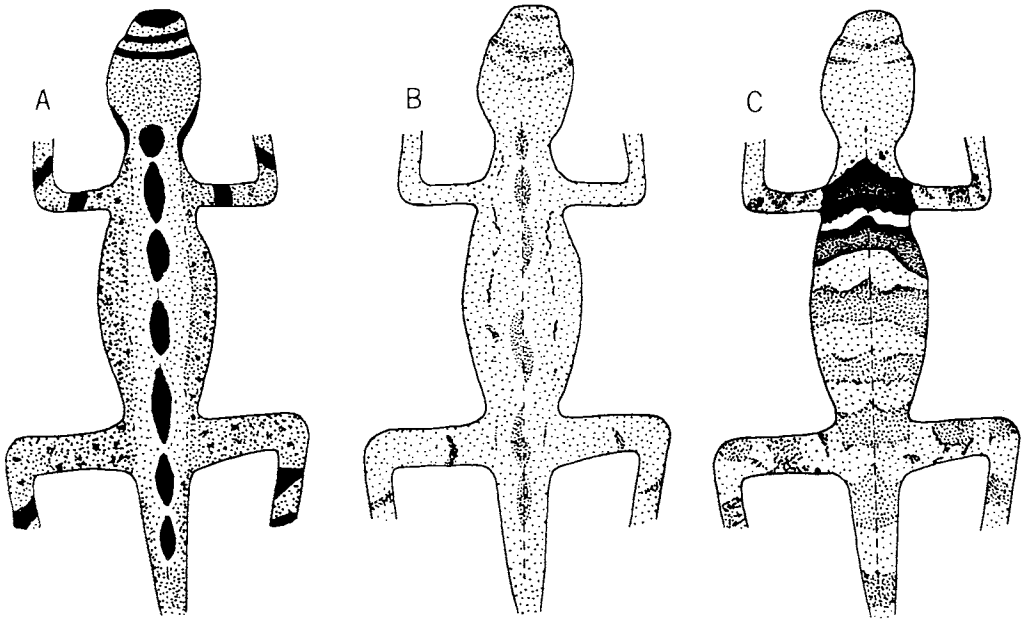


Figure 21. Dorsal patterns of A) female *E. c. catenatus* MRCN 4727, B) female *E. c. pictus* MZUSP 39539, C) male *E. c. pictus*.

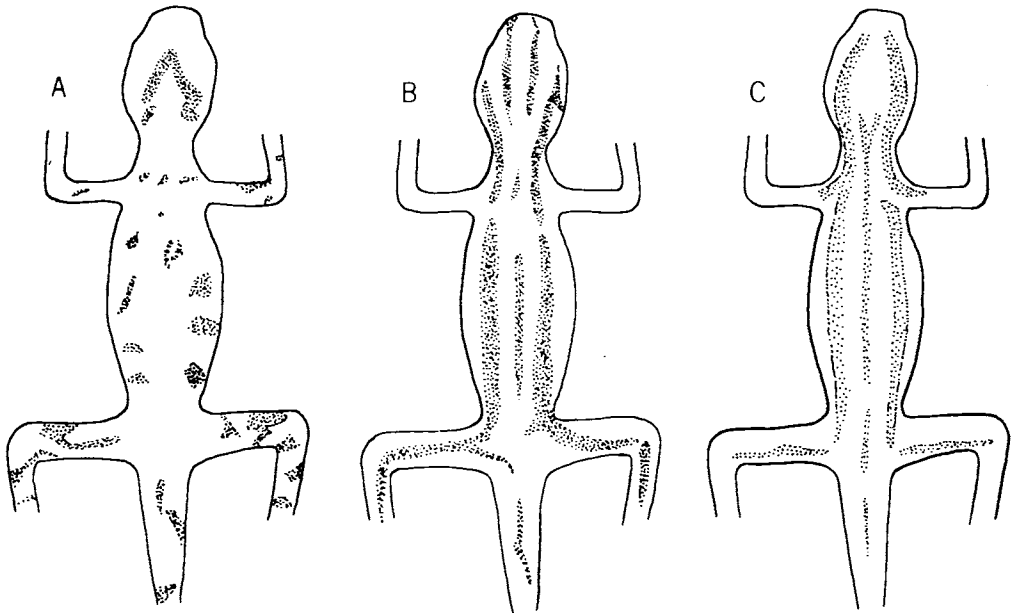


Figure 22. Ventral patterns of A) female *E.c. pictus* MZUSP 30748, B) female *E.c. bibronii* MRCN 4728, C) male *E. bilineatus* MZUSP 39525.

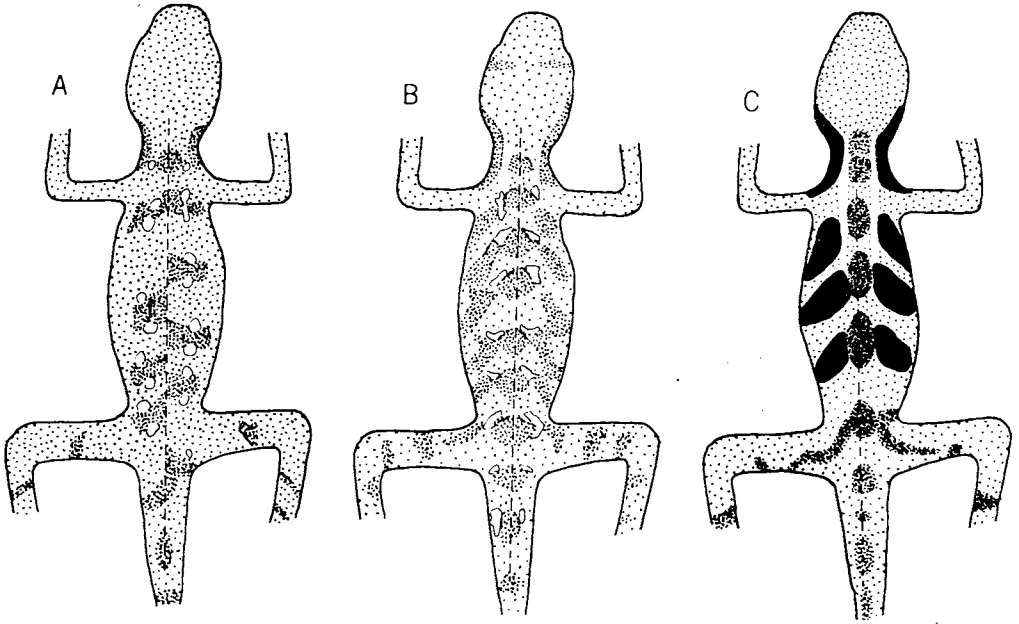


Figure 23. Dorsal patterns of A) female *E. c. hibronii* BM 1869. 11.3.8, B) female *E. bilineatus* ZMC R37701, C) male *E. bilineatus* MZUSP 39525.

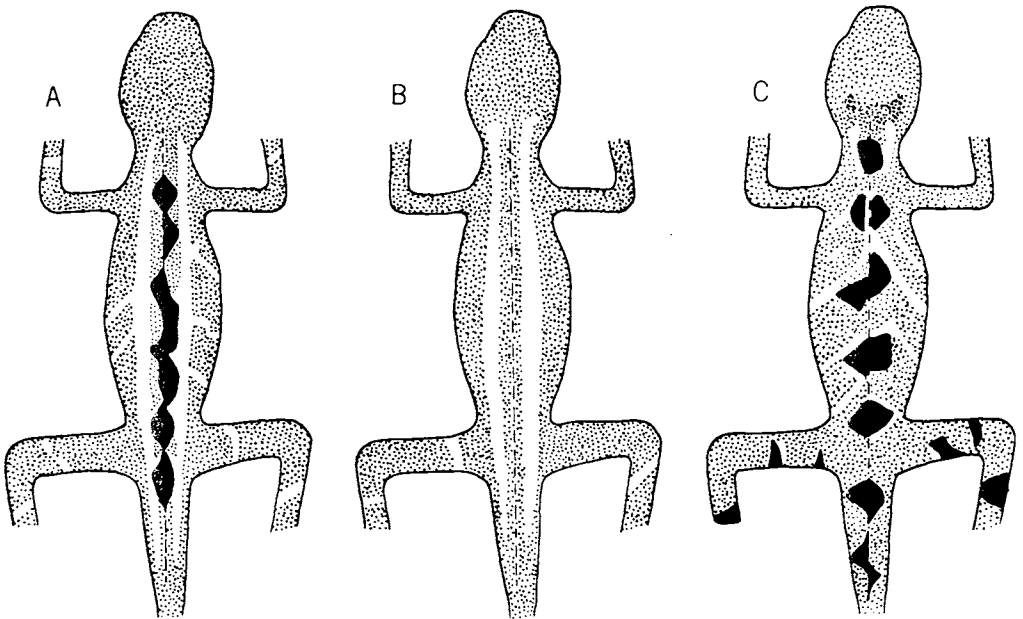


Figure 24. Dorsal patterns of female *E. iheringii* A) NMW 12967, B) MZUSP 40759, C) NMW 12961(5).

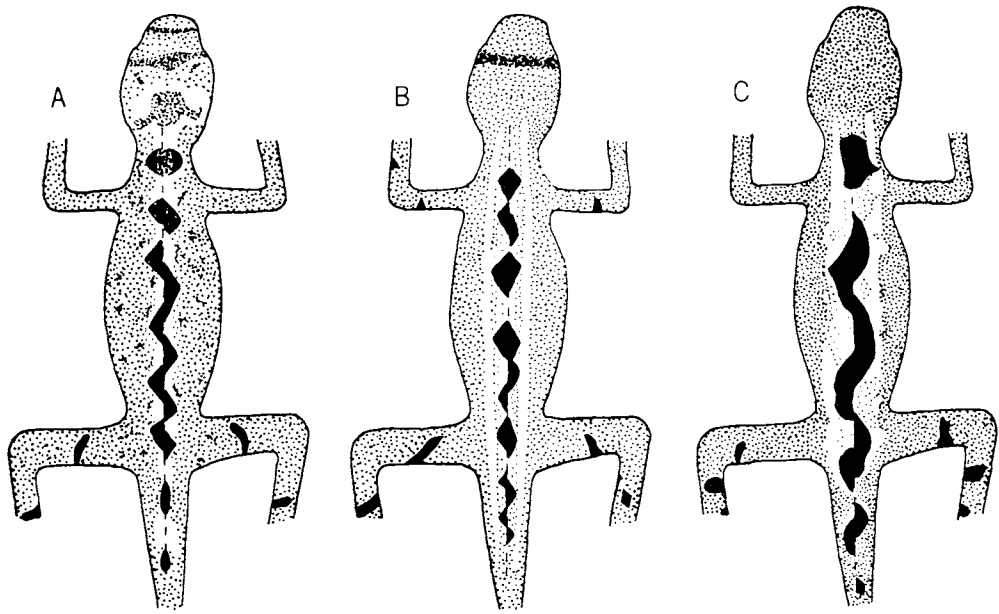


Figure 25. Dorsal patterns of A) female *E. perditus* MZUSP 11464 B) female *E. b. brasiliensis* MZUSP 10247, C) female *E. b. boulengeri* MZUSP 39537.

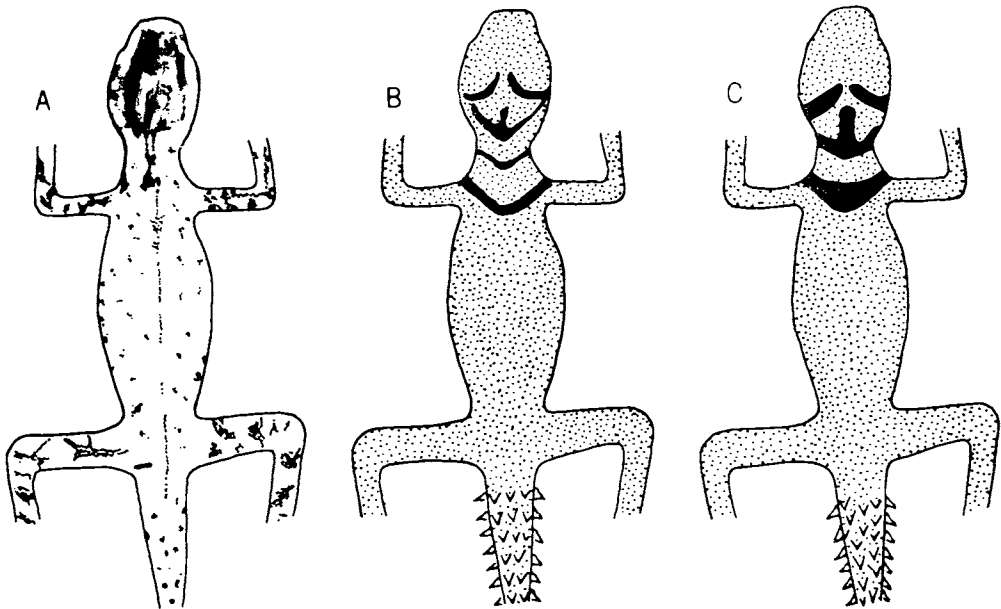


Figure 26. A) ventral pattern of female *E. perditus* MZUSP 11464, B) dorsal pattern of southern male *Strobilurus torquatus* MZUSP 39581, C) dorsal pattern of northern male *Strobilurus torquatus* MZUSP 23081.

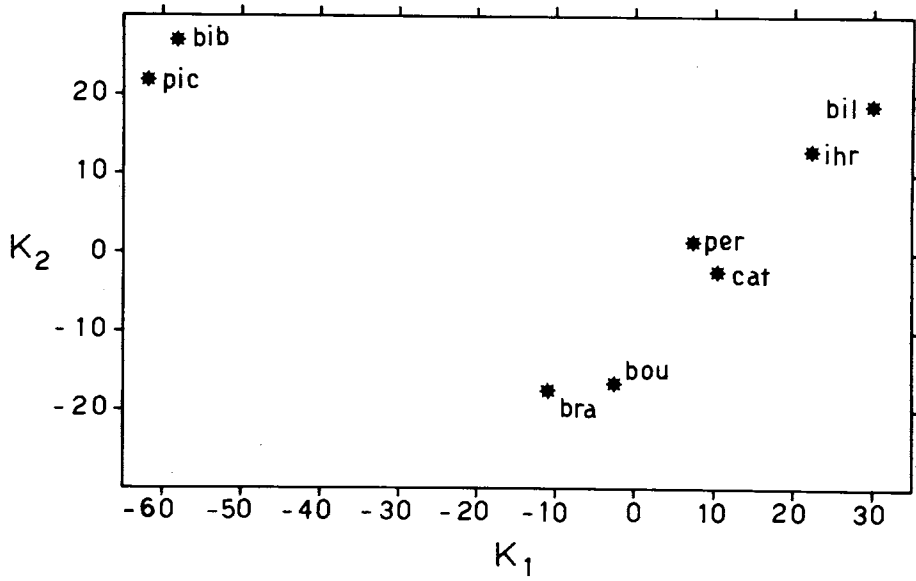


Figure 27. Means for *Enyalius* taxa plotted on the first two multiple discriminant axes generated from the meristic-morphometric data set.

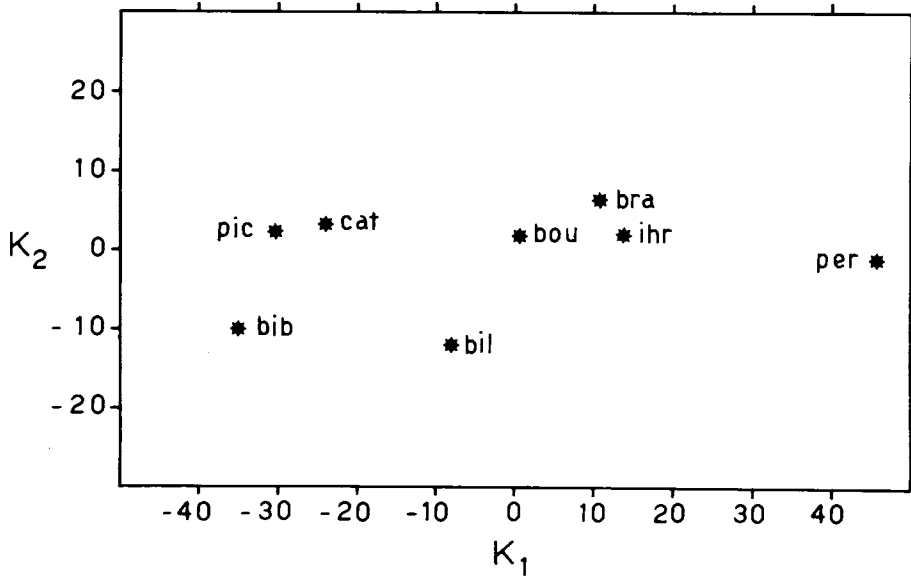


Figure 28. Means for *Enyalius* taxa plotted on the first two multiple discriminant axes generated from the cranial data set.

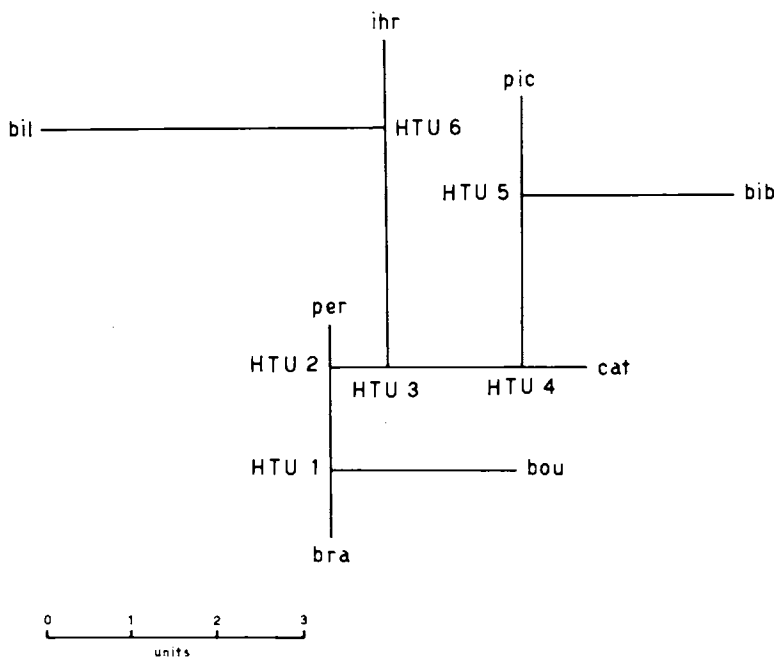


Figure 29. Wagner Tree depicting the hypothetical phylogeny of *Enyalius* in eastern South America based on the meristic-morphometric data set.

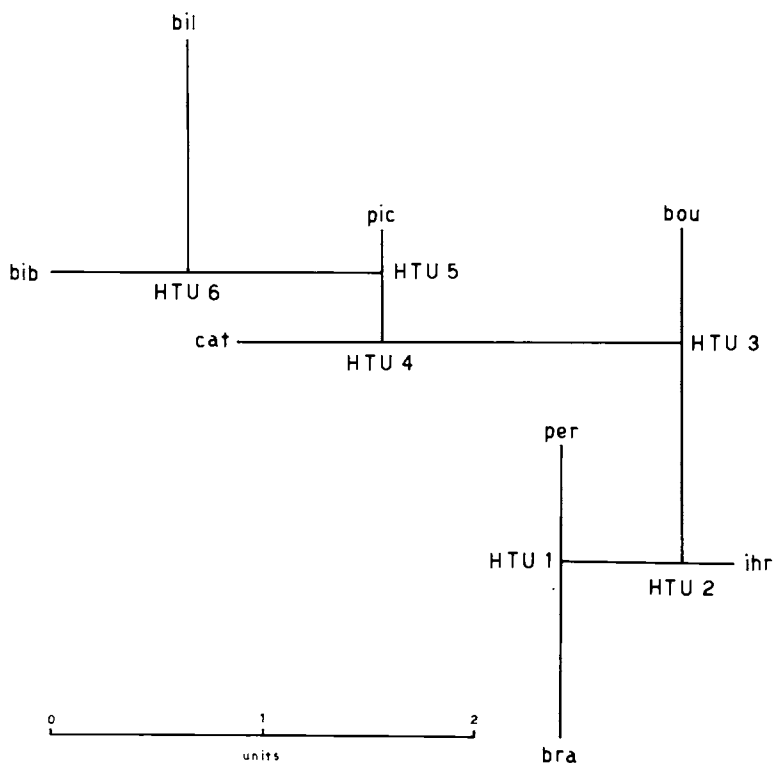


Figure 30. Wagner Tree depicting the hypothetical phylogeny of *Enyalius* in eastern South America based on the cranial data set.

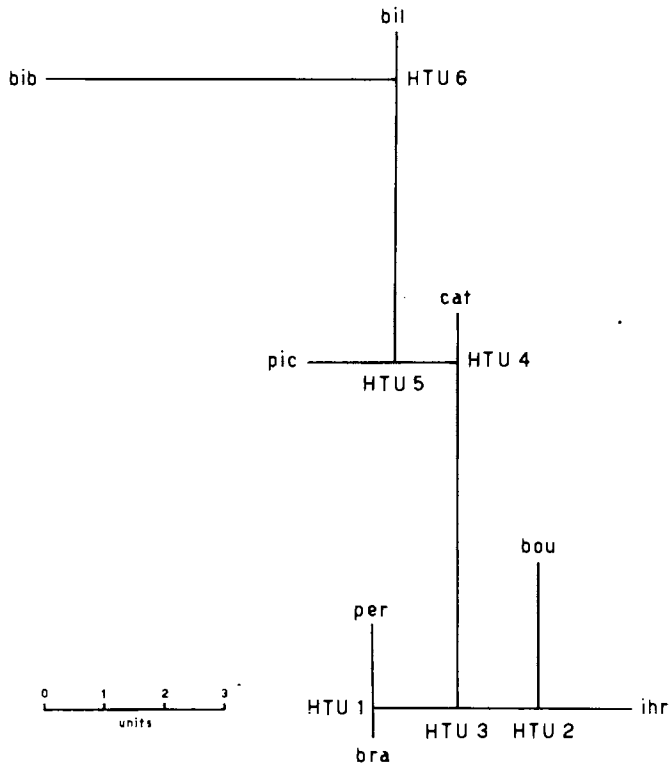


Figure 31. Wagner Tree depicting the hypothetical phylogeny of *Enyalius* in eastern South America based on the color pattern data set.

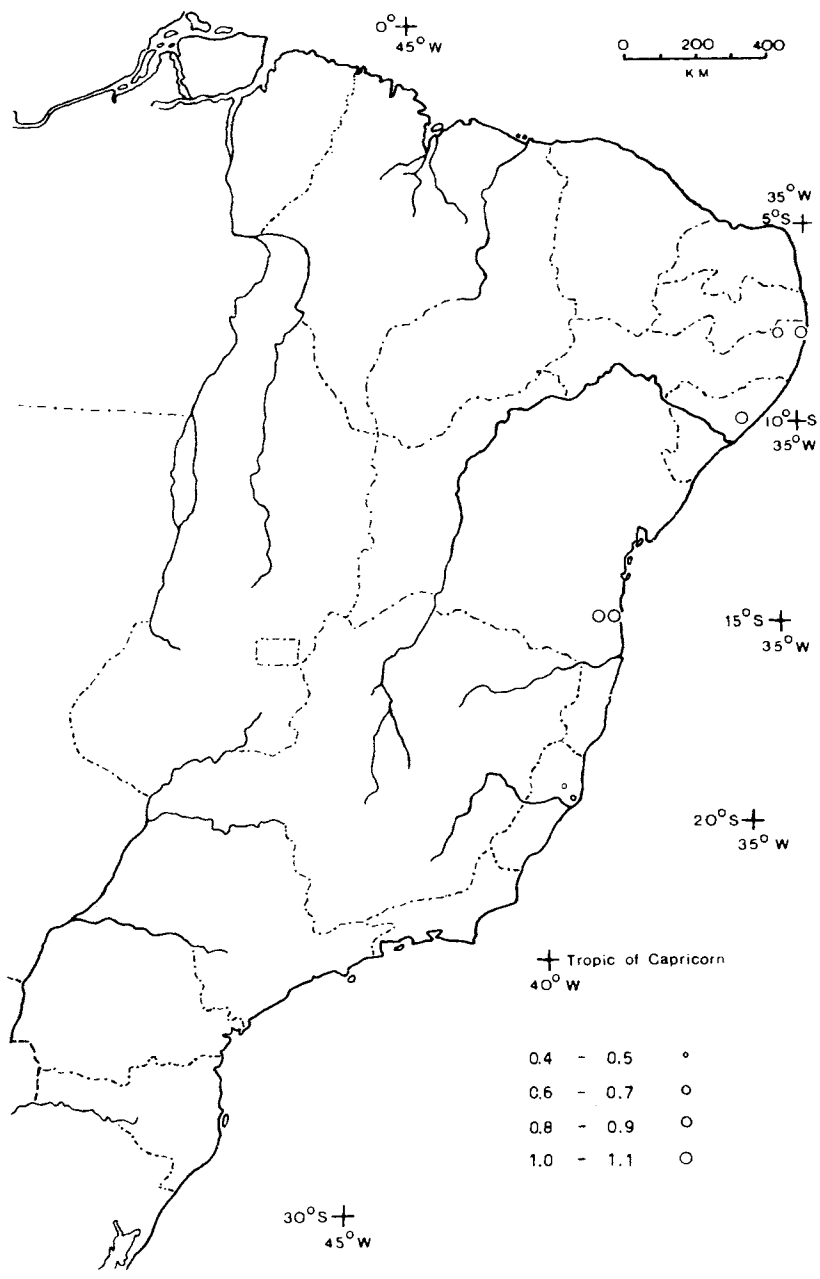


Figure 32. Geographic variation in presence of a median anterior extension on the second nuchal collar in *Strobilurus torquatus*.

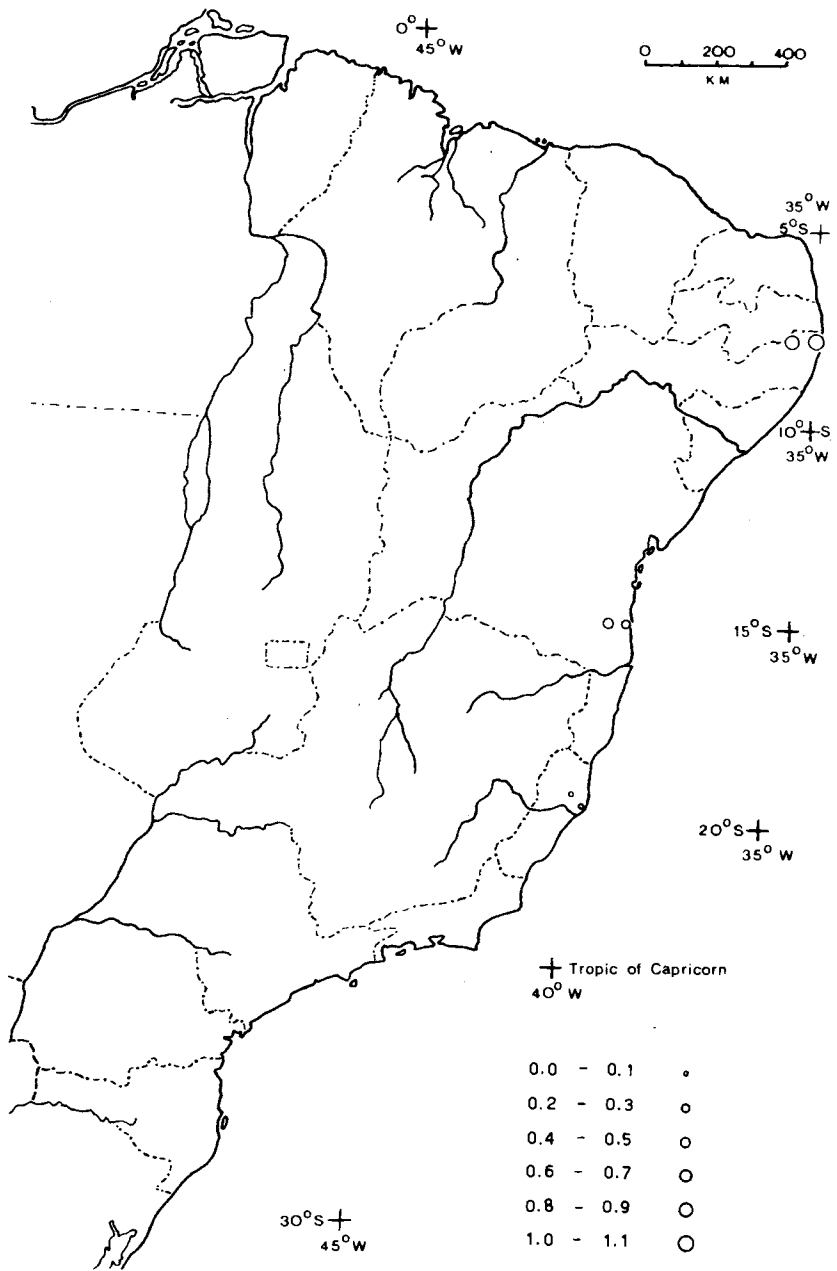


Figure 33. Geographic variation in presence of dark reticulation on throat in *Strobilurus torquatus*.

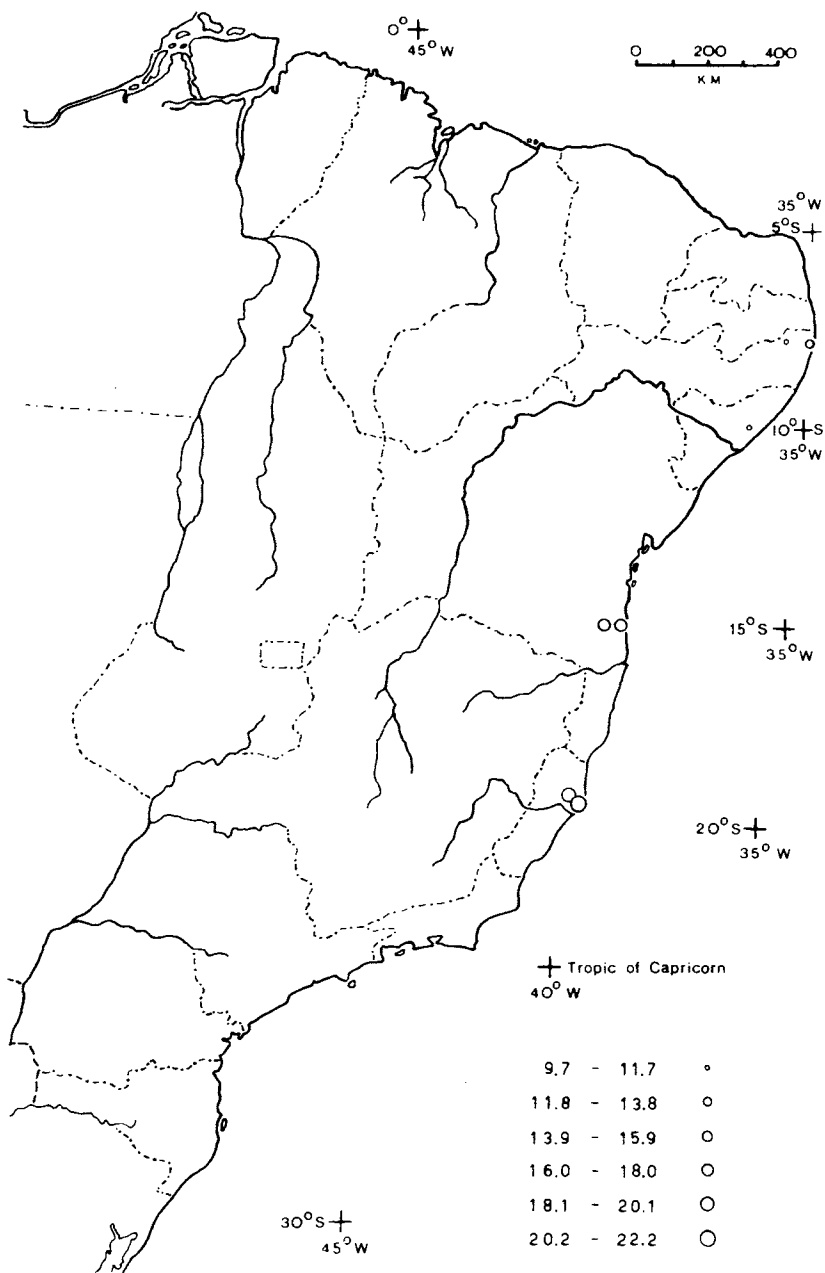


Figure 34. Geographic variation in number of scales in loreal region in *Strobilurus torquatus*.

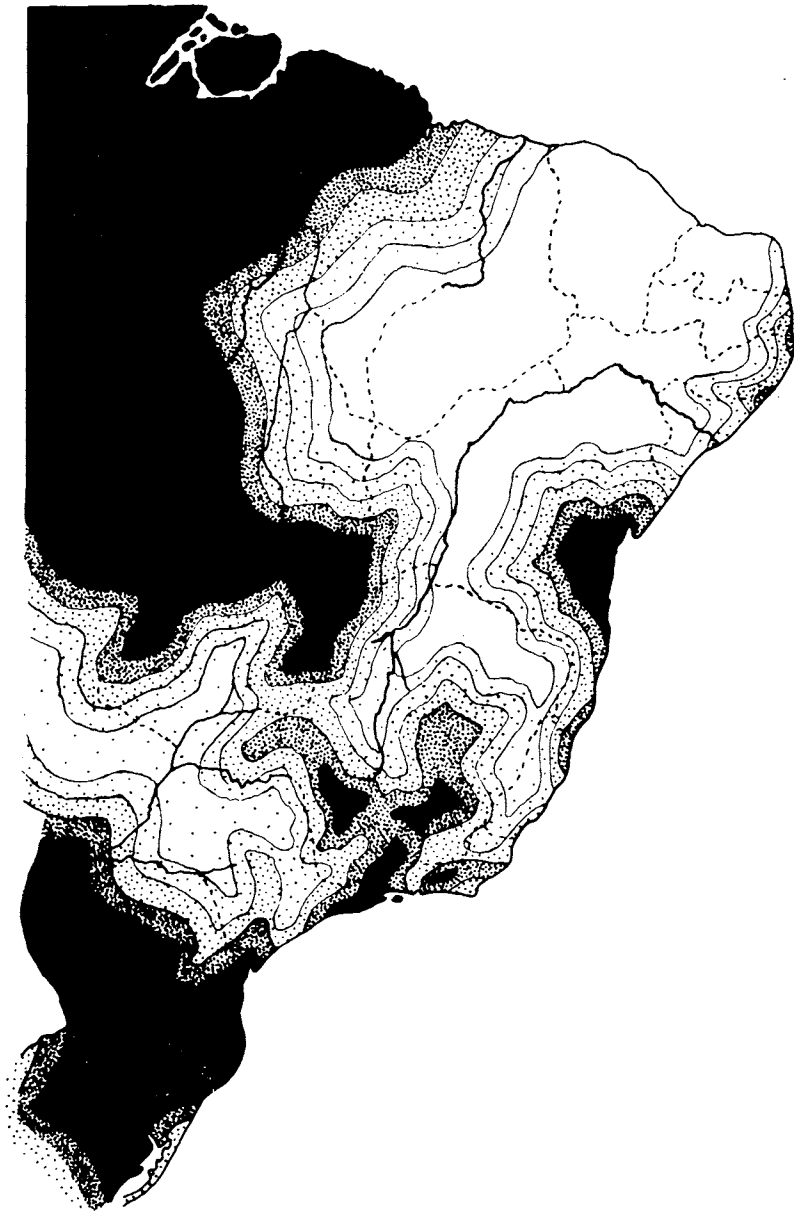


Figure 35. Relative aridity expressed by Meyer's Index ($I = \text{mm annual precipitation} / \text{mm annual saturation deficit}$). The darker the area, the less arid. Contours represent I as follows, beginning with black: 500, 500-400, 400-300, 300-200, 200-150 and 150. Simplified from Atlas Climatológico do Brasil (1969).

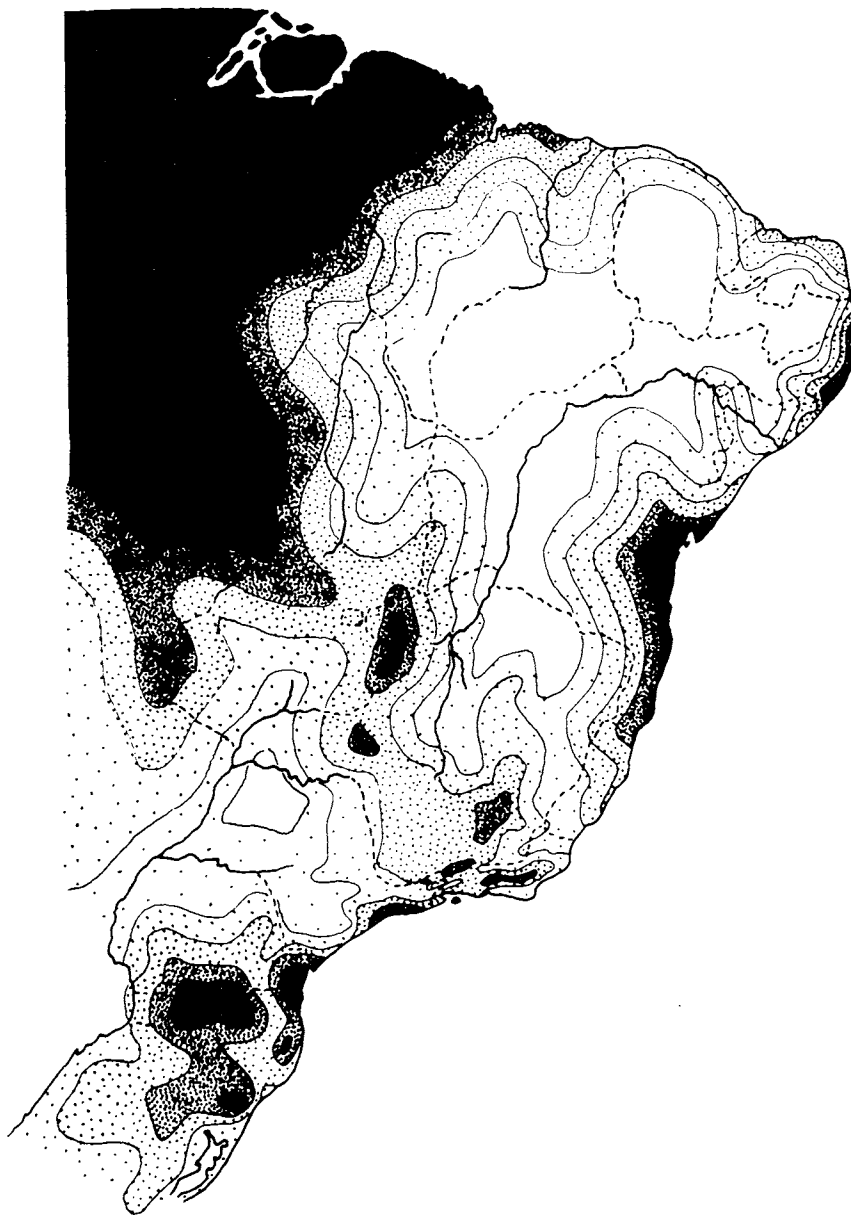


Figure 36. Relative aridity expressed by Knoche's Index ($I = \text{number of rainy days per year} \times \text{mm annual precipitation} / \text{annual mean temperature plus ten}$). The darker the area, the less arid. Contours represent I as follows, beginning with black: 100, 100-80, 80-60, 60-40, 40-20 and 20. Simplified from Atlas Climatológico do Brasil (1969).

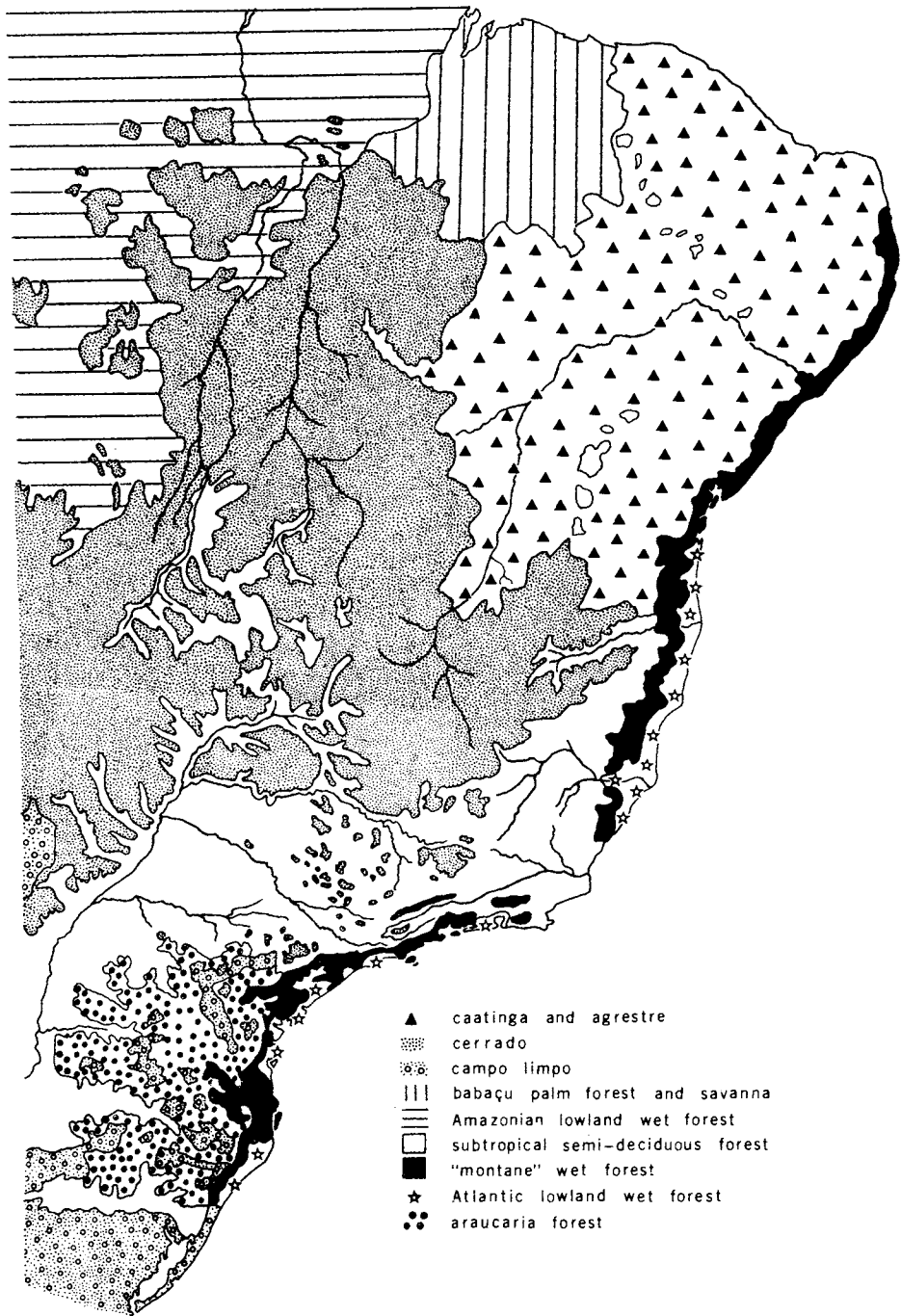


Figure 37. Vegetation of eastern Brasil. Simplified from Hueck (1972 a).

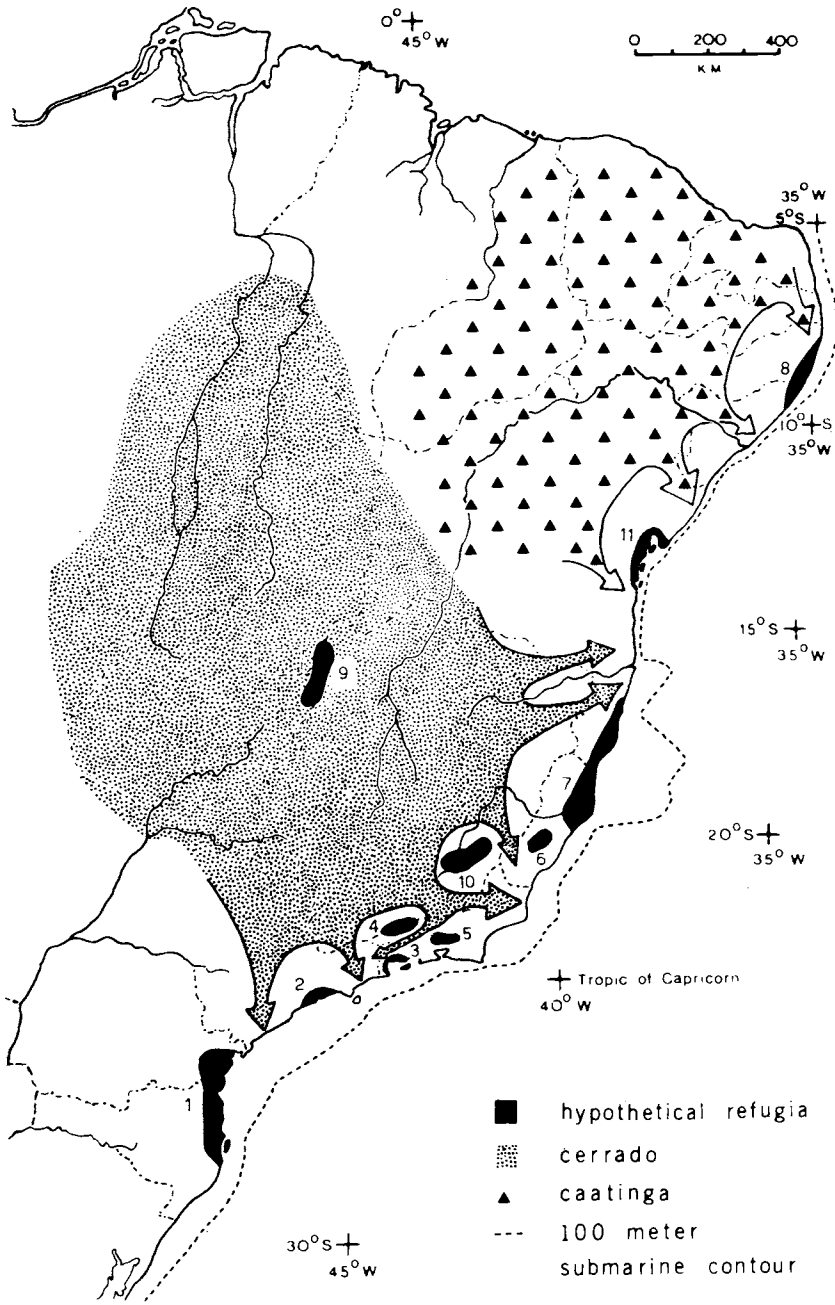


Figure 38. Hypothetical wet forest refugia and hypothetical expansions of open formations in eastern Brasil during dry periods of the Pleistocene.

Table 1. Means (above) and standard deviations (below) of meristic and morphometric characters in female *Enyalius*. The sample size for each taxon is given by N. See text for geographic origin of samples.

character	<i>theringii</i>	<i>perditus</i>	<i>brasiliensis</i>	<i>brasiliensis</i>	<i>catenatus</i>	<i>catenatus</i>	<i>catenatus</i>	<i>silineatus</i>
	N=11	N=7	N=11	<i>boulengeri</i> N=11	N=5	<i>pictus</i> N=3	<i>bibronii</i> N=3	N=5
1	1.136 0.234	1.000 0.000	2.864 0.234	3.000 0.000	1.000 0.000	1.000 0.000	1.000 0.000	1.000 0.000
2	1.045 0.151	1.000 0.000	1.045 0.151	1.818 0.751	3.000 0.000	3.000 0.000	3.000 0.000	1.000 0.000
3	3.000 0.000	2.928 0.189	3.000 0.000	3.000 0.000	3.000 0.000	1.000 0.000	1.000 0.000	3.000 0.000
4	2.773 0.344	3.000 0.000	3.000 0.000	3.000 0.000	2.400 0.894	1.000 0.000	1.000 0.000	1.000 0.000
5	80.82 4.24	85.43 8.32	86.00 7.46	87.36 5.26	88.40 12.20	91.67 15.31	77.67 8.96	70.20 3.49
6	46.54 5.05	66.28 7.67	60.27 3.13	44.73 2.15	50.80 13.61	54.00 5.00	56.33 8.39	61.60 4.16
7	140.45 8.13	198.43 13.00	213.54 17.07	184.09 10.14	182.40 19.54	193.67 16.80	165.33 11.72	125.80 9.23
8	55.45 3.53	72.00 6.40	80.00 4.94	62.64 3.75	64.60 6.66	73.33 3.21	56.00 3.61	47.60 2.30
9	13.18 1.99	14.71 1.95	15.45 1.69	13.82 1.72	14.20 1.79	15.00 1.00	11.67 1.15	12.20 1.10
10	3.818 0.751	2.714 0.756	3.045 0.568	3.864 0.778	2.600 0.548	2.000 1.000	2.667 0.577	2.200 1.170
11	3.273 0.467	3.143 0.690	3.727 1.104	4.454 0.522	3.600 0.548	3.333 0.577	3.333 0.577	2.200 0.447
12	15.00 1.26	13.43 1.27	14.54 1.57	16.73 1.49	13.60 2.07	15.00 1.00	12.00 1.00	11.80 1.10
13	11.73 1.35	11.28 0.95	10.00 0.89	11.36 0.81	10.40 1.52	12.33 1.15	10.33 0.577	7.80 0.45
14	17.91 1.92	17.00 1.63	18.73 1.56	18.64 0.92	17.80 2.39	15.33 2.89	15.67 1.53	9.20 2.49
15	6.182 1.080	7.143 1.215	7.273 1.009	7.454 0.690	6.000 0.707	6.333 0.577	7.000 1.732	5.600 0.548
16	10.73 0.65	10.57 0.53	10.09 0.83	10.36 1.03	11.40 0.89	10.00 0.00	12.00 1.00	7.20 0.45
17	10.00 0.63	9.43 0.98	9.54 1.04	10.18 0.40	11.40 1.14	10.00 1.00	11.33 1.53	7.20 0.84
18	39.45 3.47	45.43 3.82	50.00 2.32	50.27 3.10	44.00 5.24	45.00 2.65	38.33 2.08	37.00 2.55
19	15.64 1.03	15.00 1.29	15.54 1.13	16.18 0.98	15.00 1.00	13.33 1.15	15.33 0.58	14.40 0.55
20	34.00 1.67	33.71 1.80	35.36 2.25	35.82 1.17	33.60 1.82	32.67 0.58	35.00 1.00	36.40 2.19
21	10.36 0.81	10.14 0.69	10.54 0.82	10.54 0.69	9.40 0.55	9.00 0.00	9.67 0.58	9.60 0.55
22	23.54 2.11	23.00 2.00	23.45 1.92	23.64 1.29	19.60 0.89	18.33 0.58	19.33 1.53	21.20 0.84
23	21.64 1.57	23.00 1.91	23.82 1.17	23.36 1.75	25.80 2.59	25.33 1.53	23.00 2.65	21.80 1.92
24	16.00 1.34	16.86 1.07	16.45 1.21	15.00 1.18	15.80 1.30	17.33 0.58	15.33 2.31	14.00 1.87
25	11.09 0.80	10.21 0.86	10.00 0.84	9.54 0.52	9.20 0.45	9.33 0.58	9.33 0.58	10.30 0.91
26	47.45 3.47	49.86 3.44	50.18 4.71	45.54 3.33	44.40 3.21	52.67 4.73	54.67 2.08	42.40 3.13
27	62.54 13.98	19.57 7.34	23.27 2.97	25.54 4.93	20.40 6.27	24.33 10.97	7.00 3.00	61.60 8.65
28	27.27 10.83	23.29 10.00	24.46 9.68	22.73 6.65	20.80 7.29	22.33 13.58	27.67 9.61	32.60 11.37
29	9.09 7.88	24.71 8.18	17.82 5.98	23.09 9.82	29.80 12.24	27.33 20.01	24.67 21.38	5.80 8.84
30	1.09 3.62	32.29 15.25	34.36 9.15	28.46 10.24	29.00 15.35	25.67 14.57	40.67 23.24	0.00 0.00
31	210.13 10.14	225.73 4.77	205.00 8.99	167.41 10.54	202.82 5.95	205.63 13.68	198.93 3.62	270.44 8.15
32	30.33 1.24	32.06 2.33	33.49 1.50	31.96 1.59	35.10 1.14	31.93 2.12	28.83 0.60	30.78 0.88
33	25.97 1.01	29.24 2.31	32.06 1.98	29.68 1.36	34.94 1.20	32.93 2.42	28.17 0.64	29.28 1.31
34	54.59 1.75	51.27 1.35	52.36 1.80	48.87 0.97	45.06 1.91	47.03 1.19	45.30 1.76	48.80 0.82
35	40.18 2.71	40.46 2.74	38.54 2.44	33.66 1.42	32.50 2.40	34.70 2.82	35.73 2.48	41.54 2.80
36	16.02 1.57	15.64 1.44	15.67 0.92	16.72 1.00	16.34 0.34	16.10 0.95	15.97 0.31	14.32 1.15
37	3.000 0.000	3.000 0.000	3.000 0.000	3.000 0.000	3.000 0.000	1.500 0.500	1.333 0.577	3.000 0.300

Table 2. Standardized discriminant coefficients of the first three multiple discriminant functions for the meristic-morphometric data set.

character	K ₁	K ₂	K ₃
1	- .320	- .506	.034
2	- .075	- .031	.005
3	.848	- .182	- .028
4	- .838	- .285	- .236
5	1.740	- .061	.722
6	.862	- .114	- .933
7	- 2.546	- 2.012	- 1.813
8	- .483	- .141	- .759
9	.000	- .201	- .211
10	1.885	.191	.550
11	- .260	.161	.965
12	1.012	- .171	.651
13	1.198	.320	.782
14	.438	.392	.198
15	- .251	.427	- .541
16	.955	.156	.713
17	- .288	.238	.919
18	.251	.723	.233
19	- .861	- .585	.924
20	1.496	.967	.721
21	- 1.053	- .267	.031
22	- .414	- .100	- 1.020
23	.350	.706	.396
24	.461	- .538	- .443
25	- .837	.167	.762
26	.056	.743	- .806
27	-15.808	2.434	- 4.765
28	-22.679	3.339	- 7.126
29	-26.812	2.531	- 7.094
30	-25.187	3.126	- 6.402
31	.785	.319	- .431
32	- .080	.042	- .082
33	- 1.269	- .613	- .001
34	- .939	.137	- 1.039
35	1.842	.997	.184
36	1.574	- .262	.845
37	.873	- .284	.563

Table 3. Means of osteological characters in *Enyalius*. The number of skulls examined is given by N.

character	<i>iheringii</i>		<i>perditus</i>		<i>brasilienis</i>		<i>brasilienis</i>		<i>boulengeri</i>		<i>catenatus</i>		<i>catenatus</i>		<i>catenatus</i>		N=3
	N=3	N=2	N=2	N=2	N=2	N=2	N=2	N=2	N=2	N=2	N=2	N=2	N=2	N=2	N=2	N=2	
1	35.74	33.50	30.71	32.86	33.82	33.82	32.66	36.46	35.27								
2	2.667	2.500	2.500	2.000	2.667	2.667	2.000	2.000	1.000								
3	17.40	15.88	13.14	17.96	17.86	17.86	19.24	11.76	12.04								
4	29.24	25.74	31.01	25.25	21.01	21.01	22.97	26.25	21.12								
5	3.000	3.000	1.750	1.500	1.067	1.067	1.000	1.000	1.000								
6	43.35	44.50	38.33	31.78	28.65	28.65	24.86	27.22	19.15								
7	9.10	7.60	7.45	8.18	5.78	5.78	7.75	4.98	5.00								
8	23.09	24.00	21.16	14.76	79.05	79.05	85.18	69.23	84.93								
9	2.86	1.69	2.70	4.18	5.61	5.61	5.91	10.61	6.73								
10	1.29	2.58	2.46	0.89	3.10	3.10	2.26	2.43	3.43								
11	189.97	151.30	206.05	161.25	203.57	203.57	176.90	151.20	125.00								

Table 4. Standardized discriminant coefficients of the first three multiple discriminant functions for the osteological data set.

character	K ₁		K ₂		K ₃	
	K ₁	K ₂	K ₂	K ₃	K ₃	K ₃
1	- 1.581	-	.848		.084	
2	2.405	1.136	- 1.759		- 1.759	
3	- 1.411	1.345	.971		.971	
4	- .494	.181	- 1.030		- 1.030	
5	2.227	- .344	.986		.986	
6	not included					
7	- 3.053	1.233	.151		.151	
8	- 4.018	.706	.800		.800	
9	- 3.501	.162	.231		.231	
10	3.622	.981	- .079		- .079	
11	- 5.288	1.349	1.166		1.166	

Table 5. Color character frequencies in *Emyalius*. Upper number gives percentage occurrence. Lower number represents conversion of data to range 0,1.

character	<i>iheringii</i>	<i>penditus</i>	<i>brasiliensis</i>	<i>brasiliensis</i>	<i>boulengeri</i>	<i>catenatus</i>	<i>catenatus</i>	<i>catenatus</i>	<i>catenatus</i>	<i>bilineatus</i>
1	27.1	5.7	9.7	14.3	18.5	25.0	0.0	30.8	0.0	1.00
2	.879	.184	.315	.464	.602	.812	.000	1.00	.000	0.0
3	4.7	0.0	0.0	5.7	0.0	0.0	0.0	0.0	0.0	0.0
4	.825	.000	.000	1.00	.000	.000	.000	7.7	.000	0.000
5	17.6	34.0	25.8	8.6	14.8	0.0	0.0	7.7	0.0	.226
6	.520	1.00	.760	.252	.436	.000	.000	0.0	.000	0.0
7	17.6	39.6	35.5	17.1	7.4	0.0	33.3	0.0	.841	.000
8	.446	1.00	.896	.433	.187	.000	.000	0.0	.000	0.0
9	32.9	18.9	16.1	34.3	3.7	0.0	0.0	0.0	0.0	0.0
10	.961	.550	.470	1.00	.108	.000	.000	46.2	.000	.000
11	0.0	0.0	0.0	2.9	29.6	50.0	0.0	0.0	0.0	0.0
12	.000	.000	.000	.057	.593	1.00	.000	.923	.000	.000
13	0.0	1.9	12.9	17.1	25.9	25.0	0.0	7.7	0.0	.297
14	.000	.073	.498	.661	1.00	.964	.000	7.7	.000	.000
15	0.0	0.0	0.0	0.0	0.0	0.0	66.7	7.7	.000	.115
16	0.0	.000	.000	.000	.000	.000	1.00	100.0	1.00	.000
17	0.0	0.0	0.0	4.6	31.6	0.0	66.7	1.00	.667	1.00
18	0.0	0.0	.000	.046	.316	.000	0.0	63.6	0.0	.000
19	77.9	28.6	44.4	36.4	52.6	33.3	0.0	18.2	16.7	.816
20	1.00	.367	.570	.466	.675	.428	.000	18.2	.000	.500
21	5.9	11.4	5.6	36.4	10.5	0.0	16.7	18.2	.458	.500
22	.162	.314	.153	1.00	.290	.000	83.3	18.2	1.00	.218
23	0.0	0.0	0.0	4.6	0.0	0.0	1.00	10.0	0.0	.000
24	.000	.000	.000	.055	.000	.000	0.0	10.0	0.0	.100
25	78.6	7.1	44.4	68.8	58.3	100.0	1.00	100.0	1.00	.100
26	.786	.071	.444	.688	.583	1.00	.000	100.0	.000	.100
27	0.0	0.0	0.0	0.0	100.0	100.0	100.0	100.0	100.0	100.0
28	.000	.000	.000	.000	1.00	1.00	1.00	1.00	1.00	1.00
29	0.0	0.0	0.0	0.0	100.0	100.0	100.0	100.0	100.0	100.0
30	.000	.000	.000	.000	1.00	1.00	1.00	1.00	1.00	1.00
31	0.0	0.0	0.0	0.0	26.3	0.0	100.0	88.9	100.0	.000
32	.000	.000	.000	.000	.263	.000	0.0	88.9	1.00	.889
33	0.0	0.0	0.0	0.0	89.5	100.0	100.0	88.9	100.0	.889
34	.000	.000	.000	.000	.895	1.00	1.00	77.8	1.00	.889
35	0.0	0.0	0.0	0.0	0.0	0.0	100.0	77.8	1.00	.889
36	.000	.000	.000	.000	.000	.000	1.00	.778	1.00	.778
37	32.7	85.2	69.2	20.0	0.0	0.0	0.0	0.0	0.0	0.0
38	.384	1.00	.813	.235	0.0	.000	.000	0.0	.000	.000
39	0.0	55.6	53.8	65.0	63.6	100.0	0.0	0.0	.000	.000
40	.000	.556	.538	.650	.636	1.00	.000	0.0	.000	.000

Table 6. Phenetic distances separating eight taxa of *Enyalius* for the meristic-morphometric characters. Each distance is the sum of all character state differences between the two taxa.

	<i>iheringii</i>	<i>perditus</i>	<i>brasiliensis</i> <i>brasiliensis</i>	<i>brasiliensis</i> <i>boulengeri</i>	<i>catenatus</i> <i>catenatus</i>	<i>catenatus</i> <i>pictus</i>	<i>catenatus</i> <i>bibronii</i>
<i>perditus</i>	4.601						
<i>brasiliensis</i> <i>brasiliensis</i>	5.209	2.474					
<i>brasiliensis</i> <i>boulengeri</i>	5.161	3.876	2.938				
<i>catenatus</i> <i>catenatus</i>	6.137	3.488	4.566	4.392			
<i>catenatus</i> <i>pictus</i>	7.657	4.968	6.192	6.298	3.906		
<i>catenatus</i> <i>bibronii</i>	7.492	5.577	6.945	6.935	4.625	3.597	
<i>bilineatus</i>	5.012	7.061	8.265	9.157	8.137	8.825	8.218

Table 7. Phenetic distances separating eight taxa of *Enyalius* for the osteological characters. Each distance is the sum of all character state differences between the two taxa.

	<i>iheringii</i>	<i>perditus</i>	<i>brasiliensis</i> <i>brasiliensis</i>	<i>brasiliensis</i> <i>boulengeri</i>	<i>catenatus</i> <i>catenatus</i>	<i>catenatus</i> <i>pictus</i>	<i>catenatus</i> <i>bibronii</i>
<i>perditus</i>	1.193						
<i>brasiliensis</i> <i>brasiliensis</i>	1.648	1.391					
<i>brasiliensis</i> <i>boulengeri</i>	1.826	2.065	1.882				
<i>catenatus</i> <i>catenatus</i>	3.190	2.949	2.498	2.636			
<i>catenatus</i> <i>pictus</i>	3.224	2.933	2.656	1.980	1.216		
<i>catenatus</i> <i>bibronii</i>	3.933	3.258	2.927	2.819	1.987	1.761	
<i>bilineatus</i>	4.869	4.046	3.819	3.663	1.943	1.985	1.742

Table 8. Phenetic distances separating eight taxa of *Enyalius* for the color characters. Each distance is the sum of all character state differences between the two taxa.

	<i>iheringii</i>	<i>perditus</i>	<i>brasiliensis</i> <i>brasiliensis</i>	<i>brasiliensis</i> <i>boulengeri</i>	<i>catenatus</i> <i>catenatus</i>	<i>catenatus</i> <i>pictus</i>	<i>catenatus</i> <i>bibronii</i>
<i>perditus</i>	5.710						
<i>brasiliensis</i> <i>brasiliensis</i>	4.815	1.922					
<i>brasiliensis</i> <i>boulengeri</i>	3.997	6.052	4.854				
<i>catenatus</i> <i>catenatus</i>	9.039	9.157	7.542	8.088			
<i>catenatus</i> <i>pictus</i>	10.114	10.818	9.216	9.315	3.387		
<i>catenatus</i> <i>bibronii</i>	13.714	11.770	12.435	13.990	9.650	11.171	
<i>bilineatus</i>	11.345	12.396	11.887	12.336	5.835	7.059	6.689

Table 9. Means of meristic and morphometric characters in *Strobilurus torquatus* from three regions. Sample size is given by N.

character	Females			Males		
	ES N=1	BA N=2	PE N=2	ES N=3	BA N=4	PE N=7
1	71.0	58.0	55.5	63.7	60.8	56.1
2	34.0	30.5	30.0	30.7	30.8	30.7
3	80.0	68.5	74.0	74.3	68.5	73.6
4	40.0	39.0	43.0	43.0	40.0	44.7
5	18.0	17.0	17.0	18.0	17.2	17.1
6	32.0	29.5	28.0	28.7	28.5	28.4
7	13.0	11.5	10.5	11.7	12.0	11.3
8	27.0	22.5	24.5	25.0	24.0	24.7
9	14.0	13.0	14.0	14.0	13.5	14.3
10	13.0	12.0	12.0	14.0	11.8	12.4
11	12.0	12.0	11.5	12.7	12.5	12.0
12	4.0	2.8	3.5	4.0	2.6	3.2
13	17.0	14.0	15.0	14.0	12.2	15.0
14	32.0	23.5	23.0	26.3	24.5	23.4
15	46.0	36.5	33.5	40.7	35.5	33.6
16	46.0	36.5	27.5	41.3	34.5	29.9
17	20.0	16.0	12.0	20.7	17.8	11.9
18	0.0	1.0	1.0	0.3	1.2	1.6
19	16.0	16.0	15.5	15.3	17.5	17.0
20	3.7	4.5	5.9	2.5	5.2	5.3
21	0.5	0.5	1.0	0.0	0.4	0.9
22	1.0	1.0	1.0	0.3	1.0	1.0
23	0.5	1.0	1.0	0.3	1.0	0.9

Table 10. Distribution of characters in *Strobilurus torquatus* among patterns of geographic variation.

	Pattern						
	1	2	3	4	5	6	7
1 ♀		5 ♀	4 ♀	2 ♂	8 ♀	4 ♂	1 ♂
5 ♂		7 ♀	11 ♂	3 ♂	12 ♂		2 ♀
6 ♂		10 ♂	13 ♂	3 ♀	19 ♂		6 ♀
7 ♂		10 ♀	21 ♀	9 ♀			11 ♂
8 ♂		12 ♀					16 ♂
9 ♂		13 ♀					16 ♀
14 ♂		15 ♂					17 ♂
14 ♀		15 ♀					17 ♀
19 ♀		18 ♀					18 ♂
20 ♀		20 ♂					21 ♂
22 ♀		22 ♂					
		23 ♂					
		23 ♀					
Totals	11	13	4	4	3	1	10