ZOOLOGISCHE MEDEDELINGEN

UITGEGEVEN DOOR HET

RIJKSMUSEUM VAN NATUURLIJKE HISTORIE TE LEIDEN
(MINISTERIE VAN WELZIJN, VOLKSGEZONDHEID EN CULTUUR)
Deel 62 no. 2 25 mei 1988 ISSN 0024-0672

MORPHOLOGY, ECOLOGY AND BIOGEOGRAPHY OF THE SOUTH AMERICAN CAECILIAN *CHTHONERPETON INDISTINCTUM* (AMPHIBIA: GYMNOPHIONA: TYPHLONECTIDAE)

by

EDUARDO GUDYNAS,

JORGE D. WILLIAMS

and

M. DE LAS MERCEDES AZPELICUETA

Gudynas, E., J.D. Williams and M. de las Mercedes Azpelicueta: Morphology, ecology and biogeography of the South American Caecilian *Chthonerpeton indistinctum* (Amphibia: Gymnophiona: Typhlonectidae).

Zool. Med. Leiden 62 (2), 25-v-1988: 5-28, figs. 1-10, tables 1-2. — ISSN 0024-0672.

Key words: Morphology; redescription; ecology; biogeography; Gymnophiona; *Chthonerpeton indistinctum.*

This study of *Chthonerpeton indistinctum* (Reinhardt & Lütken, 1861) considers 25 morphometric characters, teeth-counts and sex, based on 96 specimens. A multivariate analysis of characters and comparisons of geographically arranged samples is carried out by graphic and statistical methods. No trends in geographical variation were found. Subsequently a redescription of the species is presented, including measurements and counts. Sexual dimorphism was observed for four characters related to the cloacal region. The results are discussed and compared with previous reports. Character-variation is also studied. Primary annuli counts show very low variation; sample variation profiles were similar for the remaining characters. A revision of biological data shows that *C. indistinctum* is a viviparous, nocturnal, fossorial to aquatic species. The caecilian is found in the subtropical to temperate areas of Uruguay, southern Brazil and central-north Argentina. A biogeographic model is developed to explain the close similarity between individuals transported with water-hyacinths and those from southern Brazil, assuming a colonization of the Jacuí river basin at the time of its formation in Quaternary times. The origin of individuals transported with water-hyacinths is assumed to be the middle Paraná river basin, and its importance in the founding or maintenance of the Río de la Plata coastal population is stressed. Lastly, relationships within the genus are briefly discussed, and it is pointed out that the species *C. corrugatum* Taylor, 1968, *C. erugatum* Taylor, 1968, and *C. hellmichi* Taylor, 1968, remain poorly defined.

RESUMEN

Se hace una revisión de *Chthonerpeton indistinctum* considerando 25 caracteres morfométricos, conteos de dientes y sexo, basados en 96 especímenes. Se realizó un análisis multivariante de caracteres y comparaciones de muestras geograficamente ordenadas por medios gráficos y estadísticos. No se observaron tendencias en la variación geográfica. Consecuentemente se presenta una redescripción de la especie, incluyendo medidas y conteos. Se observó dimorfismo sexual para cuatro caracteres relacionados con la morfología cloacal. Estos resultados se discuten y comparan con reportes previos. Se estudió también la variación de los caracteres. Los conteos de anillos primarios fueron de muy baja varación; los perfiles de variación entre muestras para los demás caracteres fueron similares. Una revisión de datos biológicos mostró que *C. indistinctum* es vivípara, nocturna, y fosorial a acuática. Se distribuye en las áreas subtropicales a templadas de Uruguay, sur de Brasil y centro-norte de Argentina. Se presenta un modelo biogeográfico para explicar la estrecha similaridad entre los individuos transportados por agua por "camalotales" y aquellos del sur de Brasil, el que asume una colonización de la cuenca del Rio Jacuí al tiempo de su formación en el Cuaternario. El origen de los individuos de los "camalotales" se asume en la cuenca media del Río Paraná, y se subraya su importancia en la fundación o mantenimiento de las poblaciones costeras del Río de la Plata. Finalmente, se discuten las relaciones dentro del género, destacándose que las especies *C. corrugatum, C. erugatum* y *C. hellmichi* continuan mal definidas.

E. Gudynas, Div. Zoología Experimental, Instituto de Investigaciones Biológicas C. Estable, Av. Italia 3318, Montevideo, Uruguay.

J. D. Williams and M. de las M. Azpelicueta, Museo de Ciencias Naturales de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina.

CONTENTS

INTRODUCTION

The Gymnophiona is one of the three Recent orders of Amphibians and doubtlessly the least known. This is partly due to the characteristics of the group: they are wormlike limbless amphibians, with fossorial to aquatic behaviour and most of them are restricted to tropical forest areas, so specimens rarely have been collected. The Typhlonectidae is a family of viviparous caecilians endemic to South America. As is the case for most gymnophions, they are poorly represented in collections and knowledge of species morphology and biology is based on very small samples.

Among the Typhlonectidae, *Chthonerpeton indistinctum* (Reinhardt & Lütken, 1861) is noteworthy for it reaches the southernmost distribution of a gymnophion in temperate subtropical Uruguay. Although there is some information on this species scattered in several notes (e.g. Gaggero, 1934; Liebermann, 1939; Dunn, 1942; Barrio, 1969; Prigioni, 1980a, b, 1981; Prigioni & Langone, 1983a, b) the most recent revision is that of Taylor (1968) based on 23 individuals. Since then new material has been collected which permits a thorough study of morphology.

The objective of this paper is to study in detail the external morphology, tooth counts, biology, ecology and biogeography of *C. indistinctum*. First, all available material is analyzed to confirm its specific identity, and then a morphological redescription of the species is presented, followed by a study of variation. Second, we present all available data on its biology, and particularly ecology, followed by a discussion of the caecilian's distribution and a possible biogeographical model.

MATERIAL AND METHODS

A total of 96 specimens of *C. indistinctum* was examined. They are in the following collections: Museo Argentino de Ciencias Naturales "B. Rivadavia" (MACN), A. Barrio's collection, now at the MACN (CENAI-MACN), Buenos Aires; Museo de Ciencias Naturales de La Plata (CHMLPA), Instituto de Limnología de La Plata (ILLPA), La Plata, Argentina; Centro Educativo Don Orione (CEDO), Montevideo, Uruguay; Museu de Ciencias Naturais, Fundação Zoobotanica do Rio Grande do Sul (MCN), Porto Alegre, Brasil; Rijksmuseum van Natuurlijke Historie (RMNH), Leiden, The Netherlands; and Field Museum of Natural History (FMNH), Chicago, USA.

Material. — Uruguay. Dpto. Montevideo. Pajas Blancas: CEDO 191-204, 294, RMNH 23191. Playa Pocitos y Buceo (collected in water-hyacinths): CEDO 458-9, 460-468, 471-479, 481-494, RMNH 23192-5, MLP 656 (RMNH 23472). Dpto. Colonia. Punta Gorda: CEDO 345.

Argentina. Pcia. Buenos Aires. Punta Lara (collected in water-hyacinths): MLP 521, RMNH 23468-9. Punta Blanca (collected in water-hyacinths): ILLPA, 5 individuals uncatalogued, RMNH 23471. Palo Blanco: MLP 374. Quilmes: MACN 613. San Isidro: MACN 1048. Buenos Aires: MACN 4460. FMNH 206619-625. Las Conchas: MACN 14739. Club de Pesca, Costanera Norte, Capital Federal: MACN 24801. Ingeniero Maschwitz: CENAI 1134. Pcia. Corrientes. Bella Vista: MLP 295. Pcia. Entre Rios. Pasaje Talavera, Recreo Zapata, Brazo Largo sobre Paraná Guazú: MACN 24821. Pcia.

Chaco. Laguna Moreno, Resistencia: CENAI 1018. Near Barranqueras: MLP 652-4. No data: MACN 1335.

Brazil (all material from Rio Grande do Sul state). Porto Alegre: MCN 1673, 2102, 4406-8, 12220. Rio Grande: MCN 7424, 7426-7, Capão da Canoa: MCN 7660. Triunfo: MCN 10452. Montenegro: MCN 11520, 11921, 12638. No data: MCN 1881.

2. Characters. — The following characters were recorded (measurements were taken as shown in fig. 1, otherwise we follow Taylor, 1968): A. Measurements and counts. 1. primary body annuli, excluding nuchal collar (PA); 2. total length (TL); 3. body width at the neck (WN); 4. body width at midbody (WM); 5. body width at the cloacal terminal tip (WC); 6. eye-snout distance (E-S); 7. eye-naris distance (E-N); 8. eye-tentacle distance (E-T); 9. naris-naris distance (N-N); 10. eye-eye distance (E-E), measured on the dorsum of the head; 11. snout-mouth distance (S-M), measured from the tip of the snout to the extreme anterior margin of the lower jaw; 12. head length (HL), measured from the snout to the first groove; 13. last groove-body terminus length (LGT); 14. length of the vent (LV); 15. width of the vent (WT).

B. Ratios (all, except 16, x 100). 16. LV/WT; 17. E-S/TL; 18. E-N/TL; 19. E-T/TL; 20. N-N/TL; 21. E-E/TL; 22. HL/TL; 23. WN/TL; 24. (LV/WT)/TL.

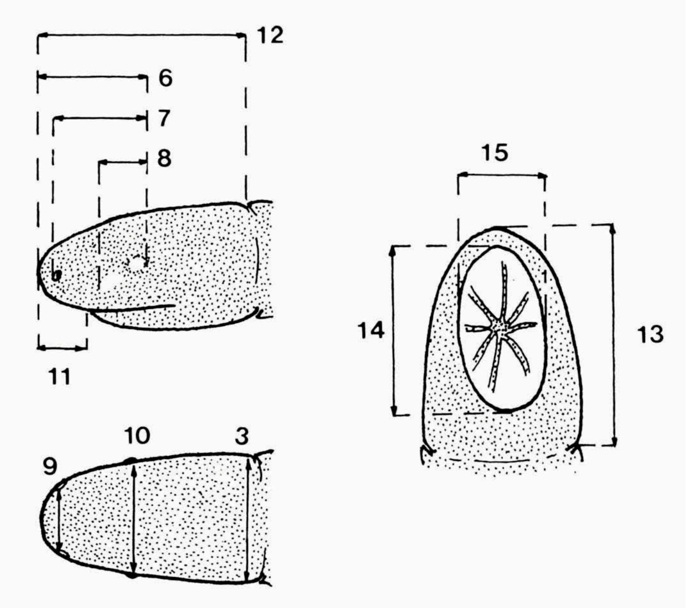


Figure 1. Sketch diagram of head (lateral and dorsal views) and vent of *Chthonerpeton indistinctum* showing measurements recorded for each examined specimen. Numbers refer to characters as in Material and methods.

C. The white area around the tentacle (25) was coded as follows: A, the white area not in contact with the eye; B, white area united to the ocular area by a thin arm; C, a large white area that included both the tentacle and eye.

D. Tooth counts: the number of teeth was counted on each side of the head for all specimens in which mouth conditions permitted this; 26. premaxillary-maxillary teeth; 27. prevomeropalatine teeth; 28. dentary teeth; 29. splenial teeth.

E. Sex. When possible, sex was determined after dissection and recognition of the musculus retractor cloacae.

3. Samples. — A total of 83 specimens, from more or less restricted geographical areas was grouped in samples for statistical analysis. These samples only include specimens defined as adults (see below). Although, we cannot prove that these samples represent populations, it is more probable that breeding occurs between geographically related specimens, than between those in distant locations. As there is no evidence against this reasoning, we consider these samples an useful tool for the study of variation. Another set of multivariate quantitative techniques was done considering only individual specimens to test the validity of our results, and they are presented elsewhere. The samples are:

1. Specimens from Pajas Blancas, Dpto. Montevideo, Uruguay (PBlancas); n = 14.
2. Individuals collected in several localities of the Province of Buenos Aires and adjacent area of the Province of Entre Rios, Argentina (BAires); n = 14.
3. Individuals arrived at the southern coasts of Uruguay, transported by water-hyacinths, in 1983 (Cam-UY); n = 27.
4. Specimens arrived under similar conditions but at the coasts of the Province of Buenos Aires (Cam-ARG); n = 14.
5. Individuals from several localities in Rio Grande do Sul state, Brasil (RGS); n = 14.

The arrival of this species at the Argentinian and Uruguayan coasts of the Rio de la Plata, transported by water-hyacinths ("camalotes") from the Rio Parana basin, has been reported by Ihering (1911) and Achaval et al. (1979), and observed by the present authors in 1983.

4. Sexual dimorphism. — We compared adult males and females for all characters, by way of a Student "t" test for means.

5. Statistical procedures. — The following statistics were obtained: $\bar{x}$, mean; SD, standard deviation; SE, standard error of the mean; and CV, coefficient of variation. Statistical procedures follow Sokal & Rohlf (1979). Student "t" test for means was done without sample variance restrictions. Significance level otherwise noted was $P < 0.01$. Multivariate Principal Factor Analysis was

done through the PRESTA program developed at the Centro Ramon y Cajal, Spain, and operating in a Digital PDP 11/34 computer at the Instituto de Investigaciones Biologicas "C. Estable", Uruguay. For details on this analysis see Marriot (1974). The clustering techniques follow Sneath & Sokal (1973).

RESULTS

1. Morphometric character analysis

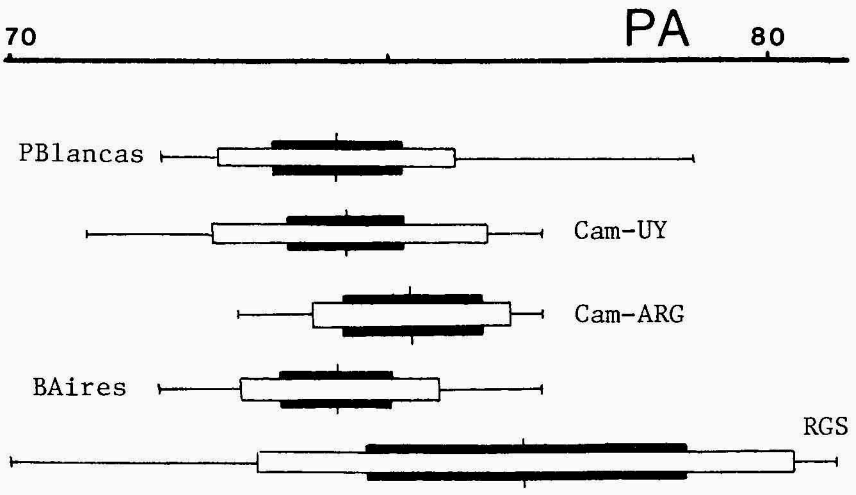
Morphometric characters were studied by Principal Factor Analysis (PFA) for 69 individuals. Four Principal Factors account for 81.6% of the total variation in the sample. The distribution of the variables shown for the first and second Principal Factors was almost identical to that illustrated by Gudynas, Williams & Azpelicueta (1985), so we will not repeat their figure. Two different trends were recognized in the analysis: some variables formed a highly correlated group, while others were less correlated. The first group included the body measurement characters, which were very homogeneous (a lower correlation was observed for variables 2, 7 and 8). The second group included ratios and PA. The PA was found isolated and not closely related to any other character. On the other hand, the ratios were clustered in two subgroups (one included variables 17-19, 21 and 23, and the other 16 and 22) while 20 and 24 were isolated.

The study of morphometric characters permits the identification of empirically correlated characters that may distort phenetic classifications (Sneath & Sokal, 1973). Although the PFA showed that body measurements were highly correlated they are not identical. It seems that one morphological feature (most probably a function of the individual's total length) may be responsible in part for this high correlation. In order to assess these factors in the present study we will work with all these characters.

Some authors have criticized the use of ratios because they do not remove size-effect and other limitations in multivariate analysis (e.g. Atchley & Anderson, 1978). This point was further investigated by comparing the results of morphometric, ratio and morphometric-ratios character sets in multivariate Principal Component Analysis. The results of these analyses were similar and supported the use of ratios. These findings will be presented elsewhere (Gudynas et al., in prep.).

2. Comparisons between samples

Samples were compared for all 24 morphometric characters and ratios through (1) Student's "t" test for samples means; (2) modified Dice Leraas diagrams (Simpson et al., 1960), and (3) a cluster analysis. A total of 240 comparisons was done among the five samples. Of these, 18 comparisons were significantly different (7.5%). The tables presenting these results are not all included because of space limitations, but the relevant results are summarized as follows: there are no significant differences between the samples for 17



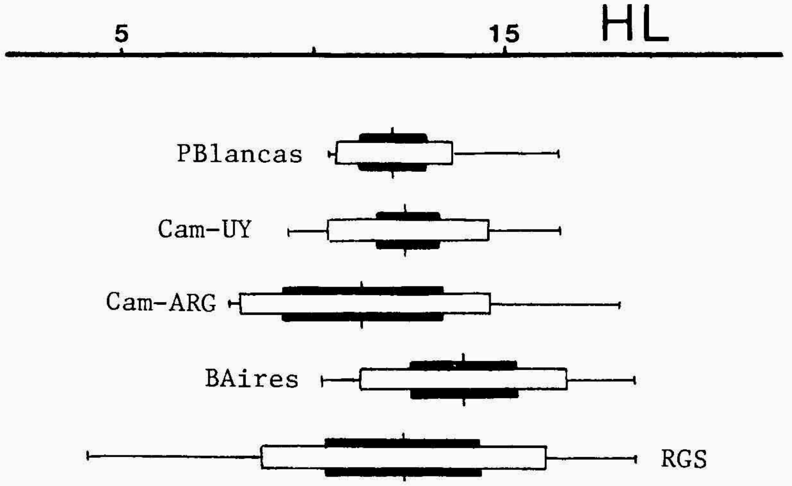


Figure 2 (above). Modified Dice Leraas diagrams for the primary annuli character in five samples of *C. indistinctum*. Sample abbreviations as in text. Horizontal line shows ranges; open and full rectangles show one SD and two SE at each side of the mean respectively; the vertical line shows mean.

Figure 3 (below). Modified Dice Leraas diagram for the head length character. See fig. 2 for further details.

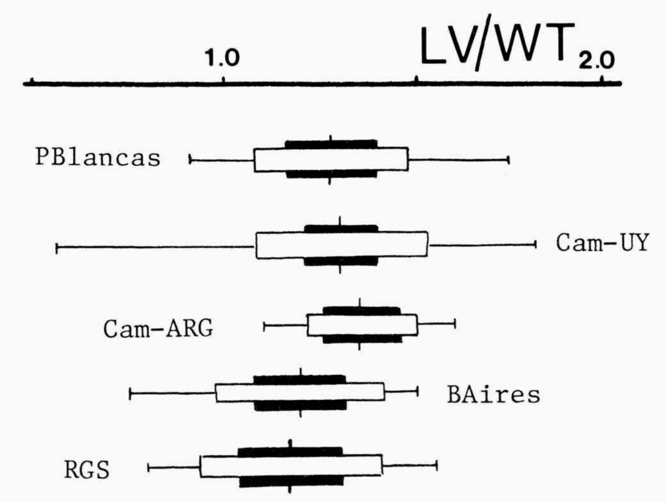


Figure 4. Modified Dice Leraas diagram for the length of the vent to width of the vent ratio. See fig. 2 for further details.

characters (1, 3-9, 11-12, 15-16, 20-24). The highest number of significant differences was found for character 10, with four significant differences, and characters 17-19 with three. The highest number of differences was recorded from sample BAires with eight significant differences (2, 10, 13 and 14).

The Dice Leraas diagrams are presented as examples for three different characters in figs. 2-4. These examples show that the RGS sample presented a wide range which was confirmed by the statistical analyses.

The results of the cluster analyses are presented in fig. 5 for PA counts and body measurements (except total length) and WT/TV ratio, using "Taxonomic Distance" as a similarity coefficient. Gudynas, Williams & Azpelicueta (1985) further explore these techniques with raw data, and both

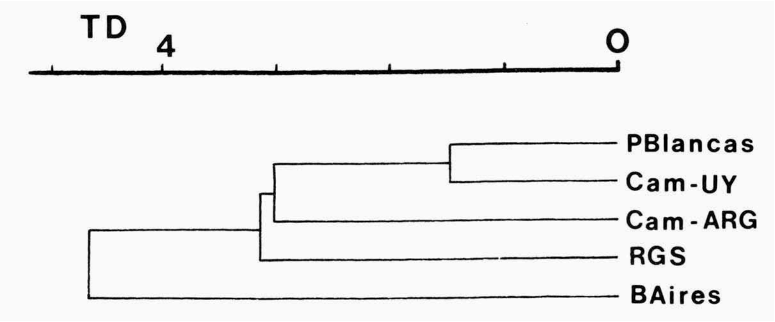


Figure 5. Clustering of *C. indistinctum* samples (abbreviations as in Material and methods); Taxonomic Distance similarity coefficient; UPGMA procedure.

standardized and log transformed data, and the incidence on classifications. We will not repeat their findings here, but only present for a brief discussion a new cluster not shown in the previous paper.

The differences between the samples were not significant for most of the comparisons. Furthermore, the Dice Leraas diagrams did not allow the recognition of trends among the samples. Gudynas, Williams & Azpelicueta (1985) found a high proportion of significant differences in a BAires sample of seven individuals. They interpreted these results keeping in mind that these specimens had been collected over almost a century, during which time preservation may have altered the specimen's size and measurements. In the present analysis, the new specimens added to the BAires sample caused a drastic reduction in the number of significant differences, supporting our previous statements. The cluster showed the highest similarity for Cam-UY and PBlancas samples, while RGS, Cam-ARG and BAires, respectively, entered the cluster at higher similarity values.

3. Size distribution

A histogram for total length is shown in fig. 6. Two groups were observed: most of the specimens were grouped at total lengths greater than 190 mm. The other group, with smaller total lengths is most probably composed of newly born to juvenile specimens. Thus, we have arbitrarily chosen the 200 mm total length: smaller specimens are considered juveniles, and longer ones, adults. Regrettably, at present, there are not enough data to support this conclusion with a study of gonad maturation (see Berois & Sá, 1985; Sá & Berois, 1985).

4. Redescription of *Chthonerpeton indistinctum*

The study of samples from various geographical regions did not show clear geographical variation that might lead to subspecific recognition, and samples

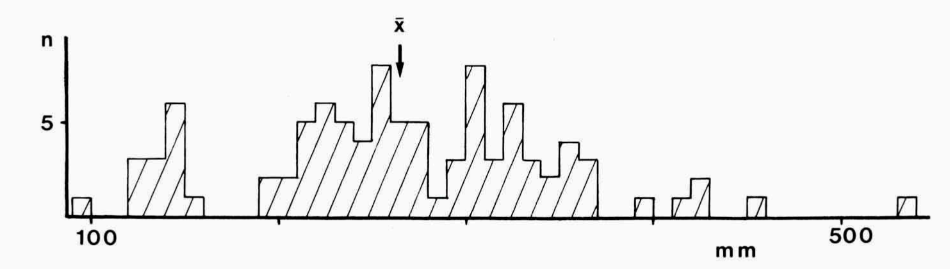


Figure 6. Histogram of total length distribution in 95 *C. indistinctum* examined. Measurements are in mm. The TL ranged from 99 to 530 mm, $\bar{x}$ = 266.05 (arrow), SD = 79.22; CV = 29.77. Specimens longer than 200 mm have been arbitrarily designed as adults (see text for further details).

are similar. Furthermore, the differences among samples and the characters of these specimens fall within the known variation and the description of *C. indistinctum* as given by the latest reviewers (Dunn, 1942; Taylor, 1968). Consequently, we conclude that these specimens have been correctly identified, and we present a redescription and a study of variation.

Chthonerpeton indistinctum (Reinhardt & Lütken, 1861)

Siphonops indistinctus: Reinhardt & Lütken, 1861: 202-203; Dumeril 1863: 317-318; Wiedersheim, 1879: 19, 23; Hensel, 1867: 162.

Chthonerpeton indistinctum: Peters, 1880: 940; Boulenger, 1882: 104; Boulenger, 1886: 445; Cope, 1889: 34; Boulenger, 1895: 411; Berg, 1896: 155; Ihering, 1911: 107; Nieden, 1913: 24; Serié, 1915: 41-42; Procter, 1923: 230; Gliesch, 1928: 428-431; Gliesch, 1929: 229-230; Gaggero, 1934: 173-182; Liebermann, 1939: 84; Dunn, 1942: 530-532; Cei, 1956: 36; Taylor, 1968: 295-305; Barrio, 1969: 499-503; Klappenbach, 1969: 4; Barrio et al., 1971: 435-445; Langguth, 1976: 30; Achaval et al., 1979: 196; Engelke & de Paula, 1979: 97-109; Aguiar, 1979: 45-53; De Carlo, 1980: 27-36; Braun & Braun, 1980: 123; Cei, 1980: 151; Prigioni, 1980a: 43-44; Prigioni, 1980b: 45-46; Prigioni, 1981: 39; Prigioni & Langone, 1983a: 81-83; Prigioni & Langone, 1983b: 97-99; Gudynas et al., 1984: 79; Berois & Sa, 1985: 10-11; Sa & Berois, 1985: 11-12; Gudynas, Williams & Azpelicueta, 1985: 15-18; Gudynas, Azpelicueta & Williams, 1985: 56; Skuk, 1985a: 40-41, 1985b: 46-47; Azpelicueta et al., 1986: in press; Fox, 1986: 154-167; Gudynas & Williams, 1986: 250-253; Sa & Berois, 1986: 510-514.

Lectotype: specimen No. 13-RO-235 in the Universitetets Zoologiske Museum, Copenhagen, Denmark, from Buenos Aires, Argentina (Taylor, 1968). The following redescription is based on 96 individuals (see Material and methods for examined specimens). Table 1 shows morphometric characteristics for adult individuals.

C. indistinctum is a subcylindrical typhlonectid (fig. 7), whose total length in the examined specimens ranged from 99 to 530 mm. The skin is smooth; primary annuli are incomplete at the dorsal and ventral midlines and their number shows lower variation (extremes 70-81 for adults; and low SD and CV; see table 1); secondary annuli are absent. Head dorso-ventrally compressed; prominent snout projecting beyond the mouth; nostrils oval, directed dorsolaterally and clearly closer to the snout than to the eyes. Tentacle in a white area that projects posteriorly to the eye and is in contact with it (43% of the specimens) or not (56% of the specimens). The head is wider posteriorly and the distance between the eyes is greater than that between the nostrils. Body width is greatest at the middle of the body, followed by the width at the neck and is smallest at the terminal tip.

Midbody width : total length ratio yielded a $\bar{x} = 29.21$ (SD = 4.77; CV = 16.33) for adults. This ratio was used by Taylor (1968), although preservation of individuals doubtlessly affected width at midbody. We prefer the ratio of the neck width to total length, which yields a $\bar{x} = 34.01$ (SD = 0.46; CV = 11.42), over the first mentioned ratio.

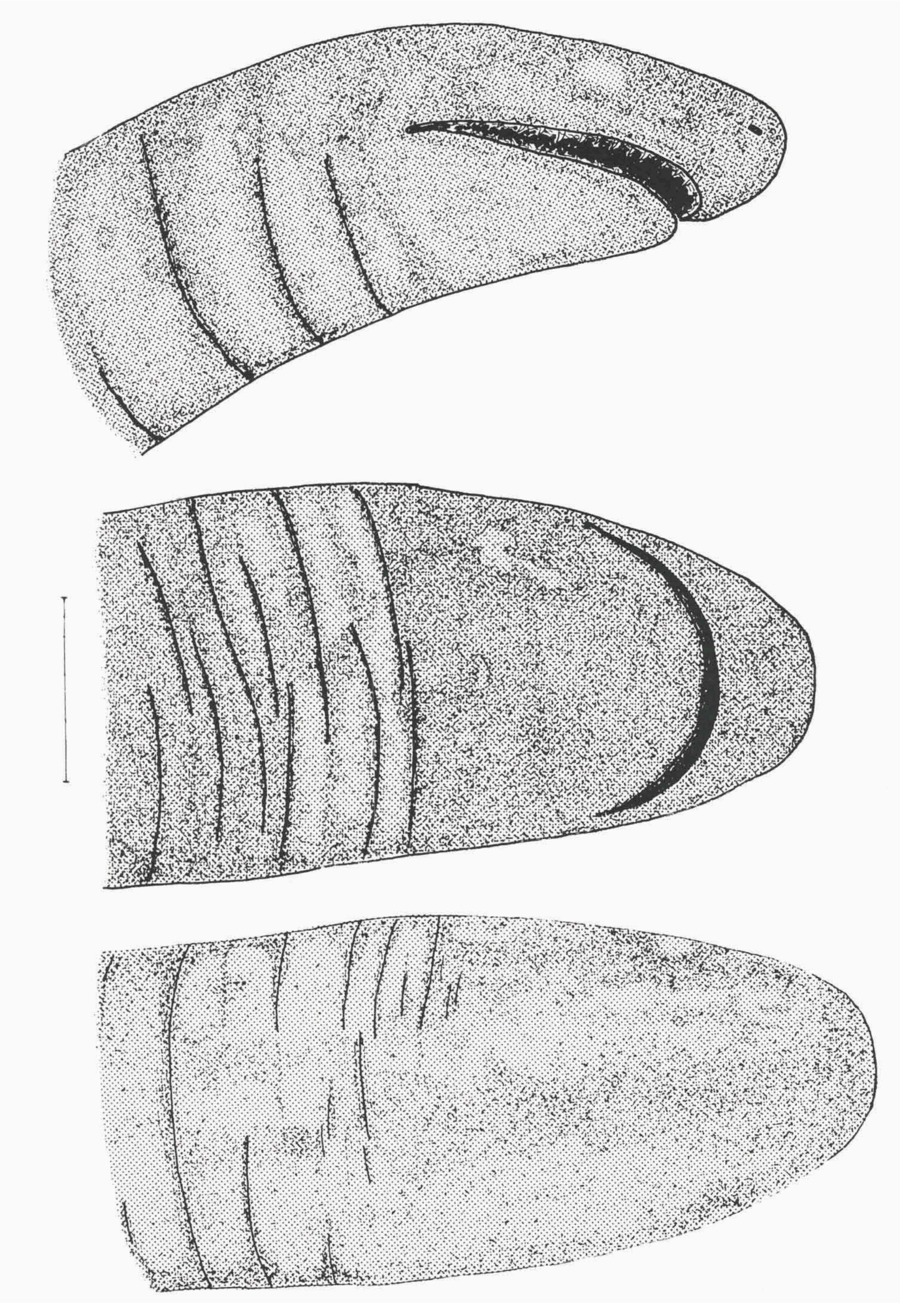


Figure 7. *Chthonerpeton indistinctum* (CHMLPA 587) from Pajas Blancas, Dpto. Montevideo, Uruguay; lateral, ventral and dorsal view of head. Line equals 10 mm

The terminal tip of the body is rounded, without a true tail. The vent is found on its ventral surface in a whitish depressed area (Taylor's 1968 "sucking disc"). Its longitudinal diameter is greater than its width (ratio $\bar{x}$ = 1.39), although it is a highly variable character (extremes 0.50 – 7.94; SD = 0.82; CV = 58.99).

Statistically significant differences between adult males and females were found only for four characters (table 2).

Teeth in four series. Counts in 43 specimens (two juveniles and 41 adults) showed premaxillary-maxillary teeth mode = 37, $\bar{x}$ = 34.35 (SD = 3.55); prevomeropalatine mode = 24, $\bar{x}$ = 27.33 (SD = 2.94); dentary mode = 26, 28 and 30, $\bar{x}$ = 28.66 (SD = 3.09); and splenial mode = 6, $\bar{x}$ = 6.59 (SD = 1.25). Correlation coefficients against total length were very low for all teeth counts, and there is no evidence of a trend to increase the number of teeth with increasing total length. The following correlation coefficients were obtained: (premaxillary-maxillary) r = 0.394, (prevomeropalatine) r = 0.376, (dentary) r = 0.407, and (splenial) r = 0.141.

Colouration: Above bright black, below black-grey; the entire body is covered with minute white spots. The tentacle and eye are surrounded by a whitish area whose shape was described above. The vent area is creamish white.

All body measurements were significantly correlated at the 95% confidence limits interval to the total length. Of 14 significant correlations, eight presented coefficients greater than 0.8.

Discussion. — The increasing number of specimens collected in recent years, compared with Taylor's (1968) study, now permits a more precise analysis of morphological features and a discussion of variation in *C. indistinctum.*

The number of primary body annuli has been the subject of several different reports: Hensel (1867) reports 82 and 86; Ihering (1911) stated 76-80; Serié (1915) reported a count of 77; Gaggero (1934) 78 and 79, and Dunn (1942) 76-87. The observed differences may be due to different counting procedures (e.g. whether the nuchal collar was included or not, as mentioned by Taylor (1968), in reference to Dunn's (1942) counts). Our counts fall between the extremes mentioned and are more similar to Taylor's (1968) range of 72-79 (and following Taylor's data we obtained a $\bar{x}$ = 75.39). Prigioni & Langone (1983a) reported a $\bar{x}$ = 76, but considered this a highly variable character. Nevertheless, according to their data, and with a SD = 4, it is clear that this is not a highly variable character, which agrees with our results.

The maximum total length of the examined specimens was 530 mm (individual CHMLP 520, Cam-ARG sample), which constitutes a new record for the

Table 1. Morphometric characters in 69 adult specimens of *Chthonerpeton indistinctum* (TL 200 mm). Characters and statistics abbreviated as in Material and methods. Measurements in mm.

	PA	TL	WN	WM	WC	E-S	E-N	E-T	N-N	E-E	S-M	HL	LGT	LV	TV
$\bar{x}$	74.94	278.34	8.09	9.71	6.58	5.96	4.59	3.04	3.29	5.68	2.52	12.37	8.22	4.09	3.23
SD	2.30	67.77	1.92	2.84	1.97	1.29	1.04	0.80	0.81	1.13	0.57	2.85	2.12	1.11	0.87
SE	0.27	8.10	0.23	0.34	0.24	0.15	0.12	0.10	0.10	0.14	0.07	0.34	0.25	0.13	0.10
CV	3.08	24.34	23.73	29.24	29.93	21.64	22.65	26.31	24.62	19.89	22.51	23.03	25.83	27.08	26.93

Table 2. Characters with sexual differences in *C. indistinctum*. For each character (abbreviations as in text) are shown mean values, the obtained "t" values after Student's test and its significance level.

	$\bar{x}$			
Character	♂	♀	t	significance
WC	6.63	5.36	2.32	0.029
TV	3.43	3.01	3.04	0.006
LV/TV	1.27	1.37	3.20	0.004
(LV/TV)/TL	0.046	0.049	2.21	0.037

species. Hensel (1867) previously reported a maximum total length of 450 mm. Body length : body width was a highly variable ratio, although similar to Taylor's (1968) figures. Body length : neck width, although less variable, also presented a high CV value.

The measurements of the vent clearly showed that there is a trend from circular to an elliptical shape, with a longitudinal axis. This measurement also revealed sexual dimorphism, which generally is poorly defined in gymnophions. Taylor (1968) stated the difficulty of sex-recognition without dissection. Barria (1969) found that the male's vent was larger than the female's in *C. indistinctum.* Other sexual differences were reported in another typhlonectid, *Typhlonectes compressicauda* (Duméril & Bibron) by Gonçalvez (1977). Barrio (1969) expressed these differences in complicated formulae. We found differences in a first level analysis for four measurements related to the cloacal region and terminal tip of the body (table 2). Probably these differences are due to the male's intromittent organ and its complex group of specialized muscles, sacs and glands, while the female's cloaca is more simple and modified as a receptor for the phallodeum and for expelling newborns (Wake, 1972).

Wake (1980) notes that the number of teeth increased during ontogeny. Our sample mostly consists of adults and no increase was evident. Furthermore correlation coefficients of teeth-counts against total length were very low.

The phallodeum of *C. indistinctum* was briefly mentioned by Wake (1972) in her analysis of cloacal morphology among gymnophions, and was briefly described in its everted position by Prigioni (1980a). The osteological description of the species and myological notes are presented elsewhere (Azpelicueta et al., 1986). Some results of a microscopic study of head anatomy dealing with tentacle morphology were presented by Skuk (1985a, b).

The variation of characters was studied by variability profiles (Sokal, 1975) (fig. 8). The CV for the number of primary annuli was very low, and very similar among all samples. The CV of body measurements were greater, and ranged from 19.89 to 29.24 ($\bar{x} = 24.83$). The highest range of CV was for RGS sample (measured as the differences between extremes) with 20.92; while the lowest range was 7.91 for the water-transported specimens samples. Variability profiles were similar between samples, and the observed differences most probably depend on the number of individuals and the collecting chance. These results also agreed with the reported pattern of similar profiles for local populations mentioned by Sokal (1975).

5. Taxonomic remarks

In the latest revision of the genus, Taylor (1968) distinguished six species in

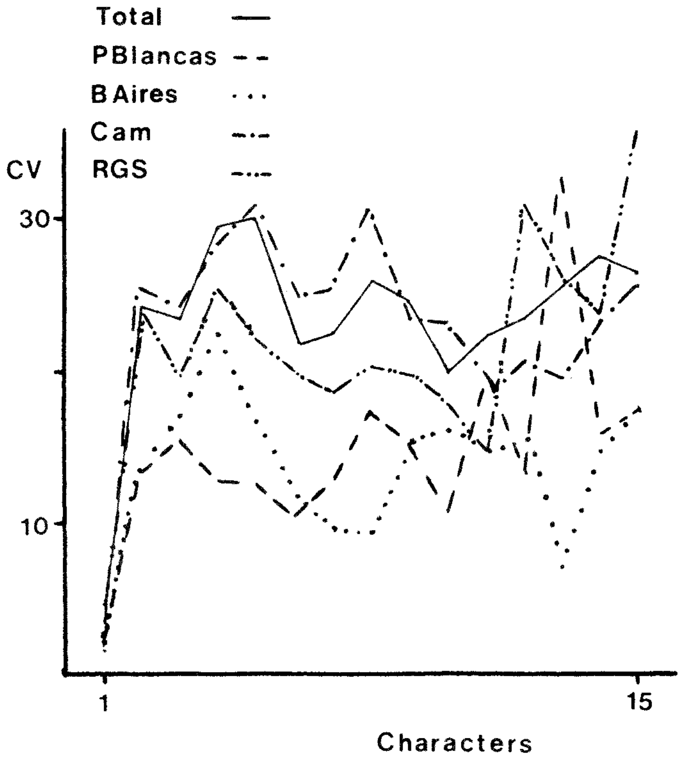


Figure 8. Variability profiles in *C. indistinctum*. Coefficient of variation values are shown for the first 14 morphometric characters (arranged as in Material and methods) and only for adult individuals. Specimens from Cam-UY and Cam-ARG samples were grouped in an unique Cam sample. Total refers CV values for the entire set of individuals.

the genus *Chthonerpeton,* of which four were new. A comparison of these species, including *C. indistinctum,* with the characters and data provided by Taylor (1968) allows us to clearly distinguish *C. braestrupi* and *C. viviparum* because of their high PA counts. The remaining three species are *C. corrugatum, C. erugatum* and *C. hellmichi,* all described as new by Taylor (1968). These three species presented PA counts within the known range of variation of *C. indistinctum.* We have compared these species with *C. indistinctum* through a modified Student "t" test of one observation against a sample (Sokal & Rohlf, 1979), considering only Taylor's (1968) PA counts. We could not reject the null hypothesis of *C. erugatum* and *C. hellmichi* coming from the same statistical population, and *C. corrugatum* was different at $P < 0.10$. All other Taylor's (1968) body measurements were highly similar for all these four species. Furthermore, other differences on sucking disc shape and tentacular area disposition, also fall within the variation observed for *C. indistinctum*. *C. corrugatum* was described from two specimens; the type locality is unknown (the holotype comes either from Africa or South America), while the paratype lacks any locality data. *C. erugatum* was described from one specimen without data. *C. hellmichi* was also described from one specimen, but the locality was "Punta Lara". Although Taylor (1968) was unable to locate this last locality, it is at the Río de la Plata coast, Buenos Aires Province, Argentina, within the known distribution of *C. indistinctum*. Thus, the situation for these three species does not permit analysis of relationships within the genus, but leads us to question their taxonomic validity. *C. corrugatum*, *C. erugatum* and *C. hellmichi* present clear morphological similarities with *C. indistinctum*, but the poor locality data preclude further analysis. Nevertheless, a type locality is available for *C. hellmichi*, which is within the range of *C. indistinctum*, and in an area where this latter species has been collected. Also, Taylor's (1968) diagnostic characters (PA counts, eye tentacle connected by white area and shape of sucking disc) fall within *C. indistinctum*. These data lead us to postulate, at least for *C. hellmichi*, a synonymy with *C. indistinctum*. Unfortunately, we can not make a decision here as we were unable to examine the type material.

6. Ecology and biology

The fossorial behavior of *C. indistinctum* has been reported repeatedly: Peters (1879) stated that the species was found burrowed in the ground according to a report by Hensel (although Hensel, 1867, did not mention the fact); Gaggero (1934) reported several specimens buried in the mud and one of them moving about on its surface; Serié (1915) stated that it does swim, but that it preferred the mud. Lema et al. (1983) reported a colubrid snake, *Liophis miliaris* (L., 1758) found in a channel at the muddy area near a marsh, eating a *C. indistinctum*. Procter (1923) obtained an individual from the colubrid *Sordellina punctata* (Peters).

On the other hand, other authors refer to this species in the aquatic component of the environment. Berg (1896) reported it from nearly stagnant waters. Gliesch (1928) stated its transport by rain water; Ihering (1911) reported it from marshes, mud and aquatic plants. Liebermann (1939) stated that it was found in wet marshes of the Río de la Plata coasts.

The most detailed ecological notes were those from the Pajas Blancas population, Uruguay (fig. 9) (Gudynas & Williams, 1986). The individuals were found active at night, swimming in small ponds at rocky points that enter the Río de la Plata waters. It was observed that individuals either entered the ponds from the mud at their margins, or if disturbed started to burrow. Thus,

Figure 9. Pond habitat at Pajas Blancas site, Dpto. Montevideo, Uruguay, inhabited by *C. indistinctum*.

the caecilian was found in both the subterranian and aquatic components of the environment. An individual collected by one of us (JDW) at the Río Paraná river bank, at Bella Vista, Corrientes, Argentina, was found under a tree.

Stomachs from Pajas Blancas individuals in two cases contained remains of pre-adults stages of the crab *Metasesarma rubripes* (Rathbun, 1897) (Decapoda: Grapsidae), sand and indeterminate vegetable matter (Gudynas & Williams, 1986). Stomach contents of the Bella Vista specimen contained remains of a Tenebrionidae and of a Formicidae.

Prigioni (1981) and Prigioni & Langone (1983b) reported on stomach contents of respectively 2 and 15 specimens (14 of them arrived at the Uruguayan coasts transported by water) that included nematodes (probably parasites), and remains of arachnids, odonata larvae and of one amphibian. As stated by Gudynas & Williams (1986) these findings only represent a potential diet as based on caecilians and preys which were heavely stressed by the journey in "camalotales". Gudynas & Williams (1986) reported parasites of the order Strongyloidea, superfamily Trichostrongyloidea.

Data on reproduction are scarce. Barrio (1969) suggested a probable four months gestation period, and the number of newborns was between six and ten. Copulations started in spring (August-September). Histology of the reproductive tract was reported by Berois & Sá (1985) and Sá & Berois (1985, 1986) for specimens collected after the 1983 water-hyacinth arrival.

7. Biogeography

An ecological biogeography analysis follows, including known distribution and brief comments on historical biogeography.

Fig. 10 shows 29 collecting sites for *C. indistinctum* based on specimens examined and literature records. In Uruguay, the caecilian is found in southern coastal localities at the Río de la Plata and Atlantic Ocean although there is an isolated record from mainland Durazno (Dunn, 1942). In Argentina it has been reported and collected at coastal localities of the province of Buenos Aires. We have examined specimens from the provinces of Entre Ríos, Corrientes and Chaco, all localities close to the Río Paraná. These are new locality records for *C. indistinctum* and they extend the known range of the species in this area about 500 km to the north. Also, a specimen from Santa Fé is known (Laurent, *in litt.*). In Brazil most localities of examined specimens were from Rio Grande do Sul state although there are two other records from Santa Catarina and Paraná states (Ihering, 1911; Dunn, 1942; Braun & Braun, 1980).

Taylor (1968) stated that most localities for *C. indistinctum* lay along the Atlantic Ocean coast, and that this most probably was the result of a higher number of collectors in that area. Our records seem to confirm Taylor's (1968) statement: our new findings show the presence of the caecilian in Atlantic coast sites in Uruguay and southern Brazil, but also in the Jacuí River-Lagoa dos Patos drainage and in the Paraná basin.

The distribution of *C. indistinctum* ranges from subtropical to temperate seasonal climates. Following Lynch's (1971) equability map of South America, these are two areas of high equability (between 50.0 and 60.0). Equability measures temperature departures from 14°C, and express temperature ranges (Lynch, 1971). This distributional pattern resembles that of some primitive leptodactylid frogs (Lynch, 1971), particularly *Limnomedusa macroglossa* (Duméril & Bibron, 1841). The known distribution of other typhlonectids in South America includes the Caribbean lowlands and the Amazonian basin (Rivero, 1980), which are both areas of low equability. Thus, *C. indistinctum* may represent a primitive distribution compared to that of other typhlonectids.

Two further points need to be considered. First, several specimens come from localities at the Rio Jacuí and Lagoa dos Patos drainage, that together with the Laguna Merin, constitute a closed basin, distinct of, and without communication with, the Paraná-Uruguay Rivers basin. The absence of con-

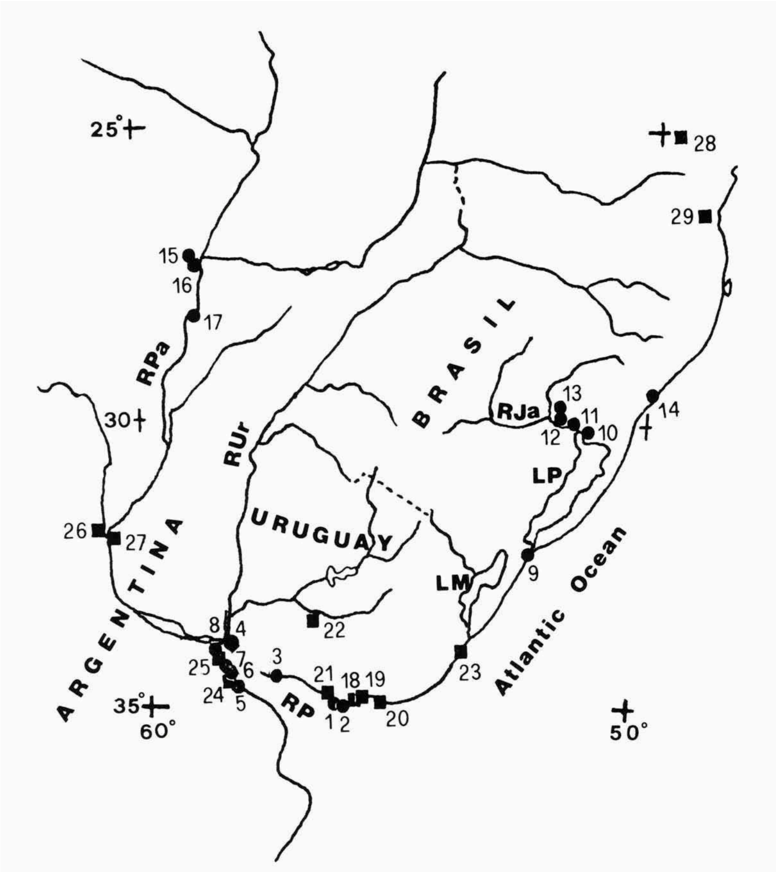


Figure 10. Distribution of *C. indistinctum*. Circles, examined specimens; squares, literature records. RPa, Río Paraná; RUr, Río Uruguay; RP, Río de la Plata; RJa, Rio Jacuí; LM, Laguna Merin; LP, Lagoa dos Patos. Uruguay: (1) Paja Blancas, Dpto. Montevideo; (2) Playa Pocitos, Dpto. Montevideo; (3) Juan Lacaze, Dpto. Colonia; (4) Punta Gorda, Dpto. Colonia. Argentina: (5) Palo Blanco, Pcia. Buenos Aires; (6) Quilmes, Pcia. Buenos Aires; (7) San Isidro, Pcia. Buenos Aires; (8) Zaraté Brazo Largo, Pcia. Entre Ríos; (15) near Barranqueras, Pcia. Chaco; (16) Laguna Moreno, Resistencia, Pcia. Chaco; (17) Bella Vista, Pcia. Corrientes. Brazil: (9) Rio Grande; (10) Porto Alegre; (11) Sapucacia do Sul; (12) Triunfo; (13) Montenegro; (14) Capão da Canoa. All localities from Rio Grande do Sul state.

Literature records: Uruguay: (3) Juan Lacaze, Dpto. Colonia (Achaval et al., 1977; Prigioni, 1981). (21) Playa Pascual, and Arroyo Tigre, Dpto. San José (Prigioni, 1981). (18) Carrasco, Dpto. Montevideo (Prigioni, 1981). (19) Arroyo Tropa Vieja, Dpto. Canelones (Prigioni, 1981). (20) Playa Las Delicias, Dpto. Maldonado (Prigioni, 1981). (22) Durazno (Dunn, 1942). (23) Arroyo Valizas, Dpto. Rocha (Prigioni & Langone, 1983b).

Argentina: (6) Quilmes (Ihering, 1911), Dock Sud (Berg, 1896; Ihering, 1911), Belgrano (Berg, 1896), Capital Federal; and Nunez, Río de la Plata, Pcia Buenos Aires (Liebermann, 1939). (7) San Isidro, Pcia. Buenos Aires (Ihering, 1911). (24) Río Santiago, Pcia. Buenos Aires (Gaggero, 1934). (25) El Tigre, Pcia. Buenos Aires (Serié, 1915). (26) Santa Fe, Pcia. Santa Fe (R.F. Laurent, in litt., specimen at the M. Lillo Foundation collection). (27) Isla Ella, Río Paraná, Pcia. Corrientes (Dunn, 1942).

Brasil: (10) Porto Alegre, Est. Rio Grande do Sul (Hensel, 1857; Lema et al., 1983). (28) Castro Tibeira, Est. Paraná (Dunn, 1942). (29) Joinville, Est. Santa Catarina (Dunn, 1942).

nections that permit a flow of individuals is supported by our review of literature (e.g. Ringuelet, 1975) and confirmed by Reis (*in litt.*) who is currently working on fishes from Southern Brazil. If we assume that *C. indistinctum* is only capable of dispersing via riparian or aquatic environments, its presence at the Brazilian localites needs some explanation. Geological and paleontological information now permits some comments on a possible historical biogeography model.

The Río Paraná started to form in the late Tertiary and developed in the Quaternary, while the Río Uruguay only developed since the Miocene (after Kullander, 1983, review). At late Miocene times the oceanic transgression ("Paranense sea") that covered western Mesopotamia, Pampa and part of the Chaco regions of Argentina to Southern Paraguay (Baez & Yané, 1979; Vuilleumier, 1971) retreated. We assume that *C. indistinctum* (or its ancestor) was present in the Río Paraná basin by that time, and considering present day ecological information, the caecilian may have occurred in riverine marshes or on river banks. During the Pliocene a humid subtropical climate and possibly gallery forests on the river banks that favoured the southward distribution of tropical species (Pascual & Rivas, 1971) were reported. The Jacuí river basin developed in the Quaternary, capturing streams from the Uruguay drainage (Kullander, 1983) and probably contained *C. indistinctum*. Thus, the basal stock that gave rise to the specimens found at the coastal lagoons and coastal sites most probably followed the development of the basin in early Quaternary times. The coastal lagoons developed from the Pleistocene to the Holocene by an alternation of marine transgressions and regressions that formed a series of coastal barriers (Soliani Jr., 1973; Zeltzer, 1976). As a result of these barriers the large lakes of dos Patos, Merín and Mangueira were closed. Although the environment consisted of large marshes and lacustrine areas, theoretically favourable for *C. indistinctum*, the alternation of marine transgressions covering part of these areas prevented a continuous presence of the species. The individuals from the mouth of the Rio Jacuí document the continuous existence of a source stock for possible colonization of these coastal areas.

Gudynas, Williams & Azpelicueta (1985) after a phenetic analysis presumed the flow of individuals between the population source for the Cam-UY and Cam-ARG samples, and the RGS sample explained the close similarity between them. These data were reanalyzed by other multivariate techniques and similar results were obtained, that will be presented elsewhere. This historical biogeographic framework suggests that, although a flow of individuals existed, it was restricted to the past.

Second, water-transported specimens represent a different problem. This transport was recognized early by Hesse et al. (1937:68): "Large streams at the flood time carry driftwood, tree trunks, even whole floating islands, and thus transport not only many small forms but a few large animals. The Paraguay brings large snakes, crocodiles, and jaguars to the neighbourhood of Buenos Aires."

The arrival of *C. indistinctum* through water-hyacinths at the Río de la Plata coasts of Uruguay and Argentina has been reported at least on three occasions in the present century: 1905 (Ihering (1911) reported on *C. indistinctum* arriving at Montevideo and La Plata); 1977 (Achaval et al. (1979) reported on specimens arriving at the Uruguayan coasts of Colonia and Montevideo departments) and in 1983 (Gudynas, pers. obs. at Uruguayan, and Williams, pers. obs. at Argentinian coasts). The transport by floating vegetation-rafts is a natural phenomenon, although catastrophic. It is observed after heavy rains and extensive floodings of the Paraná and Paraguay Rivers in Northern Argentina and Paraguay. These rafts know as "camalotales" are an association of floating hydrophytic vegetation, dominated by *Eichhornia crassipes* and *E. azurea*. The origin of these "camalotales" is assumed to be along the lower Paraguay River and the middle and lower Paraná River. Thus, the two water transported samples (Cam-UY and Cam-ARG) have a similar origin, probably including individuals from various sites along these streams, and constitute a sample from a large population with free exchange in the river system. In October 1983, a *C. indistinctum* was collected at Punta Gorda beach, Dpto. Colonia, Uruguay (fig. 10), at the base of a low cliff. This record is important because at that same time rafts of "juncos" coming from the Argentinian bank of the Río Uruguay were detected in which colubrid snakes of the genus *Helicops* Wagler, 1830 were transported. Field-evidence suggests that the specimen also may have arrived through these rafts, a transportation mechanism not previously reported.

Water-transported individuals constitute an important source for the establishment and/or maintenance of populations at the Río de la Plata coastal sites. The close similarity between the PBlancas and Cam-UY samples supports this statement.

Thus, the present day distribution of *C. indistinctum* seems to be the result of a complicated set of dispersal procedures, illustrating the dynamic boundaries of a species distribution.

ACKNOWLEDGEMENTS

We have examined specimens thanks to several curators: P.C. Braun (MCN), J.A. Cranwell and J.M. Gallardo (MACN and CENAI-MACN), and R.F. Inger (FMNH). Statistical analyses were carried out thanks to the Division of Biophysics, IIBCE, headed by the late C.M. Franchi, while D. Soto helped us with computer programms. R.M. Reis and R.F. Laurent provided relevant information for the paper. R.M. Capocasale, M.H. Wake, J.F. Thompson and M.S. Hoogmoed kindly reviewed various drafts of the paper and provided most helpful comments.

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