REVISION OF THE AFRICAN CAECILIAN GENUS *SCHISTOMETOPUM* PARKER (AMPHIBIA: GYMNOPHIONA: CAECILIIDAE)
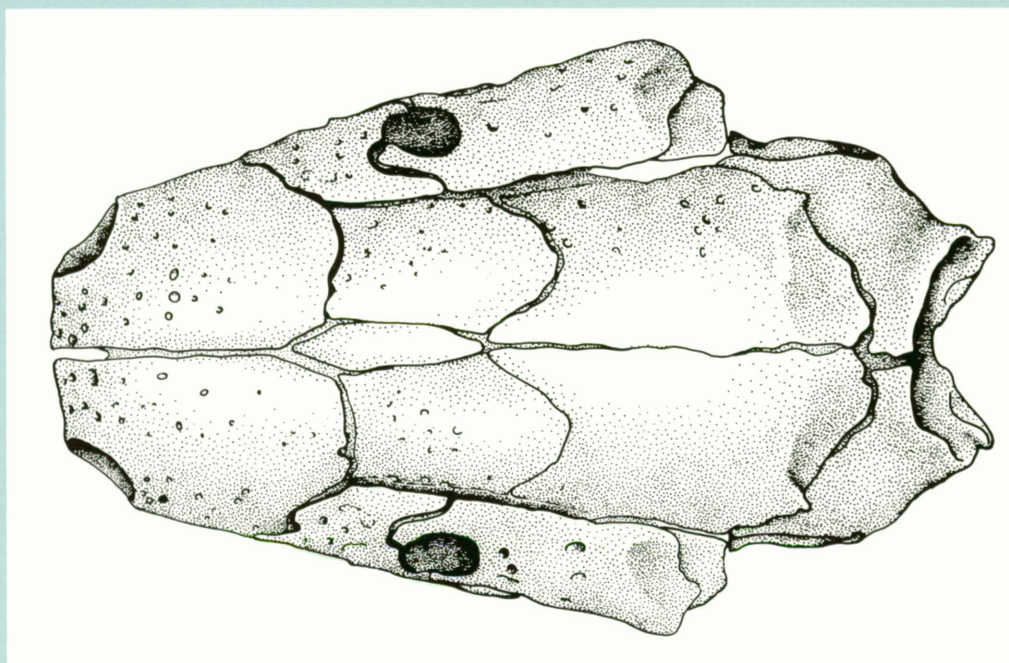
BY

RONALD A. NUSSBAUM

AND

MICHAEL E. PFRENDER

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Revision Of The African Caecilian Genus *Schistometopum* Parker (Amphibia: Gymnophiona: Caeciliidae)

by

Ronald A. Nussbaum

Division of Herpetology
Museum of Zoology
The University of Michigan
Ann Arbor, Michigan 48109-1079, USA

and

Michael E. Pfrender

Department of Biology
University of Oregon
Eugene, Oregon 97403

ABSTRACT

Nussbaum, R. A. and M. E. Pfrender. 1998. *Revision of the African caecilian genus* Schistometopum *Parker (Amphibia: Gymnophiona: Caeciliidae). Misc. Publ. Mus. Zool. Univ. Michigan 187:1-32, 15 figs., 15 tables, 2 color plates.* We revised African caecilians of the caeciliid genus *Schistometopum* Parker based on univariate and multivariate analyses of morphometric characters and coloration. *S. brevirostre* (Peters) and *S. ephele* Taylor, are junior synonyms of *S. thomense* (Barboza du Bocage), and *S. garzonheydti* Taylor and Salvador is a junior synonym of *Geotrypetes seraphini* (A. Duméril). The two valid species of *Schistometopum* occur on opposite sides of the African continent: *S. gregorii* (Boulenger) in coastal Kenya and Tanzania, and *S. thomense* on São Tomé island in the Gulf of Guinea. Two records for *S. thomense* on Príncipe Island and in the Ruwenzori region of central, equatorial Africa are problematic and require verification. Geographic variation in color and morphometric characters of *S. thomense* is pronounced and is remarkable considering the small range of this species on an island with seemingly uniform habitat. The discovery of pronounced, clinal, microgeographic variation in *S. thomense* and the erroneous taxonomic conclusions derived from it by Taylor is viewed as a strong argument against the trend to elevate "diagnosable" allopatric populations to species status without careful study both in the field and in the laboratory. Significant sexual dimorphism in head size is documented for both species of *Schistometopum*, with males having the larger heads in both cases. This same pattern of sexual dimorphism in head size is known for other caecilian species. Sexual dimorphism in head size may result from selection for sexual resource partitioning or for male combat advantage or both. Scarring and fresh bite marks on individuals from both field and laboratory populations suggest that combat may be part of the sociobiology of *S. thomense*, but the context of this aggression is unknown. *S. thomense* is abundant in disturbed habitats and does not appear to be threatened with extinction. *S. gregorii* was also abundant in anthropogenic habitats in 1934, but the species has not since been reported.

Key words: Gymnophiona, Caeciliidae, *Schistometopum*, Systematics, Africa.

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INTRODUCTION

The African caecilian genus *Schistometopum*, with five currently recognized species, has a broadly disjunct distribution in western and eastern equatorial Africa. Four species (*brevirostre, ephele, garzonheydti, thomense*) are restricted to islands in the Gulf of Guinea, and the fifth species (*gregorii*) occurs in coastal Kenya and Tanzania (Taylor, 1968). These two centers of distribution are separated by about 3,500 km, which include the vast rain forests of the upper Zaire (Congo) drainage, a region where caecilians are expected, but none has definitely been found.

The four western species are recorded from three of the four main islands of the Gulf of Guinea: Bioko (Fernando Po), Príncipe, São Tomé, and on Rolas, a satellite of São Tomé (Fig. 1). Caecilians have not been reported on Pagalu (Annobon). *Schistometopum brevirostre* is reported on São Tomé and Rolas; *S. ephele* on São Tomé; *S. garzonheydti* on Bioko; and *S. thomense* on São Tomé/Rolas and Príncipe (Taylor, 1968). The record of the latter species on Príncipe is questionable and requires confirmation.

The single eastern species, *Schistometopum gregorii*, is known from the region near the mouth of the Tana River north of Mombasa, Kenya, and from two localities (Bagamayo River and Rufigi River) in coastal Tanzania, 500-600 km south of the Kenyan locality.

The distribution of *Schistometopum*, as currently constituted, poses several questions. Why, for example, are the western species restricted to islands when seemingly good habitat exists on the nearby mainland? What are the microdistributional (niche) relationships of the three species that are reported to occur together on São Tomé island? Do the western species form a monophyletic group with respect to the single eastern species, and how closely related are the eastern and western forms?

In addition to these questions of relationships, there are some contradictions and mistakes in the literature that need to be addressed. For example, if the original description of *Schistometopum garzonheydti* Taylor and Salvador, 1978, is accurate, then the single specimen upon which the species is based cannot possibly be a *Schistometopum* (see below). Parker (1941) described and illustrated a skull of *Schistometopum* indicating that the orbit is in the squamosal bone. Taylor (1968:678) reproduced Parker's illustration of the skull, which clearly shows the orbit in the squamosal. In spite of this, Taylor (1968:663) listed one of the generic characters of *Schistometopum* as "eye in socket piercing maxillary bone".

In this paper, we review the status of the species of *Schistometopum*, present new information on morphological variation, and present a revised classification of the genus.

ACKNOWLEDGMENTS

MATERIALS AND METHODS

We visited São Tomé, Rolas, and Príncipe islands from 1 June through 4 July 1988 in order to determine the microgeographic relationships of *Schistometopum brevirostre, S. ephele*, and *S. thomense* and to obtain specimens for anatomical, morphometric, and life history studies. Samples were grouped into ten localities (Table 1, Fig. 2).

We also examined most of the specimens of *Schistometopum* in the major museums of the World, including the British Museum of Natural History (BM); Musée Royal de l'Afrique Centrale, Tervuren (MRAC); Museo Civico di Storia Naturale di Genova (MSNG); Museo National de Cienias Natureles, Madrid (MNCN); Museum of Comparative Zoology, Harvard (MCZ); Museum d'Histoire Naturelle, Bâle (MHNB); Museum of Zoology, University of Michigan (UMMZ); Natural History Museum, Wien (NHMW); Universidad Lisboa, Museu Bocage (MBL); University of Florida (UF); Zoologisches Museum und Institut für Spezielle Zoologie, Berlin (ZMB); Zoologishes Museum, Hamburg (ZMH).

Specimens collected on São Tomé were color-coded in the field while alive, and representative individuals were photographed. Specimens were assigned to one of four categories in regard to dorsal coloration: 1) yellow; 2) dark yellow, no brown flecks; 3) dark yellow, light to moderate brown flecking; 4) dark yellow, heavy brown flecking . The ventral coloration is white with variable amounts of yellow and brown bars. The colored bars tend to be restricted to individual primary folds and thus are transversely disposed. The amount of brown bars on the venter is correlated with the amount of brown dorsal flecking. Ventral coloration was scored by selecting 20 contiguous, mid-ventral, primary folds and counting the number of white, yellow, and brown folds in the 20-fold segment. The mid-ventral line was also scored as 1) continuously white; 2) white interrupted by yellow or brown; and 3) no white mid-ventral line.

The sex and state of maturity of all specimens were determined by direct examination of the gonads. All measurements are from preserved specimens and are recorded in mm. A ruler was used to record total length to the nearest 1.0 mm. Dial calipers were used for all other measurements. Body width was measured to the nearest 1.0 mm, all remaining measurements to the nearest 0.1 mm. The following measurements and counts were recorded. Total length; body width, at midbody; head length, from tip of snout to first groove of first collar on side of neck; head width, at level of posterior corner of mouth; inter-ocular distance, between medial borders of eyes; inter-narial distance, between medial borders of nares; eye-naris distance, anterior margin of eye to posterior margin of naris; eye-tentacle distance, anterior corner of eye to midpoint of tentacular aperture; tentacle-naris distance, midpoint of tentacular aperture to posterior margin of naris; primary

4°

BIOKO

GULF OF GUINEA

2°

PRÍNCIPE

SÃO TOMÉ

EQUATOR----------------------------------**0°**

6°   PAGALU   **8°**   **10°**
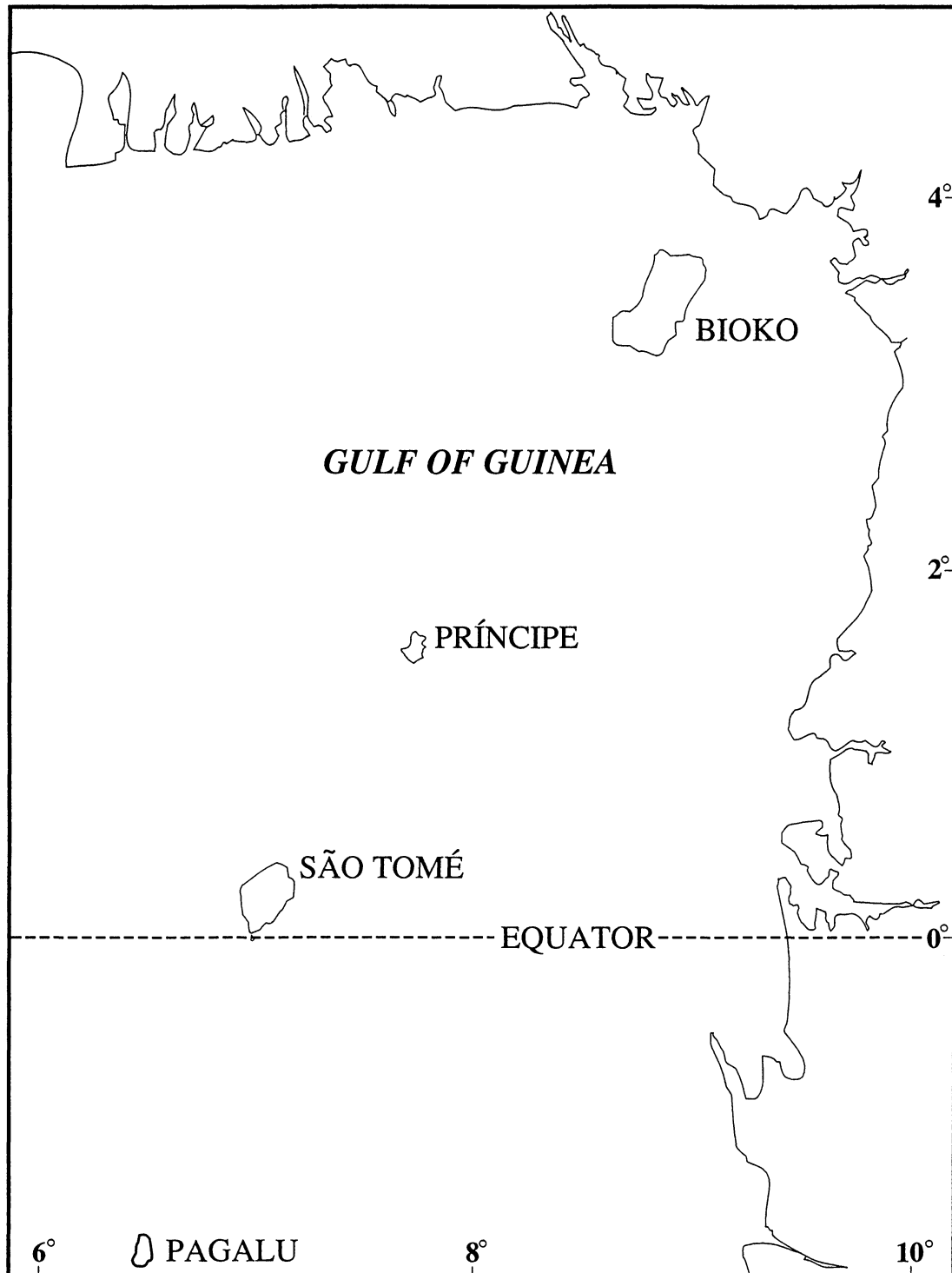
Figure 1. Major islands in the Gulf of Guinea, western equatorial Africa: Rolas is shown as the tiny island on the equator just south of São Tomé.

annuli, number of primary annuli after second collar; vent annuli, number of primary annuli interrupted by cloaca; secondary annuli, number of partial and complete secondary annuli; complete secondary annuli, number of secondary annuli that completely encircle body; vertebrae, total number of vertebrae including the atlas complex, counted from x-ray plates; scale rows, number of overlapping rows of scales in a posterior primary an-

nulus counted in the dorsal region; primary annuli with scales, number of primary annuli containing scales.

Teeth were counted only on borrowed specimens in which the jaws had already been cut. This included most of the *Schistometopum gregorii*. In addition, teeth were counted on a subsample of *S. thomense* to determine whether significant sexual differences exist. The premaxillary-maxillary teeth were counted as a unit;

Table 1. Sampling localities for *Schistometopum* on São Tomé Island (see Fig. 2) and sample sizes used for multivariate comparisons without tooth count data.

Locality			Sample size		
			elevation (m)	males	females
1	Ponta Furada	banana plantation	150	2	18
2	Pousada	plantations, Casa de Repousa	850	17	33
3	Road to Pousada*	between km posts 5 and 6	150	—	—
4	Pedroma	Pedroma cacau plantation	220	14	16
5	Rio Abade	along the river in cacau	5-10	14	16
6	Alto Douro I	1 km NW Ribeira Alfonso	150	4	10
7	Colónia Açoreana	plantation 1 km NE Col. Aço.	60	11	19
8	Ribeira Peixe	secondary coastal vegetation	70	18	32
9	Alto Douro II	hillside 2 km NW Porto Alegre	100	10	16
10	Rolas	rocky fields near village	5	2	—

* not included in multivariate comparisons

vomeropalatine teeth were also counted together; and dentary and splenial teeth were counted. For all four series of teeth, right and left sides were counted together.

Morphometric comparisons between sexes and among populations were made using a covariance model with means adjusted to body size (total length). The equality of the regression coefficients was assessed by the significance of the interaction between group and the covariate (total length) using type III sum of squares. In comparisons with equal regression coefficients (slopes), standard t-tests with Scheffé allowances for multiple comparisons were used to test for significant differences between adjusted means. Covariance analysis was done with the general linear model (GLM) procedure on the statistical package of SAS, version 6.12.

Multivariate morphometric analysis was done using discriminant functions with SPSS for UNIX, release 6.1. All variables were standardized prior to analysis with Fisher's Z-transformation to equalize the variances. The maximum resolution in all cases was achieved by setting the prior probability of inclusion equal to the frequency of occurrence. In all cases, a stepwise inclusion of variables resulted in lower resolution than inclusion of all variables. Four separate analyses were done. The first was to determine whether males and females could be discriminated morphometrically. This analysis was done separately for a population of *Schistometopum thomense* (Pousada), a putative population of *S. ephele* (Ribeira Peixe), and the Kenyan sample of *S. gregorii*. The second analysis was to compare populations by sex of specimens recently captured by us on São Tomé. Thirdly, we did a multivariate comparison by sex of the Pousada and Ribeira Peixe samples from São Tomé and the Kenyan sample of *S. gregorii*. In the latter analysis, we included two specimens of *S. gregorii* from Tanzania and a single specimen of *S. thomense* purportedly from the Ruwenzori region of central Africa, possibly eastern Zaire (recently Democratic Republic of Congo). Fourthly, we did an *a posteriori* attribution of all specimens from São Tomé to either the Pousada (*thomense*) or Rebeira Peixe (*ephele*) populations based on discriminate functions calculated from the Pousada and the Rebeira Peixe populations.

For both the univariate and the multivariate analyses of western *Schistometopum*, we used only those specimens recently captured by us on São Tomé, as many of the older museum specimens were in poor condition and could not be measured accurately. The univariate and multivariate comparisons are based on the same samples and measurements. For the East African *Schistometopum gregorii*, no recent material was available, so we were forced to rely on older museum material.

NOMENCLATURAL HISTORY

Barboza du Bocage (1873) described *Siphonops thomensis* on the basis of two specimens donated to the Lisbon Museum by Craveiro Lopes, a naval officer and sometime governor of African Portugese possessions. Barboza du Bocage did not observe living specimens and, therefore, missed the most striking feature of the species, the bright yellow-orange coloration (rapidly lost in preservative). He placed the species in *Siphonops* based on the position of the tentacle, which is close to the eye, and remarked that this is the first species of *Siphonops* found outside of tropical America. Peters (1874) established *Siphonops brevirostris* based on a single specimen of imprecise locality, "von der Westküste Africas (Guinea)", that was presented by an animal dealer. Peters did not compare *S. brevirostris* to *S. thomensis* as he apparently was unaware of Barboza du Bocage's very similar species described one year earlier. Like Barboza du Bocage, Peters did not see the specimen alive, and he described the color as bluish gray.

Peters (1879) published the first major revision of caecilians in which he attempted to define genera and arrange them hierarchically on the basis of several morphological characters. His primary division was the presence or absence of dermal scales. This resulted in an artificial classification in which the scaleless *Siphonops* and typhlonectids were placed together in Peters' "Gymnocaeciliae". Because "*Siphonops*" *thomensis* and "*S*". *brevirostris* both have scales, they had to be transferred to a different genus, and Peters placed them together in the tropical American genus *Dermophis* on the basis of having scales, visible eye in a socket, a circular tentacle pit in front of and below the eye, a globular tentacle, and two rows of teeth in the lower jaw.

Peters (1880), having received a specimen of *Dermophis thomensis* from Barboza du Bocage, decided his *Dermophis brevirostris* was the same, and this synonymy was followed by Boulenger (1882, 1895), Nieden (1913), and Gorham (1962). Gorham inexplicably corrected the type locality of *D. brevirostris* to Rolas Island. Apparently there is no justification for this change.
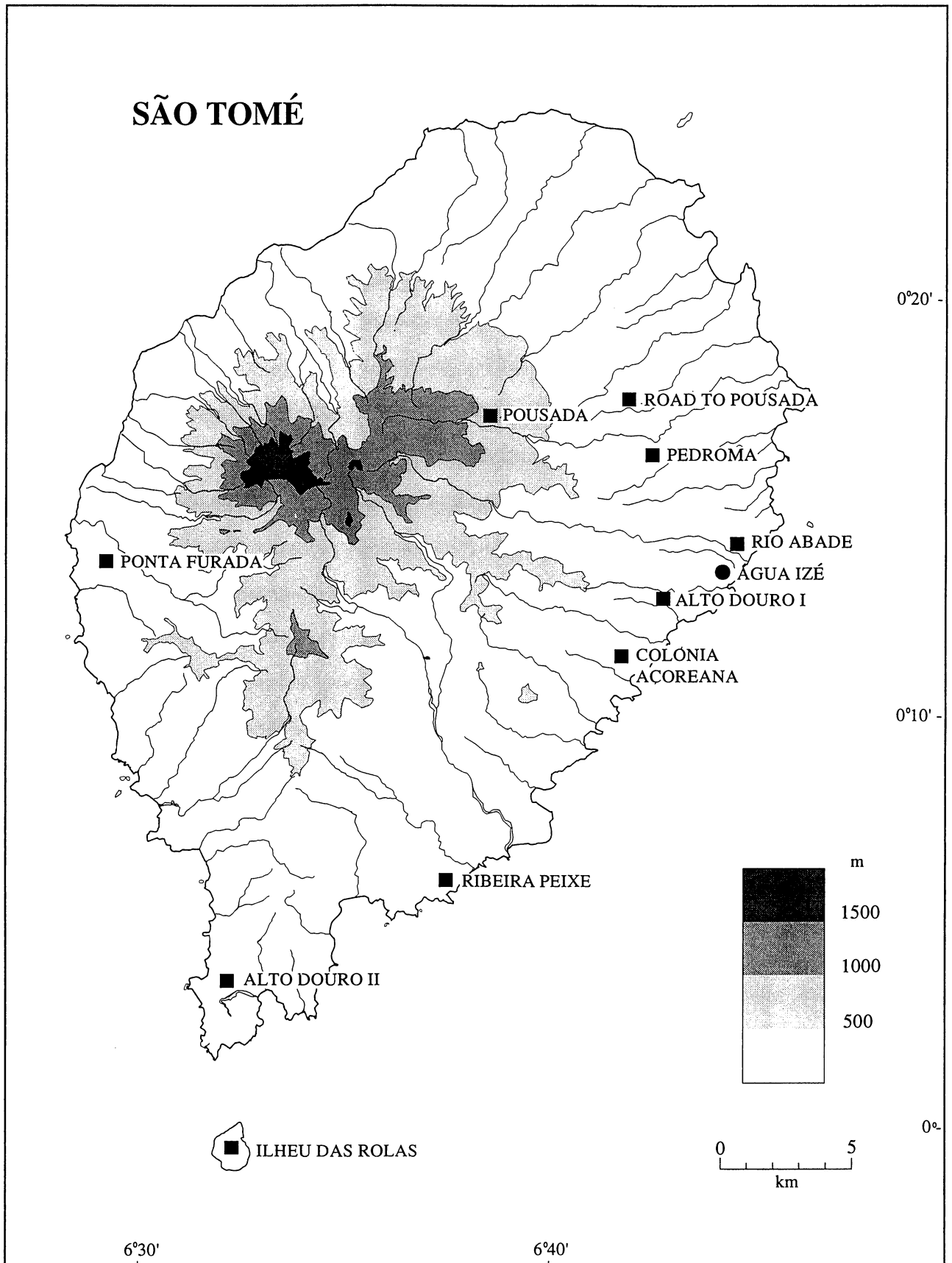
Figure 2. Map of São Tomé and Rolas Islands; solid squares indicate locations of sample sites (Table 1); the solid circle indicates the type locality (Água Izé) of *Schistometopum ephele* Taylor.

Günther (1894) listed a specimen from Ngatana, Tana River, Kenya Colony as *Dermophis thomensis*, but in the same year, Boulenger (1894) described a new species, *Dermophis gregorii*, based on the same specimen. Boulenger noted that *D. gregorii* has a longer, blunter snout and a more anteriorly placed tentacle than *D. thomensis*.

Two additional species, *Boulengerula denhardti* Nieden (1912) and *Bdellophis unicolor* Boettger (1913), from the lower Tana River of Kenya, were synonymized with *Dermophis gregorii* by Loveridge (1936). Loveridge based these synonymies on new material obtained by him at the type localities of the three "species". Taylor (1968) has since supported Loveridge's conclusions.

Parker (1941) recognized that *Dermophis*, in the sense of Werner (1931) and earlier authors, was artificial, and he placed some of the included species in the existing genus *Hypogeophis* and created a new genus, *Schistometopum*, to receive *Dermophis gregorii* and *D. thomensis*. He designated *D. gregorii* as the type species of *Schistometopum*. Parker distinguished *Schistometopum* from *Dermophis* on the basis of (1) the frontals, which are small and separated mesially in *Schistometopum* (see cover illustration of dorsal view of skull of *S. gregorii* based on UMMZ 177011) versus large with a median suture in *Dermophis*; (2) the pseudotemporalis muscle, absent in *Schistometopum* and present in *Dermophis*; and (3) the "ectopterygoids", present in *Schistometopum* and absent in *Dermophis*. Parker's action restricted *Dermophis* to the Neoptropics and *Schistometopum* to Africa, with one western (*S. thomense*) and one eastern (*S. gregorii*) species. Parker implied that *Dermophis* and *Schistometopum* are sister genera.

Taylor (1965, not 1964 as is often cited) described *Schistometopum ephele* from São Tomé, which he distinguished from *S. thomense* from the same island in having a smaller, more pointed head and different coloration. *S. ephele* was described (Taylor, 1965:297) as "light yellowish-brown with dark lilac-brown flecks over dorsum and sides of body; fewer flecks on venter chin and throat". By contrast, Taylor (1968:679) described *S. thomense* as "uniformly bright yellow". In the same paper, Taylor (1965) resurrected *S. brevirostris* (sic) from the synonymy of *S. thomense*. Without having seen a living specimen, Taylor (1965) believed that *S. brevirostre* differs in color ("bluish gray") and head shape from *S. thomense*. Loumont (1992:40), citing "Nussbaum, communication personelle", again listed *S. brevirostre* as a synonym of *S. thomense*, as did Schätti and Loumont (1992).

Taylor and Salvador (1978) established the most recently described species of the group, *Schistometopum garzonheydti*, based on a single specimen from Bioko Island. The most serious of the several mistakes in this paper is that, if the description is accurate, the unique holotype of *S. garzonheydti* cannot be a *Schistometopum*. Taylor's (1968) own list of diagnostic characters for *Schistometopum* includes a smooth tongue "without narial plugs" (p. 663). However, Taylor and Salvador (1978:60) wrote that the tongue of *S. garzonheydti* has narial plugs: "Zunge mit zwei kleinen Nasalzapfen". In addition, Taylor and Salvador indicated

that the tentacle opening is closer to the naris than to the eye ("Entfernung Tentakel zum Auge 3 mm, Tentakel zum Nasenloch 1,2 mm"), a relationship not known for any species of *Schistometopum*, and generally considered to be of generic distinction.

Taylor and Salvador (1978) indicated that *Schistometopum garzonheydti* belongs to the subfamily "Dendrophiinae". It is not clear whether this is a misspelling of Dermophiinae or an attempt to establish a new subfamily. We assume it is a misspelling.

Several lesser but important errors occur in Taylor and Salvador (1978). For example, they stated in the diagnosis that *Schistometopum garzonheydti* has 36 secondary annuli, but two paragraphs below, in the description of the holotype, the number of secondary annuli is given as 26.

There is confusion in the literature concerning the spelling of both *Schistometopum brevirostre* and *Schistometopum thomense*. For examples, Taylor (1965) incorrectly referred to the former as *Schistometopum* "*brevirostris*", and Els (1963) used the incorrect spelling *Schistometopum* "*thomensis*" for the latter. The original names were *Siphonops brevirostris* and *Siphonops thomensis* (not *Siphonops* "*brevirostre*" and *Siphonops* "*thomense*", as stated by Wake, 1985:631). The original spellings were correct, because *Siphonops* (and later *Dermophis*) is a non-neuter noun. *Schistometopum*, however, is neuter and requires the spellings "*brevirostre*" and "*thomense*".

STATUS OF *SCHISTOMETOPUM THOMENSE* (BARBOZA DU BOCAGE) AND *S. EPHELE* TAYLOR

Coloration.-Surveys on São Tomé and Rolas Islands revealed microgeographic variation in color characteristics which, according to Taylor (1965), differentiate *Schistometopum thomense* (immaculate bright yellow) from *S. ephele* (yellow with brown freckles). There is no detectable sexual dichromatism in any of the populations, therefore the sexes were combined for comparison. Two populations representing the extremes of color variation were chosen as standards for comparing the other populations. Specimens from Pousada and nearby Road to Pousada do not differ in coloration and were combined as "Pousada" for purposes of color comparisons (for morphometric comparisons, Pousada does not include the sample from Road to Pousada). Pousada (population 2) has the highest percentage of pure yellow (*thomense*) individuals, and the population at Ribeira Peixe (8) has the most heavily freckled (*ephele*) individuals. Ribeira Peixe is about 18 linear km SW along the coast from the type locality (Água Izé) of *S. ephele* (Fig. 2).

The dorsal coloration of the immaculate yellow individuals from Pousada and the heavily freckled specimens from Ribeira Peixe are illustrated in Fig. 3a. Intrapopulation variation in the intensity of dorsal brown freckling for Ribeira Peixe is shown in Fig. 4. Variation in dorsal coloration among populations is summarized in Table 2. There is obvious clinal geographic variation in dorsal coloration

Table 2. Dorsal coloration of *Schistometopum* from populations on São Tomé: frequency of individuals in populations with different dorsolateral coloration. Pousada to Alto Douro II are geographically ordered eastern localities; Ponta Furada is an isolated western locality; Pousada includes both Pousada and Road to Pousada.

	(1) light yellow, no brown freckles	(2) dark yellow, no brown freckles	(3) dark yellow, light freckling	(4) dark yellow, heavy freckling	n
2 Pousada	0.93	0.07	0.00	0.00	54
4 Pedroma	0.97	0.03	0.00	0.00	34
5 Rio Abade	0.42	0.28	0.30	0.00	43
6 Alto Douro I	0.00	0.14	0.71	0.14	14
7 Colónia Açoreana	0.00	0.07	0.80	0.14	74
8 Ribeira Peixe	0.00	0.01	0.24	0.75	193
9 Alto Douro II	0.00	0.08	0.81	0.12	26
1 Ponta Furada	0.17	0.52	0.30	0.00	23

between the two extremes as is indicated by comparing individuals from Rio Abade and Colónia Açoreana (Fig. 6). Rio Abade is only 1-2 km N of Água Izé, the type locality of *Schistometopum ephele*; Colónia Açoreana is further south, about half way between Pousada and Ribeira Peixe.

Ventral coloration shows the same pattern of variation (Table 3) as dorsal coloration. Ventral views of Pousada and Ribeira Peixe specimens are depicted in Fig. 3b, and clinal variation is demonstrated in Fig. 7.

The mid-ventral line of *Schistometopum thomense* may be white, white broken by brown or yellow, or completely obscured with brown or yellow. Only the Ribeira Peixe and Alto Douro II populations have high percentages of individuals with broken or completely obscured mid-ventral white lines (Table 4).

Morphometric and meristic comparisons.-Because all measurements and some counts vary with body size, it was necessary to use analysis of covariance with total length as the covariate in all univariate comparisons. There is no apparent sexual dimorphism in total length within populations (Table 5), but sexual dimorphism is evident in head size (head length and width), and in several other measurements associated with the head, in both the Pousada and Ribeira Peixe populations (Tables 6 and 7). Because the regressions in most of these cases are significantly different, neither the means nor adjusted means can be compared. The regressions for head length and head width are shown in Fig. 8. In both populations, males have longer and wider heads at all but the smallest body sizes, and the sexual difference is greater in the Ribeira Peixe population. In the Pousada population, for those characters with equal size regressions, only internarial distance and the number of primary annuli with scales varied sexually. Greater internarial distance in males probably is a manifestation of their larger heads. In the Ribeira Peixe population, characters with equal size regressions that were sexually different are body width, interorbital

distance, and the number of primary annuli with scales. Many females at Ribeira Peixe were gravid, which explains their greater body width. The greater interorbital distances of males is again correlated with their larger head size. The sexual difference in primary annuli with scales is reversed in this population compared to Pousada, with males having more annuli with scales than females.

A comparison of males between Pousada and Ribeira Peixe (Table 8) reveals small but significant differences in measurements associated with the head, with Ribeira Peixe males having greater distances between structures. Ribeira Peixe males also have more vomeropalatine teeth than males from Pousada. Pousada males have more primary annuli and vertebrae than males from Ribeira Peixe, a relationship also observed in females (Table 9). This could be a developmental phenomenon associated with higher elevations (Pousada) and lower temperatures, as vertebral number has been shown to be developmentally sensitive to temperature in other ectothermic vertebrates (Fox, 1948; Fox *et al.*, 1961; Lindsey, 1966; Peabody and Brodie, 1975). Females from Ribeira Peixe also seem to have larger heads than those from Pousada (Table 9), but the differences in head-associated measurements are not as great as for males. Females at Pousada have significantly more primary annuli with scales than those from Ribeira Peixe.

Because of the significant sexual dimorphism detected by univariate analysis, discriminant function analysis was also used to examine sexual dimorphism at the multivariate level. Among Pousada individuals, with all variables except tooth counts included, 64.7% of males and 90.9% of females were accurately classified to sex *a posteriori* (Table 10). The percentages are higher, 94.4 and 100.0%, for the Ribeira Peixe population, probably reflecting the stronger sexual differences in head size in this population.

The morphometric and meristic characteristics of the

Figure 3 (facing page). Dorsal (A) and ventral (B) views of two color types of *Schistometopum thomense* from São Tomé. In A, the upper, immaculate yellow individual is a female (small head) from Pousada, and the lower, freckled individual is a male (large head) from Ribeira Peixe. In B, the upper individual is from Ribeira Peixe and the lower from Pousada.

A

B
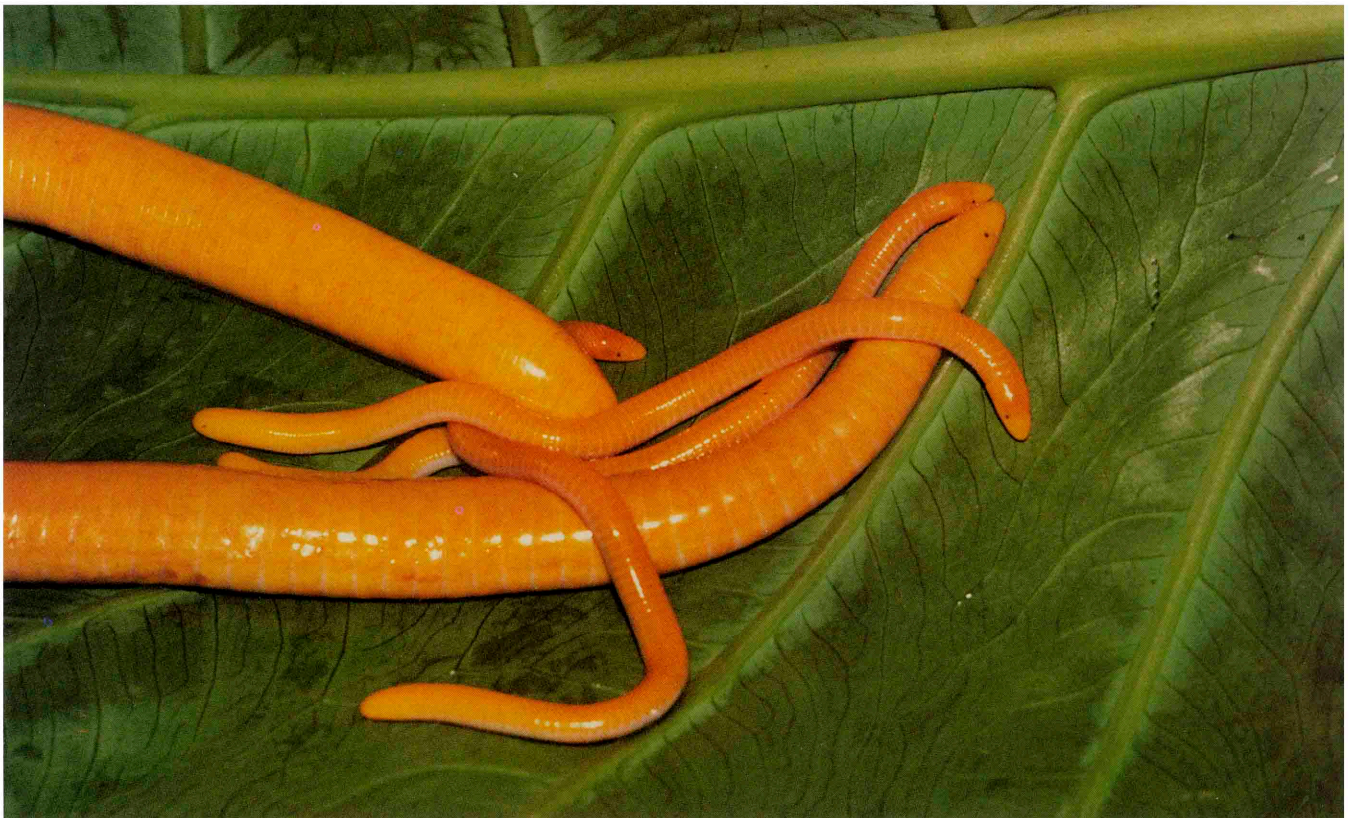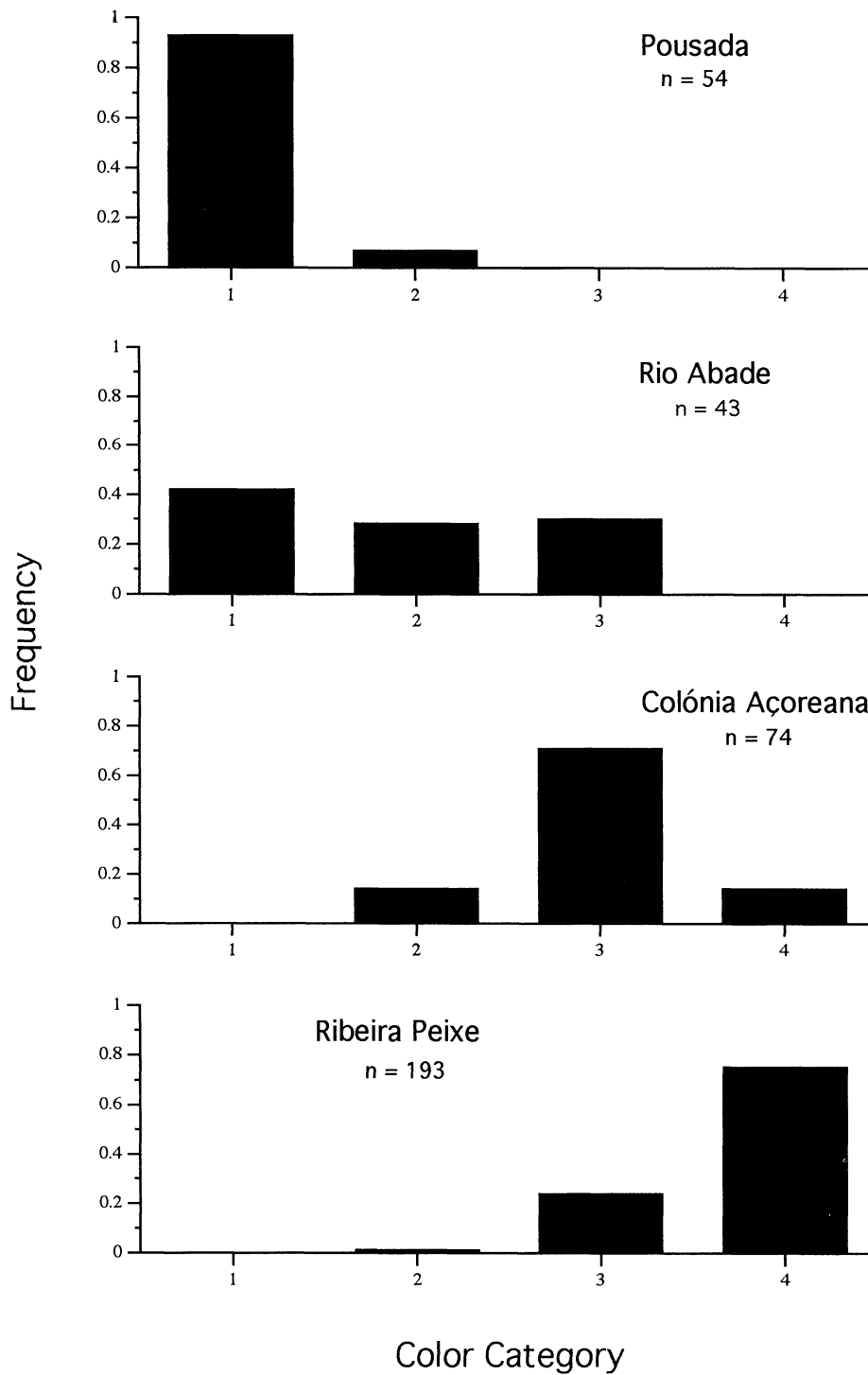
Figure 6. Clinal geographic variation in dorsal coloration of *Schistometopum thomense.* Color category (1) bright yellow, immaculate; (2) dark yellow, immaculate; (3) dark yellow, light to moderate brown flecking; (4) dark yellow, heavy brown flecking. The histograms are ordered by geographic proximity (see Fig. 2).

Figure 4 (facing page). Five *Schistometopum thomense* from Ribeira Peixe illustrating intrapopulation variation in dorsal coloration within the *ephele* color type.

Figure 5 (facing page). A female *Schistometopum thomense* from Pousada with her full complement of offspring born within a few hours of the time the photograph was taken. The adult color pattern is present at birth in both the Pousada and Ribeira Peixe (not shown) populations.

Table 3. Ventral coloration of *Schistometopum* from São Tomé by population. Means and standard errors of the numbers of annuli colored yellow, brown, and white along a randomly selected midventral segment of 20 annuli. Ponta Furada is an isolated western locality; Pousada includes both Pousada and Road to Pousada.

| | | Ventral Annulus Color | | | | | |
| | | Yellow | | Brown | | White | |
Population	n	Mean	SE	Mean	SE	Mean	SE
2 Pousada	54	8.76	1.22	0.00	0.00	11.24	1.22
4 Pedroma	34	6.85	1.08	0.00	0.00	13.15	1.08
5 Rio Abade	43	6.98	0.91	0.12	0.07	12.91	0.90
6 Alto Douro I	14	5.93	1.34	1.36	0.63	12.71	1.62
7 Colónia Açoreana	74	8.05	0.67	2.54	0.28	9.43	0.79
8 Ribeira Peixe	193	10.03	0.27	9.77	0.27	0.22	0.12
9 Alto Douro II	26	14.92	0.63	5.00	0.64	0.08	0.08
1 Ponta Furado	23	4.57	0.94	0.09	0.09	15.35	0.96

other populations were also examined, but, because no striking differences were found, and in the interest of space, the univariate results are not presented here. Instead, the multivariate technique of discriminant functions analysis was used to compare these populations to the Pousada and Ribeira Peixe populations, the two populations that are maximally different in coloration. Discriminant functions were calculated for the Pousada and Ribeira Peixe populations, and the data from specimens of the remaining populations were applied to the functions to determine which of the two base populations they would most likely be assigned to based on their overall characteristics.

Because of the strong sexual signal in the multivariate data, discriminant functions analyses for comparing populations were done separately by sex. The results are summarized in Table 11. The percentage of individuals within geographically intermediate populations assigned *a posteriori* to either Pousada or Ribeira Peixe is related to the geographic distance of the population from Pousada and Ribeira Peixe (Fig. 9), suggesting clinal variation in morphometric and meristic characteristics. Three other populations, Rolas, Alto Douro II, and Ponta Furado, are not positioned geographically between Pousada and Ribeira Peixe. The two individuals from Rolas are split between assignments to Pousada and Ribeira Peixe, even though Rolas Island is much closer to the latter. Alto Douro II is close to, and southeast of, Ribeira Peixe, and specimens from there are colored similarly to the freckled Ribeira Peixe animals. Even so, 30.0 and 12.5% of males and females, respectively, from Alto Douro II are assigned to distant Pousada. The Ponta Furado population is on the western side of the island, and specimens from there are intermediate in dorsal coloration between Pousada and Ribeira Peixe (Table 2), but more similar to Pousada in ventral coloration (Table 3). Nevertheless, a higher percentage of both males and females from Ponta Furado are assigned to Rebeira Peixe than to Pousada based on multivariate morphometrics (Table 11).

Taxonomic conclusions.–Taylor (1965) distinguished *Schistometopum ephele* from *S. thomense* on the basis of brown freckling and smaller and more pointed heads in the former. We demonstrated clinal geographic variation in coloration between immaculate yellow (*thomense*) and brown freckled (*ephele*) populations. We also demonstrated clinal variation in morphology between these populations. Taylor (1965, 1968) apparently was unaware of sexual dimorphism in head size and shape in both the *thomense* and the *ephele* morphs, as we demonstrated herein. Taylor did not identify the sex of the holotype of *S. ephele*, but based on his comments about the small and pointed head, also indicated in his accompanying photographs, we predicted accurately that it would prove to be a female. We conclude there is no justification for recognizing *S. ephele* and consider it to be a junior synonym of *S. thomense*.

STATUS OF
SCHISTOMETOPUM BREVIROSTRE (PETERS)

From 1880 (Peters) until 1965 (Taylor), *Schistometopum brevirostre* existed only as a junior synonym of *S. thomense*. Neither Peters nor Taylor clearly explained their reasons for, respectively, synonymizing and resurrecting *S. brevirostre*. Taylor (1965) was the first to assign specimens other than the holotype to *S. brevirostre*, but his determinations were obscure. He believed *S. brevirostre* is bluish gray compared to the yellowish *S. thomense*, but Peters (1880) had already pointed out that the color of the type of *S. brevirostre* resulted from fading. Taylor also believed the head was somewhat elongated compared to *S. thomense*, however he was unaware of the sexual and geographic variation in head shape and size. He also believed *S. brevirostre* has fewer splenial teeth, "4-5", (1965:299), but one and two pages later in the same publication he lists splenial tooth counts of "9-9" and "10-11" for the specimens he assigned to this species.

Taylor (1965, 1968) indicated that the holotype of
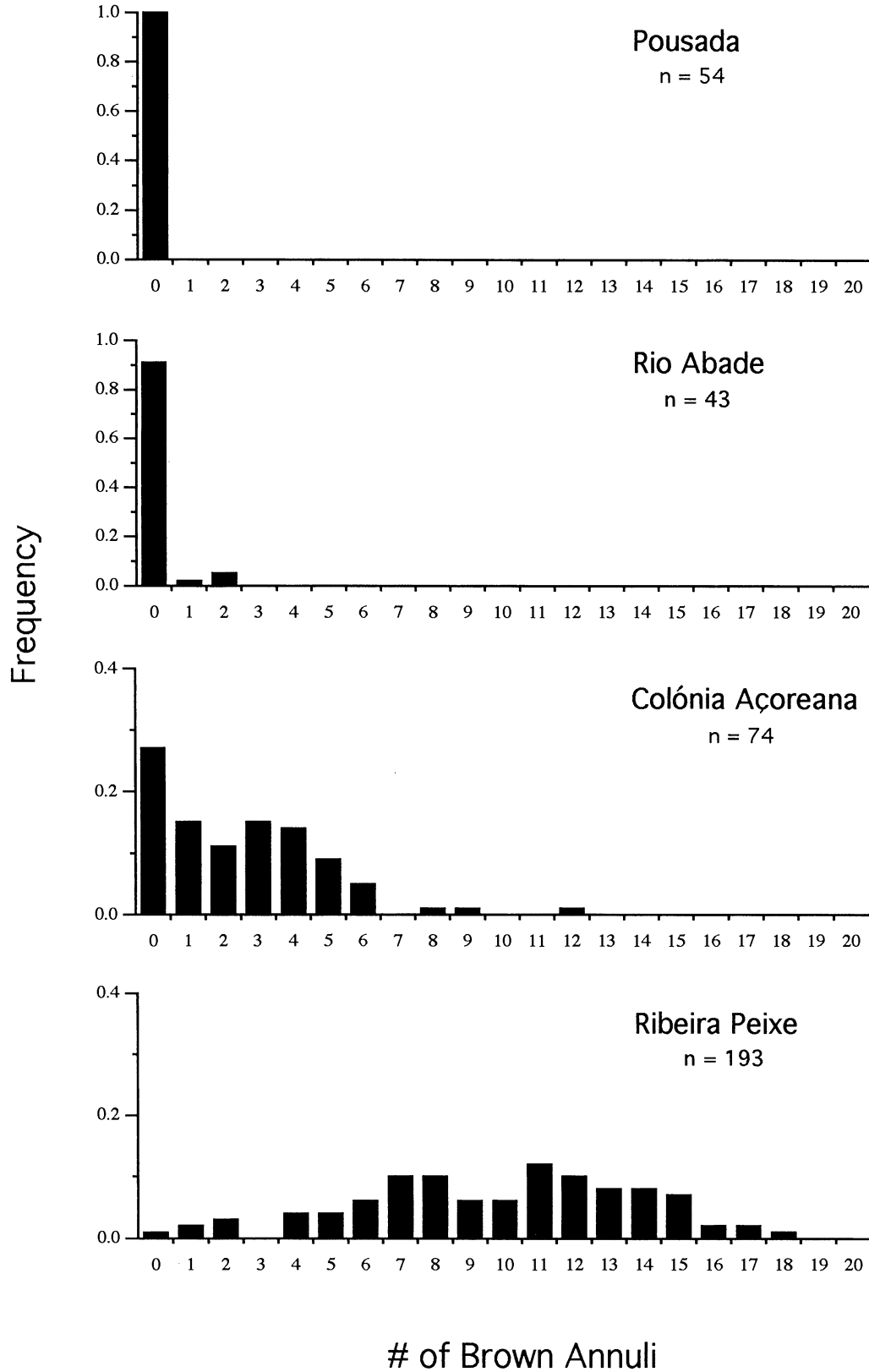
Figure 7. Clinal geographic variation in ventral coloration of *Schistometopum thomense*. The histograms show the number of brown ventral annuli (see Fig. 3b and methods) along a randomly chosen 20-annulus segment of the venter. The histograms are ordered by geographic proximity.

Table 4. Midventral coloration of *Schistometopum* from São Tomé by population: frequency of individuals in populations with different amounts of white coloration along the midventral line. Pousada to Alto Douro II are geographically ordered eastern localities; Ponta Furada is an isolated western locality; Pousada includes both Pousada and Road to Pousada.

	(1) white	(2) scattered	(3) none	n
2 Pousada	0.96	0.02	0.02	54
4 Pedroma	1.00	0.00	0.00	34
5 Rio Abade	1.00	0.00	0.00	43
6 Alto Douro I	0.93	0.07	0.00	14
7 Colónia Açoreana	1.00	0.00	0.00	74
8 Ribeira Peixe	0.06	0.23	0.71	193
9 Alto Douro II	0.00	0.46	0.54	26
1 Ponta Furada	1.00	0.00	0.00	23

Table 5. Size (total length, mm) variation in *Schistometopum*.

	Males				Females			
	Mean	SE	Range	N	Mean	SE	Range	N
S. thomense (all)	215.2	4.48	135-344	92	208.4	3.29	129-340	160
1 Ponta Furada	186.5	11.50	175-198	2	179.5	7.68	129-237	18
2 Pousada	230.1	13.41	155-344	17	220.7	6.44	161-340	33
3 Road to Pousada	——	——	——	—	——	——	——	—
4 Pedroma	184.8	5.71	158-238	14	188.2	2.74	175-208	16
5 Rio Abade	214.9	7.73	182-282	14	213.0	7.09	172-259	16
6 Alto Douro I	301.5	16.02	258-331	4	313.1	4.84	293-333	10
7 Colónia Açoreana	219.9	8.73	182-281	11	201.4	3.95	161-232	19
8 Ribeira Peixe	219.1	6.18	181-291	18	204.6	5.83	154-291	32
9 Alto Douro II	179.0	9.12	135-217	10	181.7	6.35	132-222	16
10 Rolas	281.0	25.00	256-306	2	——	——	——	—
S. gregorii (Kenya)	246.7	12.44	141-336	23	259.7	13.92	152-350	22
S. gregorii (Tanzania)	——	——	——	—	293.5	12.5	281-306	2

Siphonops brevirostris was not available for examination when he visited the Berlin Museum in 1961. Wake (1985) apparently interpreted this to mean the type is "lost". One of us (RAN) borrowed caecilians from the Berlin Museum in 1986 and among them identified two very similar specimens (ZMB A600 and 4911) one of which, presumably the latter, was likely to be the holotype of *S. brevirostris*. In a letter to RAN dated 27 October 1992, Dr. Rainer Günther confirmed that ZMB 4911 is the holotype of *S. brevirostris*. Dr. Günther wrote that Peters (1874) had incorrectly listed the holotype as number 4711, which led to the confusion and suggestion that the type was lost.

When examined by RAN in 1986, the holotype was grayish brown with somewhat lighter annular grooves. The coloration is typical of specimens that have faded with preservative and age. Our morphometric and meristic data recorded from the holotype (Table 12) differ only slightly from that of Peters (1874), and demonstrate that, in agreement with Peters (1880) and contrary to Taylor (1965, 1968), there is no basis for recognizing *Schistometopum brevirostre*. We consider it to be a junior synonym of *S. thomense*.

STATUS OF *SCHISTOMETOPUM GARZONHEYDTI* TAYLOR AND SALVADOR

Based on the original description of *Schistometopum garzonheydti* Taylor and Salvador, 1978, it was apparent that this form could not be a *Schistometopum*. This was surprising, because Taylor was the foremost authority on caecilians and had described many new families and genera and provided diagnoses for all genera (Taylor, 1968). RAN examined the holotype, MNCN 1239, in 1987 and found that it was badly dried and brittle with a broken body and cut jaws. The color was generally yellow-brown resulting from drying and perhaps bleaching, as indicated by the rather irregular and asymmetrical intensity of the yellow-brown coloration. The annular grooves are clearly edged in white, although in 1987 this was only faintly indicated on some grooves, resulting from fading. The tentacles are far forward, nearly even with the anterior margin of the mouth, much closer to the nares than to the distinct eyes. This is unlike *Schistometopum*, in which the tentacular apertures are much closer to the eyes than to the nares. Unlike *Schistometopum*, the tongue bears a pair of narial plugs

Table 6. Analysis of covariance of morphometric and meristic characters of males and females of *Schistometopum thomense:* Pousada sample only, means adjusted to size (TL), measurements in mm, variables untransformed.

	Adjusted mean	F-test (p) equal slopes	Scheffé (p) difference	r^2
Body width		0.836	0.616	
males (n = 17)	9.28			0.849[a]
females (n = 33)	9.13			0.722[a]
Head length		0.028*	——	
males	——			0.942[a]
females	——			0.837[a]
Head width		0.033*	——	
males	——			0.919[a]
females	——			0.806[a]
Interorbital distance		0.002*	——	
males	——			0.918[a]
females	——			0.817[a]
Internarial distance		0.173	0.017*	
males	1.00			0.811[a]
females	0.92			0.524[a]
Eye-naris distance		0.007*	——	
males	——			0.939[a]
females	——			0.823[a]
Eye-tentacle distance		0.072	0.121	
males	0.77			0.882[a]
females	0.72			0.631[a]
Tentacle-naris distance		0.005*	——	
males	——			0.928[a]
females	——			0.861[a]
Primary annuli		0.745	0.366	
males	96.8			0.000
females	97.3			0.009
Vent primary annuli		0.157	0.085	
males	2.06			0.057
females	1.76			0.033
Secondary annuli		0.099	0.883	
males	34.2			0.318
females	34.6			0.000
Complete secondary annuli		0.150	0.740	
males	6.3			0.201
females	6.1			0.000
Max-premaxillary teeth		0.749	0.895	
males[1]	30.8			0.248[c]
females[1]	30.9			0.207
Vomeropalatine teeth		0.305	0.877	
males[1]	32.6			0.006
females[1]	32.4			0.105
Dentary teeth		0.079	0.793	
males[1]	22.8			0.017
females[1]	22.7			0.197
Splenial teeth		0.436	0.643	
males[1]	18.7			0.119
females[1]	18.3			0.013
Vertebrae		0.909	0.200	
males	101.3			0.002
females	102.0			0.003
Posterior scales rows		0.040	0.527	
males	4.0			0.002
females	4.2			0.186[c]
Primary annuli with scales		0.778	0.038*	
males	70.7			0.401[b]
females	76.4			0.375[a]

* significant difference in mean and/or slope
[1] samples sizes for tooth counts differ from other characters: males (n = 17), females (n = 15)
a p < 0.001
b p < 0.01
c p < 0.05

Table 7. Analysis of covariance of morphometric and meristic characters of males and females of *Schistometopum thomense:* Ribeira Peixe sample only, means adjusted to size (TL), measurements in mm, variables untransformed.

	Adjusted mean	F-test (p) equal slopes	Scheffé (p) difference	r^2
Body width		0.209	0.000*	
males (n = 18)	7.91			0.667[a]
females (n = 32)	9.14			0.827[a]
Head length		0.002*	——	
males	——			0.853[a]
females	——			0.674[a]
Head width		0.001*	——	
males	——			0.751[a]
females	——			0.769[a]
Interorbital distance		0.051	0.000*	
males	3.92			0.667[a]
females	3.52			0.656[a]
Internarial distance		0.028*	——	
males	——			0.470[b]
females	——			0.271[b]
Eye-naris distance		0.001*	——	
males	——			0.846[a]
females	——			0.605[a]
Eye-tentacle distance		0.051	0.059	
males	0.95			0.477[b]
females	0.84			0.131[c]
Tentacle-naris distance		0.001*	——	
males	——			0.759[a]
females	——			0.494[a]
Primary annuli		0.447	0.097	
males	94.6			0.165
females	93.6			0.028
Vent primary annuli		0.616	0.803	
males	1.54			0.000
females	1.57			0.036
Secondary annuli		0.095	0.334	
males	35.8			0.102
females	33.1			0.028
Complete secondary annuli		0.386	0.508	
males	6.1			0.055
females	5.8			0.004
Max-premaxillary teeth		0.858	0.131	
males[1]	29.5			0.123
females[1]	31.0			0.335
Vomeropalatine teeth		0.211	0.167	
males[1]	36.0			0.409[c]
females[1]	34.2			0.113
Dentary teeth		0.678	0.819	
males[1]	23.2			0.002
females[1]	23.0			0.074
Splenial teeth		0.411	0.874	
males[1]	18.2			0.372
females[1]	18.4			0.259
Vertebrae		0.449	0.118	
males	99.2			0.087
females	98.3			0.006
Posterior scales rows		0.552	0.433	
males	4.6			0.009
females	4.4			0.009
Primary annuli with scales		0.743	0.000*	
males	75.5			0.190[c]
females	66.6			0.082

* significant difference in mean and/or slope
[1] samples sizes for tooth counts differ from other characters: males (n = 10), females (n = 10)
a p < 0.001
b p < 0.01
c p < 0.05

Schistometopum thomense
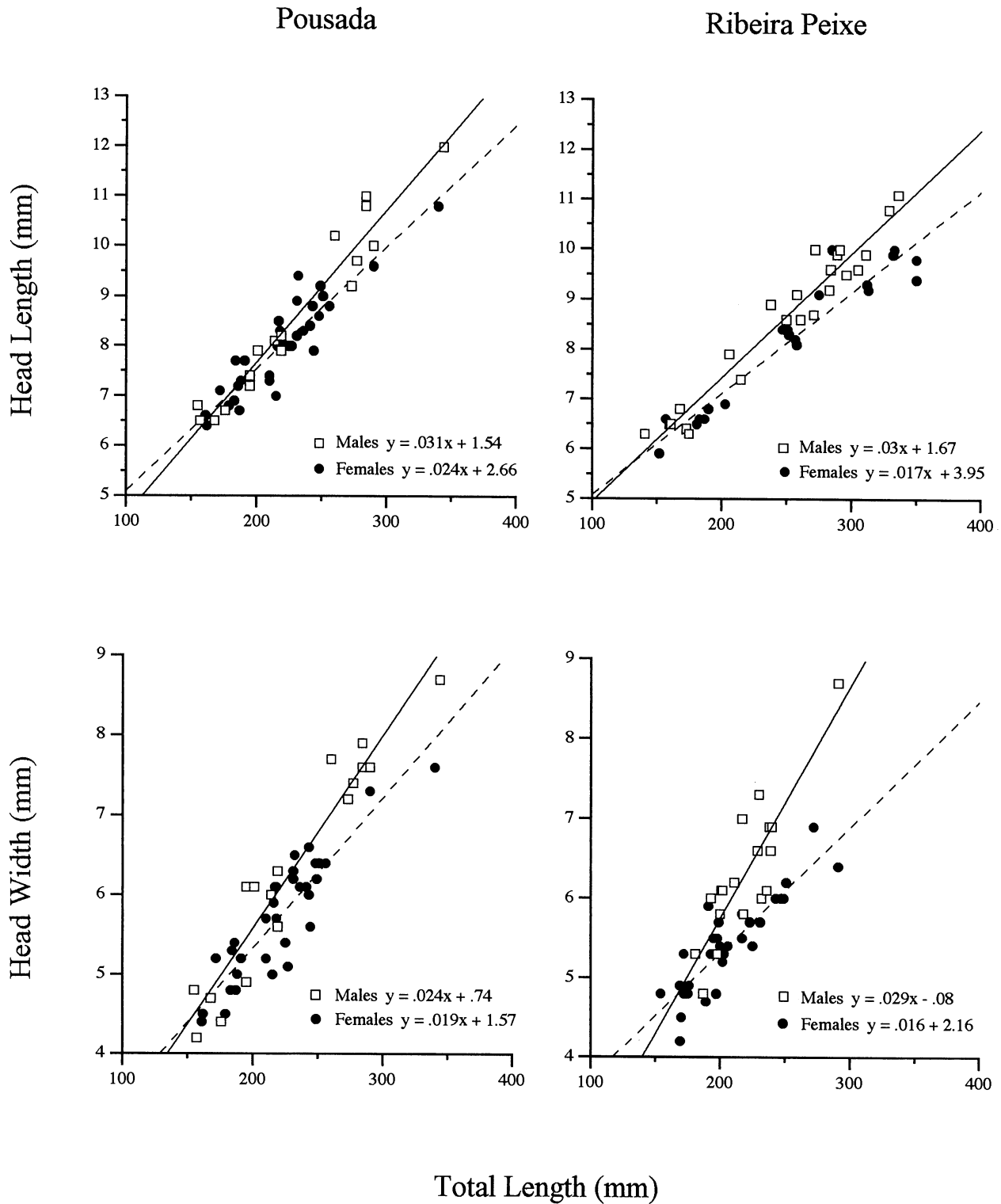
Figure 8. Regression of head length and head width on total length for males and females of the Pousada and Ribeira Peixe populations of *Schistometopum thomense*. Adult males have larger heads than females in both populations. The sexual dimorphism is greatest in the Ribeira Peixe population.

Table 8. Analysis of covariance of morphometric and meristic characters of Pousada and Ribeira Peixe populations of *Schistometopum thomense*: male samples only, means adjusted to size (TL), measurements in mm, variables untransformed.

	Adjusted mean	F-test (p) equal slopes	Scheffé (p) difference	r^2
Body width		0.442	0.061	
Pousada (n = 17)	9.29			0.849[a]
Ribeira Peixe (n = 18)	8.67			0.667[a]
Head length		0.923	0.780	
Pousada	8.42			0.942[a]
Ribeira Peixe	8.46			0.853[a]
Head width		0.275	0.072	
Pousada	6.16			0.919[a]
Ribeira Peixe	6.44			0.751[a]
Interorbital distance		0.464	0.143	
Pousada	3.97			0.918[a]
Ribeira Peixe	4.13			0.617[a]
Internarial distance		0.049*	——	
Pousada	——			0.811[a]
Ribeira Peixe	——			0.470[b]
Eye-naris distance		0.857	0.005*	
Pousada	4.11			0.939[a]
Ribeira Peixe	4.34			0.846[a]
Eye-tentacle distance		0.649	0.000*	
Pousada	0.77			0.882[a]
Ribeira Peixe	1.01			0.477[b]
Tentacle-naris distance		0.928	0.042*	
Pousada	3.41			0.928[a]
Ribeira Peixe	3.56			0.759[a]
Primary annuli		0.135	0.002*	
Pousada	96.8			0.000
Ribeira Peixe	94.8			0.165
Vent primary annuli		0.661	0.023*	
Pousada	2.05			0.057
Ribeira Peixe	1.57			0.000
Secondary annuli		0.707	0.423	
Pousada	33.9			0.318[c]
Ribeira Peixe	36.3			0.102
Complete secondary annuli		0.640	0.932	
Pousada	6.3			0.201
Ribeira Peixe	6.2			0.000
Max-premaxillary teeth		0.821	0.219	
Pousada[1]	30.8			0.248[c]
Ribeira Peixe[1]	29.7			0.123
Vomeropalatine teeth		0.099	0.008*	
Pousada[1]	32.6			0.006
Ribeira Peixe[1]	36.6			0.409[c]
Dentary teeth		0.751	0.660	
Pousada[1]	22.8			0.017
Ribeira Peixe[1]	23.2			0.002
Splenial teeth		0.159	0.956	
Pousada[1]	18.7			0.119
Ribeira Peixe[1]	18.8			0.372
Vertebrae		0.329	0.004*	
Pousada	101.3			0.002
Ribeira Peixe	99.2			0.087
Posterior scales rows		0.757	0.072	
Pousada	4.1			0.002
Ribeira Peixe	4.6			0.009
Primary annuli with scales		0.445	0.053	
Pousada	70.8			0.401[b]
Ribeira Peixe	77.0			0.190

* significant difference in mean and/or slope

[1] samples sizes for tooth counts differ from other characters: Pousada (n = 17), Ribeira Peixe (n = 10)

a p < 0.001

b p < 0.01

c p < 0.05

Table 9. Analysis of covariance of morphometric and meristic characters of Pousada and Ribeira Peixe populations of *Schistometopum thomense*: female samples only, means adjusted to size (TL), measurements in mm, variables untransformed.

	Adjusted mean	F-test (p) equal slopes	Scheffé (p) difference	r²
Body width		0.008*	——	
Pousada (n = 33)	——			0.722[a]
Ribeira Peixe (n = 32)	——			0.827[a]
Head length		0.011*	——	
Pousada	——			0.837[a]
Ribeira Peixe	——			0.674[a]
Head width		0.191	0.462	
Pousada	5.59			0.806[a]
Ribeira Peixe	5.53			0.769[a]
Interorbital distance		0.775	0.456	
Pousada	3.58			0.817[a]
Ribeira Peixe	3.54			0.656[a]
Internarial distance		0.929	0.000*	
Pousada	0.89			0.524[a]
Ribeira Peixe	1.09			0.271[b]
Eye-naris distance		0.016*	——	
Pousada	——			0.823[a]
Ribeira Peixe	——			0.605[a]
Eye-tentacle distance		0.106	0.000*	
Pousada	0.67			0.631[a]
Ribeira Peixe	0.85			0.131[c]
Tentacle-naris distance		0.001*	——	
Pousada	——			0.861[a]
Ribeira Peixe	——			0.494[a]
Primary annuli		0.278	0.000*	
Pousada	97.3			0.009
Ribeira Peixe	93.6			0.028
Vent primary annuli		0.147	0.132	
Pousada	1.76			0.033
Ribeira Peixe	1.56			0.036
Secondary annuli		0.514	0.449	
Pousada	34.6			0.000
Ribeira Peixe	33.0			0.028
Complete secondary annuli		0.789	0.539	
Pousada	6.1			0.000
Ribeira Peixe	5.8			0.004
Max-premaxillary teeth		0.817	0.736	
Pousada[1]	30.7			0.207
Ribeira Peixe[1]	30.9			0.335
Vomeropalatine teeth		0.709	0.262	
Pousada[1]	32.1			0.105
Ribeira Peixe[1]	34.2			0.113
Dentary teeth		0.118	0.540	
Pousada[1]	22.5			0.197
Ribeira Peixe[1]	22.9			0.074
Splenial teeth		0.146	0.832	
Pousada[1]	18.2			0.013
Ribeira Peixe[1]	18.4			0.259
Vertebrae		0.561	0.000*	
Pousada	102.0			0.005
Ribeira Peixe	98.3			0.006
Posterior scales rows		0.187	0.180	
Pousada	4.1			0.186[c]
Ribeira Peixe	4.4			0.009
Primary annuli with scales		0.152	0.000*	
Pousada	75.0			0.375[a]
Ribeira Peixe	67.1			0.082

*significant difference in mean and/or slope
[1]sample sizes for tooth counts differ from other characters: Pousada (n =15), Ribeira Peixe (n = 10)
[a] $p < 0.001$
[b] $p < 0.01$
[c] $p < 0.05$

Table 10. Discriminant functions analysis: *a posteriori* classification of all individuals of *Schistometopum thomense* from Pousada and Ribeira Peixe and *S. gregorii* from Kenya as either male or female; two sets of discriminant functions were calculated for *S. thomense*, the first included the total sample without the four tooth count variables and the second included a subset of the samples with the four tooth count variables; values are numbers and percent of individuals.

		Predicted Group Membership	
Actual group	n	males	females
Schistometopum thomense			
A. without tooth counts			
Pousada			
males	17	11 [64.7%]	6 [35.3%]
females	33	3 [9.1%]	30 [90.9%]
Ribeira Peixe			
males	18	17 [94.4%]	1 [5.6%]
females	32	0 [0.0%]	32 [100.0%]
B. with tooth counts			
Pousada			
males	17	16 [94.1%]	1 [5.9%]
females	15	1 [6.7%]	14 [93.3%]
Ribeira Peixe			
males	10	10 [100%]	0 [0%]
females	10	0 [0%]	10 [100%]
Schistometopum gregorii			
A. with tooth counts			
males	21	19 [90.5%]	2 [9.5%]
females	22	1 [4.5%]	21 [95.5%]

Table 11. Discriminant functions analysis: *a posteriori* assignment of all individuals from São Tomé populations of *Schistometopum* to either the Pousada or the Ribeira Peixe populations; all variables included; data are number of individuals and percentage of total population.

			Predicted Group Membership			
	n		2 Pousada		8 Ribeira Peixe	
Actual group	males	females	males	females	males	females
1 Ponta Furado	2	18	0 0.0%	6 33.3%	2 100.0%	12 67.6%
2 Pousada*	17	33	17 100.0%	33 100.0%	0 0.0%	0 0.0%
4 Pedroma	14	16	14 100.0%	14 87.5%	0 0.0%	2 12.5%
5 Rio Abade	14	16*	10 71.4%	12 80.0%	4 28.6%	3 20.0%
6 Alto Douro I	4*	10	1 33.3%	1 10.0%	2 66.7%	9 90.0%
7 Colónia Açoreana	11	19	8 72.7%	3 15.8	3 27.3%	16 84.2%
8 Ribeira Peixe	18	32	0 0.0%	0 0.0%	18 100.0%	32 100.0%
9 Alto Douro II	10	16	3 30.0%	2 12.5%	7 70.0%	14 87.5%
10 Rolas	2	0	1 50.0%	—— ——	1 50.0%	—— ——

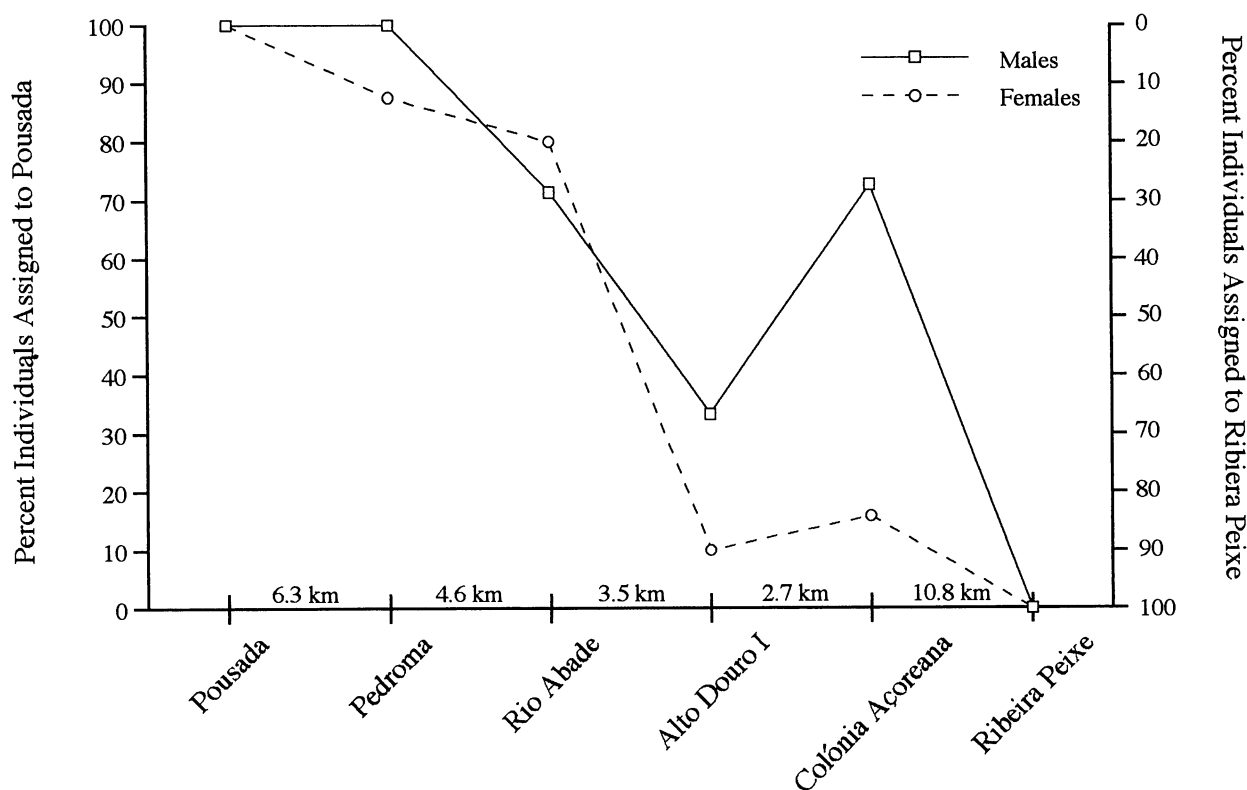* missing case disallowed for one specimen

Figure 9. Similarities between adjacent populations of *Schistometopum thomense* based on multivariate analysis of morphometric and meristic data. The graphs show the percent of males and females of geographically ordered populations that are assigned *a posteriori* through discriminant functions analysis to either the Pousada or the Ribeira Peixe populations. Population sample sizes given in Table 1.

Table 12. Morphometric and meristic comparisons of holotypes of *Schistometopum* (measurements in mm).

	brevirostre ZMB 4911	*ephele* MSNG 8773	*garzonheydti* MNCN 1239	*gregorii* BM 1946.9.5.53
Sex	female	female	unknown	unknown
Maturity	adult	adult	adult (?)	adult (?)
Total length	208	185	225	289
Body width	7	8	10	10
Head length	7.6	7.3	7.7	11.0
Head width	5.2	5.7	6.5	7.3
Interorbital distance	3.3	3.1	3.6	4.9
Internarial distance	0.8	0.9	1.6	2.6
Eye-naris distance	3.5	3.4	3.2	4.5
Eye-tentacle distance	0.7	0.7	3.1	1.7
Tentacle-naris distance	2.8	2.6	1.2	3.4
Primary annuli	97	96	90	114
Vent primary annuli	2	2	2	3
Secondary annuli	34	40	42	46
Complete secondary annuli	5	8	7	11
Max-premaxillary teeth	29	29	40	32
Vomeropalatine teeth	35	—*	36	27
Dentary teeth	23	24	30	26
Splenial teeth	16	18	34	2
Vertebrae	100	99	95	118
Posterior scale rows	3	1	4	5
Primary annuli with scales	71	64	40	94

*vomeropalatine teeth uncountable

Table 13. Analysis of covariance of morphometric and meristic characters of males and females of *Schistometopum gregorii*: Kenya sample only, means adjusted to size (TL), measurements in mm, variables untransformed.

	Adjusted mean	F-test (p) equal slopes	Scheffé (p) difference	r²
Body width		0.540	0.637	
males (n = 23)	8.73			0.845[a]
females (n = 22)	8.62			0.887[a]
Head length		0.018*	——	
males	——			0.946[a]
females	——			0.923[a]
Head width		0.046*	——	
males	——			0.901[a]
females	——			0.898[a]
Interorbital distance		0.075	0.010*	
males	4.20			0.889[a]
females	3.97			0.872[a]
Internarial distance		0.310	0.033*	
males	2.28			0.791[a]
females	2.12			0.683[a]
Eye-naris distance		0.072	0.005*	
males	3.49			0.885[a]
females	3.25			0.844[a]
Eye-tentacle distance		0.056	0.000*	
males	1.16			0.857[a]
females	0.96			0.810[a]
Tentacle-naris distance		0.003*	——	
males	——			0.925[a]
females	——			0.826[a]
Primary annuli		0.690	0.724	
males	114.3			0.019
females	114.5			0.082
Vent primary annuli		0.278	0.602	
males	2.25			0.004
females	2.40			0.064
Secondary annuli		0.783	0.734	
males	42.6			0.137
females	43.1			0.272[c]
Complete secondary annuli		0.724	0.559	
males	8.8			0.026
females	8.5			0.111
Max-premaxillary teeth		0.558	0.139	
males	29.8			0.646[a]
females	28.8			0.814[a]
Vomeropalatine teeth		0.345	0.621	
males	25.6			0.773[a]
females	25.9			0.796[a]
Dentary teeth		0.216	0.012*	
males	25.7			0.759[a]
females	24.3			0.909[a]
Splenial teeth		0.099	0.353	
males	2.9			0.357[b]
females	2.6			0.012
Vertebrae		0.685	0.628	
males	117.1			0.037
females	117.4			0.092
Posterior scale rows		0.665	0.005*	
males	4.3			0.469[a]
females	3.5			0.630[a]
Primary annuli with scales		0.563	0.227	
males	78.8			0.788[a]
females	73.5			0.692[a]

* significant difference in mean and/or slope
a p < 0.001
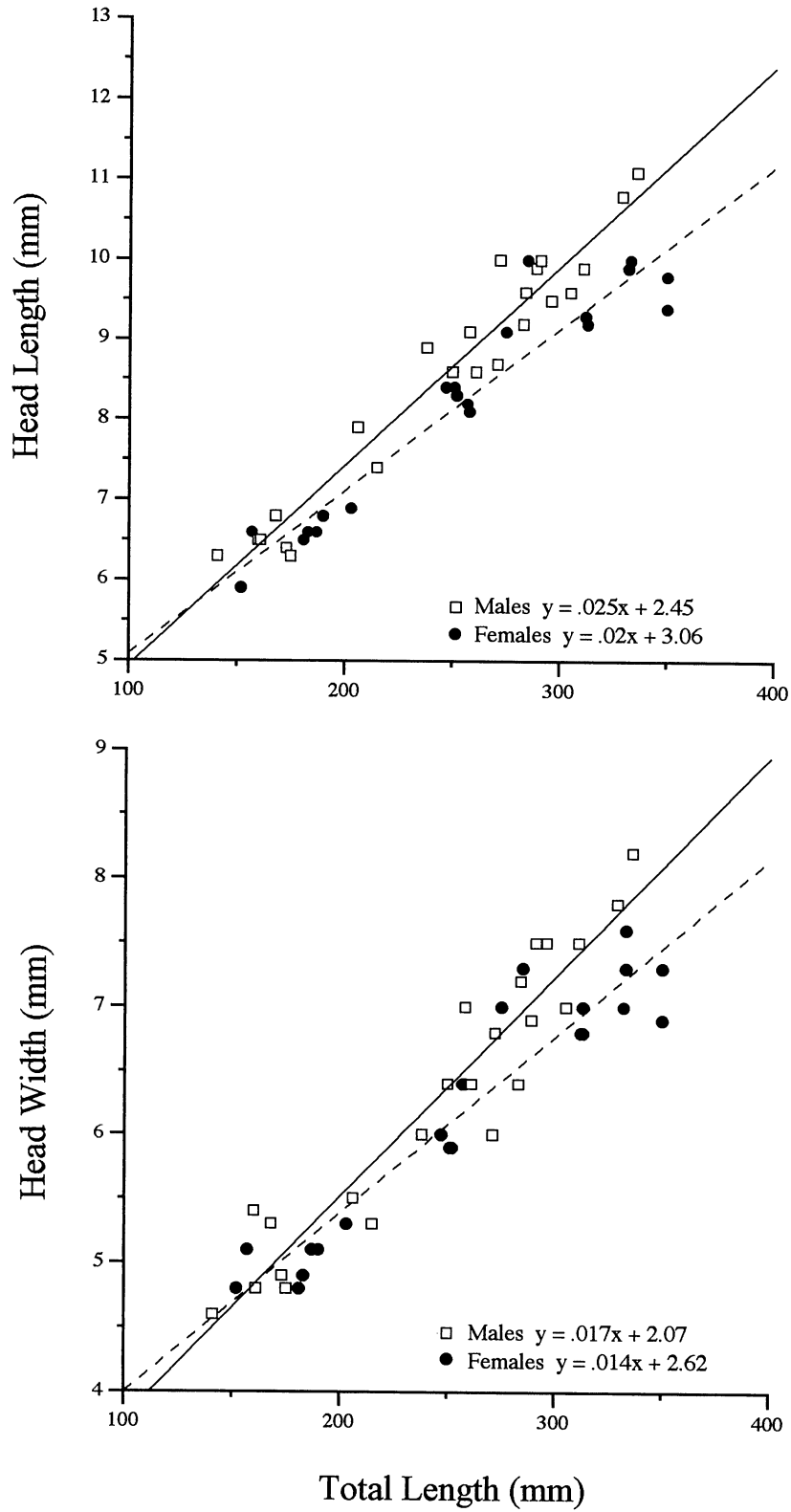b p < 0.01
c p < 0.05

Schistometopum gregorii

Figure 10. Sexual dimorphism in head size of *Schistometopum gregorii* parallels that observed in *S. thomense*. Graphs show scatter and least squares regression line. Sample sizes given in Table 13.

(smooth in the former). The teeth of all series are bicuspid, especially noticeable in the smaller more posterior teeth. The splenial teeth are very small. No attempt was made to determine the sex and condition of the gonads because of the fragility of the specimen.

Morphometric and meristic data for the holotype of *Schistometopum garzonheydti* are summarized in Table 12. These data differ only slightly from those presented by Taylor and Salvador (1978). The largest discrepancy is in the number of secondary annuli, stated to be 26 and 36 by Taylor and Salvador. The former value is probably a typographical error, as their 36 is much closer to RAN's count of 42 secondary annuli.

The holotype cannot be distinguished from *Geotrypetes seraphini*, a common caeciliid known from western equatorial Africa. Taylor and Salvador (1978) apparently were misled by the abnormal yellowish color of the holotype (*G. seraphini* is dark lavender or bluish black with white-edged annular grooves increasingly boldly marked posteriorly), and perhaps also by the type locality, "Fernando Po" (= Bioko), an island to the northeast of São Tomé where yellowish *Schistometopum* are known to occur. The holotype was reportedly collected in 1885 by Amado Osorio. If the locality is correct, then this is the first record of *G. seraphini*, or any caecilian, from Bioko, a large island close to the coast of Cameroon and perched upon the continental shelf, with a maximum depth of 60 m separating it from the nearby (32 km) mainland (Amadon, 1953; Exell, 1944). Príncipe, São Tomé, and Pagalu, all further to the southwest, are smaller, off the continental shelf, surrounded by deep water, and more depauperate. Bioko undoubtedly was connected to Cameroon by dry land during the last glacial maximum when sea-levels around the mid-latitudes were as much as 130 m lower than present (Milliman and Emory, 1968). Given the continental connection of Bioko and the observation that *G. seraphini* is common in Cameroon, the presence of this species on Bioko would not be surprising.

However, there is reason to believe the locality may be in error. There is another specimen in the Madrid collection, which, by its number (MNCN 1237), apparently was catalogued two specimens before the holotype of *Schistometopum garzonheydti*. It was reportedly collected in June, 1886, also by Amadio Osario on "Fernando Po". MNCN 1237 is also poorly preserved and obviously old, but it is readily identifiable as a typical specimen of *Caecilia tentaculata*, a caecilian restricted to northern South America. It is extremely unlikely that *C. tentaculata* occurs outside the Neotropics, which indicates an error in cataloguing. Interestingly, MNCN 1236 is another old, poorly preserved specimen of *C. tentaculata*, and it is plausibly recorded as being from Quito, Ecuador. MNCN 1238 is accurately identified as a *Herpele squalostoma* from "Rio Muni, continental Equatorial Guinea", and MNCN 1232, also accurately identified, is listed as *H. squalostoma* from Fernando Po. Both of the *H. squalostoma* specimens were collected in 1865 by Amado Osorio. Thus, it is clear that caecilians from both the Neotropics and the region of the Gulf of Guinea were

being cataloged at the same time in the Madrid Museum. It seems most likely that the holotype of *S. garzonheydti* (MNCN 1239, = *Geotrypetes seraphini*) and the specimen of *C. tentaculata* (MNCN 1237) were both wrongly recorded from Fernando Po at the same time and for the same (unknown) reason. Until additional specimens of *C. tentaculata* and/or *G. seraphini* are found on Bioko, they should not be considered to be part of the fauna of that island. Similarly, the record of *H. squalostoma* for Fernando Po is suspect.

STATUS OF
SCHISTOMETOPUM GREGORII (BOULENGER)

There has never been any doubt that *Schistometopum gregorii* is a valid and highly distinctive species. Two outstanding questions regarding this species are, firstly, whether or not *S. gregorii* and *S. thomense* form a natural group and, secondly, whether or not the Tanzanian population(s) of caecilians that are currently assigned to *S. gregorii* really belong to that species.

The broad geographic separation of *Schistometopum gregorii* (East African Coast) and *S. thomense* (island off the coast of West Africa), in addition to the large color and morphometric differences between the two species, is justification for questioning their monophyletic status. The question will have to be resolved in the context of a broad-based phylogenetic study that includes many other caeciliid genera. Here, we propose only to point out some of the differences and similarities between the two species.

Most specimens of *Schistometopum gregorii*, including the holotype, are from near the mouth of the Tana River, north of Mombasa, Kenya, and these were grouped together for morphometric analysis. Two specimens are from coastal Tanzania about 560-640 km south of the Tana River locality, and these were analyzed separately.

The results of a morphometric comparison of sexes within the Tana River sample of *Schistometopum gregorii* are summarized in Tables 5 and 13. It seems likely that females will prove to be the larger sex in this species, as females in our sample average 13 mm longer than males and have a maximum total length 14 mm greater than that of males (Table 5). As in *S. thomense*, there is sexual dimorphism in head length and width in this species, and in the same direction, with males having longer and wider heads than females at larger sizes. The adjusted means cannot be compared, because there are significant slope differences between the sexes in the regressions of head size on total length (Fig. 10), with the heads of males increasing in size in relation to total length at a faster rate. Correspondingly, males have significantly larger adjusted means than females for other head measurement with the exception of the distance between the tentacle and the naris, which can't be compared because of unequal slopes (Table 13). Here also males have the faster rate of increase relative to total length (slope for males =0.008; for females = 0.006). Two other morphometric characters are sexually dimor-
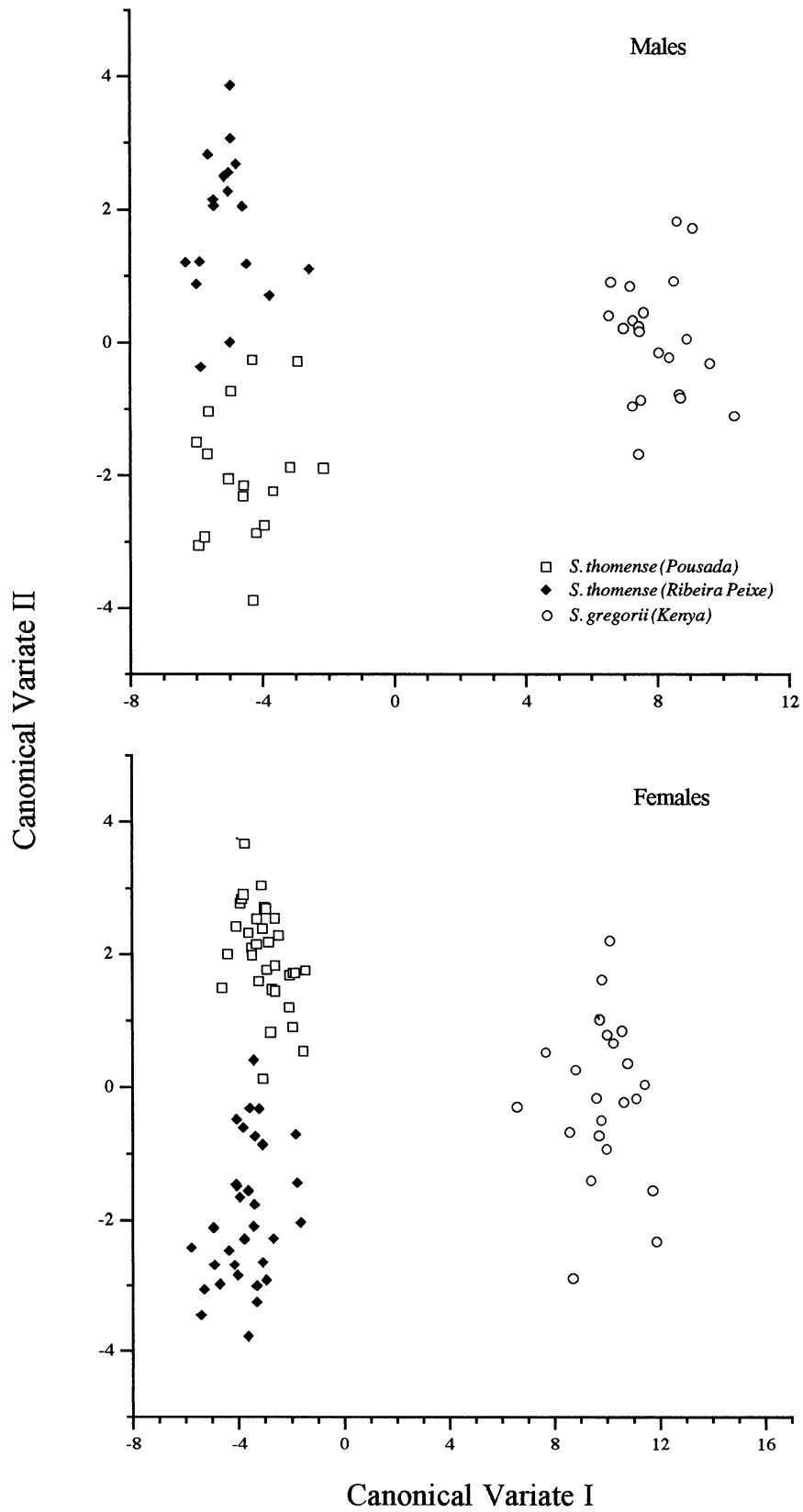
Figure 11. Distribution of individuals of *Schistometopum gregorii* (Kenya sample only) and *S. thomense* by sex on the first two canonical variates based on all morphometric and meristic characters except tooth counts. The first canonical variate accounts for 94.61 (males) and 91.97 (females) %, and the second canonical variate for the remaining 5.39 (males) and 8.03 (females) %, of the total variance. The results demonstrate microgeographic variation in morphometric and meristic characters of *S. thomense* that parallel microgeographic variation in color.

Table 14. Analysis of covariance of morphometric and meristic characters of *Schistometopum thomense* (Pousada and Ribeira Peixe combined) and *S. gregorii:* males only, means adjusted to size (TL), measurements in mm, variables untransformed; sample size same as indicated for body width throughout, except interorbital distance for *S. gregorii* sample.

	Adjusted mean	F-test (p) equal slopes	Scheffé (p) differences	r^2
Body width		0.077	0.000*	
thomense (n = 27)	9.68			0.809[a]
gregorii (n = 23)	8.20			0.845[a]
Head length		0.011*	——	
thomense	——			0.934[a]
gregorii	——			0.945[a]
Head width		0.001*	——	
thomense	——			0.879[a]
gregorii	——			0.901[a]
Interorbital distance		0.726	0.005*	
thomense	4.25			0.851[a]
gregorii (n = 22)	3.99			0.889[a]
Internarial distance		0.312	0.000*	
thomense	1.19			0.387[a]
gregorii	2.07			0.791[a]
Eye-naris distance		0.001*	——	
thomense	——			0.899[a]
gregorii	——			0.885[a]
Eye-tentacle distance		0.619	0.014*	
thomense	0.95			0.613[a]
gregorii	1.08			0.857[a]
Tentacle-naris distance		0.000*	——	
thomense	——			0.885[a]
gregorii	——			0.925[a]
Primary annuli		0.870	0.000*	
thomense	96.18			0.007
gregorii	114.21			0.019
Vent primary annuli		0.300	0.014*	
thomense	1.88			0.042
gregorii	2.13			0.004
Secondary annuli		0.216	0.003*	
thomense	34.19			0.223[c]
gregorii	41.89			0.137
Complete secondary annuli		0.116	0.000*	
thomense	6.41			0.182[c]
gregorii	8.69			0.026
Max-premaxillary teeth		0.022*	——	
thomense	——			0.197[c]
gregorii	——			0.646[a]
Vomeropalatine teeth		0.006*	——	
thomense	——			0.027
gregorii	——			0.773[a]
Dentary teeth		0.000*	——	
thomense	——			0.004
gregorii	——			0.759[a]
Splenial teeth		0.149	0.000*	
thomense	18.95			0.158[c]
gregorii	2.72			0.357[b]
Vertebrae		0.623	0.000*	
thomense	100.60			0.001
gregorii	116.98			0.037
Posterior scale rows		0.001*	——	
thomense	——			0.017
gregorii	——			0.469[a]
Primary annuli with scales		0.000*	——	
thomense	——			0.362[a]
gregorii	——			0.788[a]

* significant slope and/or difference
[a] $P < 0.001$
[b] $p < 0.01$
[c] $p < 0.05$

Table 15. Analysis of covariance of morphometric and meristic characters of *Schistometopum thomense* (Pousada and Ribeira Peixe combined) and *S. gregorii*: females only, means adjusted to size (TL), measurements in mm, variables untransformed.

	Adjusted mean	F-test (p) equal slopes	Scheffé (p) differences	r²
Body width		0.000*	——	
thomense (n = 25)	——			0.845[a]
gregorii (n = 22)	——			0.887[a]
Head length		0.319	0.001*	
thomense	8.31			0.890[a]
gregorii	7.91			0.923[a]
Head width		0.073	0.351	
thomense	6.02			0.838[a]
gregorii	5.93			0.898[a]
Interorbital distance		0.481	0.224	
thomense	3.93			0.832[a]
gregorii	3.84			0.872[a]
Internarial distance		0.036*	——	
thomense	——			0.255[b]
gregorii	——			0.683[a]
Eye-naris distance		0.081	0.000*	
thomense	4.07			0.854[a]
gregorii	3.11			0.844[a]
Eye-tentacle distance		0.478	0.618	
thomense	0.88			0.391[a]
gregorii	0.91			0.810[a]
Tentacle-naris distance		0.001*	——	
thomense	——			0.826[a]
gregorii	——			0.826[a]
Primary annuli		0.942	0.000*	
thomense	96.03			0.023
gregorii	114.36			0.082[c]
Vent primary annuli		0.213	0.002	
thomense	1.72			0.023
gregorii	2.36			0.064
Secondary annuli		0.185	0.000*	
thomense	32.04			0.011
gregorii	42.64			0.272[c]
Complete secondary annuli		0.464	0.000*	
thomense	5.73			0.000
gregorii	8.40			0.111
Max-premaxillary teeth		0.105	0.000*	
thomense	31.31			0.240[c]
gregorii	28.22			0.814[a]
Vomeropalatine teeth		0.270	0.000*	
thomense	33.56			0.079
gregorii	25.20			0.796[a]
Dentary teeth		0.000*	——	
thomense	——			0.064
gregorii	——			0.909[a]
Splenial teeth		0.186	0.000*	
thomense	18.53			0.084
gregorii	2.6			0.012
Vertebrae		0.827	0.000*	
thomense	100.7			0.015
gregorii	117.3			0.092
Posterior scale rows		0.035*	——	
thomense	——			0.069
gregorii	——			0.630[a]
Primary annuli with scales		0.005*	——	
thomense	——			0.211[c]
gregorii	——			0.692[a]

* significant slope and/or difference
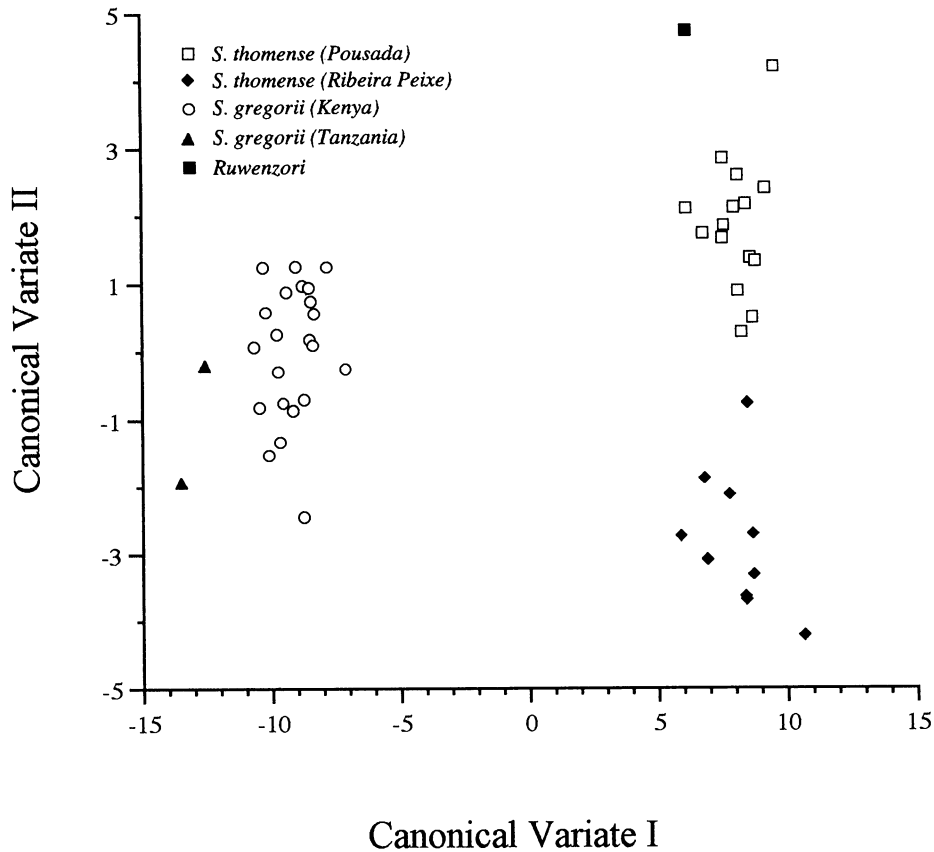[a] P < 0.001
[b] p < 0.01
[c] p < 0.05

Figure 12. Distribution of female *Schistometopum gregorii* and *S. thomense* on the first two canonical variates based on all morphometric and meristic data including the four tooth counts. The first canonical variable accounts for 96.35 %, and the second canonical variable for the remaining 3.65 %, of the total variance. All groups are clearly distinguished, as in the analysis without tooth counts (Fig. 11). The two Tanzanian females of *S. gregorii* and the putative Ruwenzori female of *S. thomense* are isolated.

phic. Males have more dentary teeth and more scale rows in the posterior annuli than females (Table 13). A *posteriori* assignment of individuals to sex indicates that discriminant functions analysis using all morphometric characters accurately distinguishes 90.5% of males and 95.5% of females, which suggests the overall degree of sexual dimorphism is greater than in the Pousada sample of *S. thomense*, but less than the Ribeira Peixe sample of the latter species (Table 10).

As expected, there is an ontogenetic increase in tooth number on all four rows for both sexes and no ontogenetic increase in annuli and vertebral counts (Table 13), with the exception that there is a slightly positive correlation between total length and the number of secondary annuli in females. There is a strong positive correlation in both sexes between total length and the number of primary annuli that have scales. This latter ontogenetic pattern is common to most caecilians that have scales (Nussbaum, unpublished). Scales appear first in the posteriormost annuli and develop progressively in the anterior direction. At any stage in development, the anteriormost scales that appeared late in ontogeny are tiny compared to the larger posteriormost scales that appeared early in ontogeny. As the animal grows, tiny anterior scales, at first undetectable, grow to the size at which they can be

seen macroscopically and recorded.

There is no ontogenetic nor sexual variation evident in coloration, but all of the available specimens are old, and their color in life is unknown, except for Loveridge's (1936:375) brief indication that they are "Uniform glossy black resulting in a lacquered appearance." Sexual dichromatism is unreported in caecilians and apparently does not occur in this species.

There are only two specimens, both females (MCZ 27901, 28601), available from southern coastal Tanzania that have been assigned to *Schistometopum gregorii*. Taylor (1968:676) indicated in a table that the type specimen (Senckenberg Museum 28) of *Bdellophis unicolor* (= *S. gregorii*) is from "Usambara, German East Africa", which if true would be a third record of *S. gregorii* from Tanzania. However, Boettger (1913:353) stated clearly that the specimen is from "Peccetoni im Wituland", which places it in Kenya near the type locality of *S. gregorii*. Taylor (1968:673) elsewhere in the same publication recorded the type locality of *Bdellophis unicolor* in accordance with Boettger.

Taylor (1968) reported differences in the number of secondary annuli between the two coastal Tanzanian specimens and the typical population to the north, but he was uncharacteristically reluctant to describe them as a new species on the basis of too few specimens. We also exam-

ined these two specimens, and, although our annuli counts differ slightly from those of Taylor (1968), we confirmed that they differ from the typical population mainly in having fewer secondary annuli (17-24 versus 26-56 among a sample of 46 from the Kenyan population). These two specimens also stand apart in a discriminant functions comparison of *Schistometopum gregorii* and *S. thomense* (Fig. 12). Although there is no overlap in the number of secondary annuli between the two populations, the intermediate geographic area has not been thoroughly explored for caecilians, and the possibility exists that populations intermediate in counts might exist in this region. We therefore concur with Taylor, that until further data are available, these southern forms are best included in typical *S. gregorii*.

A within sex, morphometric comparison of *Schistometopum gregorii* and *S. thomense* using covariance analysis reveals many differences between these two species (Tables 14 and 15). Compared to males of *S. thomense*, males of *S. gregorii* have a narrower body, shorter distance between the eyes, greater internarial distance, greater distance from the eye to the tentacle, more primary annuli, more primary annuli interrupted by the vent, more secondary annuli, more complete secondary annuli, far fewer splenial teeth, and more vertebrae. Several other characters (see Table 14) differ in their regressions on total length. Compared to females of *S. thomense*, females of *S. gregorii* have shorter heads, shorter distance from the eye to the naris, more primary annuli, more primary annuli interrupted by the vent, more secondary annuli, more complete secondary annuli, fewer premaxillary-maxillary teeth, far fewer splenial teeth, and more vertebrae. Among females, several characters differ between species in regression on total length (see Table 15).

In a multivariate comparison, using all variables except tooth counts, the first canonical variate strongly separates all specimens of *Schistometopum thomense* from Pousada and Ribeira Peixe from all specimens of *S. gregorii* (Fig. 11). The second canonical variate, accounting for much less of the variance, nevertheless nearly completely separates the male and female subpopulations of *S. thomense* from Pousada and Ribeira Peixe, two population separated by only 18 linear km.

A separate multivariate comparison of females was done using all data, including the four tooth counts, in order to assess the taxonomic importance of tooth counts, to further evaluate the morphometric relationships of the two females of *Schistometopum gregorii* from Tanzania, and to examine the morphometric position of a female *S. thomense* reputedly from the Ruwenzori region of central Africa. In this analysis (Fig. 12), the first canonical variate again separates all individuals of *S. thomense* and *S. gregorii*, but their positions on the axis are switched, and the first axis also separates the two Tanzanian females from the remaining female *S. gregorii*. All females of *S. thomense* from Pousada and Ribeira Peixe are separated completely along the second canonical axis when tooth counts are included. The female thought to be from the Ruwenzori region of

Zaire is also clearly separated from the other *S. thomense*, but is much closer to the Pousada population of that species. This is of interest, because the putative Ruwenzori female is also immaculate like Pousada individuals and unlike the strongly freckled individuals from Ribeira Peixe. We view this as evidence that the Ruwenzori specimen might be a mislabeled specimen from São Tomé.

SYNOPSIS

Schistometopum Parker

Schistometopum Parker, 1941:17. Type species *Dermophis gregorii* Boulenger, 1894, by original designation.

Diagnosis.–Caeciliids with eye not under bone, in socket formed mostly by squamosal, anterior border formed by maxilla; no temporal fossae; mesethmoid exposed dorsally between separated frontals; splenial teeth present; secondary annuli present; scales present; tentacular aperture closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content.–Two species, *gregorii* and *thomense*.

Distribution.–Restricted to eastern and western equatorial Africa: Kenya, Tanzania, and São Tomé Island in the Gulf of Guinea, and possibly Príncipe Island in the Gulf of Guinea and eastern Zaire.

Etymology.–From Latin, a neuter noun meaning "split forehead", apparently in reference to the separated frontal bones (see cover illustration), compared to the juxtaposed frontal bones of *Dermophis*.

Remarks.–The distribution of the two species of *Schistometopum* is unusual in that the two species are separated by great distances. However, the large region of the upper Zaire River is largely unexplored for caecilians, and it may be that other species of the genus remain to be discovered in this region (but see remarks under *S. thomense*). The two genera of the gymnophionan family Scolecomorphidae, *Scolecomorphus* and *Crotaphatrema*, share a distributional pattern similar to that of *Schistometopum* (Nussbaum, 1985; Nussbaum and Hinkel, 1994). The life history and ecology of both species of *Schistometopum* are poorly understood. *S. thomense* is independent of water and gives birth to living young. The reproductive mode of *S. gregorii* is unknown (but see below).

Schistometopum gregorii (Boulenger)

Dermophis gregorii Boulenger, 1894:646. Type locality, "Ngatana, E. Africa" [Ngatana is on the Tana River, Kenya]. Holotype, British Museum of Natural History (BM) 1946.9.5.53, collected by J. W. Gregory.

Boulengerula denhardti Nieden, 1912:199. Type locality, "Gebiet des Tanaflusses im südlichen Britisch-Ostafrika [Tana River region, Kenya]. Holotype, Zoologische Mu-

seum Berlin (ZMB) 22350, collected by C. Denhardt. Synonymized with *Dermophis gregorii* Boulenger by Loveridge 1936:375.

Bdellophis unicolor Boettger 1913:353. Type locality, "Peccetoni im Wituland" [Lake Peccatoni near the mouth of the Tana River, Kenya]. Holotype, Natur-Museum und Forschungs-Institut Senckenberg (SMF) 28, collected by A. Voeltzkow. Synonymized with *Dermophis gregorii* Boulenger by Loveridge 1936:375.

Schistometopum gregorii: Parker 1941:17. First use of combination.

Specimens examined.–BM 1946.9.5.53 (Ngatana, Kenya). **MCZ** 27901 (Bagamoyo River, Ruvu Ferry, Tanzania), 28601 (close to Kilindi near Rufigi River, Tanzania), 85083-93, 109729-70, 109771-2, 20054 (Mombosasa, near Witu, Kenya) 20055-71, 20073, 20075, 20077-82, 20084-92 (Kau, north bank Tana River, Kenya), 20093-5 (Laini, south bank Tana River, Kenya), 20096-7 (Ngatana, north bank Tana River, Kenya), 20101-3, 20105, 20107-11, 20113-6, 20124-46, 20148-50 (Lake Peccatoni, Kenya), 20151-4 (Mkonumbi, near Witu, Kenya). **UF** 11645 (Peccatoni near Witu, Kenya). **UMMZ** 147009-18, 177011 (Lake Peccatoni near Witu, Kenya); 147019-23 (Kau, Tana River, Kenya).

Identification.–A *Schistometopum* with nearly uniformly plumbeous to dark brown (glossy black in life) dorsolateral coloration (somewhat lighter ventrally); 110-119 primary annuli (89-105 in *thomense*); 112-122 vertebrae (94-109 in *thomense*), and 1-5 splenial teeth (12-25 in *thomense*).

Distribution.–Western Kenya near the mouth of the Tana River and central, coastal Tanzania.

Etymology.–The name "*gregorii*" is a noun in the genitive case, commemorating J. W. Gregory, the collector of the holotype.

Remarks.–Other than the various types and the two specimens from Tanzania, collected in 1953 and 1956, all known specimens of *Schistometopum gregorii* were obtained by A. Loveridge in 1934. To our knowledge, the species has not been collected in Kenya since 1934 and in Tanzania since 1956.

Schistometopum thomense (Barboza du Bocage)

Siphonops thomensis Barboza du Bocage, 1873:224. Type locality, "Ile Saint Thomé (côte occidentale d'Afrique)". Bocage mentioned two unnumbered specimens given to the Lisbon Museum (later to become the Museu Bocage Lisboa) by M. Craveiro Lopes, which are syntypes. These specimens presumably were lost (see remarks) in the 1978 fire that destroyed the Lisbon Museum (E. G. Crespo, 1986, *in litt.*).

Siphonops brevirostris Peters, 1874:617. Type locality, "Westküste Africas (Guinea)". Gorham (1962) listed Rolas

Island as the type locality, but the basis for this is unknown and there is no evidence for this in the records of the Berlin Museum (R. Günther, 1992, *in litt.*). Holotype, Zoologisches Museum Berlin (ZMB) 4911 (not 4711 as listed by Peters), obtained from Mr. Frank, a dealer of natural history specimens. Synonymized with *Siphonops* (*Dermophis*) *thomensis* by Peters (1880:223), resurrected by Taylor (1965:299), and here placed again in synonymy of *Schistometopum thomense*.

Dermophis brevirostris: Peters (1879:937). First use of combination.

Dermophis thomensis: Peters (1879:938). First use of combination.

Schistometopum thomensis (sic): Parker (1941:17). First use of combination.

Schistometopum ephele Taylor, 1965:295. Type locality, "Água Izé (400-700M.) Ihla São Thomé." Holotype Museo Civico di Storia Naturale, "G. Doria", Genoa (MSNG) 8773. Paratype, British Museum (BM) 1933.11.16.1-4 (see remarks), from Ihla São Thomé. **NEW SYNONYM**.

Specimens examined.–MBL 23.001-3 (Lagoa, Amélia, São Tomé). **MCZ** 24551-2 (Monte Casca, São Tomé), 29429 (São Tomé). **MRAC** 121099 (50 km along route from Mbau to Watalinga, N. W. Ruwenzori River, 750 m altitude, Zaire ?, see remarks). **MSNG** 8773 (holotype, *Schistometopum ephele*). **NHMB** 17-8, 2796-7 (São Tomé, 2796-7 wrongly listed as Ceylon in earlier references). **NHMW** 9112, 9113.1-3 (São Tomé). **UMMZ** 118065 (Ihla de São Tomé); 186675-88 (Alto Douro, Ihla de São Tomé); 186696-721 (Alto Douro at Porto Allegre, Ihla de São Tomé); 187044 (Capela, Ihla de São Tomé); 186841-914 (Colónia Açoreana, Ihla de São Tomé); 186689-95 (Monte Cafe, Ihla de São Tomé); 186745-78 (Pedroma, Ihla de São Tomé); 186722-44 (Ponta Furada, Ihla de São Tomé); 186947-75, 187020-53, 187555-61, 187565, 188017, 188027, 189396-400, 189488, 189695, 190123, 190385 (Pousada, Ihla de São Tomé); 187054-327, 187334-44, 187540-54, 187560, 187562-4, 187566-71, 189119-21, 190387, 190466-7, 192925, 193284, 193365-6, 195785, 201278-9, 210895, 210899-900, 214092, 217709-10 (Ribeira Peixe, Ihla de São Tomé); 186798-840 (Rio Abade, Ihla de São Tomé); 186673-4 (Ilhéu das Rolas); 186915-35 (Route 3, between km 4 and 5, Ihla de São Tomé); 186936-46, 186976-187019, 187328-33, 187345-60, 187572-3, 188028-9 (Route 3 from São Tomé City, between km posts 5 and 6, Ihla de São Tomé). **ZMB** 4911 (holotype of *Siphonops brevirostris*), 8738 (São Tome). **ZMH** A00979 (locality not registered, presumably São Tomé), A00980-89 (Monte Café, São Tomé).

Identification.–A *Schistometopum* with dorsolateral coloration ranging from immaculate bright yellow to darker yellow with heavy brown freckling in life, yellow color fades to light tan or cream in preservative; 89-105 primary annuli (110-119 in *gregorii*); 94-109 vertebrae (112-122 in *gregorii*); 12-25 splenial teeth (1-5 in *gregorii*).

Distribution.–Known only from Ihla São Tomé in the Gulf of Guinea, tropical West Africa. Records for nearby Príncipe Island and distant Zaire (Ruwenzori Region) are doubtful.

Etymology.–The name "*thomense*" refers to the geographical range of the species (São Tomé Island) at the time the species was described.

Remarks.–R. Günther (letter to RAN dated 27 October 1992) informed us that a specimen of *Schistometopum thomense*, ZMB A600 (= 8738) in the Berlin Museum is "a (probably the last) type of *Siphonops thomensis* Bocage, which our museum received from Lisbon in the past century." Bauer *et al.* (1993:288) subsequently listed ZMB 8738 as the only surviving syntype of *S. thomense*. We believe, however, that this is incorrect, mainly because ZMB 8738 is too small to be one of the syntypes. Bocage had only two specimens ("deux exemplaires") of *S. thomense* available in 1873 when he described the species. Bocage (1873:225) gave the total length of the two types as follows "Le plus grand, longueur totale 32 centimètres...Le plus petit, longueur totale 258 millimetères". In 1987, RAN carefully examined the putative syntype (ZMB 8738) and recorded its total length as 212 mm, which is 46 mm shorter than Bocage's smallest type specimen. The specimen, although softened and faded somewhat, is in good condition and was fixed in a straightened position, so it is highly unlikely that an error of 46 mm would have been made in measuring its length.

Perhaps Bauer *et al.* (1993) were mislead into thinking that ZMB 8738 is one of the types of *Schistometopum thomense*, because the specimen was sent by Bocage to Berlin shortly after Bocage described the species. However, recorded history shows that it need not have been one of the syntypes. Peters (1880:223), the curator at Berlin at that time, reported that "Hrn. Barboza du Bocage" sent one of his specimens to Berlin, which caused Peters to synonymize his *Siphonops brevirostris* with Bocage's *Siphonops thomensis*. That Peters had not received the specimen prior to 1879 is proved by Peters' (1879) publication in which he listed both *Siphonops brevirostris* and *Siphonops thomensis* (as *Dermophis*) as valid species and did not mention receiving a specimen of the latter from Bocage. Six years after Bocage described *Siphonops thomensis* on the basis of the two syntypes, he received at Lisbon many ("muitos") more specimens of *Siphonops thomensis* (Barboza du Bocage, 1897:206) from two different sources, and undoubtedly it was one of these that he sent to Peters. It seems highly unlikely that Bocage would have sent a type to Peters if he had abundant other material available, and it may be that the receipt of the many new specimens in 1879 was the impetus to send specimens to other museums.

There is a specimen of *Schistometopum thomense* in the Muséum d'Histoire Naturelle Bâle, MNHB 2797, with a badly corroded metal tag attached, which is engraved with the word "paratypoid". This specimen is erroneously recorded as being from "Ceylon". The specimen is almost certainly not a paratype or a syntype. RAN examined the specimen and recorded its total length as 206 mm, which in much smaller than either of the syntypes. Paul and Fritz Sarasin were associated with the Bâle Museum in the late 1800's, and some of their research material is catalogued there. The Sarasins were interested in both caecilians and Ceylon, and it seems likely that they may have received a gift of a *Schistometopum thomense* from the 1879 collections received by Bocage, which later became confused with the Sarasin's Ceylonese collection of caecilians.

We believe the two syntypes of *Schistometopum thomense* are lost or were destroyed in the Lisbon fire of 1978. Because there is no doubt about the identification of the species, there is no reason to designate a neotype.

Taylor (1965) designated one of four specimens listed as BM 1933.11.16.1-4 as a female paratype of *Schistometopum ephele*. He believed that perhaps one of the remaining three, a damaged specimen, also represented this species, and that the other two were *S. thomense*. Taylor (1968:670) presented data in a table for *S. ephele* which included BM 1933.11.16.1 and 1933.11.16.4. The tabular measurements and counts for these two specimens differ considerably from the data he presented for the paratype in the accompanying text, which he did not identify with a museum number. He also provided a photograph (his Fig. 367) of BM 1933.11.16.1, a freckled ("*ephele*") individual, which is not identified as the paratype in the figure legend; but the legend includes the comment that the specimen is an adult 327 mm long, which matches the total length given for this specimen in his table. The specimen is obviously a female, based on the size and shape of the head and the robust body. Taylor (1968:670) included tabular data for seven other *S. ephele* from the British Museum, but, in the text, he mentions that there is only one other specimen (1927.2.10.1) of *S. ephele* in the British Museum, and this is not one of the specimens listed in his table. It is clear that part of the confusion results from Taylor having included in his 1968 monograph text taken verbatim from his 1965 paper, without adjusting for new information, a common problem with accounts in Taylor's 1968 monograph. The identity of the paratype of *S. ephele* is, therefore, uncertain, but perhaps it is either BM 1933.11.16.2 or 3.

We tentatively identified a specimen in the Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC 121099) as *Schistometopum thomense*, although the locality is far removed from São Tomé and from a region (eastern Zaire/southwestern Uganda) where caecilians are otherwise unknown. The specimen was collected by Rev. R. P. Lejeune (no date) at "km 50, route Mbau-Watalinga, N. W. de la riv. Ruwenzori, forêt humide, alt. 750 m". Although the country was not recorded, the locality appears to be in Zaire. There are two villages named "Mbau" in Zaire, and none that we could find in Uganda. The first is at 3° 26' N latitude, 23° 13' E longitude, and is relatively far from the Ruwenzori region. The second, at 0° 38'N latitude and 29° 30' E longitude, is much closer to the Ruwenzori area, and we suspect this is the site reported by Lejuene. The specimen, a mature female 216 mm total length, differs somewhat from typical *S. thomense*. The tentacle is very
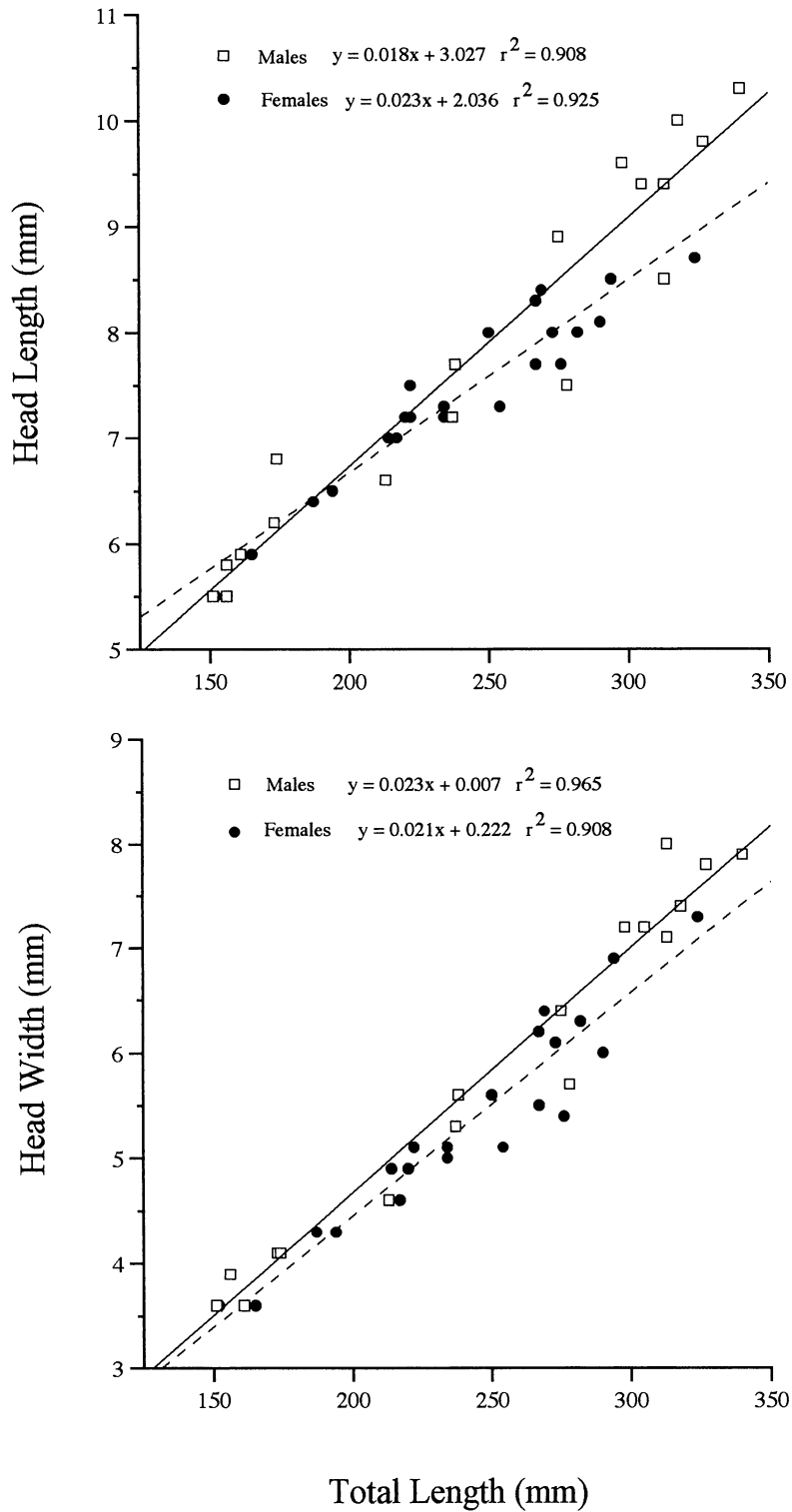
Hypogeophis rostratus

Figure 13. Regression of head length and head width on total length for a population of the caeciliid, *Hypogeophis rostratus* from Frégate Island, Republic of Seychelles. The same pattern of sexual dimorphism observed in *Schistometopum thomense* and *S. gregorii* (males with larger heads) is observed in this species.

close to the eye, and it has a higher number of maxillary-premaxillary teeth (38) than recorded for *S. thomense*, which is especially noteworthy given the relatively small size of the specimen. The other tooth counts are either near the maximum (vomeropalatine) or minimum (dentary, splenial) recorded for S. *thomense* from São Tomé. The number of primary and secondary annuli and vertebrae fall well within the range of *S. thomense*. The specimen represents either a remarkable range extension for *S. thomense*, or a cryptic species closely related to the latter, or perhaps it is a mislabeled specimen actually from São Tomé, although there is no apparent reason to doubt the record.

DISCUSSION

Taylor (1965) was intemperate in describing *Schistometopum* "*ephele*" because he had access to information that should have invoked caution and because he had not done any field work aimed at resolving the status of the forms of *Schistometopum* on São Tomé. S. "*ephele*" differs, according to Taylor (1965:297), from *S. thomense* only in that the former has a "proportionally small, more pointed head than *thomense*" and has a dorsolateral yellowish coloration "with dark lilac-brown flecks", whereas *S. thomense* is immaculate yellow. Had Taylor recorded the sex of specimens and carefully studied variation in the sample of *S. thomense* that was available to him, he would have understood the significance of head size and shape in the holotype of *S.* "*ephele*" and realized that its head is small and pointed because it is a female, and not because it is a different species. In regard to color pattern, the range of variation in specimens from São Tomé examined by Taylor should have given him pause, and apparently he was uncertain about the status of some individuals as indicated by his remark (1965:297) that a second specimen with the same catalogue number as the type of *S. ephele* "*may* likewise belong here".

We suspected *Schistometopum ephele* was invalid, but deemed it necessary to conduct systematic field surveys on São Tomé and Príncipe Islands to resolve with certainty the taxonomic status of this form. Our field work revealed intergradation between nominal *S. thomense* and the *ephele* morph, and more interestingly showed that dramatic geographic variation within a species can occur over very short distances in seemingly uniform habitat, even within a small island system. Similar unexpectedly high amounts of microgeographic variation in island populations was recorded for three lizard species (Brown and Thorpe, 1991; Brown et al., 1991; Thorpe and Báez, 1987; Thorpe and Brown, 1989), which suggested to the authors that strong natural selection along environmental gradients and/or sexual selection, rather than hybridization in secondary contact zones, might be responsible for the sharply clinal variation that was documented. However, the reasons for strong microgeographic variation within these island populations of lizards and of *S. thomense* are unknown and invoke questions about evolution and the process of speciation that transcend in importance the issue of species definitions.

In addition to the taxonomic changes derived from this study, there are two additional results that are of particular interest. Firstly, the results dispute the attitude of some proponents of the evolutionary and phylogenetic species concepts (ESC and PSC), who argue that if an allopatric group of individuals is "diagnosable" then it is a species (Cracraft, 1983, 1987; Rosen, 1978, 1979; Highton, 1990; Howard et al. 1993; Ridley, 1989), and argue against the wholesale elevation of distinguishable, closely related, allopatric populations to species level without careful field studies, as was suggested by Collins (1991, 1992). Secondly, sexual dimorphism has rarely been reported in caecilians, and the discovery of marked sexual dimorphism in both species of *Schistometopum* raises questions about the social interactions of these and other caecilian species.

There is a trend in herpetology to name new species based on minimal character differences between obviously closely related forms that are allopatric. This is especially true among molecular systematists who often use genetic distances based on allozymes or DNA sequences as evidence that polytypic species should be resolved into two or more species. Often, the ESC or PSC is cited to justify these proposals (e.g., Collins, 1991, 1992; Daugherty et al., 1990; Howard et al., 1993). These investigators seem not to have noticed that there is nothing axiomatic in the ESC nor in the PSC that unquestionably justifies these actions. Therefore, to accept diagnosability as justification for naming allopatric species is to accept a conventional and/or authoritarian solution to the complex issue of species recognition. We fear that acceptance of simplified, conventional solutions to the species problem, such as is advocated by some extreme proponents of the ESC and PSC, will obscure much interesting biology and worse yet may reduce the amount of field research that goes into studying distributions, geographic variation, speciation, and biodiversity. For example, in response to one of his critics, who suggested that additional field work might resolve the status of some allopatric populations, Collins (1992) replied that the possible "discovery of new records [that might show intergradation] is speculation and has no bearing on the situation". By this we presume Collins means that allopatry and diagnosability alone are enough under the concept of the ESC to justify taxonomic revision, even before field work and careful analysis of variation are done. We disagree with Collins, and believe that exhaustive field work and extensive data analysis should precede any taxonomic revision that involves uncertain status of allopatric populations.

Caecilians are poorly studied from most aspects, so it is not surprising that sexual dimorphism in this group is largely unknown. It has long been known that males of many species of most families have a pair of "anal glands" anteriorly on either side of the cloacal opening and that these glands are absent or very rarely present in females (Taylor, 1968; Nussbaum, personal observations). Sexual dimorphism in the size and shape of the "anal plate", or the area around the cloacal opening has been documented in typhlonectids (Gonçalves, 1977; Taylor, 1968; Wilkinson, 1989). Nussbaum

(1985) reported sexual dimorphism in the number of vertebrae and primary annuli in all three currently recognized species of *Scolecomorphus*. The pattern is particularly striking in *S. uluguruensis*, the only species in which a large homogeneous sample exists. In *S. uluguruensis*, there is virtually no overlap in the number of vertebrae and primary annuli, with females, the larger sex, having greater numbers of both. Nussbaum (1985) suggested that more body segments in females may be related to reproductive potential, in that added segments might provide additional space for developing embryos in these viviparous species.

In regard to head size, Nussbaum (1985) found that males of *Scolecomorphus uluguruensis* have significantly longer (p < 0.00) and wider (p < 0.000) heads than females. In *S. kirkii*, the adjusted mean head length and width of males and females could not be compared, because the slopes of head size regressed on total length were significantly different. The slope for both head length and width was greater (b = 0.024 vs. 0.010 and 0.021 vs. 0.011) for males than females, indicating that head size increases faster with growth in males than in females. Neither the slopes nor head size were significantly different between sexes in the third species, *S. vittatus*. However, only a few specimens per population of widely scattered populations were available for the latter species, and specimens assigned to *S. vittatus* may represent several cryptic species (Nussbaum, unpublished). Males have significantly longer and wider heads among a homogeneous population of *Hypogeophis rostratus* from Frégate Island (Fig. 13) in the Seychelles Archipelago (Pfrender and Nussbaum, in preparation).

There is only one example that suggests apparent lack of sexual dimorphism in head size in caecilians. Wake (1980) stated that head width in a population of *Dermophis mexicanus* is not sexually dimorphic, but we note that her regressions of head width on total length (her Fig.4), while not significant at the 0.01 level, indicate that males have a steeper regression (slope = 0.041) than females (slope = 0.034). Wake did not report data on head length. Therefore, there are no examples that clearly demonstrate lack of head size dimorphism in caecilians, but this may only reflect the dearth of large homogeneous samples that could be used to test for this.

Whether or not head size dimorphism proves to be general in caecilians, its clear presence in *Hypogeophis rostratus*, *Schistometopum gregorii*, *Schistometopum thomense*, *Scolecomorphus kirkii*, and *Scolecomorphus uluguruensis* provokes speculation about its cause. Larger heads in males might reflect intraspecific resource partitioning or sexual selection for combat advantage among males, or both. However, because in every case, males have the larger head, it seems that combat advantage is the most likely explanation, presuming that larger heads and wider gapes might be advantages in combat. Caecilians of many species bite each other (personal observations), but, because caecilians live in burrows, it is difficult to know whether one or the other sex is more prone to bite, although it is clear that individuals of both sexes are bitten, both in the field and in laboratory colonies. This is evident from the signature scars present on the bodies of both freshly caught and captive individuals.

Teodecki *et al.* (in press) demonstrated that females of *Schistometopum thomense*, with their smaller and more pointed heads, burrow significantly faster than the larger and blunter headed males, which suggests a cost to males of having larger heads. These observations, while intriguing, are limited and subject to various interpretations. Detailed and cleverly designed studies are needed to reveal the mating system and other aspects of the social lives of caecilians, so that secondary sexual dimorphism in head size and the number of body segments might be understood.

The life history and ecology of *Schistometopum gregorii* and *S. thomense* have not been studied in detail. Arthur Loveridge, who obtained most specimens of *S. gregorii* presently in museums, provided brief observations on *S. gregorii* in the field. Using specimens of *S. thomense* obtained for the research presented here, Ducey *et al.* (1993) studied the burrowing behavior of this and several other caecilian species, and Smits and Flanagin (1994) presented data on its respiration. Nothing seems to have been reported on *S. thomense* in its natural environment.

Loveridge (1936) collected his series of *Schistometopum gregorii* in May, 1933 one month after the "big rains had broken". The first specimen was captured by Loveridge in a small tussock or island of soil that projected above the water on the flood plain of Lake Peccatoni (now Lake Kenyata). The remainder of his large series was collected by natives at three sites. Loveridge visited the first after the collecting was completed, and he described it as "black mud, which had a slight admixture of sand, beneath the waters of the lake [Peccatoni]." Natives informed Loveridge that *S. gregorii* lives under water. However, a second smaller series collected by native children near Kau was taken from mud near the village. At Ngatana, only two specimens were taken, one from mud under sedges on a river bank, the other from drier earth at the base of banana plants about 100 m from the river. Although none was collected at Golbanti and Mpokomo, natives there informed Loveridge that the species is common in mud associated with rice plantations.

Loveridge (1936) reported only minute ova present in specimens of *Schistometopum gregorii* he examined, and we confirm his observations. There is nothing in the reproductive tract of Loveridge's series that indicates the reproductive mode of the species. Natives at Lake Peccatoni informed Loveridge that during the rainy season, *S. gregorii* deposit many eggs in the water. This seems unlikely, as in all verified cases, caecilians either deposit their eggs in terrestrial nests which are attended by the female or give birth to living young. Perhaps the natives had mistaken frog or fish eggs for caecilian eggs. In Seychelles, the senior author has observed *Hypogeophis rostratus* in the water on nu-

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Figure 14 (facing page). View of southeastern coast of São Tomé island looking to the southwest. The rocky, volcanic shore line and highly modified vegetation typify the area where most samples of *Schistometopum thomense* were collected.

merous occasions. In these cases, the caecilians were either mating or feeding in the water; their eggs are deposited on land. *H. rostratus* are attracted to dead fish placed in the water by Seychellois for cooling, or to offal discarded in water, both of which they attempt to eat. It would not be surprising if *S. gregorii*, which apparently is semi-aquatic, occasionally feeds on frog and/or fish eggs, which might give natives the impression these eggs are deposited by caecilians. Loveridge (1936) reported only termites in the stomachs of the specimens taken from more terrestrial sites and only earthworms in stomachs of specimens from the shallows of Lake Peccatoni.

We observed *Schistometopum thomense*, or "cobra bobo" (silly or foolish snake), from sea level up to about 1,000 m elevation on São Tomé, and they almost certainly occur at higher elevations. They were collected in June during the dry season, in relatively undisturbed forest, but they are common in a variety of habitats, including highly heterogeneous, rocky, coastal, habitats (Fig. 14) and completely denuded and degraded habitats (Fig. 15) such as cacau plantations, sugar cane plots, and trash piles. They were found in wet soil, under discarded cacau husks, under stones and logs, and in litter. They were usually found at considerable depth in mineral soil at drier sites and closer to the surface at wetter sites such as in seeps and muddy talus at edges of streams. In a cacau plantation at Pedroma (220 m), smaller specimens were found closer to the surface than larger individuals. Early afternoon soil temperatures at 12 sites where individuals were collected 8-17 June at 850 m in degraded habitat ranged from 21.4 to 25.2° C. They tended to be concentrated at some sites, but it is uncertain whether this was due to social interactions or favorable local habitat conditions. Occasionally, two large individuals were found very close together, nearly touching. Many had bite marks on them, which we confirmed as conspecific bites by later laboratory observations.

Schistometopum thomense is viviparous, with 2 to 7 young being born usually at the same time in captivity. The young (n = 27) are 91-118 mm (mean = 105.6) total length at birth, weigh 0.90-1.99 g (mean = 1.52), and are fully formed with no evidence of gill scars and with essentially adult coloration (Fig. 5). In June, most of the adult females we captured were pregnant, many giving birth within a few days of capture. Stomach contents of the few specimens examined contained sand (probably from earthworms), earthworms, and insects.

Occasionally dead specimens were found under litter, especially under cacau husks. At Pedroma, three dead individuals were found with pustules on their skin. They were being eaten by ants and other insects, which are particularly abundant in the litter and piles of cacau husks in plantations. It was unclear whether the insects had killed the caecilians. We often found healthy and uninjured caecilians in litter with dense populations of biting ants.

The brilliant yellow coloration of *Schistometopum thomense*

is unusual in that most other caecilians are not brightly colored, although some species of the South American genus *Epicrionops* and the Asian genus *Ichthyophis* have yellow, lateral stripes. Bright yellow is usually associated with aposematic or pseudoaposematic coloration, but during our brief stay of about one month on São Tomé, we observed no interactions suggesting a function for the bright coloration. The only potential models observed were millipedes.

Both *Schistometopum gregorii* and *S. thomense*, although known from relatively few specimens from small geographic areas, appear not to be threatened with extinction. *S. gregorii* is apparently abundant on the Tana River delta, an area heavily used for agriculture, and they occur in muddy areas around villages and in plantations. Similarly, *S. thomense* is common and does not seem to be adversely affected by deforestation and other habitat disturbance. Although the current status of *S. gregorii* is uncertain (it hasn't been seriously sought recently), both species of *Schistometopum* thrive in anthropogenic habitats, as do some other African species such as *Boulengerula taitanus* (Nussbaum and Hinkel, 1989), some Indian species such as *Gegeneophis ramaswamii* (Nussbaum and Gans, in preparation), and some species of Seychellean caecilians (Nussbaum, unpublished). For these species, forest cover is not important, but rather the critical factors are an abundance of moisture, soil and litter, and abundant food in the form of soil and litter-layer invertebrates. Deforestation and traditional native agricultural practices may actually benefit these species by increasing the amount of moist soil (rice paddies, banana plantations) available to live in and the amount of decaying organic matter at the soil surface, which results in higher productivity of invertebrate prey available to the caecilians. A switch from traditional to modern agricultural practices involving the heavy use of pesticides and synthetic fertilizers could, however, change this picture.

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Figure 15 (facing page). Coastal plateau at Ribeira Peixe. This region was being cleared for planting oil palm in 1988. Caecilians were found in the degraded forests shown in the background.

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