SUPERSPECIFIC RELATIONSHIPS WITHIN THE GENUS CTENOPOMA (PERCIFORMES, ANABANTOIDEI) A MORPHOMETRIC ANALYSIS AND PRELIMINARY PHYLOGENY

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PREFACE

Initially, this was a study on the comparative ethology of fishes of the genus Ctenopoma. Towards that end, aquaria were set up, a plethuora of support equipment and supplies laid in, living specimens obtained and observations begun. After a year and a half (though exhaustive efforts were made to make the specimens 'feel at home') the fishes would not engage in any vigorous behavior--and they certainly were not breeding. To add to this strain, the specimens obtained were not always easy to identify. All we really had to go on in the way of identification guides were the questionable names on photographs in aquarium hobbyist works. So, I undertook a tour of North American museums to examine specimens and learn to identify the species of Ctenopoma. In my naivete, I felt that this would be an easy enough task and perhaps, upon its completion, the live fishes would begin to cooperate. They did not, and the morphological work soon grew into a pre-revision of the African Anabantidae when it became obvious how little reliable systematic work had been done on these fishes. The systematic work soon took over and the project meandered steadily away from the live fishes (who remain relatively inactive) and the original design of the study. Eventually, I ended up in Europe, pouring over thousands of specimens in old world institutions.

This thesis presents much of the morphological data that have been gathered and analysed over a period of almost three years.

ACKNOWLEDGEMENT

This study in its various incarnations has been underway for sometime and many persons have contributed in numerous ways. Firstly, I need to acknowlege my advisor, Dr. Rudolph J. Miller, for constant interest, ideas, senarios and the skeptical eye. Dr. Michael E. Douglas provided absolutely essential aid with statistics and the computer and contributed the modern look at things and an outsiders view of *Ctenopoma*. Dr. Tony Echelle posed important questions and critically read the thesis. Dr. Barry Chernoff aided greatly in the original design of the study and was very important in my introduction to museums and modern systematics.

Above all, this has been a museum study, and curators and staffs of a number of institutions have provided lists, information, specimen loans and assistance during visits: The Academy of Natural Sciences of Philadelphia, E.B. Böhlke and W. Saul; The American Museum of Natural History, C.L. Smith and N. Feinberg; The Royal Museum of Central Africa, D. Thys van den Audenaerde; The National Museum of Natural History (Paris), G. Teugels, M.L. Bauchot; The British Museum (Natural History), K.E. Banister, B. Brewster, G. Howes, A. Wheeler. The California Academy of Natural Sciences, the Field Museum of Natural History, The Royal Museum of Natural History (Leiden), The Museum of Zoology, Univeristy of Bergen (Norway) and The United States

National Museum all provided important loans of material. Dr. H.-J. Paepke (Museum of Zoology of the Humboldt University of Berlin) and Pekka T. Lehtinen (University of Turku, Finland) generously sent to me important type material from their collections. I am especially grateful for their efforts. I am particularly indebted to Jos and Eviline Snoeks-Moons and L. Risch and family for hospitality and assistance during my visit to Belgium and to Jim and Dawn Hodgson during my stay in England. David M. Armitage of the U.K. re-examined some types in the British Museum for me and provided photographs of them.

Funding for the various phases of this work has been provided by the Dept. of Zoology, Oklahoma State Univeristy (J. Wilhm, Head), The OSU Foundation, The Jessup/McHenry Fund of the Academy of Natural Sciences of Philadelphia and my parents.

Finally, for useful views in science, its role and processes, I would like to acknowledge Rudolph J. Miller and Alexandra Vargo of The Colorado College.

To my parents, who never questioned the value of having an ichthyologist in the family---and never asked (or apparently even wondered):

"...so what good is it?"

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CHAPTER I

INTRODUCTION

Fishes of the perciform suborder Anabantoidei are widely distributed in tropical and subtropical Asia and Africa. The most primitive of the five extant anabantoid families is the Anabantidae (Liem, 1963; Lauder and Liem, 1983). This family, with two nominal African genera and one Asian genus, is the only anabantoid family represented in Africa and the only one shared between Asia and Africa. Africa and Asia share no anabantoid genera.

In Africa the Anabantidae is represented by two genera, *Sandelia* (two species) and *Ctenopoma* (approximately 16 species in three species groups of undetermined taxonomic rank). Liem (1963) hypothesized that the proto-African anabantid migrated from Asia to Africa in the Eocene. Since all reported anabantoid fossils come from Asia and are relatively recent in origin (Liem, 1963; Romer, 1967) there is little fossil support for this or any other view. Attempts have been made to include the South American nandid genera in the Anabantoidei (Donn E. Rosen, pers. comm.), though a close relationship between nandid and anabantoid is not likely (Liem and Greenwood, 1983). There is no recent or fossil anabantoid presence in South America, which might indicate Gondwanic origin of the Anabantidae. Athough lacking firm historical data, this possibility should not be discounted.

Whatever its origin, the early anabantid arrived or was present in Africa early enough to have modern representatives in most major drainage basins and ichthyofaunal regions of modern Africa. Furthermore, enough time has passed to allow two or more important radiations in the African anabantid line. A pre-Miocene origin or arrival of the ancestral stock is probably necessary to account for the present wide-spread distribution of the family (Beadle, 1981, summarizes the various hypotheses regarding the histories and relationships of the African waterways). Anabantids are air-breathing fishes and can be fairly mobile (one is known to traverse overland, Ricardo-Bertram, 1940). This potentially allows for more rapid and extensive dispersal than that found in non-airbreathing fishes.

General Biology

Anabantoid fishes are distinguished from other perciform fishes by having a suprabranchial accessory breathing structure (the labyrinth), derived from the first epibranchial gill arch. The degree of development and dependence upon this organ varies greatly among anabantoid taxa (Day, 1869; Foersch, 1976). Some species will drown if denied access to the surface (e.g., *Anabas*), while others rarely utilize atmospheric oxygen (e.g., *Parosphomenus*). Even within one family (e.g., Anabantidae) the labyrinth can show tremendous variation in development (Elsen, 1976). Such variation is presumably related to the ecology as well as the phylogeny of a species.

Aerial respiration has allowed anabantoid fishes to exploit anoxic habitats such as swamps and backwaters, which seem to be the preferred habitats for most species of *Ctenopoma* (Matthes, 1964; Greenwood, 1966;

Berns and Peters, 1969; K.E. Banister, pers. comm.). *Sandelia*, on the other hand, exist in potentially more strongly oxygenated temperate waters. *Sandelia capensis*, in fact, is found in waters cool and oxygenated enough to support introduced *Salmo gairdneri* (Jubb, 1965), Its labyrinth is strongly reduced (Barnard, 1943; Elsen, 1976), though apparently still functional (Jubb, 1965). Habitation in temperate waters has probably reduced the benefit of having a well-developed labyrinth.

Life in oxygen-poor waters has affected other areas of anabantoid biology as well. A number of reproductive specializations in *Ctenopoma* such as, natant (bouyant) eggs, bubblenest building and extended parental care may all be viewed as adaptations to this harsh environment. Two basic reproductive strategies occur in *Ctenopoma*: bubblenest building and egg scattering (or "free spawning"). The bubblenest builders are small animals with marked sexual dimorphism. In these species the male builds a bubblenest which is the center of a defended territory. He attempts to attract a ripe female into the territory and when he succeeds, a spawning embrace is performed and gametes released. The eggs float up into the nest where they are tended by the male. The male provides all parental care, which terminates when the brood hatches. So far as is known, all other species of *Ctenopoma* spawn without elaborate courtship, bubblenests or parental care. They instead pair with a series of short courtship displays, clasp, and release natant eggs which drift away without further attention from either parent. Brood sizes in these species are probably larger than those of the small, sexually-dimorphic species (Matthes, 1964). Richter (1981) summarizes many anecdotal observations on the breeding behavior and biology of *Ctenopoma*.

According to some sketchy observations (Harrison and Du Plessis, 1947; Siegfried, 1963), *Sandelia* spawn near the substrate, where a pair deposits demersal eggs in a depression (possibly similar to a centrarchid nest). The male guards the brood in this nest. However, M. Bruton (pers. comm.) has indicated that *Sandelia* (as with some *Ctenopoma*) are possibly bubblenest builders. There is certainly more known about these fishes, which are considered endangered in The Republic of South Africa and are under study (M. Bruton, pers. comm.), but such information has not been published in an accessible form.

Ctenopoma feed mainly on arthropods--terrestrial and aquatic (Matthes, 1964), though two species have behavioral and morphological specializations for piscivory (S. Norris, aquarium observations) and consume small fishes in nature (Matthes, 1964). *Sandelia* are reported to be omnivorous, and larger specimens are "avid predators on small fishes" (Jubb, 1965, p. 61). The piscivorous *Ctenopoma* have highly protrusile jaws and employ an ambush-and-suction strategy to capture their prey. *Sandelia* have relatively large mouths, but without tremendously protrusile jaws. If they are consuming many fishes, their prey-capture tactics probably involve more of a 'chase-and-run-down' procedure, perhaps similar to the strategy of blackbass (*Micropterus*), to which *Sandelia* bears superfical resemblance in body form.

Systematics

The most complete, though very dated, systematic review of the African Anabantidae is found in Boulenger's *Catalogue of the Freshwater Fishes of Africa*, Volume IV (1916). The small number of good specimens available to Boulenger and the subsequent addition of ten species and subspecies to the genus severely limit the usefulness of this work. Since Boulenger, discussion of *Ctenopoma* taxonomy has not extended much beyond that of small groups of geographically-associated or phylogenetically-related species (e.g. Poll, 1939; Daget, 1958; Matthes, 1964). As a result, the stability of the nomenclature has suffered. Species have been described without a full understanding of such factors as ontogenetic change and/or geographic variation (e.g. Banister and Bailey, 1979; Ahl, 1923, 1927). Other workers (Blanche *et al.*, 1964; Matthes, 1964; Bell-Cross, 1976; Skelton, et al., 1985) have suggested synonymies, apparently without having seen the type specimens involved.

Recent work (cited below) and the present study indicate that the approximately sixteen species in the genus *Ctenopoma* can be divided into three distinct morphological groups. Elsen (1976) first defined these groups using internal morphology. Banister and Bailey (1979), in a cursory review of the Zairian *Ctenopoma*, arrived at a nearly identical set of groupings. Elsen (1976) referred to his groups as possible "*sous-genres*" (subgenera), though the taxonomic status and rank of these groups has yet to be rigorously determined or formally defined.

CHAPTER II

MATERIALS AND METHODS

Specimens

Specimens of all but four of the forty-one nominal taxa of _Ctenopoma_ have been examined. In addition, data were taken from several specimens of _Sandelia capensis_ and _Anabas sp._ Type material for all but the four unseen _Ctenopoma_ species and _Anabas_ has also been examined. Except for taxa of which there are only a few known specimens (usually, in these cases, only a small type series or holoype), complete data were taken from a minimum of 12 specimens per taxon. See Table I for summary of material examined and Appendix B for a comprehensive list of material examined. For each taxon an attempt was made to collect data from roughly the same number of males and females in the most common size class(es) and to use specimens from as many areas of the range of the taxon as possible. Data were taken from only a few juveniles (specimens smaller than 35 mm SL), as such specimens can be difficult to identify and/or measure accurately.

Sexing

All specimens were sexed. Almost all adult specimens could be identified as either males or females, from their external morphology (see below for discussion of sexual characters). The sex assigned to a specimen on the basis of external morphology was occasionally confirmed

TABLE I

NOMINAL *CTENOPOMA* (AND ANABANTID) TAXA EXAMINED

Taxon	No. of Specimens Examined	Type(s) Examined
acutirostre	28	y
ansorgei	52	y
argentoventer	1	y
ashbysmithi	5	y
breviventralis	1	y
brunneus	2	y
caudomaculatum	1	y
congicum	35	y
congicum longipinnis	6	y
ctenotis	2	y
damasi	12	y
davidae	2	y
denticulatum	1	y
fasciolatum	1	y
fasciolatum filamentosum	2	y
garuanus	1	y
gabonense	1	y
houyi	2	y
intermedium	174	y
kingsleyae	30	y
lineatus	1	y
maculatum	19	y
machadoi	42	y
multifasciatum	1	y
multispine	59	y
muriei	38	y
muriei ocellifer	5	y
nanum	250	y
nigropannosum	20	y
ocellatum	13	y
oxyrhynchum	12	y
pekkolai	1	y
pellegrini	13	y
petherici	38	y
petherici chadensis	6	y
pleurostigma	1	y
rhodesianus	0	n
riggenbachi	1	y
smithii	0	n
togoensis	0	n
vernayi	0	n
weeksii	2	y
Sandelia capensis	5	y
Anabas sp.	6	n

by examining gonads. Though sexing using external morphology proved accurate, juvenile or small specimens frequently could not be sexed with confidence using either method. These specimens were recorded as juveniles, though they may have represented young non-breeding individuals.

Characters and Analyses

To rigorously evaluate similarity and the presumed phylogenetic proximity of the various taxa of *Ctenopoma*, 34 phenetic morphological (linear) measurements per specimen were taken to a tenth of a millimeter using dial calipers (Table II). The variables were chosen to be easily identifiable, replicable and homologous from taxon to taxon. It was further intended that the measurements contain information on the relative shape of the specimen. The data set can be considered a "truss" (Bookstein *et al.*, 1985), though it is somewhat less complex (fewer measurments) than usually seen in truss analyses. The log-transformed (base 10) values for these data were subjected to principal components analysis (PCA) (NTSYS) based on the correlation matrices of these values. PCA groups specimens without regard to the names or groupings applied to them by the researcher. This is important as it removes the biases or desires of the researcher from the analyses. Once clusters of specimens were identified using PCA or simple examination of specimens, the data were subjected to a discriminant function analysis (BMPD). This procedure takes groupings of specimens as defined by the researcher *a priori* and identifies those characters most important in separating the given groups.

TABLE II

MORPHOLOGICAL CHARACTERS

CHARACTER
1. total length
2. standard length
3. origin of dorsal fin to terminus of anal fin
4. origin of anal fin to terminus of dorsal fin
5. dorsal fin base
6. anal fin base
7. origin of dorsal fin to origin ofanal fin
8. origin of dorsal fin to pelvic fin base (body depth)
9. origin of dorsal fin to posterior edge of isthmus
10. terminus of dorsal fin to terminus of anal fin
11 caudal peduncle length
12. caudal peduncle depth
13 terminus of dorsal fin to center of caudal fin base
14. terminus of anal fin to center of caudal fin base
15. predorsal length
16. pre-anal length
17. pre-pelvic length
18. pre-isthmus length
19. pelvic base to posterior border of isthmus
20. body width at the dorsal upper edge of gill slit
21. origin of dorsal fin to upper edge of gill slit
22. upper edge of gill slit to upper edge of pectoral fin base
23. origin of anal fin to upper edge of pectoral fin base
24. upper edge of pectoral fin base to pelvic fin origin
25. head length (as measured from snout to upper edge of gill slit
26. snout length
27. orbit diameter (horizontal)
28. interorbital length
29. length of premaxilla
30. length of pectoral fin
31. length of pelvic fin
32. length of terminal dorsal fin rays
33. length of terminal anal fin rays
34. length of longest caudal fin rays

Twenty meristic traits and a variable number of miscellaneous, often qualitative, characters were evaluated separately using PCA or univariate statistics or simply noted for their presence or absence in a particular specimen or taxon (Table III).

Using various combinations of the analyses outlined above, species groups and species were compared. Juveniles, outliers and specimens missing data values were eliminated from most analyses. Certain values (such as caudal fin length) were eliminated from many analyses because such values were not available for many specimens (or a few important specimens) due to specimen damage. Other values were eliminated from some analyses, if confidence in the accuracy of their measurment for certain species or specimens was questionable (e.g., caudal peduncle length for *C. petherici* and *C. kingsleyae*). The morphological data for at least one species per species group were subjected to PCA in order to evaluate the extent of external sexual dimorphism present in the data for that species (and its species group). For taxa in which the data contained strong sexual dimorphism, all subsequent analyses were run using only one sex at a time (usually males). Where the data did not demonstrate great sexual dimorphism, the sexes were run together.

TABLE III

MERISTIC AND MISCELLANEOUS CHARACTERS

CHARACTER

Merisitic Characters

1. dorsal fin spines
2. dorsal fin rays
3. anal fin spines
4. anal fin rays
5. pectoral rays
6. caudal fin rays
7. pelvic fin spine and rays
8. scales in lateral series
9. scales in lateral line (upper and lower)
10. scales in vertical series (upper and lower)
11. spines above notch on operculum
12. spines within notch on operculum
13. spines below notch on operculum
14. spines on the interoperculum
15. spines on the suboperculum
16. spines on the preoperculum
17. spines on the lachrymal

Miscellanous Characters

1. pelvic fin overlap with anal fin
2. length of jaw in relation to orbit
3. character of post-ocular spines (if present)
4. character of pre-caudal fin spines (if present)
5. character of genitle papillae
5. presence of a single pore or a pair of CCL pores in interorbital space
7. color pattern
8. state of gonads (not on all specimens)
9. scale type (ctenoid or cycloid) on:
    - forehead
    - cheek
    - throat
    - trunk
    - bases of unpaired fins

CHAPTER III

RESULTS

The Three Species Groups of *Ctenopoma*

As noted earlier, *Ctenopoma* is composed of at least three distinct groups. Elsen (1976), using characters of the axial skeleton, labyrinth and swimbladder (as visualized on cleared and stained specimens of seventeen nominal species of *Ctenopoma* and *Anabas* and *Sandelia*), first outlined these groups. Though he suggested in passing that his groups might represent subgenera, he made no other systematic or taxonomic comments on the Anabantidae. He instead largely confined his work to the descriptive morphology of the family. Banister and Bailey (1979) outlined a nearly identical set of groupings based mainly on meristic characters, size and general body form.

Morphology

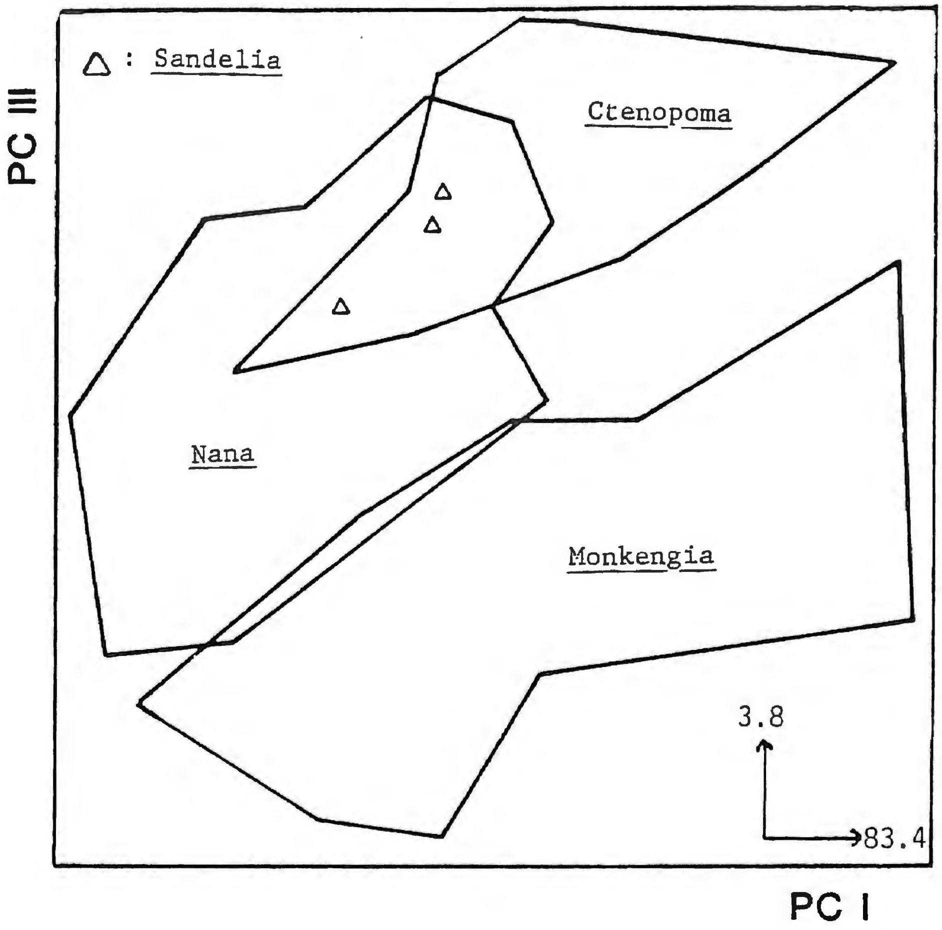
The three species groups of *Ctenopoma* are easily separated by superficial appearance alone. Most easily distinguished is the *Nana* species group. These animals, as adults, are smaller (65 mm SL maximum) than their congeners and show strong sexual dimorphism. Males of these species are more colorful than the females (especially when in breeding condition) and the males are larger with elongated anal, dorsal and pelvic fins. Species of both the *Ctenopoma* and *Nana* species groups are long shallow-bodied fishes, but members of the former group are much larger (adults 80mm SL +) and lack the strong sexual dimorphism seen in member of the Nana species group. Fishes of the third species group, Monkengia, are much deeper bodied than their congeners, and are for the most part large (adults 80 mm SL +).

Figure 1 shows the overall PCA projections for the first and third principal components (PCI and PCIII, respectively) for all specimens for all specimens of Ctenopoma and Sandelia. PC I primarily reflects size, while PC III is a shape axis. The characters having the highest loadings on the shape PC are length of fins (dorsal, anal and pelvic), eye diameter and caudal peducle form. Of slightly less importance on this factor are several characters involving body depth. This analysis shows the Monkengia species with strong differences in shape as compared to either the Nana or Ctenopoma species. Specimens of the latter two cluster separately, but are close. There is a common trend in shape change vs. size. The Ctenopoma specimens can be regarded as being larger versions of the same basic shape (e.g., long and shallow).

While the above analysis indicates that there are three basic body forms of Ctenopoma, shape alone is not sufficient evidence to support the existence of natural evolutionary groups within the genus. Similar shapes could result from convergence (homoplasy) and therefore additional characters are necessary to support the monophyly of the groups. Several series of such characters exist, each supporting the unity or separation of the same species and species-groups.

Behavior and Life History

Members of the Nana species group exhibit the more specialized reproductive strategy involving complex courtship, bubblenest building



The relative amount of variance accounted for by these axes is noted on the PCA plot (and on all subsequent plots).

Figure 1. PCA Plot (Morphological Data) for all the African Anabantidae.

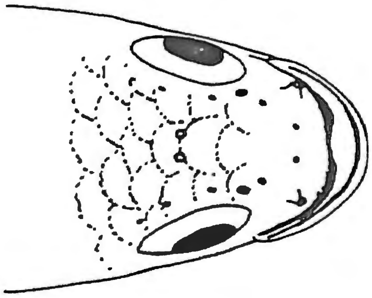
and parental care. These traits are apparently absent from the Ctenopoma and Monkengia species groups both of which practice the simpler free spawning strategy without parental care.

General Morphology

Members of the Nana species group have a closely associated pair of cephalic lateral line (CLL) pores in the interocular region. All other Ctenopoma have a single cephalic lateral line pore in this region (see Figure 2). Species of Monkengia may be distinguished from the other two species groups on the basis of caudal ray counts: 16 total caudal rays for Monkengia, 14 total caudal rays for the Ctenopoma and Nana species groups. Both Sandelia and Anabas have a single interocular pore and 16 total caudal rays.

As noted earlier, members of the Nana species group exhibit a great deal of sexual dimorphism (elongate fins and bright colors in males). While not so marked, members of the other two species groups do exhibit some degree of sexual dimorphism. Males of both species groups bear patches of strongly-spined scales just posterior to their orbits. The spines are highly developed and stout scale ctenii. Daget and Iltis (1965) first noted these spines in C. kingslyae (of the Monkengia species group), and I have noted them in all other members of the Monkengia and Ctenopoma species groups. Large females may have poorly developed, though visible 'fringing,' on their post-ocular scales (Cambray, 1980). Males as small as 50 mm SL may show development of their post-ocular spines. Males of Monkengia also have a patch of similarly spined scales just anterior to the base of the caudal fin (Peters, 1976). This posterior patch is not present in any

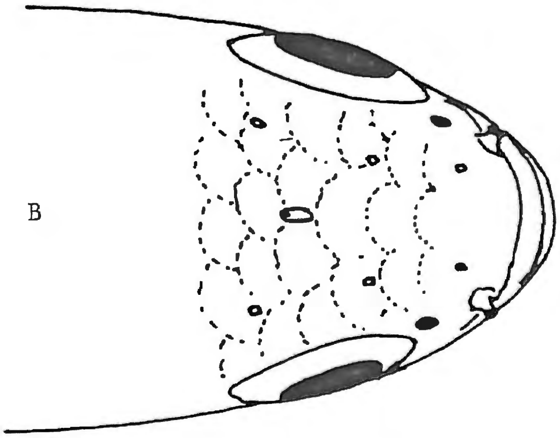
A



Ctenopoma nanum

SL: 56.70 mm
Interorb. space: 4.0 mm
MRAC 76-1-P: 753-756

B



Ctenopoma nigropannosum

SL: 84.60
Interorb. space: 7.9 mm
CAS 64609

Figure 2. Dorsal view of the head of two *Ctenopoma*: A. *Nana* species group, B. *Ctenopoma* species group.

other anabantid taxon. Cambray (1980) reported the post-ocular spine patches from Sandelia bainsii, but interestingly, the spines are lacking from male S. capensis. Post-ocular and pre-caudal peduncle patches of spined scales are not reported from Anabas (or any other anabantoid group) and I have been unable to find them on any of numerous specimens of Anabas examined. Neither patch occurs in any members of the Nana species group.

Peters (1976) hypothesized that the spine patches enhance the ability of the male to grasp the female during their quick and often frantic spawning embrace, though this has not been verified experimentally.

There are slight sexual differences in body length frequencies among the subgenera (Table IV). Male Nana are larger in standard length than females, while females of the Ctenopoma species group are larger than males. This character is correlated nicely with the differences in life history. Males of the Nana species group must defend territories and attract females with body and fin displays--increased size is clearly helpful in both of these activities. Without such tasks, males of the Ctenopoma species group are under less pressure to attain great size. Large females can produce greater numbers of eggs and, in species affording no parental care, a large brood size is more adaptive.

The relative size data for the Monkengia species group are not as clear. Males tend to be larger than females in some species, females are larger in others. This could be random or an artifact of the data, but it is more likely that it is correlated with some unknown aspect of the life histories of these species. Perhaps there are feeding or

TABLE IV

MEAN STANDARD LENGTHS FOR REPRESENTATIVE *CTENOPOMA*.

Species	Mean SL (mm)		N	
	male	female	male	female
Ctenopoma				
multipsine	70.2	83.8	29	31
nigropannosum	70.4	80.9	11	9
pellegrini	75.9	94.5	5	4
Monkengia				
acutirostre	92.2	85.5	11	15
muriei	45.7	54.4	11	26
oxyrhynchum	63.6	68.8	8	7
Nana				
ansorgei	41.7	37.7	46	22
congicum	43.1	42.6	27	18
damasi	42.3	39.6	8	4
fasciolatum	47.5	47.3	27	17
intermedium	44.8	39.1	68	56
nanum	49.6	39.9	125	102

breeding territories in some species, and larger males have better mating success.

I have no data on the length/sex ratios of *Sandelia* or *Anabas*. *Sandelia*, who do nest and may be territorial, possibly produce larger males which must complete for nesting sites. *Anabas* spawn near the surface without any nesting behavior or parental care and probably produce larger females.

Elsen (1976) defined his subgroups largely on the relative development of the labyrinth. It is most strongly developed in members of the *Ctenopoma* species group (and *Anabas*), weakly developed in the *Monkengia* species group and nearly absent in *Sandelia*. Members of the *Nana* species group show an intermediate state of development. Differences were also present in swimbladder morphology. Members of the *Ctenopoma* species group have a vertically divided swimbaldder, which does not contact the posterior wall of the suprabranchial chamber. Posteriorly, the swim bladder is horizontally divided by a fine membrane. The swimbladder of members of the *Nana* species group contacts the posterior wall of the suprabranchial chamber--perhaps allowing enhanced sound perception--and is only weakly divided vertically by a broken membrane. No horizontal division is reported. As with the *Ctenopoma* species group, the members of the *Monkengia* species group have horizontal and vertical divisions in their swim bladder. Unique to this *Ctenopoma* group and to *Sandelia* is the presence of two diverticulations of the swimbladder which extend anteriorly and contact the posterior walls of the suprabranchial chamber.

Data from the present study support the contention that there exist three phenetically defined natural groups of Ctenopoma (outlined in Table V), though groups slightly different in composition than those offered by either Elsen or Banister and Bailey (see discussion). Each of these species groups or 'subgenera' is a very cohesive unit with monophyly for each strongly indicated by a series of characters. Table VI summarizes the important characters separating the anabantid genera and Ctenopoma species groups. As monophyly is assumed for these species groups, for the purposes of this thesis, they will be given the taxonomic rank of subgenus. Final determination of the most appropriate rank for these groups will require additional study.

TABLE V

THE SPECIES GROUPS OF CTENOPOMA

Ctenopoma	Monkengia	Nana
ashbysmithi	acutirostre	ansorgei
machadoi	kingsleyae	congicum
multispine	maculatum	damasi
nigropannosum	muriei	fasciolatum
pellegrini	ocellatum	intermedium
	oxyrhynchum	nanum
	petherici	

TABLE VI

SUMMARY TABLE OF ANABANTID PHYLOGENETIC CHARACTERS

	Anabas	*Ctenopoma*	*Monkengia*	*Nana*	*Sandelia*
Caudal Rays	14	12	14	12	14
Interopercular pores	1	1	1	2	1
Post ocular fringed scales	-	+	+	-	+
Pre-Caudal fringed scales	-	-	+	-	-
Strong ext. sexual dimorph.	-	-	-	+	-
Swim bladder	tubular	tubular	bifurcated	tubular	bifurcated
Larger sex	?	female	either	male	?
labyrinth	strongly developed	strongly developed	weakly developed	intermediately developed	very weakly developed
Egg type	natant	natant	natant	natant	demersal
Nest building	-	-	-	+	++
Parental care	-	-	-	+	++

The Subgenus *Ctenopoma*

Description

Fishes of the typical subgenus large and shallow bodied; adults, 70 to 100 mm SL; fourteen total caudal rays (12 branched caudal rays); opercle, subopercle and interopercle all strongly spined in specimens 40 mm SL and larger; preopercle usually not spined or serrate; lachrymal (preorbital) not spined or serrate; thirty-four (rarely 29) scales in lateral series; single CLL pore between eyes in interorbital space; coloration generally fairly plain, some broad vertical bars present on many specimens, more pronounced in younger animals; faint streaks frequently radiating posteriorally off eyes; caudal peduncle often marked with an oblong horizontal band; juvenile (up to 50 mm SL) specimens bear 8-10 very narrow (one scale row wide) vertical stripes; pelvic fins short and unmarked; little or no sexual dimorphism in the morphometry or color pattern; females larger in size.

Sexual Dimorphism

Figure 3 depicts the PCA scatter plot of specimens of *C. multispine* with sexes noted. There is no clear pattern of sexual dimorphism in *C. multispine* or the subgenus *Ctenopoma*. Since the sexes have only slight, mostly size related dimorphism, they are not separated in further analyses of the subgenus *Ctenopoma*.

Species Groups and Alpha Taxonomy

Based on morphometric data, the three or four species of this subgenus can be placed into two groups. *Ctenopoma multispine* and the

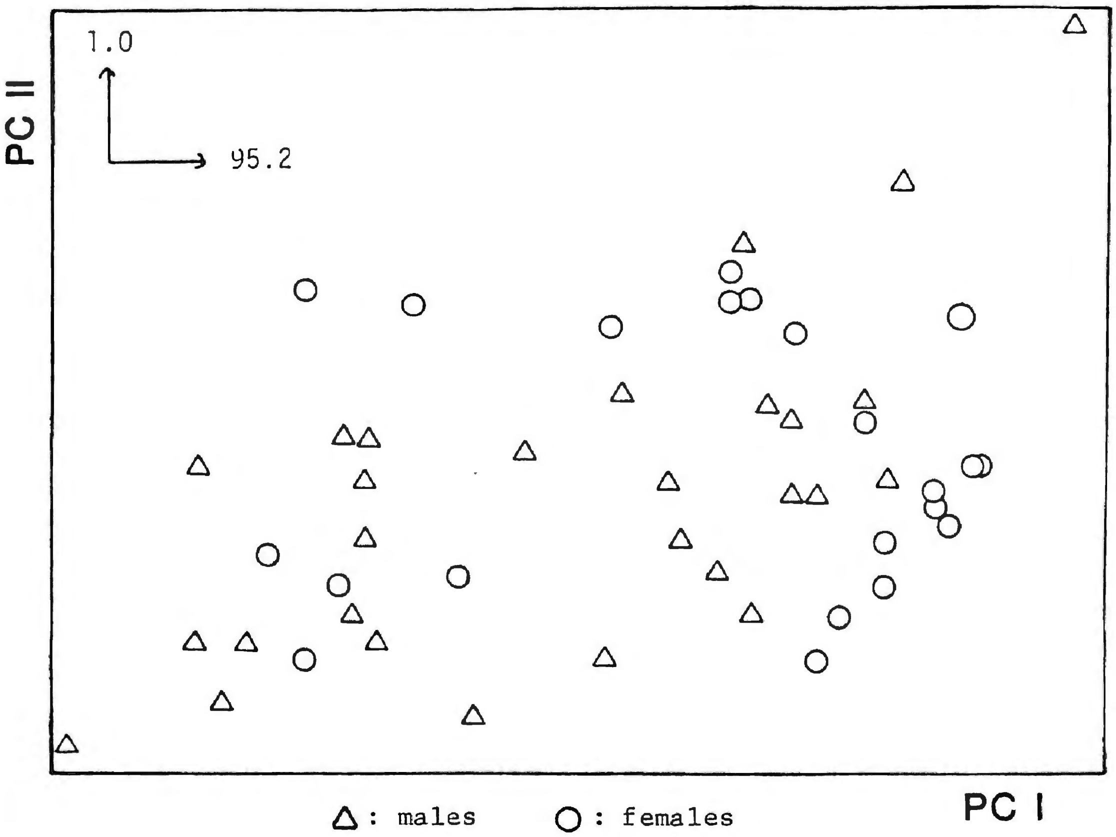


Figure 3. PCA Plot (morphological Data) for all *C. multispine* with with sexes noted.

very similar (probably identical) *C. machadoi* are distinguished from *C. pellegrini* and *C. nigropannosum* by slightly lower meristic values for the unpaired fins and higher opercular spine counts (Table VII). Figure 4 presents a plot of PCA scores based on the morphological data for all species of the subgenus. A similar pattern of separation is apparent.

Ctenopoma multispine and C. machadoi

Fowler (1936) described *C. machadoi* differing from *C. multispine* largely in color pattern. It was synonymized with *C. multispine* by Skelton, et al. (1985), though Poll (1967) had previously suggested that it was merely a "race" of of the latter. My data support the synonymization. Figure 5 is a typical result of several attempts to separate the two nominal forms. There is no discernable pattern, and a discriminant function analysis based on the morphological data for the two forms failed to find any characters on which to separate them. The *C. machadoi* specimens in the analysis are Fowler's types (the only known specimens of either taxon from the Cuanza River in Angola) and a few specimens identified as *machadoi* by Poll. The *C. multispine* specimens are representatives of the species from throughout its range. (See Figure 27 for a general map of modern African hydrology. Distribution maps for all species are in Appendix A.)

Ctenopoma nigropannosum and C. pellegrini

Ctenopoma nigropannosum and *C. pellegrini* are similar close in many ways, clearly distinct. difficult to separate. Figure 6 presents a typical PCA result for them. There is a regular pattern of shape

TABLE VII

CTENOPOMA SPECIES GROUP KEY MERISTIC VALUES

	Standard length	Dorsal spines	Anal spines	Dorsal rays	Opercular spines	Interop. spines	Subop. spines	Preop. spines
machadoi n=42	43-114 x=77.2	15-19 x=17.4	7-10 x=8.3	7-10 x=8.2	13-55 x̄=34.6	9-23 x=17.7	0-12 x̄=7.0	0-5 x̄=1.0
multispine n=59	43-99 x̄=73.0	16-19 x̄=17.7	7-10 8.7	7-10 x̄=8.7	10-56 x=35.2	10-27 x=19.0	0-15 x̄=6.0	0
nigropannosum n=20	49-141 x̄=75.2	18-21 x=19.1	8-10 x̄=8.8	9-12 x̄=10.3	5-36 x̄=24.2	10-17 x=13.5	0-9 x̄=4.2	0-7 x=.3
pellegrini n=13	31-110 x=76.6	18-20 x=18.7	7-9 x̄=7.8	10-13 x̄=10.8	4-39 x̄=25.3	12-16 x=14.1	0-9 x̄=4.2	0

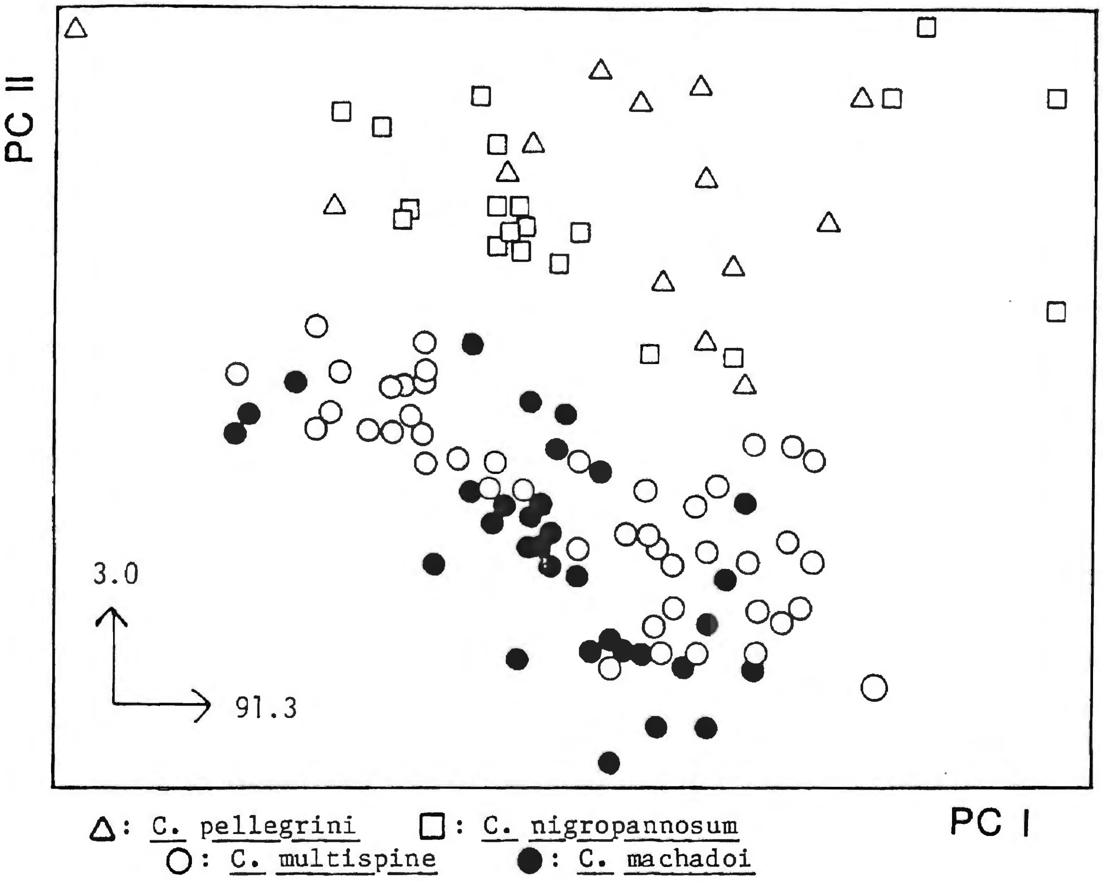


Figure 4. PCA Plot (Morphological Data) for all *Ctenopoma*.

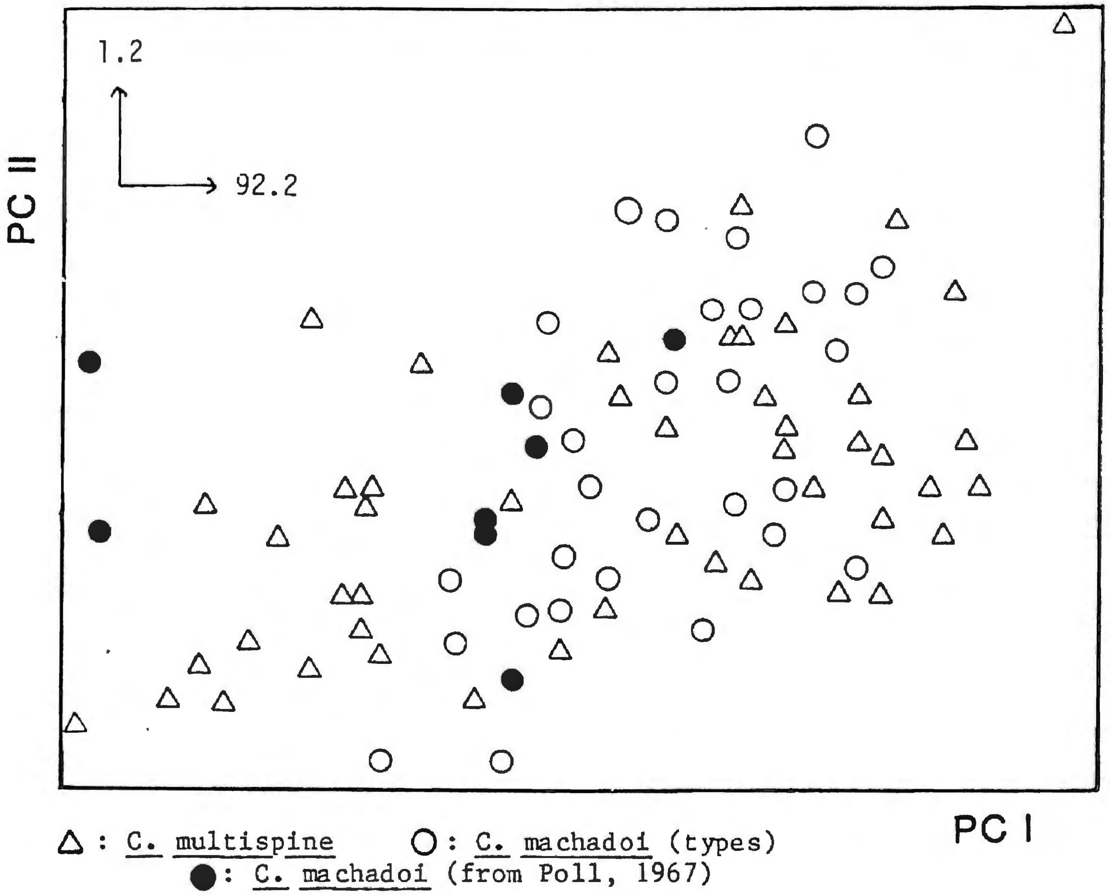


Figure 5. PCA Plot (Morphological Data) for *C. multispine* and *C. machadoi*.

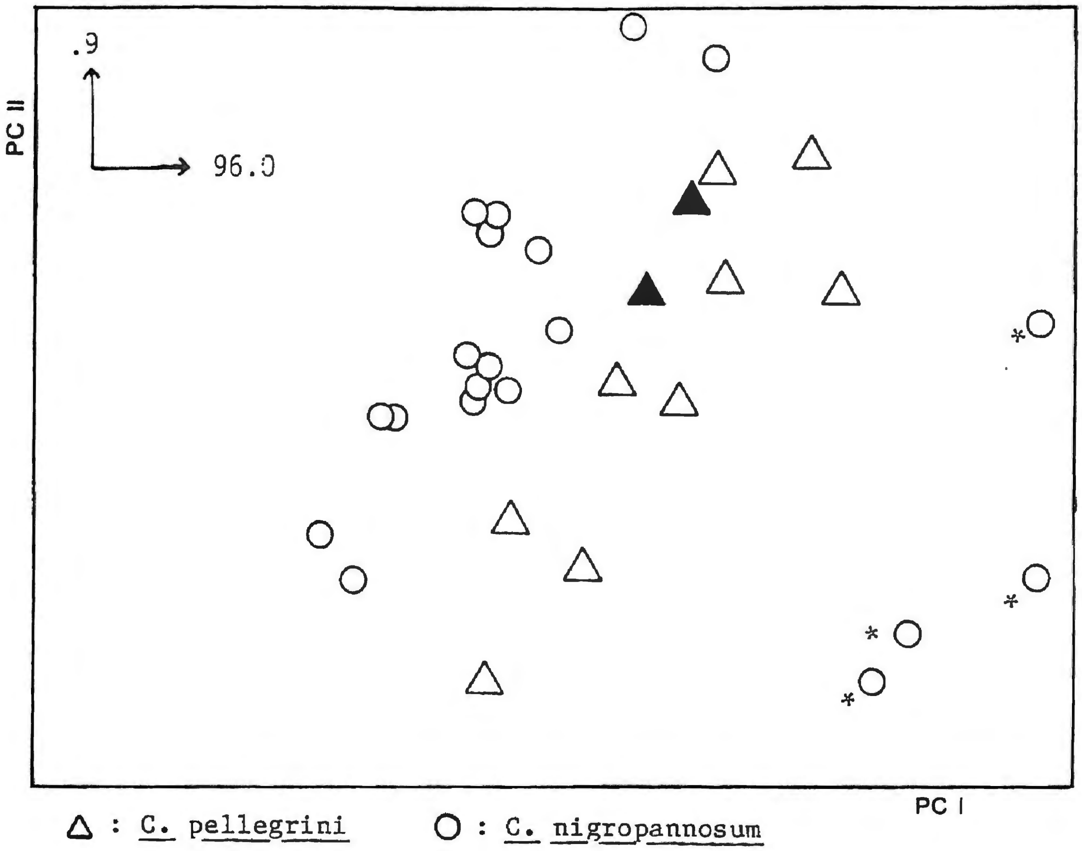


Figure 6. PCA Plot (Morphological Data) for *C. nigropannosum* and *C. pellegrini*.

difference with size between the two, though the factors are not very significant and the discriminant function analysis based on the morphological data could not separate the two forms. The four *C. nigropannosum* noted on figure 6 with an "*" are extremely large specimens compared to all others examined.

Ctenopoma pellegrini appears to be less common than *C. nigropannosum*, with a slightly more restricted distribution (see Appendidix A). It is generally a more cylindrical, long-bodied fish than *C. nigropannosum*. The snout is rounded in *C. pellegrini* and somewhat elongate and acute in the former. The body of *C. nigropannosum* is laterally compressed giving it a deeper, flatter and more angular appearance than *C. pellegrini*. This difference is particularly apparent in the caudal peduncle region. Color patterns of preserved specimens are similar, though there are some qualitative differences. *Ctenopoma pellegrini* frequently shows an elongate dark horizontal bar on the caudal peduncle. This bar, formed by the fusion of several vertical bars, is not as well defined in *C. nigropannosum*, specimens of which tend to be much darker overall. Matthes (1964) described other differences, such as smaller scales on the opercle in *C. pellegrini*, which I found difficult to use.

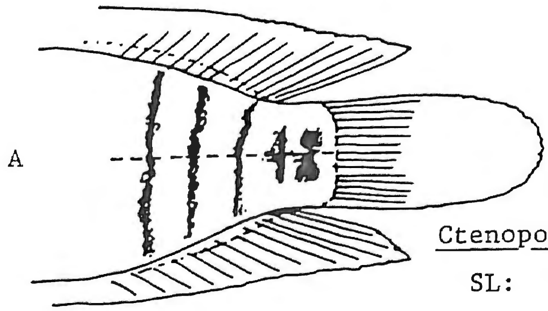
Ctenopoma ashbysmithi

There is one additional nominal member of the subgenus *Ctenopoma*, *C. ashbysmithi* Banister and Bailey, 1979. *Ctenopoma ashbysmithi* presents an identification problem and has not been included in any of the above analyses because all known specimens (a single collection of 40 individuals) are juveniles. The largest specimen (35 mm SL) is the holotype, and is far below the adult size of any other known member of the subgenus *Ctenopoma*. Of the specimens which were opened (not by me), none was observed to have identifiable gonadal tissue. Many specimens had greatly distended abdomens, which is a common indicator of gravid female *Ctenopoma*. However, similar distention was also observed in juvenile *C. nigropannosum*, and examination of these specimens demonstrated that the swelling was due to distended guts--full of arthropod fragments--and not to active ovaries.

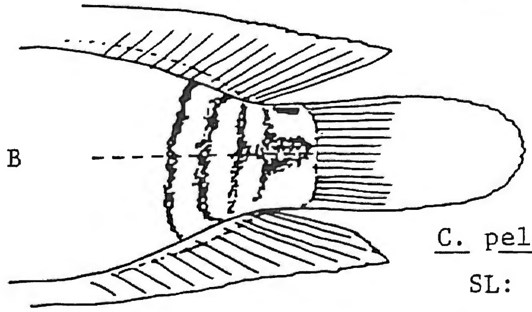
The meristic characters of *C. ashbysmithi* indicate that it belongs to the subgenus *Ctenopoma*. Unfortunately the characteristics used in the original description to separate it from other *Ctenopoma* species (shape and development of opercular spines, head proportions, lachrymal serrations and color pattern) are probably all strongly influenced by ontogeny, and taken alone are not useful diagnostic characters.

I am unable to distingush *C. ashbysmithi* from juvenile *C. nigropannosum* and *C. pellegrini*, which as juveniles are especially difficult to separate from each other. Some subtle meristic characters separate the two latter species (Matthes, 1964) and on the basis of these, *C. ashbysmithi* is tentatively listed under the more common *C. nigropannosum*. *Ctenopoma multispine* is eliminated from consideration as the possible identity for *C. ashbysmithi* because of differences in juvenile color patterns (see Figure 7).

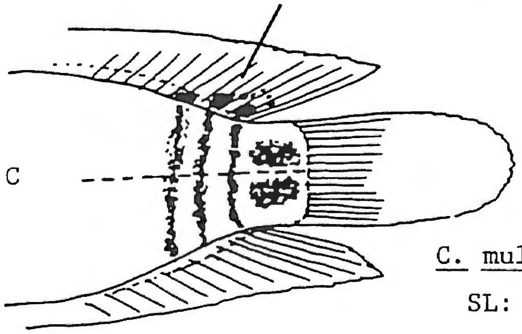
Ctenopoma ashbysmithi was collected in a marsh outside the known ranges for any other *Ctenopoma* species and final determination of its status awaits the collection of adult specimens from this region. Banister (pers. comm.) found the marsh was extremely acidic and suggested that the fishes present appeared dwarfed.



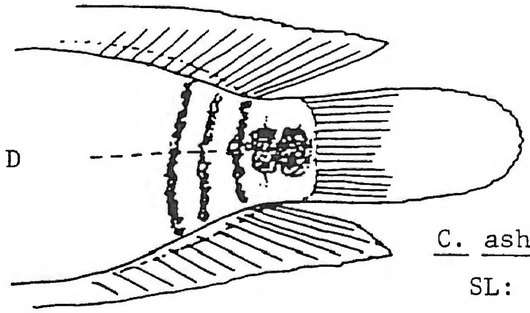
Ctenopoma nigropannosum
SL: 22.5 mm
MRAC 39465



C. pellegrini
SL: 31.40
MRAC 94914-915



C. multispine
SL: 32.20
MRAC 36385-417



C. ashbysmithi
SL: 35.70
BMNH 1976-10-21: 2
(holotype)

Figure 7. Juvenile color patterns of *Ctenopoma*.

The Subgenus Monkengia

Description

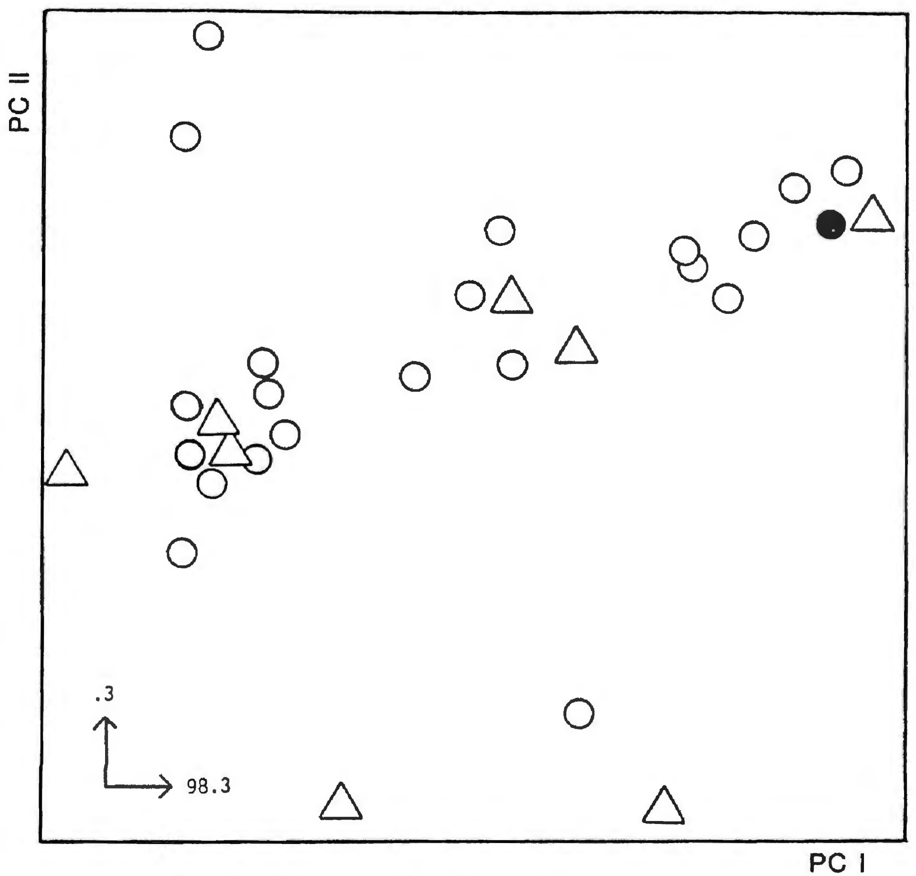
Fishes of the subgenus Monkengia are generally large (80+ mm SL), deep-bodied fishes; sixteen total (14 branched) caudal rays; opercle and interopercle usually spined or finely serrate; subopercle and preopercle freqently spined or serrate; a single CLL pore in the interorbital space; adult and young adult males have a patch of strongly spined scales just posterior to the orbit and a similar patch just anterior to the base of the caudal fin; coloration variable, uniform grey or olive or brown or dark mottled pattern of yellows and browns; dark spot (sometimes an ocellus) at base of caudal peducle or on the flank; pelvic fins short and uncolored or somewhat more expansive and decorated; upper jaws highly protrusile with lengthy ascending process of premaxilla, or non-protrusile with short ascending process of premaxilla; little or no sexual dimorphism in morphometry, possible sexual dimorphism in color patterns or color intensity.

Sexual dimorphism

Figures 8 and 9 show PCA plots of, respectively, a non-protrusile jawed species, C. kingsleyae and a protrusile-jawed species, C. acutirostre. Little or no size free sexual dimorphism is evident in these plots, and the sexes are not separated in further analyses.

Species Groups and Alpha Taxonomy

There are at least two clades within this subgenus. Figure 10 presents a PCA scatter plot of all species of Monkengia. Ctenopoma



△ : males ○ : females
(solid figure = syntype)

Figure 8. PCA Plot (Morphological Data) for C. kingsleyae with sexes noted.

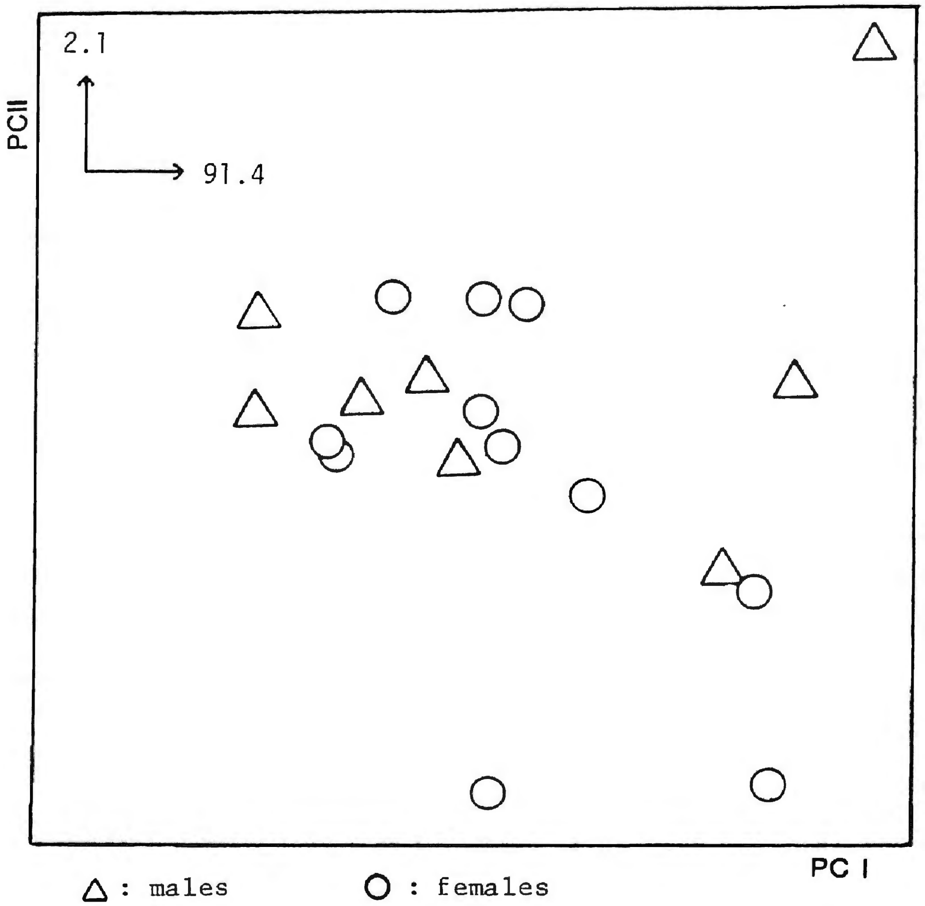


Figure 9. PCA Plot (Morphological Data) for *C. acutirostre* with sexes Noted.

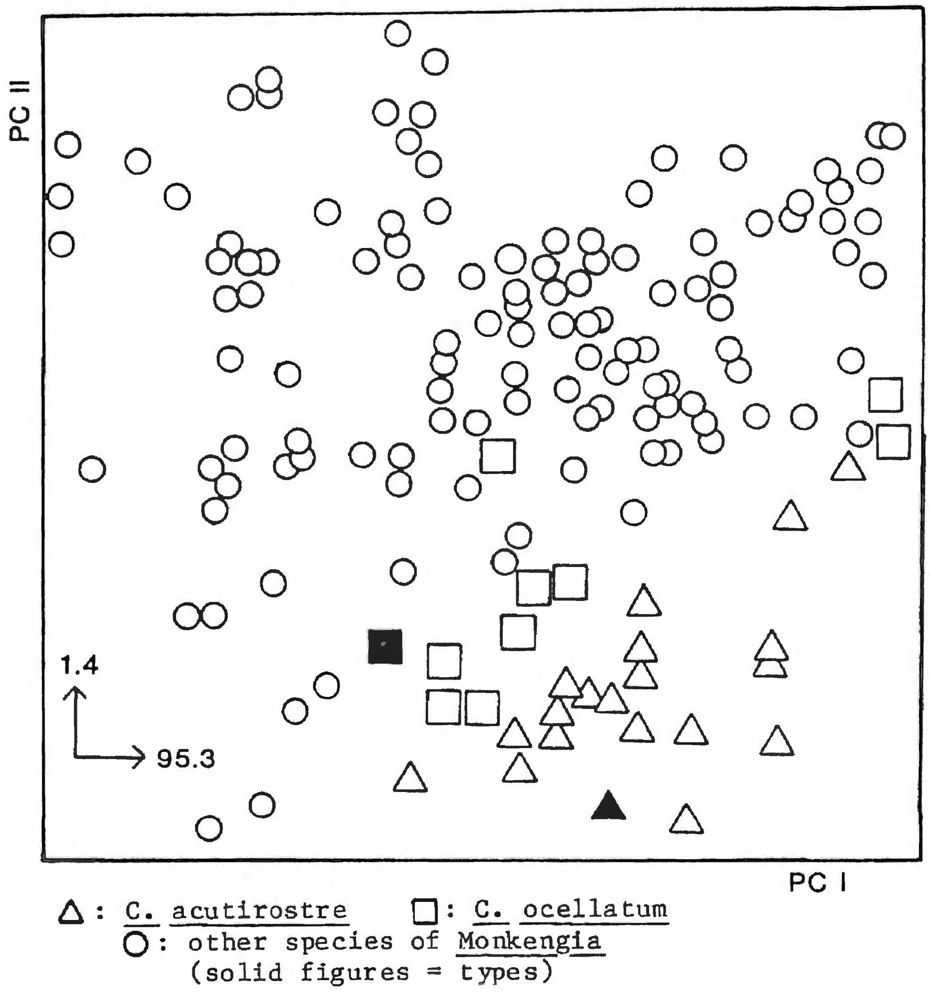


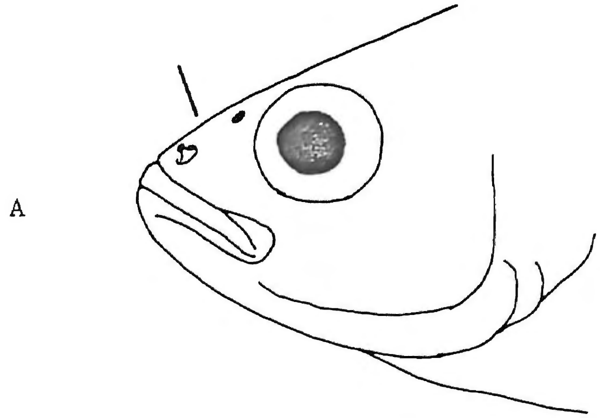
Figure 10. PCA Plot (Morphological Data) for all *Monkengia* with with *C. acutirostre* and *C. ocellatum* indicated.

acutirostre and *C. ocellatum* form a separate group in this comparison, are further distinguished by their jaw morphology. Both have highly protrusible jaws with the ascending process of the premaxilla extending well beyond the middle of the orbit. The jaws of other *Monkengia* are less protrusible, and the ascending process of the premaxilla does not extend to the anterior border of the orbit. The lachrymal (suborbital shelf) of *C. acutirostre* and *C. ocellatum* is also quite different from that found in other *Monkengia*, being narrow and blade-like antero-ventrally to the orbit. In all other *Ctenopoma* (and *Anabas* and *Sandelia*) the lacrhymal is broad and flat (see Figure 11). *Ctenopoma acutirostre* and *C. ocellatum* have strongly-spined preopercles, whereas other *Monkengia* generally have fewer (if any) and weaker preopercular spines.

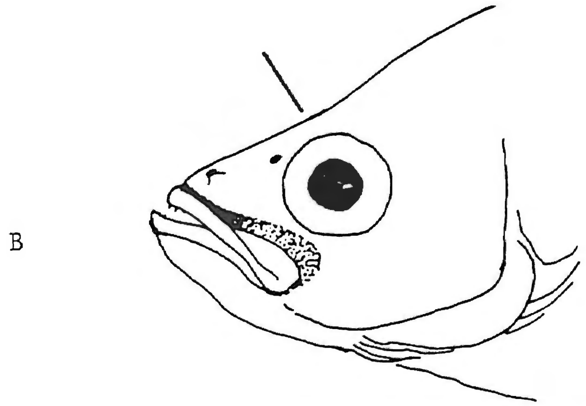
Protrusible-Jawed Species

Ctenopoma acutirostre and *C. ocellatum* are clearly different, though in the past the two species have been confused. Boulenger (1916) synonymized the two forms without comment. Pellegrin (1928) revived *C. acutirostre* as a subspecies of the other and later Poll (1939) returned it to full specific status, based on coloration and snout profile.

As noted by Poll and Pellegrin, the two species show differences in coloration and body form. *Ctenopoma acutirostre* is irregularly blotched with large dark-brown spots on a tan background, one oblong spot occurs at the base of the pectoral fin. *Ctenopoma ocellatum* has a distinct spot at the base of the caudal fin, anterior to which



Ctenopoma maculatum
SL: 110.5 mm
CAS 15783



Ctenopoma acutirostre
SL: 90.9 mm
Aquarium specimen

Length of ascending process of the premaxilla indicated by bar.

Figure 11. Head Profiles of *C. acutirostre* and *C. maculatum*.

are a series of concentric rather irregular, roughly vertical bars. The irregular barring is less distinct on older specimens. *Ctenopoma ocellatum* lacks the spot at the pectoral fin base. The jaws of *C. acutirostre* are more protrusible than those of *C. ocellatum*. The snout of the former is much more acute and the profile of the head is concave, as opposed to convexly rounded or straight in *C. ocellatum*. In *C. acutirostre*, the articulation between the dentary and the subopercle forms an angular and convex bulge, while it is more rounded in *C. ocellatum*.

In both species the ascending process of the premaxilla extends well beyond the anterior border of the orbit (see Figure 11A). In *C. acutirostre* the track made by the process is clearly visible on the forehead between the eyes. Two scale rows thinly cover and outline the tissue overlying the process, allowing their length to be easily gauged without manipulation of the jaws or dissection. The track of the ascending process is hidden in *C. ocellatum* and the jaws must be manipulated or scales removed to determine its length.

The holotype of *C. denticulatum* Pellegrin (the only known specimen) differs from many specimens of *C. acutirostre* only in the development of serrations on the inter-and sub-opercles. These bones are highly serrate in the *C. denticulatum* holotype. Boulenger (1916) listed *C. denticulatum* in his synonymy of *C. ocellatum*, but, as noted above, he referred all specimens of *C. acutirostre* to *C. ocellatum*. Based on the characters outlined above, the holotype of *C. denticulatum* is clearly not a specimen of *C. ocellatum*. The serrations on the inter-and sub-opercles show great variation in *C. acutirostre*

(0-31 serrations for each bone), and do not represent characters of sufficient taxonomic value to separate *C. denticulatum* from *C. acutirostre*.

Non-Protrusible Jawed Monkengia

Species of this group have short ascending processes of the premaxilla and broad flat lachrymals. Within this group are two further subdivisions, based mostly on color pattern: 1. species with a large spot at the base of the caudal fin, and 2. species with a spot mid-laterally on the flank. There is also some differentiation evident in the morphological data. Figure 12 presents a typical PCA scatter plot for all species of non-protrusile jawed *Monkengia*. Length of the premaxilla and eye diameter account for most non-size related variance in this analysis.

Species with Mid-body Spot. *Ctenopoma maculatum* is restricted to the coastal rivers from southern Cameroun to the upper Ogooue River, and to an extreme northwestern tributary of the Zaire basin (The Dja River). Gosse (1963) erroneously recorded *C. maculatum* from near Yangambi in the middle Zaire basin. Examinantion of Gosse's specimens reveals them to be *C. oxyrhynchum*, the other species with a mid-body spot. *Ctenopoma maculatum* does not extend so far into the Zaire basin, while *C. oxyrhynchum* is widespread in the lower and middle reaches of the basin. The two forms are not sympatric, except possibly in the Sangha River (western Zaire River drainage).

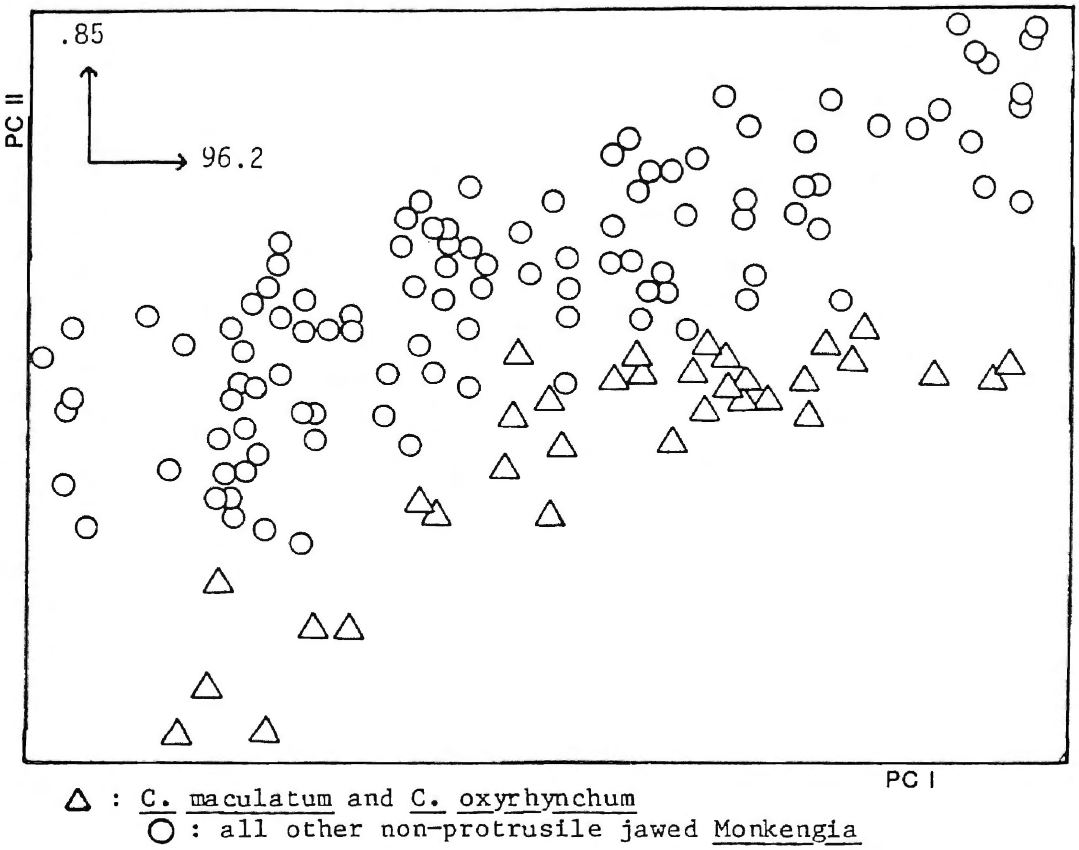


Figure 12. PCA Plot (Morphological Data) of non-protrusile jawed *Monkengia* with *C. maculatum* and *C. oxyrhynchum* noted.

These two species are similar both in shape (Figure 13) and general appearance and have been confused. The most useful characters in separating them are size and color pattern. *Ctenopoma oxyrhynchum* does not exceed 100 mm SL while *C. maculatum* is frequently much larger. Except for the midbody spot, *C. maculatum* is drab brown (or grey in alcohol). *Ctenopoma oxyrhynchum*, by comparison, often shows dark mottling againt a tan background. Two streaks radiate posteriorly from its eyes and its pelvic fins are always darkly pigmented. The pelvic fins of *C. maculatum* are always clear except in very small specimens (25 mm SL). The snout of *C. maculatum* is more rounded than that of *C. oxyrhynchum*. Though specimens of *C. oxyrhynchum* tend to be smaller, the interopercle is more stongly spined. The subopercle of *C. maculatum* is never spined, though in *C. oxyrhynchum* it is normally heavilly spined.

Boulenger (1916) erroneously listed *C. weeksii* Blgr. as a synonym of *C. maculatum*. The *C. weeksii* syntypes are *C. oxyrhynchum*.

Species with a Caudal Spot. *Ctenopoma muriei* is the most easily identified of the three species of this group. Both size and shape differences between *C. muriei* and the other species are clear in the plot of PCA scores for this group (Figure 14). *Ctenopoma muriei* adults are never larger than 80 mm SL, while adults of the other species are much larger.

The syntypes of *Ctenopoma ctenotis* (Boulenger) are specimens of *C. muriei* (SMN et al., in prep.) as are the types of *Anabas houyi* Ahl (first suggested by Blanche *et al.*, 1964; verified by SMN). In 1928 Nichols described what he perceived to be a new subspecies of *C. muriei*, *Anabas muriei ocellifer*, from Ankoro on the upper Lualaba River

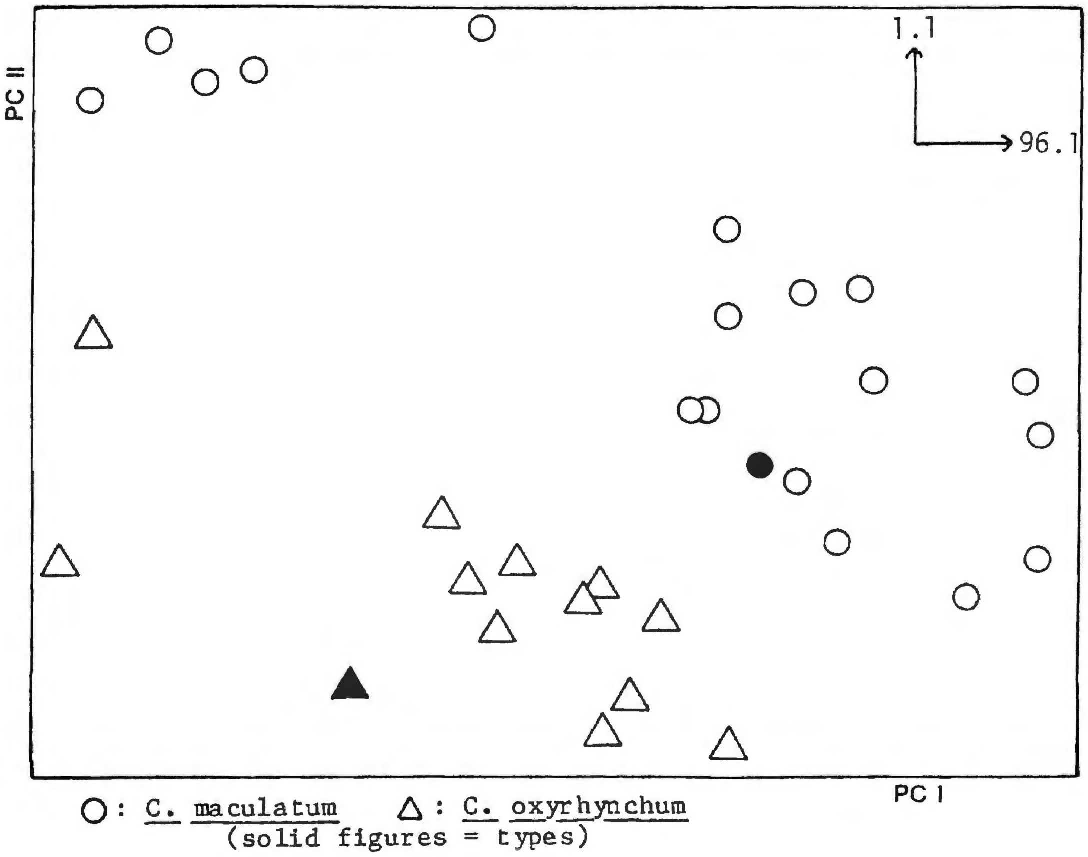


Figure 13. PCA Plot (Morphological Data) for *C. maculatum* and *C. oxyrhynchum*.

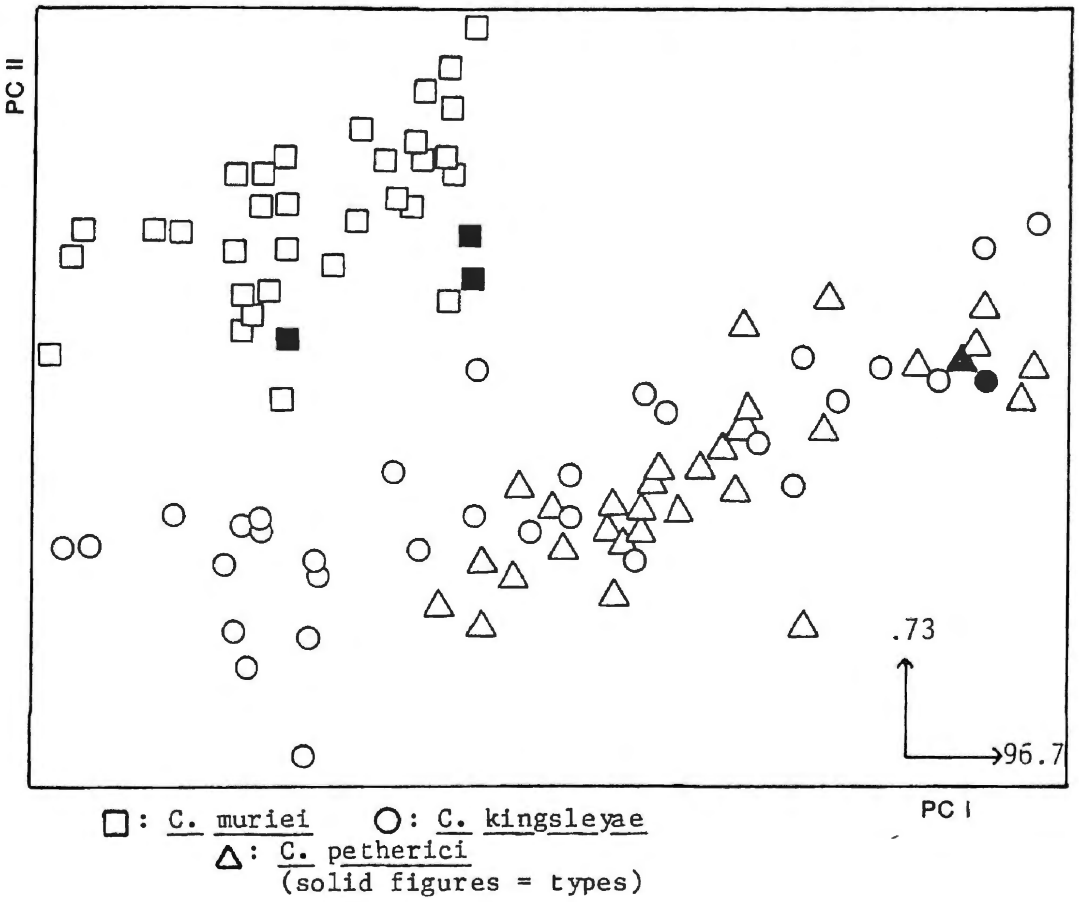


Figure 14. PCA Plot (Morphological Data) for *Monkengia* forms bearing caudal spots.

(upper Zaire drainage). Banister and Bailey (1979) questioned the identity of Nichol's specimens, suggesting instead that they represent *C. ctenotis*. The type series of *A. muriei ocellifer* is not *C. muriei*, and in fact does represent the taxon which has been known as "*C. ctenotis*" (now *C. intermedium*, Skelton, in prep., see below).

Ctenopoma kingsleyae and *C. petherici* are more difficult to separate from each other. Figure 15, a PCA of the morphological data, indicates two overlapping groups with the holotypes of both species unconfortably close together. The meristic data are of more use. In general, *C. petherici* has higher counts for several meristic variables, though overlap occurs for each case (see Figures 16 and 17). Figure 18, a PCA plot of the meristic data, shows good differentiation, though as in the PCA of morphological data, the holotype of *C. kingsleyae* is in the scatter for *C. petherici*. In both PC plots, the same series of *C. kingsleyae* specimens are placed in the *C. petherici* scatter. These specimens are indicated in both figures and are very likely specimens of the latter species. They are all from regions that probably support populations of *C. petherici* rather than *C. kingsleyae* (see below). The occurence of the *C. kingsleyae* holotype in the *C. petherici* scatter is puzzling; it is from the Ogooue River, well beyond the known range of *C. petherici*. The *C. kingsleyae* holotype is an unusually large specimen and this could push it away from 'normal' *C. kingsleyae*.

The two forms apparently have different distribution patterns with only limited sympatry. *Ctenopoma kingsleyae* is found in the Zaire basin and in coastal drainages from Zaire to the Senegal River. These regions are primarily rain forest. *Ctenopoma petherici*, on the other hand, inhabits sub-Saharan waterways from the Nile to the Senegal River

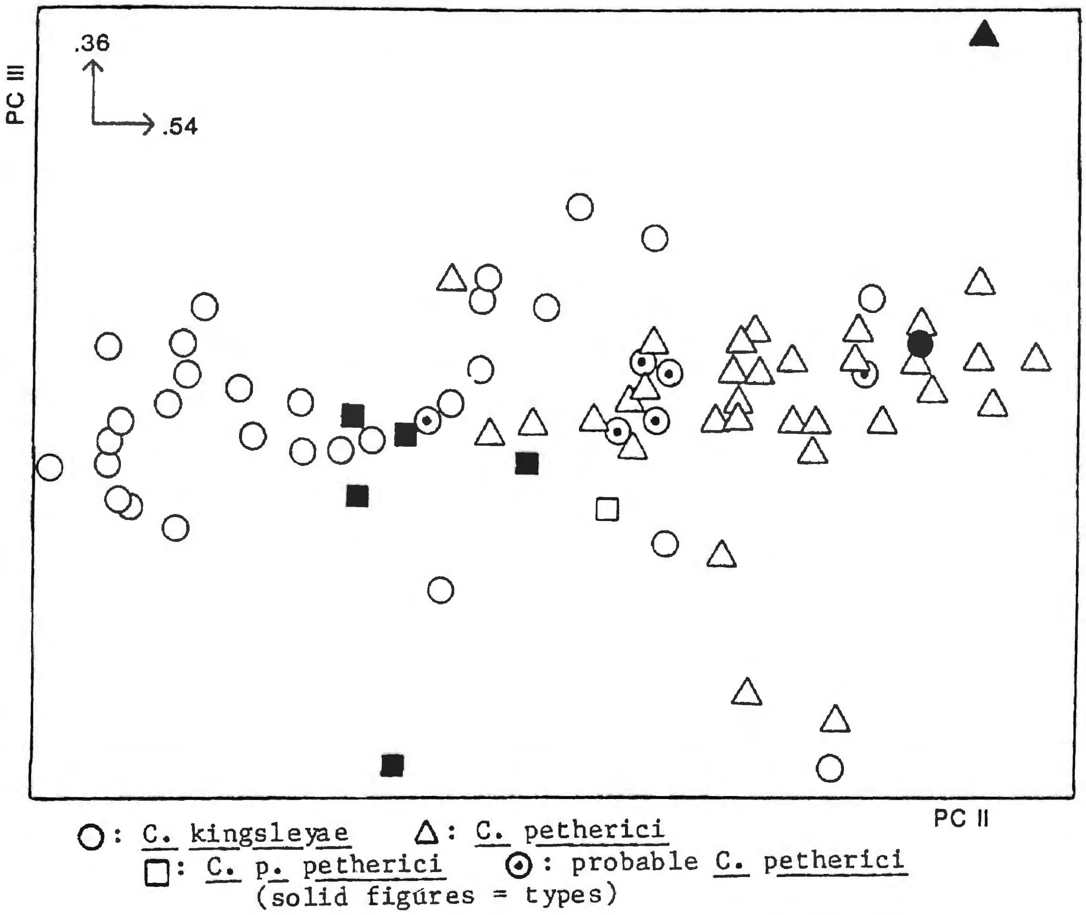
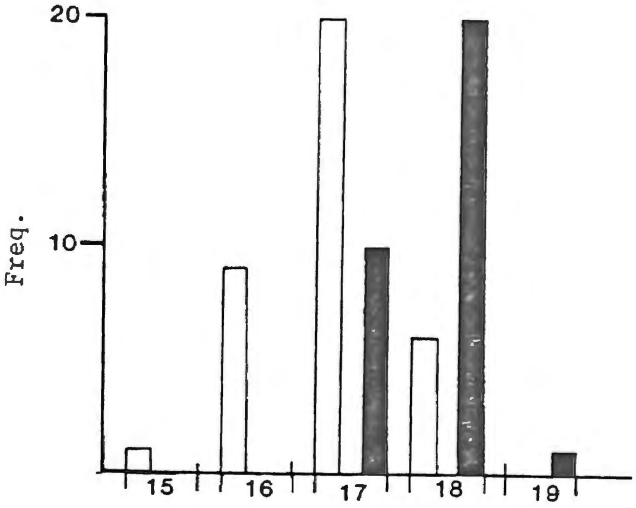
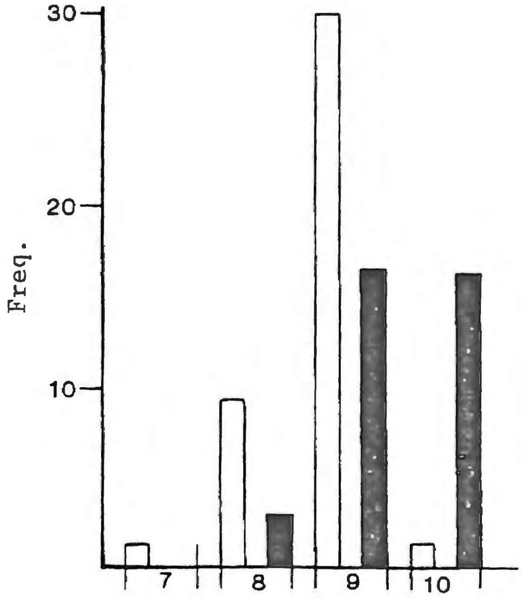


Figure 15. PCA Plot (Morphological Data) for *C. petherici* and *C. kingsleyae*.



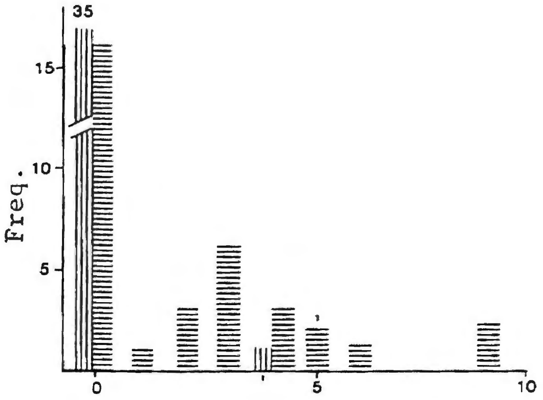
A. Dorsal spines



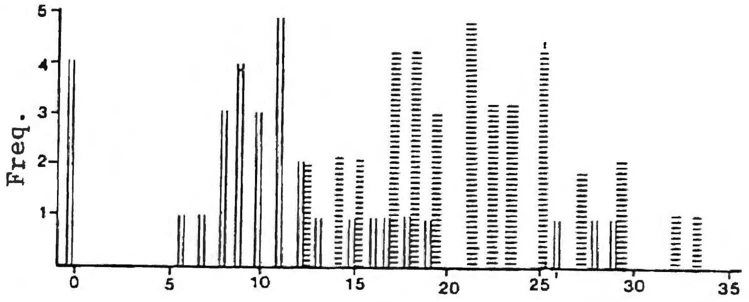
B. Anal spines

open bars = *C. kingsleyae* closed bars = *C. petherici*

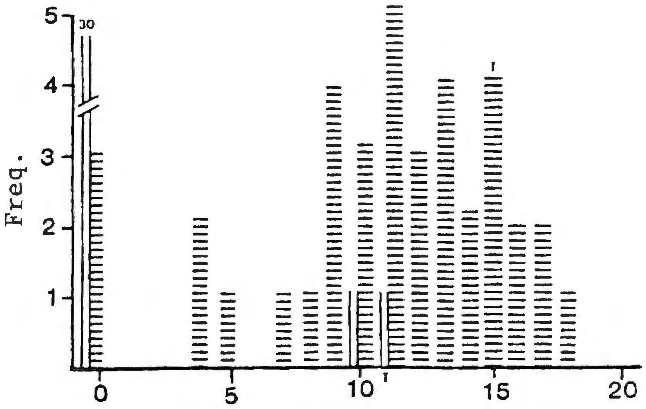
Figure 16. Frequency of Anal and Dorsal Spine counts for *C. kingsleyae* and *C. petherici*.



A. Preopercular spines



B. Interopercular spines



C. Subopercular spines

vertical bars = C. kingsleyae   horizontal bars = C. petherici
"T" = Value for Type Specimen

Figure 17. Frequency of Opercular spine counts for C. kingsleyae and C. petherici.

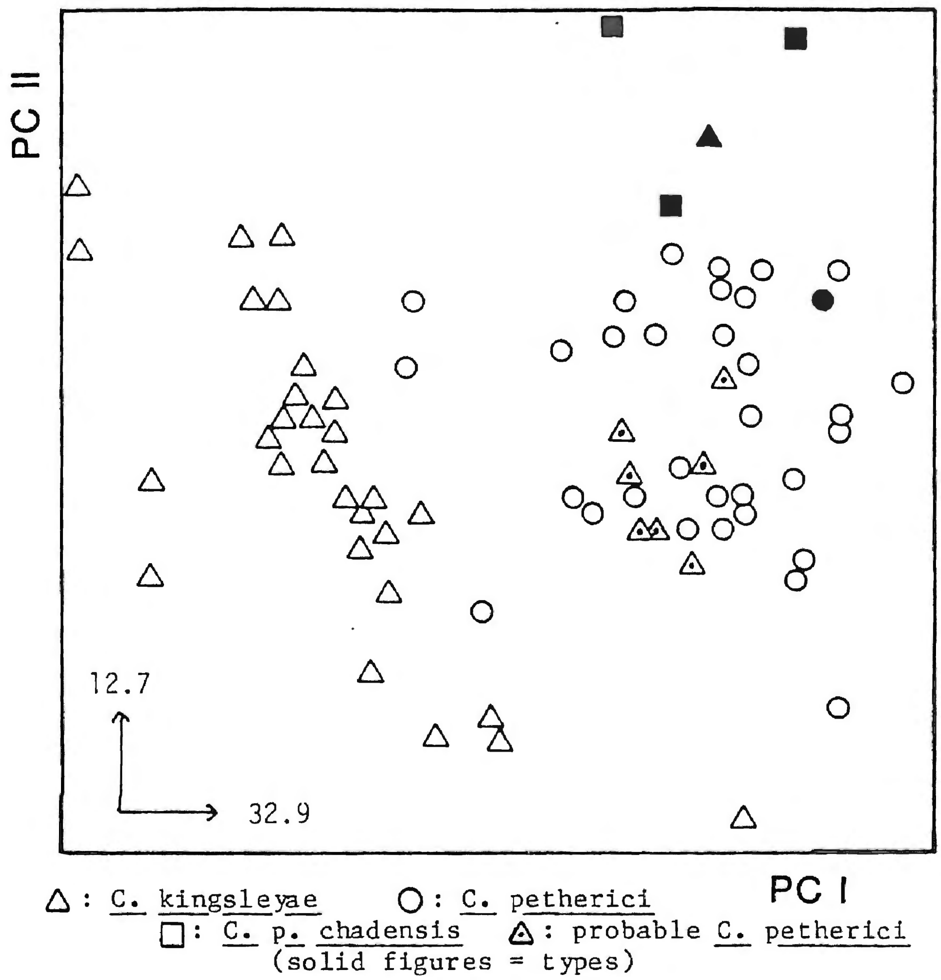


Figure 18. PCA Plot (Meristic Data) for *C. kingsleyae* and *C. petherici*.

and rivers with historic ties to the above waterways. The two forms are apparently sympatric in northern Nigeria (Niger River System)(G. Mc. Reid, pers. comm.). The overall distribution patterns of these species is unclear at present and literature and museum register records are unreliable.

Anabas argentoventer was described by Ahl (in Schreitmuller and Ahl) in 1922. His holotype apparently came from live specimens imported to Germany before The First World War and circulated for some years in the German aquarium trade under the name "*Anabas africanus*" (*nomen nudem*). The reported origin of this stock is Wari on the Niger River Delta. The holotype, an emaciated aquarium specimen (?), is a specimen of *C. kingsleyae*. A recent photograph circulated by German aquarists (e.g. Linke, 1980, p. 100) under the name *C. argentoventer* is quite different. The specimen in this photograph has colored pectoral fins and a blade-like lachrymal and may represent a young *C. ocellatum*).

Anabas breviventralis Pellegrin is known only from the holotype, a very poorly preserved specimen. It is soft, its median fins are greatly damaged and the head is broken or deeply torn in several places. The specimen is also largely descaled, though a pigmented spot at the base of the caudal fin is still evident. Identification of the specimen is also confounded by poor locality information. Pellegrin gave its origin as "Afrique equatorial francais." This region includes elements of both the Lake Chad and Zaire River basins. The meristic values of the median fins of the holotype of *A. breviventralis* place it within the range of variation of *C. kingsleyae* of the Zaire basin. On that basis, I am designating the former name as a junior synonym of the latter.

Anabas togoensis Ahl is known by a single specimen from Togo (west Africa). Daget (1958) listed this taxon in his synonymy of *C. kingsleyae*. He noted that there is nothing in the original description of *A. togoensis* indicating any differences between it and *C. kingsleyae* from west Africa, though he apparently did not see the holotype. H.-J. Paepke, Curator of Fishes of the Zoological Museum of Berlin, informs me that the holotype cannot be located. There is little possibility that *A. togoensis* represents a valid species and, in the absence of any type material, I agree with Daget's synonymization, at least until the distributional picture for *C. kingsleyae* and *C. petherici* is clarified. The holotypes of both *A. caudomaculatus* Ahl and *A. riggenbachi* Ahl are specimens of *C. petherici*. Blanc et at. (1964) first suggested this synonymy for *A. caudomaculatus* (subsequently verified by during the present study by examination of the holotype). The holotype of *A. riggenbachi* is another poorly preserved specimen without locality data and identification of this specimen is based largely on meristic characters and the presumed type locality.

The Subgenus *Nana*

Description

Fishes of the *Nana* subgenus are 75 mm SL or less and have the following characteristics: fourteen total caudal rays (12 branched); opercle and interopercle spined, sub -and preopercle and lachrymal never spined or serrate; single pair of close set CLL pores in the interorbital space; highly developed sexual dimophism, most evident in body and anal, dorsal and pelvic fin size, all are larger in males; pelvic fins colored in both sexes at all ages.

Sexual dimorphism

Figure 19 presents a PCA of morphological data from all specimens of *C. nanum*. Marked sexual differences are clearly demonstrated along both axes. In PC I differences in size account for most of the variance, male specimens being generally larger. Of most importance in separating the sexes on PC II are caudal peduncle length and anal dorsal, pelvic fin length. Of only slightly less importance are variables reflecting body depth and dimensions of the abdomen. Because of strong sexual dimorphism exhibited by this subgenus, all subsequent morphological analyses on *Nana* are conducted on data from male specimens only (unless otherwise specifically noted).

Species Groups and Alpha Taxonomy

The species of *Nana* separate into two main groups on the basis of dorsal and anal spine counts: 1. D. XVII-IXX (XVI-XVII rare);

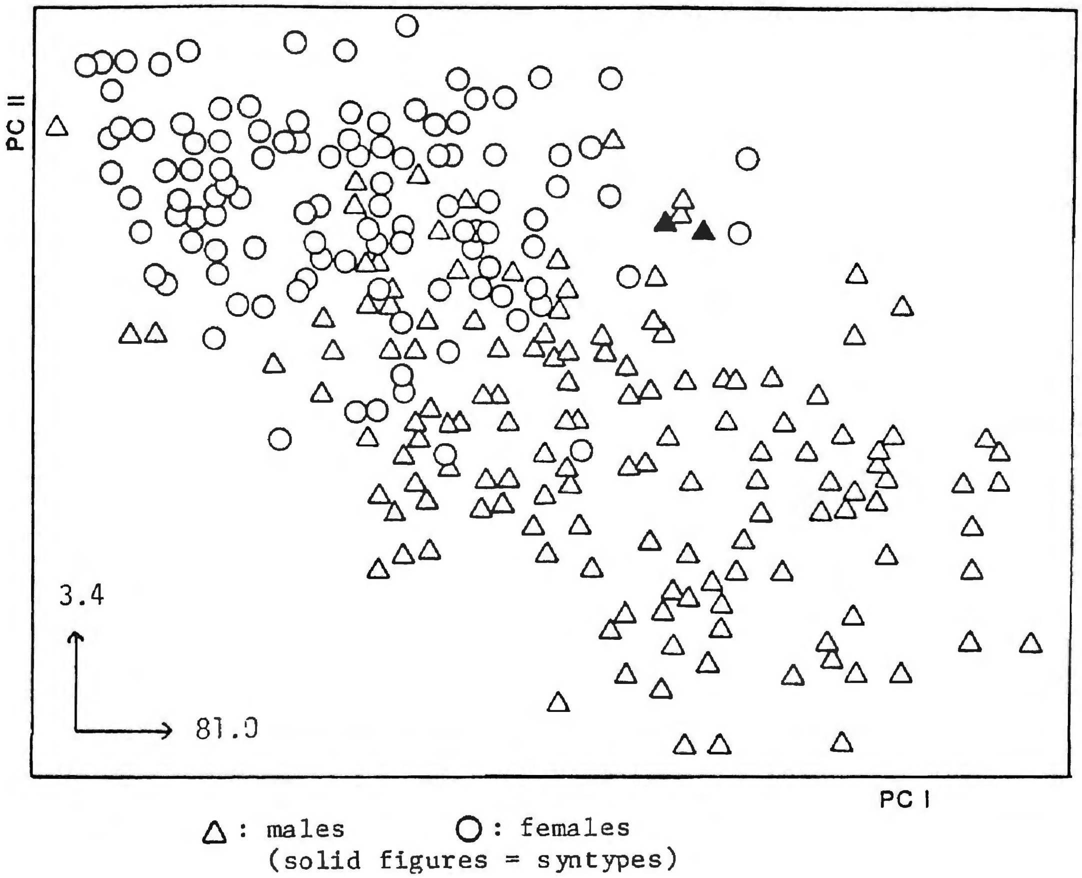


Figure 19. PCA Plot (Morphological Data) for *C. nanum* with Sexes Noted.

A. X-XII (X uncommon); 2. D. XIV-XVI (uncommonly XVII); A. VI-X (rarely X).

Species with Higher Spine Counts

Ctenopoma ansorgei is found throughout the *cuvette centrale* (the central forested region of the Zaire River basin) and in some of the closely-associated west-coast drainages of the central African rain-forest belt. *C. ansorgei* is smaller than most other species of *Nana* (60 mm SL or smaller), and is more brightly colored. There are 6-8 dark vertical bars on the flanks; these are usually slightly narrower than the interspaces and extend onto the median fins. The interspaces are orange in living specimens, especially on the fins and in breeding males. The membranes towards the tips of the anal and dorsal spines and rays are white, as is the tissue along the leading edge of the pelvic fins. Breeding males have markedly elongated and filamentous terminal rays on the anal and dorsal fins. The leading rays of the pelvic fins are also greatly elongated, often reaching almost to the terminus of the anal fin. Both sexes have 2 or 3 streaks radiating posteriorly from their eyes.

Anabas davidae was described by Poll (1939), from two specimens from Pool Malebo (Stanley Pool) on the lower Zaire River. Presently, one of the syntypes is partly disentegrated, the other is a young adult, which is slightly dehydrated with little color pattern still apparent. The Meristic traits of the two syntypes are well within the range for *C. ansorgei*. Poll (1939) provided no reason for separating the two species, nor can I find any. At the time of the description, *C. ansorgei* was not known from Pool Malebo, but subsequent collections in the region yielded good numbers of *C. ansorgei*. Boesman (1959) reported a series of *Ctenopoma* which he identified as *C. davidae* from Pool Malebo. To separate *C. davidae* from *C. ansorgei*, he cited slight differences in body depth: 3.25-3.35 % of the SL for *C. ansorgei* and 3.5-4.0 % SL for *C. davidae*. I cannot separate the two forms using this character which varies greatly in such a small species depending on the condition of the specimen and the quality of preservation. Figure 20 presents a PCA for the morphological data for all specimens (males and females) of *C. ansorgei* with a syntype of *C. davidae* and specimens from Pool Malebo noted. The syntypes of *A. davidae* and the specimens cited by Boesman are fairly poor, but I identify them unquestionably as *C. ansorgei*.

Ctenopoma damasi is apparently endemic to the Lake Edward basin in the Nile headwaters. It is easily separated from *C. ansorgei* on the basis of this distribution (the two are not sympatric) and color pattern. *Ctenopoma damasi* (preserved) show no banding. The fins and dorsum are dark brown, and the belly is pale tan or yellow. The head is frequently darker than the rest of the body, with a dark border along the posterior margin of the opercle. Photographs of living specimens (Richter, 1982, p. 123) show it to be dark blue or black with lighter blue flecks on the sides and fins. *Ctenopoma damasi* is stouter with a less acute snout than C. *ansorgei* (see figure 20).

Species with Lower Spine Counts

Among these forms, *C. fasciolatum* is easily identifiable by its deeper body, and very short caudal peduncle. All other species of *Nana* except *C. ansorgei* have well-developed caudal peduncles. Table VIII

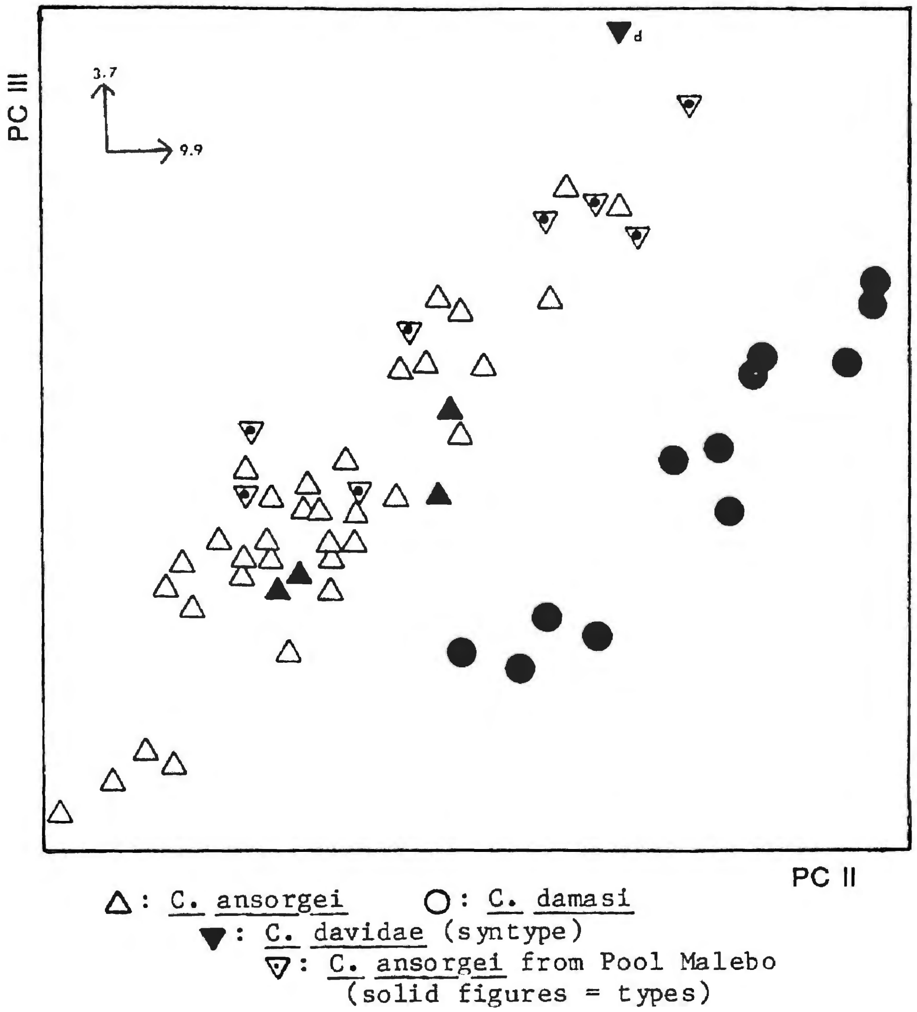


Figure 20. PCA Plot (Morphological Data) of *C. ansorgei* and *C. damasi* with *C. davidae* noted.

presents key proportional values for all species of Nana. Ctenopoma fasciolatum does not usually exhibit the vertical bars found in some or all age classes of all other species of Nana (except C. damasi?). Preserved males and females of C. fasciolatum are black or deep blue overall. When vertical bars are present they are very wide, separated only by a single uneven row of lightly pigmented scales. Overall the appearance is frequently more mottled than barred. The anal, dorsal, caudal and pelvic fins are also dark with pale flecks. In breeding males the posterior rays of the anal and dorsal fins and the rays of the pelvic fins are extending into long filaments. Non-breeding males also have elongated fin rays, though they are not extended into long filaments. The same fins, especially the pelvics, may be pointed in females, but they are not usually filamentous. Breeding females and some preserved females show a pale horizontal stripe which extends from just behind the opercule posteriorly along the flank (C. Ferraris, pers. comm.). Ctenopoma congicum, the species most easily confused with C. fasciolatum, has a very similar color pattern, though the banding in C. congicum is usually more distinct. Ctenopoma congicum is also shallower-bodied and has a well developed caudal peduncle (refer to Table VIII).

Ctenopoma fasciolatum is confined to the forested regions of the cuvette centrale.

In 1925 Pellegrin described a subspecies of C. fasciolatum, which he named C. fasciolatum filamentosa. The holotype is a small male, and the character used by Pellegrin to distinguish his subspecies is the "development" (i.e., elongation) of its fin rays. As suggested by Matthes (1964), the holotype is a normal male specimen with elongate

TABLE VIII

NANA SPECEIES GROUP KEY PROPORTIONAL VALUES

Species	Caudal ped. lngth/ SL	Interorb. dist./ head lngth	Pect. to Pelv. dist./SL	Caudal ped. depth/SL	Body depth/ SL
ansorgei	16.2-51.7 $\bar{x}=25.8$	3.9-4.7 $\bar{x}=4.2$	6.5-9.1 $\bar{x}=7.8$	5.8-7.2 $\bar{x}=6.4$	3.2-3.9 $\bar{x}=3.5$
congicum	29.2-46.7 $\bar{x}=37.6$	3.1-3.2 $\bar{x}=3.2$	6.2-7.0 $\bar{x}=6.6$	5.4-5.7 $\bar{x}=6.0$	2.6-3.1 $\bar{x}=2.9$
c. longipinnis	12.7-32.8 $\bar{x}=21.8$	2.8-3.2 $\bar{x}=3.2$	6.0-8.4 $\bar{x}=7.1$	5.5-6.6 $\bar{x}=6.0$	2.7-3.0 $\bar{x}=2.9$
damasi	17.5-30.5 $\bar{x}=22.5$	3.2-3.7 $\bar{x}=3.4$	6.7-7.6 $\bar{x}=7.1$	5.9-6.9 $\bar{x}=6.2$	2.9-3.0 $\bar{x}=3.0$
fasciolatum	19.0-71.2 $\bar{x}=36.8$	2.9-3.4 $\bar{x}=3.1$	6.0-7.2 $\bar{x}=6.5$	5.0-6.0 $\bar{x}=5.5$	2.3-3.0 $\bar{x}=2.6$
intermedium	11.3-29.9 $\bar{x}=15.3$	3.3-4.2 $\bar{x}=3.8$	6.3-8.5 $\bar{x}=7.3$	5.5-7.3 $\bar{x}=6.3$	2.8-3.5 $\bar{x}=3.1$
nanum	9.8-35.3 $\bar{x}=16.4$	3.4-4.5 $\bar{x}=3.9$	6.0-8.7 $\bar{x}=7.0$	5.0-7.6 $\bar{x}=6.0$	2.3-3.0 $\bar{x}=3.1$

fin rays. The subspecies is not valid.

Ctenopoma congicum is found throughout the *cuvette centrale* and occupies some of the central African west coast drainages. In the northern areas of the Zaire basin, where the rainforest ends, *C. congicum* is present where other *Ctenopoma* (e.g., *C. fasciolatum*, *C. ansorgei*) are not found--presumably the latter two species cannot survive outside rainforested areas. *Ctenopoma congicum* also occurs in Nilo-Sudanic waters; it is found in southern headwaters of the Lake Chad basin, and I have identified several specimens of *C. congicum* from the White Nile. Adult specimens strongly resemble *C. fasciolatum* in color pattern, though banding is more pronounced in *C. congicum*. These bands are narrowly spaced and mottled or broken at the edges. Pale flecks are present on the body, soft anal and dorsal and caudal fins. When the color pattern is ambiguous, body proportions (body depth and caudal peduncle length separate *C. congicum* from *C. fasciolatum* and interorbital distance (or eye diameter which is usually nearly equal to interorbit distance in species of *Nana*) separates it from *C. nanum* and *C. intermedium*. The eye diameter (or interorbital space) is contained in the head length (tip of snout to the upper edge of the operclular opening) 2.8-3.2 times in *C. congicum* and 3.4-4.5 times in *C. nanum* and *C. intermedium*. *C. nanum* is also slightly shallower-bodied that *C. congicum*.

Anabas pekkolai Rendahl, 1939 is known only by the holotype which was taken in 1914 at Tonga on a tributary of the While Nile. I have identified the specimen as a young male *C. congicum* (very well preserved).

Ctenopoma congicum longipinnis (Fowler, 1939) is based on a single collection of 11 specimens from a northern tributary of the Zaire River. Fowler based his new subspecies on some obscure differences between his specimens and the figure of *C. congicum* published in Boulenger (1916). The specimens of his type series appear to be *C. fasciolatum*. Figure 21 is a PCA of morphological data for these two species with types of *C. c. longipinnis* noted. The types will have to be re-examined to confirm their identity.

Ctenopoma nanum is the most widespread of the species of *Nana*. It is found throughout the Zaire basin (excepting some extreme southern tributaries), in the west coast central African drainages and in at least one tributary of the Nile. The very similar *C. intermedium* replaces *C. nanum* in southern tributaries of the Zaire system, and occurs southward into the Zambesi River system and several east coast rivers south of the Zambesi.

Ctenopoma nanum usually is strongly barred. The 6 to 8 vertical bars are regularly spaced, sharply edged and usually slightly wider than the pale interspaces. The first band is at the pectoral fin base and the most posterior is at the caudal fin base. The posterior bar forms an ocellus in specimens 30 mm SL and less). The bars usually extend onto the median fins and are more distinct in males than in females. Males of *C. nanum* are larger than females, more intensely colored and have the elongated fin rays described for other species of *Nana*. The elongation in *C. nanum* is usually not as pronounced as that found in *C. fasciolatum* or *C. ansorgei*.

Since *C. nanum* is so widespread, existing in many separate rivers and sections of rivers, some of these populations (e.g., those in the Nile or in the west coast central African drainages) must be isolated

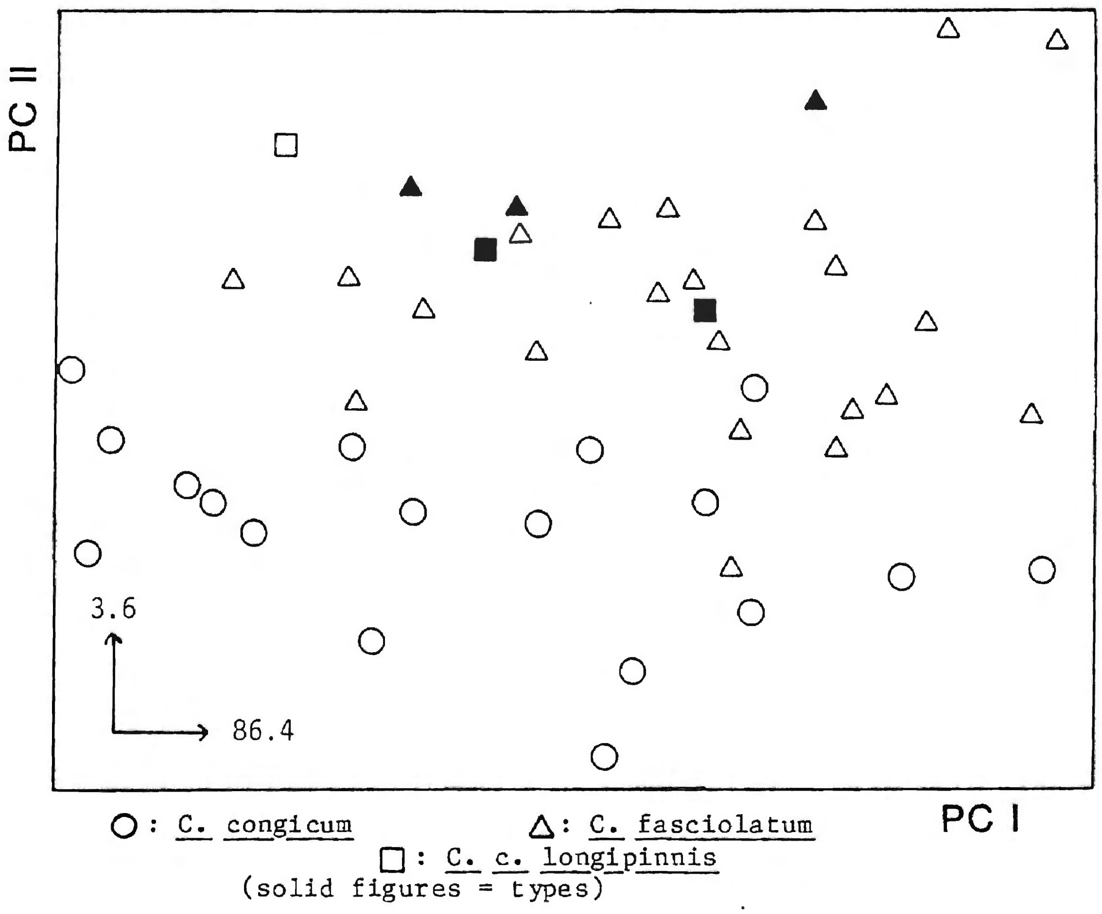


Figure 21. PCA Plot (Morphological Data) for *C. fasciolatum*, *C. congicum* and *C. c. longipinnis*.

from each other. Geographic variation was perceived in qualitative examination of specimens from various parts of the distribution. Variation in shape is noticable particularly in the head and snout profiles, and in color patterns. In an attempt to quantify this variation complete morphometric data were taken from each of over 500 specimens of C. nanum and C. intermedium from all areas of the distribution. However, the morphological data failed to provided any easily quantifiable geographic variation. A scatter of PCA scores showed complete overlap between different regions.

Two populations are qualitatively unique. Specimens of C. nanum from the headwaters of the northeastern tributaries of the Zaire River (beyond the rain forest belt) are less distinctly barred than specimens from more central areas of the basin. This is possibly an ecophenotypic responce to the habitat in the region or an artifact of preservation (though the same pattern was found in specimens from several collections in several different musuems). Interestingly, C. intermedium, which replaces C. nanum in the southern tributaries of the Zaire basin upstream from the rainforested areas, are also less distinctly barred. Another variant comes from some western tributaries of the Zaire, where specimens are very deep-bodied and humpbacked. Since only 5 specimens of this form have been identified, its status and distribution are at present not clear.

There are several junior synonyms for C. nanum. Anabas lineatus Nichols, 1923, is based on a single poorly preserved juvenile with no known locality. Synonymy was suggested by Matthes (1964), and verified after examination of the holotype (S. Norris, pers. obs.). Ernst Ahl described 5 species of Ctenopoma in a 1928 paper. The holotype of his Anabas garuanus from the "Hinterland" (back country) of Cameroun is a gravid female *C. nanum* (S.Norris, pers. obs.). *Anabas brunneus* Ahl was synonymized with *C. nanum* by Holly (1930). The two syntypes of *A. brunneus* which I have seen are large male specimens of the humpbacked variant of *C. nanum* noted above.

Ctenopoma intermedium (Pellegrin, 1928) was described from four specimens from the upper Zambesi River. Bell-Cross (1976) incorrectly listed the name as a synonym of *C. multispine*, but otherwise the name has remained unused until present. The species to which the name is now applied (Skelton, in prep.) has previously been known as *C. ctenotis* (Boulenger). Skelton *et al.* (1985) noted that the syntypes of *C. ctenotis* do not match the taxon to which that name has been most commonly applied. The two syntypes of *C. ctenotis* have subsequently been identified as *C. muriei* (S.Norris *et al.*, in prep.), and I have data supporting Skelton's opinion that *C. intermedium* is the only name available for the specimens previously known as *C. ctenotis*.

Morphologically, *C. intermedium* is poorly separated from *C. nanum*, and distribution is the most useful distinguishing character. *Ctenopoma intermedium* is found in the southern tributaries of the Zaire basin all along the southern headwater region of the basin and into the Zambesi River system. Recognizable *C. nanum* are not found much farther south than the southern border of the dense forest. Mixed populations have not been identified nor have any potential hybrids; however, the two species are so similar that such populations might be difficult to identify morphologically.

Figure 22 presents the PCA of morhological data for the males *C. nanum* and *C. intermedium*. There only poor differentiation based on these data. *Ctenopoma intermedium* is stouter, with a longer caudal

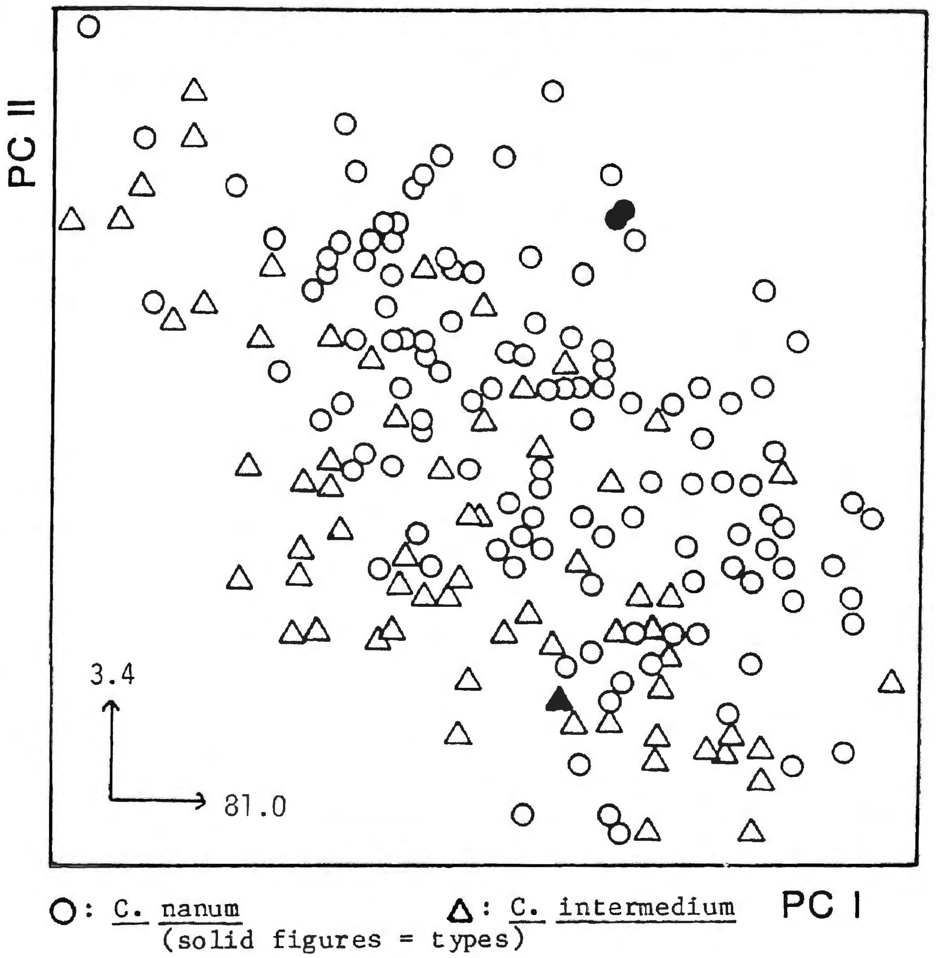


Figure 22. PCA Plot (Morphological Data) for C. nanum and C. intermedium.

peduncle and blunter face. Factors reflecting these traits load higher than others on the shape axis (PC II). PCAs of the meristic data (Figure 23 and 24) show more differentiation, but overlap is still extensive. The most important characters on PC II are numbers of dorsal spines, anal spines and opercular spines. Figures 25 and 26 show the frequencies for these characters for both species. *Ctenopoma intermedium* tends to have higher counts for these meristic elements, though there is considerable overlap.

Color pattern differences also exist. The final band in *C. intermedium* is frequently present in the form of a vertically oblong spot with a pale ring (hence the name "blackspot climbing perch" used by Skelton, et al. 1985). Anterior to this spot, the first few vertical bars are curved slightly around the spot. The bars are narrower and slightly less even than those of *C. nanum*. Some specimens of *C. intermedium* from the Zaire and Zambesi basins in Angola (which Poll, 1967) listed as unusual *C. nanum*) are not banded but show an uneven, mottled ("marbled") pattern. The median fins of *C. intermedium* are often dark and the bands do not pass onto them. Breeding males have the filamentous fins as in other species *Nana*, but the bands in breeding males disappear as the specimens become very dark all over (almost black in preserved specimens). Breeding *C. nanum* also darken, but the banding is still very clear on the body and median fins.

Based on distribution qualitative differences in color pattern and quantifiable (but not extensive) differences in morphometry, I feel that *C. intermedium* is distinct from *C. nanum*, though very similar.

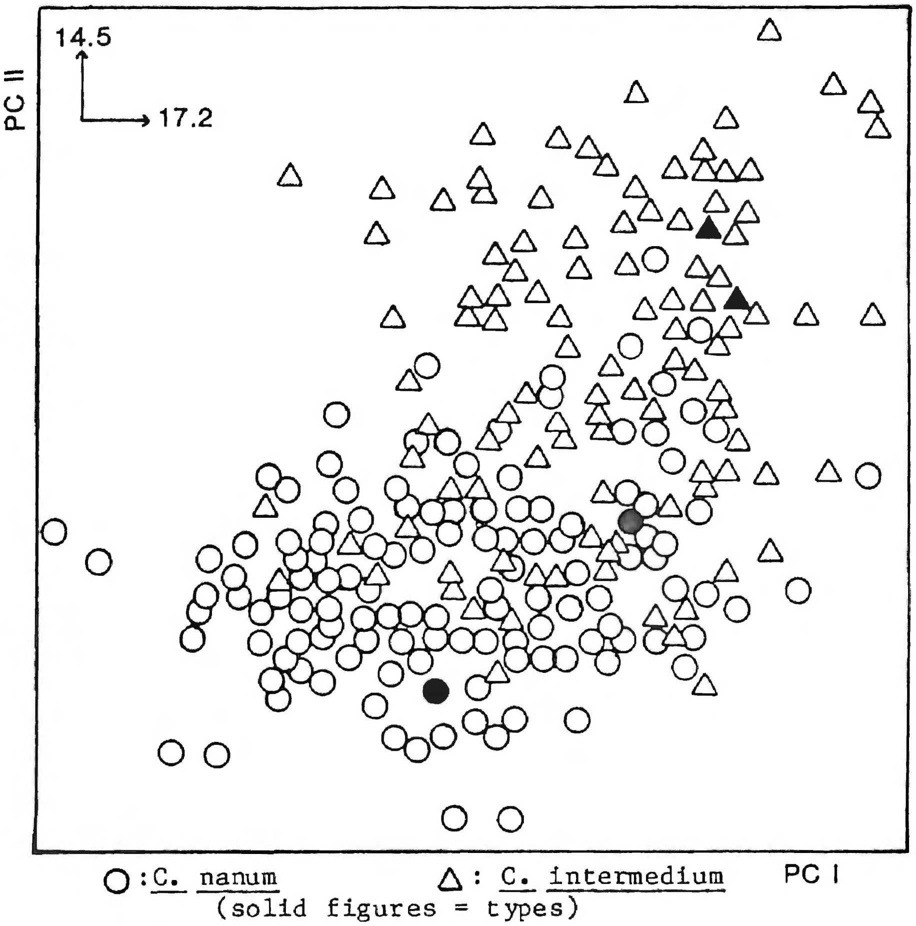


Figure 23. PCA Plot (Meristic Data) for *C. nanum* and *C. intermedium* (males and females).

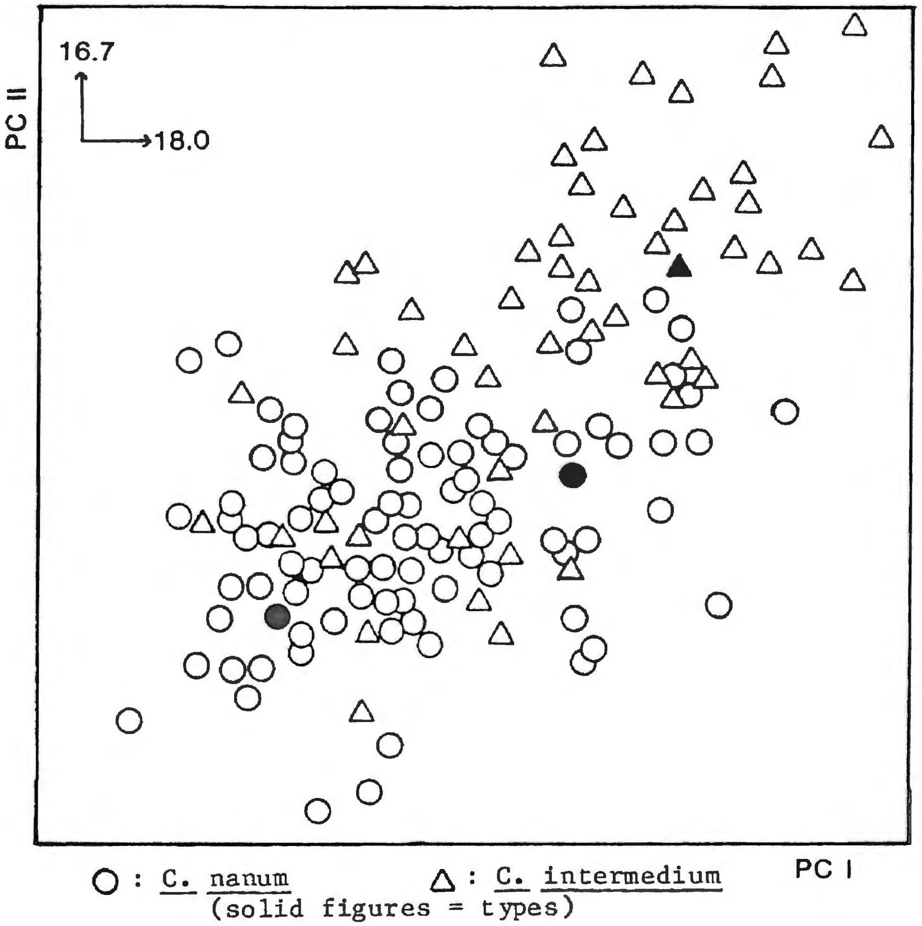
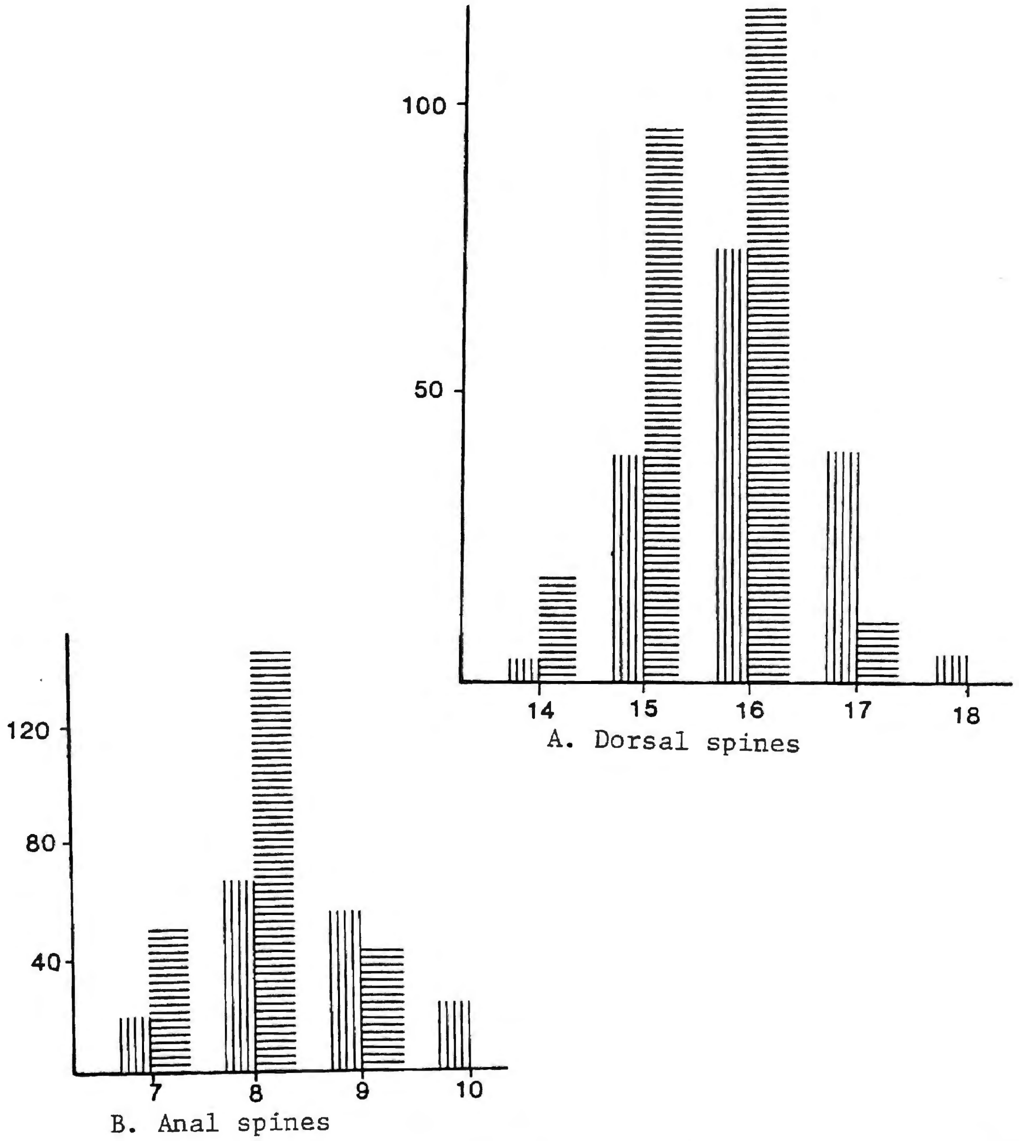


Figure 24. PCA Plot (Meristic Data) for _C._ _nanum_ and _C._ _intermedium_ (Males Only).

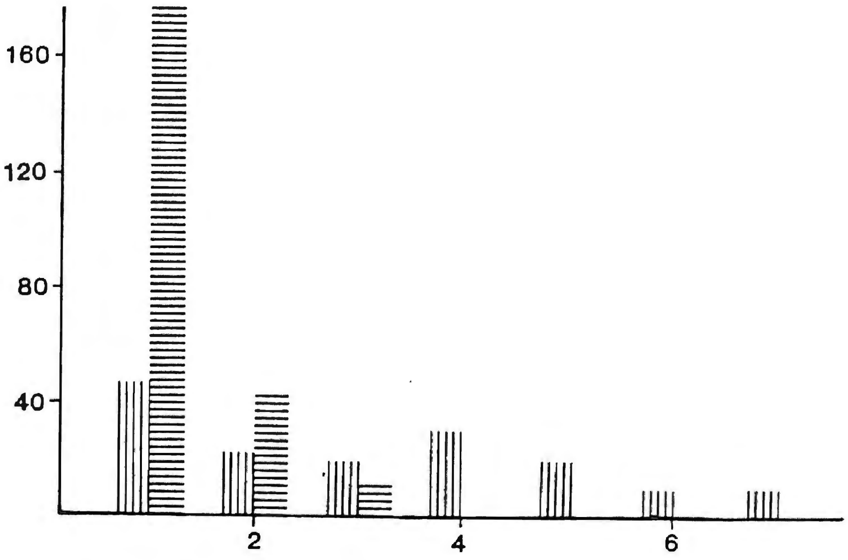


A. Dorsal spines

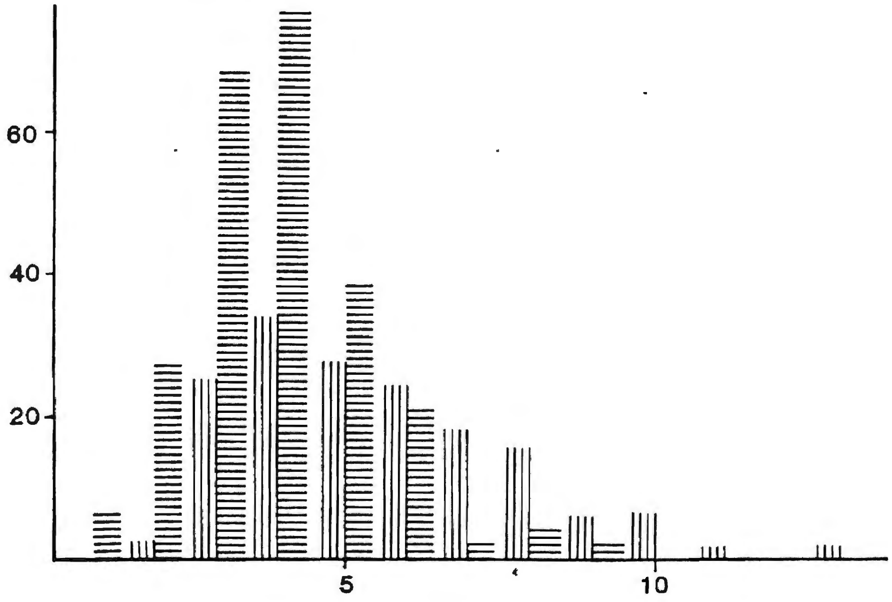
B. Anal spines

vertical bars *C. intermedium* horizontal bars = *C. nanum*

Figure 25. Anal and Dorsal Spine Frequencies of *C. nanum* and *C. intermedium*.



A. Spines above opercular notch



B. Spines below opercular notch

vertical bars = *C. intermedium* horizontal bars = *C. nanum*

Figure 26. Opercular Spine Frequencies for *C. nanum* and *C. intermedium*.

CHAPTER IV

DISCUSSION AND CONCLUSIONS

Zoogeography

Sandelia and *Ctenopoma* are presently allopatric. The two species of *Sandelia* are confined to several coastal rivers in extreme southeastern Africa. *Sandelia capensis* is more widespread and common than *S. bainsii*, though neither species is extremely abundant anywhere (M. Bruton; P. Skelton, pers. comm.). Conversely, *Ctenopoma* is much more widely distributed, and is found in suitable habitat in almost all drainages south of the Sahara and north of the Cape Region. It is convenient to discuss *Ctenopoma* distribution within the framework of 'ichthyofaunal provinces'--areas of endemism, frequently (and not coincidentally) corresponding to major drainage basins (defined and discussed by Poll, 1957, 1973; Roberts, 1975; critiqued by Greenwood, 1983). Figure 27 presents the modern hydrology of Africa with important elements labeled; Figure 28 presents the ichthyofaunal provinces hypothesized by Roberts (1975), which are very similar to those advocated by other authors.

The diversity of species of *Ctenopoma* is greatest in the four million square kilometers of lowland tropical forest and savanna drained by the Zaire River. This region, the Zaire Ichthyofaunal

Figure 27. General Hydrology of Africa.

Modified from Roberts (1975)

Figure 28. Ichthyofaunal Provinces of Africa.

Province, has the richest fish fauna in Africa. As recently as the Pliocene, this basin was an immense swampy lake (Beadle, 1981). An outlet to the Atlantic Ocean drained the lake in the Pleistocene, and later, the central region of the basin became arid during a severe interpluvial period (Roberts, 1975). These past phases of the Zaire basin must have produced a varied series of habitats. The diversifying effects of these changes, evident in the extensive ichthyofauna of the region, have been enhanced at least in recent times by several series of falls or rapids which isolate parts of the basin from one another.

Much of the Zaire River basin is covered by dense tropical rain forest. This forested region, the lower and middle reaches of the basin, often refered to as the *cuvette Centrale*, is the habitat where the diversity of *Ctenopoma* species is richest. In this region, all three subgenera are represented with a combined total of twelve species. Five of these species appear to be endemic to the basin. Three additional species are known from the non-rainforested areas of the basin; none of these species occurs in the rainforested areas.

There are several smaller drainages flowing to the Atlantic which are also within the central African rain forest belt. These have an ichthyofauna distinct enough to be considered a separate ichthyofaunal province by Roberts (1975), though it shows strong affinities to that of the Zaire basin, with which the coastal basins are contiguous. Of the five or six species of *Ctenopoma* represented in the west coast drainages, only one is not widely distributed in the *cuvette centrale*.

To the north of the Zaire basin, extending to the extreme western coast of Africa and bounded on the north by the Sahara, is the

Nilo-Sudanic ichthyofaunal province. The major hydrologic elements of this region are the Nile River System south to Lakes Albert and Edward, the Lake Chad drainage and the entire courses of the Niger, Senegal and Volta rivers. Though in recent times some of these elements are separated by great stretches of extremely arid desert, they share a remarkably uniform fish fauna. Only a few species are known to exhibit notable differences among populations in the now-isolated drainages (Beadle, 1981).

In west Africa to the south of much of the Nilo-Sudanic region, a belt of coastal rainforest drains southward into the Atlantic by way of a series of small rivers. These waterways have many typical Nilo-Sudanic species; however, they have sufficient numbers of endemic forms that Roberts (1975) recognized them as a separate zoogeographic unit, the Upper Guinean Province (Roberts, 1975).

Little rainforest is drained by the main Nilo-Sudanic waterways, and the diversity of *Ctenopoma* is correspondingly low. The subgenus *Ctenopoma* is absent and only three species each from the other subgenera are known from this province. The three species of *Nana* are very restricted in their Nilo-Sudanic distributions. Two of these (*C. nanum* and *C. congicum*) probably are recent invaders from the Zaire basin; their Nilo-Sudanic ranges are primarily in waters close to those of the Zaire basin. The third restricted form, *C. damasi*, apparently is endemic to the Lake Edward drainage of the upper Nile. The only other Nilo-Sudanic endemic is *C. petherici*, which is primarily restricted to savanna rivers such as the Nile or stretches of the Niger and Lake Chad drainages. Its close relative, *C. kingsleyae*, is more common in the coastal rainforest rivers of the Upper Guinean Province and lower Zaire basin, though it is found in some Nilo-Sudanic waters (Daget, 1958). These two forms are very similar and apparently are rarely sympatric. *Ctenopoma muriei* is most commonly found in eastern Nilo-Sudanic waters, but is also represented by several specimens in the upper Zaire drainage. This extremely unusual distribution (K.E. Banister, pers. comm.) has been of great interest and controversy to biogeographers (see Poll, 1963; Banister and Bailey, 1979; and Appendix A).

Adjacent to the Zaire ichthyofaunal province and interdigitating with much of its southern watershed is the Zambesi ichthyofaunal province, consisting of the Zambesi River, its sometimes disconnected tributary systems, and several smaller rivers south of the Zambesi. These streams do not drain any rainforest and support to only two (possibly three) species of *Ctenopoma*: *C. intermedium* and *C. multispine*. *Monkengia* is absent. Both species are found commonly in the upper (southern) Zaire tributaries, though they are most widely distributed in Zambesian waters. Stream capture at the shared watershed and/or faunal movement across interdrainage swamps can easily account for the co-occurence of the two forms in these two faunal regions (Bell-Cross, 1965), as it probably does for the presence of Zairean species in Nilotic waters. *Ctenopoma multispine* has a problematic relative from the Cuanza River (a poorly known and biogeographically distinct river in western Angola).

Previous Systematic Work

Liem (1963) described the osteology of the Anabantoidei and offered hypotheses on the phylogeny of the suborder. He regarded the anabantid taxa as modern remnants of the ancestral anabantoid. Since their origin in the upper Tertiary, anabantoid fishes have diverged and specialized greatly and there is no longer any single taxon that clearly represents the ancestral form. Instead, presumed traits of the ancestral form are found scattered throughout the Anabantidae, particularly among the more generalized anabantids, *Anabas* (Asia) and *Ctenopoma* (Africa). *Sandelia* shows extensive specialization and modification from the presumed ancestral type--probably due to its adaptation to a temperate climate.

Though he examined in detail specimens from all three nominal anabantid genera, Liem did not see any specimens of the subgenus *Nana*, and the only species of *Monkengia* that he examined was *C. muriei*, which is aberrant in some respects (see below). He therefore obtained an imcomplete picture of *Ctenopoma* and listed some advanced (or derived) characters as being absent in the genus whereas they are actually present in taxa he did not examine. These characters include, development of protrusible jaws, which are not the norm in *Ctenopoma*, but are found in *C. acutirostre* and *C. ocellatum*, and the loss of parasphenoid teeth, in some species of *Nana*. In fact, some the major phylogenetic trends he identified for the suborder as a whole can be seen clearly in the African Anabantidae: e.g., the trend towards increased jaw protrusibility and the trend towards edentulation on the parasphenoid.

Liem's phylogeny is presented in Figure 29. He theorized that the ancestral anabantid arose in Asia in the upper Tertiary and that an early form of this fish migrated to Africa, perhaps in the Eocene. The Asian and African forms subsequently diverged. In Asia, the ancestral form gave rise to *Anabas* and the three (or four) other Asiatic Anabantoid families. In Africa, *Ctenopoma* evolved and gave rise to *Sandelia*. Lauder and Liem (1983), in a review of the evolution and interrelationships of the Actinopterygii added the monotypic and extremely specialized Luciocephaloidei to the Anabantoidei and linked the Anabantidae and the highly specialized Helostomatidae ('kissing grouami') as sister groups in the suborder.

Elsen's (1976) study of the Anabantidae included a taxonomically complete range of anabantid material, but Elsen provided only a few superficial phylogenetic comments on the family. Most interestingly, suggested a link between the species of *Monkengia* and *Sandelia*. Both possess strongly reduced labyrinths and have a swimbladder with two anterior bifurcations. Other characters, particularly the development of the labyrinth and the structure of swimbladder provide characters for separating *Anabas* and the other *Ctenopoma* species groups.

Elsen placed *C. muriei* in the *Nana* species group, apparently because it lacks the anterior bifurcations of the swimbladder. However, it has 16 total caudal rays and a single interocular pore, and does not show the type of sexual dimorphism seen in other members of the subgenus *Nana*. Rather, males have patches of spined postocular and precaudal scales as in the subgenus *Monkengia*, and do not build bubblenests but are free spawners (Berns and Peters, 1969).

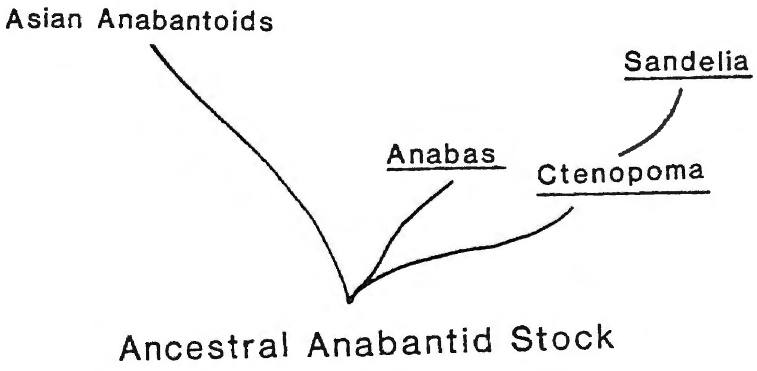


Figure 29. Anabantid Phylogeny Presented by Liem (1963).

Ctenopoma muriei are much smaller (never in excess of 80 mm SL) than other Monkengia, so it seems probable that this species is a dwarfed, perhaps paedomorphic, member of the subgenus, and has lost some typical traits of the subgenus Monkengia, such as the bifurcated swimbladder.

A New Phylogeny

Using Liem and Elsen's characters, plus those found in the present study, a preliminary cladogram can be constructed for the Anabantidae (Figure 30), characters listed in Table IX. Anabas is used as the base or outgroup for the African anabantids.

The position of Sandelia in this phylogeny is the most problematic and tentative. Available data for Sandelia (number of caudal rays, structure of the labyrinth and swimbladder) link it more closely to the subgenus Monkengia than to Anabas or any other Ctenopoma species group. With Sandelia so placed, the genus Ctenopoma becomes a paraphyletic taxon (and the subgeneric status of the species groups becomes inappropriate). An alternative placement of Sandelia (dashed line on figure 30) avoids paraphyly, but creates a somewhat less parsimonious cladogram, as some characters (swimbladder bifurcations, reduction in the labyrinth) become homoplasic between Sandelia and Monkengia and would have to have evolve twice.

Sandelia exhibits several unique traits as would be expected from its history of isolation and habitation in an ecosystem unused by any other modern anabantid. Some of these (e.g., differences in the labyrinth) most likely involve adaptation to local conditions (i.e., temperate vs. tropical). Others, such as differences in cranial osteology or number of branchiostegal rays are perhaps random divergences from the ancestral form, possibly resulting from genetic

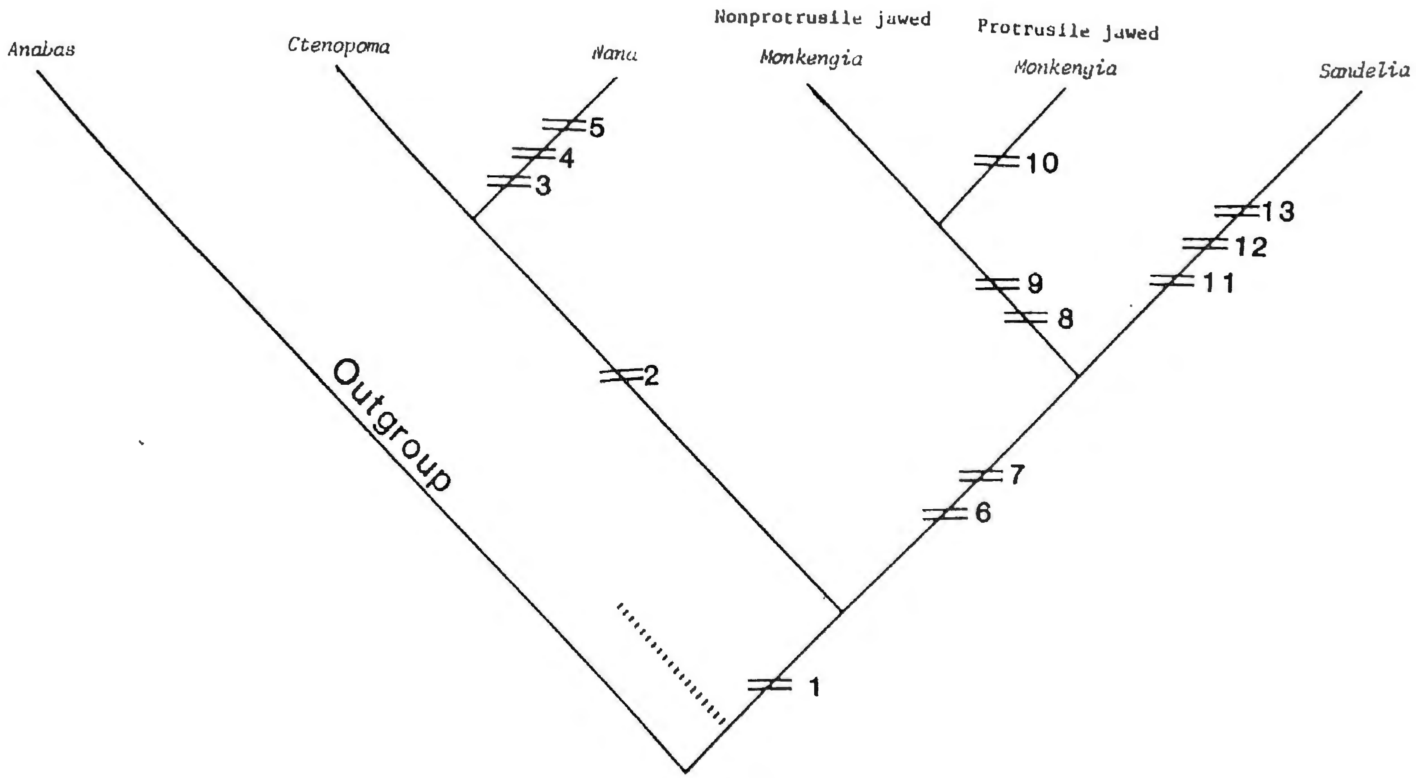


Figure 30. Phylogeny of the Anabantidae

TABLE IX

CHARACTERS FROM FIGURE 30.

Number (Figure 30)	Character (Synapomorphy)
1	spined postocular scales
2	14 total caudal rays
3	strong external sexual dimorphism
4	2 interorbital CLL pores
5	parental care and bubble nest building
6	bifurcated swim bladder
7	reduced labyrinth
8	precaudal fin base fringed scales
9	deep body
10	protrusile jaws
11	absence of ctenoid scales
12	5 branchiostegal rays
13	demersal eggs

drift during isolation.

The spined postocular scales of males are synapomorphic to the African Anabantidae. Anterior bifurcations of the swimbladder are synaopomorhies uniting *Monkengia* and *Sandelia* to a common ancestor not shared with other African anabantids. Spined scales near the base of the caudal fin of males and a generally deeper body profile are synapomorphies of the *Monkengia* species group, separating it from *Sandelia*. Uniting the two species of *Sandelia* are synapomorphies such as the loss of one branchiostegal ray and the near complete lack of ctenoid scales.

Within the subgenus *Monkengia* there are two main clades. One comprises *C. acutirostre* and *C. ocellatum*. Monophyly of these species is indicated by several traits, such as the extremely long ascending process of the premaxilla, the acute snout and the narrow blade-like lachrymal. These traits are not found in any other anabantid taxon.

Ctenopoma muriei has some apomorphic traits (described above) separating it from the other members of the *Monkengia* clade which lack protrusile jaws.

The other species of *Monkengia* those having non-protrusible jaws are not united by any known synapomorphic traits, but form a cohesive unit and are probably monophyletic. They may be divided on the basis of color pattern (dark spot on the caudal fin base vs. dark spot on the midbody), but the cladistic value of this character is not clear. Certainly, *C. kingsleyae* and *C. petherici* (caudal spot) are extremely similar and probably closely related to each other and to *C. muriei* (to which they are superficially quite similar in form and color pattern), which I view as a dwarfed version of the *kingsleyae*/*petherici* form.

Conversely, beyond the shared presence of a midbody spot, *C. oxyrhynchum* and *C. maculatum* do not appear to be as close, and more data on these two forms is needed.

Uniting the subgenera *Ctenopoma* and *Nana* is the shared presence of 14 total caudal rays. The species of *Nana* are united by synapomorphies such as presence of a pair of CCL pores in the interocular space and the cluster of characters associated with their unique (to the Anabantidae) mode of reproduction: characters such as the extreme sexual dimorphism, (presumed) secondary loss of postocular spined scales and presence of nestbuilding and parental care.

I know of no clear synapomorphic characters uniting the species of the subgenus *Ctenopoma*. However, the subgenus is easily separable from other anabantids and is almost surely monophyletic. It separates from *Monkengia*, *Anabas*, and *Sandelia* on the basis of caudal ray counts and from the species of *Nana* by the presence of spiney postocular scales and a single interocular CCL pore in the former. The sub-and interopercle are spined in *Ctenopoma* and never so in *Nana*. Fishes of *Ctenopoma* have 29-34 (rarely 29) scales in the lateral series as opposed to 24-28 in *Nana* and *Monkengia*. *Anabas* has 26-31 scales in the lateral series (Weber and de Beaufort, 1922) and *Sandelia*, 27-35 (Boulenger, 1916).

There are no clear clades within *Nana*. *Ctenopoma ansorgei* and *C. damasi* both have a higher number of anal and dorsal spines, but otherwise do not bear great resemblance to each other. The other four species of *Nana* (those with lower spine counts) exist in two color patterns: vertically barred vs. unevenly barred or speckled. The color patterns grade into each other and overlap strongly in juveniles. The phylogentic value of these color pattern characters is not clear, but is probably not great. In the species groups with higher spine counts, one, *C. ansorgei*, is barred and the other, *C. damasi*, is speckled.

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APPENDIX A

ANNOTATED SPECIES LIST

THE SUBGENUS CTENOPOMA

Ctenopoma multispine Peters, 1844

Synonymy. *Anabas rhodesianus* Gilchrist and Thompson, 1917
Synonymy by Jubb, 1963

Anabas machadoi Fowler, 1930
Synonymy by Skelton, et al., 1985

Anabas vernayi Fowler, 1935
Synonymy by Jubb, 1963

Distribution. See Figure 31. *Ctenopoma multispine* is found in the upper tributaries of the Zambesi and Zaire River basins, in the Okavango River and swamp system, the lower reaches of the Zambesi River, the Cuanza River in Western Angola, and in coastal drainages to the south of the Zambesi River mouth. It is apparently absent from the middle Zambesi River, presumably due to the lack of suitable habitat.

Comments. Skelton et al. (1985) added *Anabas machadoi* to the synonymy of *C. multispine* without examining Fowler's types. The present study supports the synonymy, though qualitative differences in color patterns and opercular spine counts do exist between the western (= *C. machadoi*) and eastern populations of *C. multispine*. The *C. machadoi* types are the only specimens or either taxon which I have been able to locate from the Cuanza River, which is poorly known but ichthyologically distinct from closely associated drainages (Roberts, 1975). The suggestion by Poll (1967) that *C. machadoi* is a "race" (=subspecies) of *C. multispine* is possible.

Anabas rhodesianus Gilchrist and Thompson and *A. vernayi* Fowler were both listed as synyonyms of *C. multispine* without comment by Jubb (1967) and Jubb and Gaigher (1971). I have not seen the types of either of the two former species.

△ : C. machadoi ○ : C. multispine
("t" = type specimens, solid figures
= specimens examined)

Figure 31. Distribution of C. multispine.

Ctenopoma nigropannosum Reichenow, 1875

Synonymy. *Ctenopoma gabonense* Gunther, 1896
Synonymy by Boulenger, 1899

?*Ctenopoma ashbysmithi* Banister and Bailey, 1979

Distribtution. See Figure 32. *Ctenopoma nigropannosum* commonly is found throughout the *cuvette centrale* of the Zaire basin. Specimens are also reported from the Chilogango River, just to the north of the Zaire River mouth. I have seen a single specimen reportedly from the Ogooue River, further north along the coast. *Ctenopoma ashbysmithi* is known only from its type locality on the Zaire River near Kinda indicated with on Figures 31 to 33 with an "A."

Comments. *Ctenopoma gabonense* was synonymized with *C. nigropannsosum* by Boulenger (1899); I have seen the types of both species and concur. The problems with *C. ashbysmithi* are discussed at length in the main body of the text.

Ctenopoma pellegrini (Boulenger, 1902)

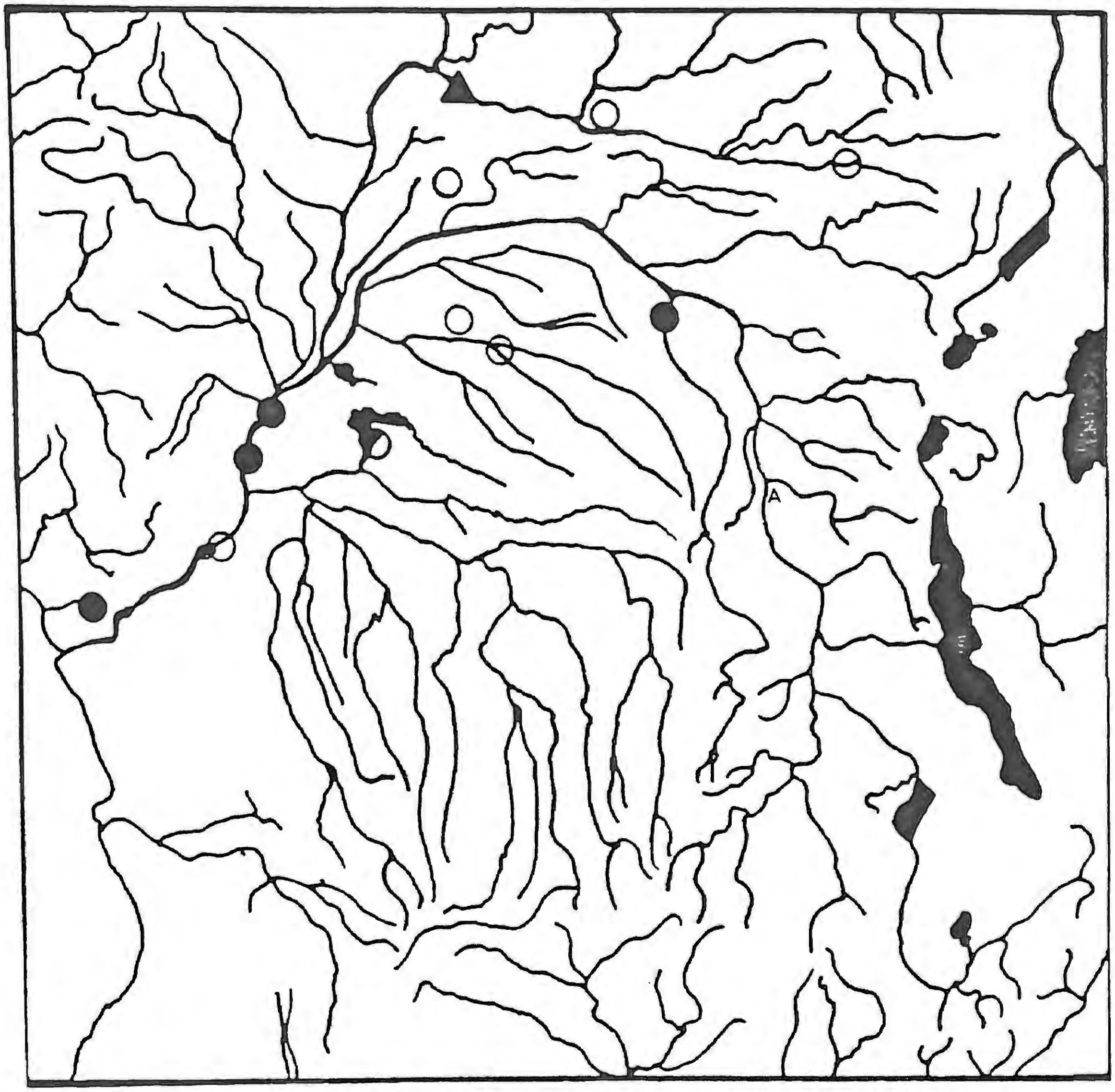
Synonyms. None

Distribution. See Figure 33. *Ctenopoma pellegrini* has a nearly identical distribution to that of *C. nigropannosum*, but is absent from the Ogooue River.

Comments. *Ctenopoma pellegrini* appears to be less common than *C. nigropannosum* (if relative museum holdings of the two species can be used as a measure of abundance).

△ : type ○ : confirmed locations
(solid figure = specimens examined)

Figure 32. Distribution of *C. nigropannosum*.



△ : type ○ : confirmed locations
(solid figures = specimens examined)

Figure 33. Distribution of C. pellegrini.

THE SUBGENUS *MONKENGIA*

Ctenopoma acutirostre Pellegrin, 1899

Synonyms. *Ctenopoma denticulatum* Pellegrin, 1899
(*syn. nov.*)

Anabas ocellatus (part.) Boulenger, 1916

Anabas ocellatus acutirostris Pellegrin, 1928

Distribution. See Figure 34. *Ctenopoma acutirostre* is endemic to the Zaire River basin, found throughout the *cuvette centrale*, and in tributaries of the Kasai River.

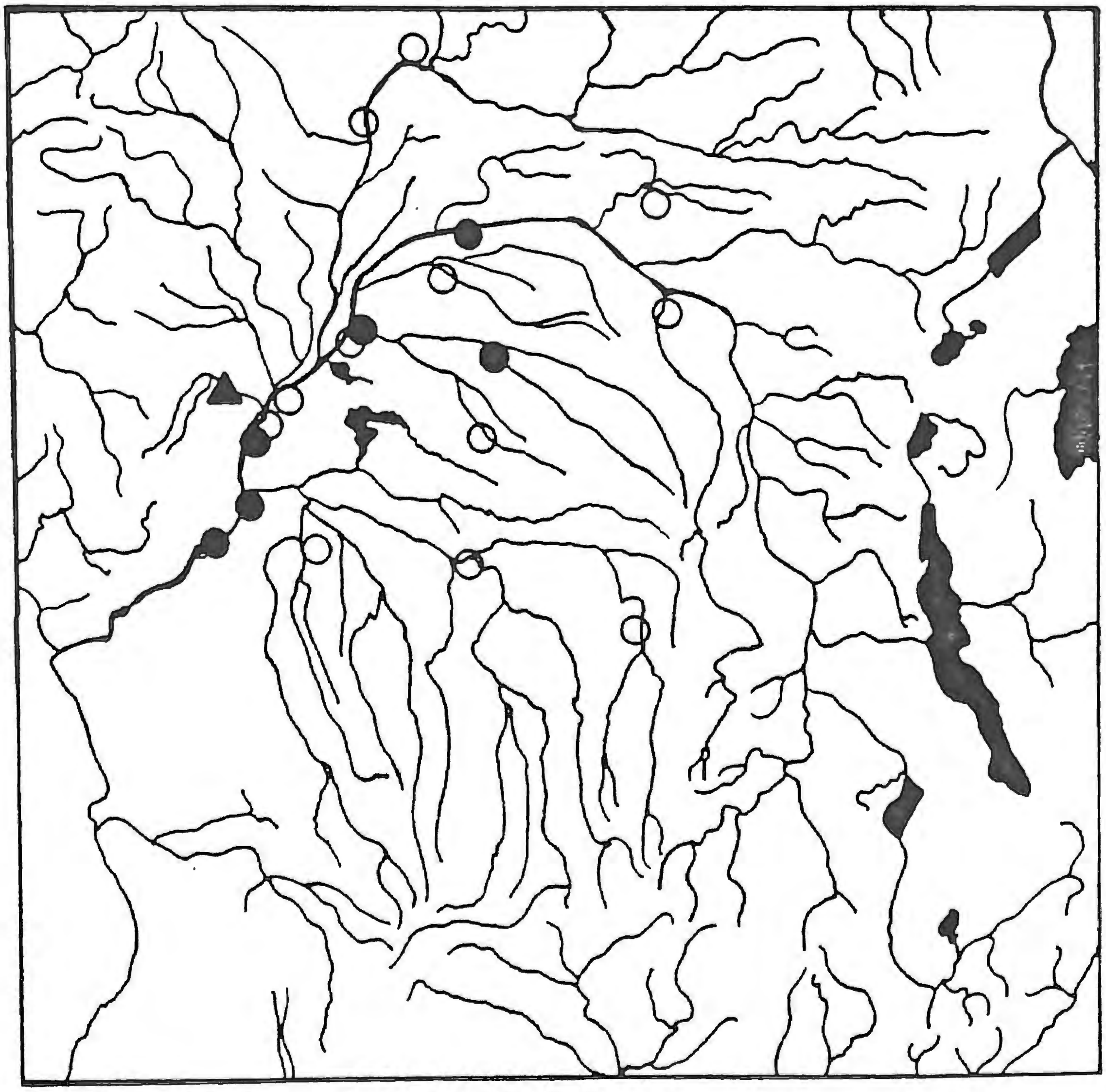
Comments. The past confusion with this species and *C. ocellatum*, and the identity of *C. denticulatum*, are discussed in the text.

Ctenopoma ocellatum Pellegrin, 1899

Synonyms. None

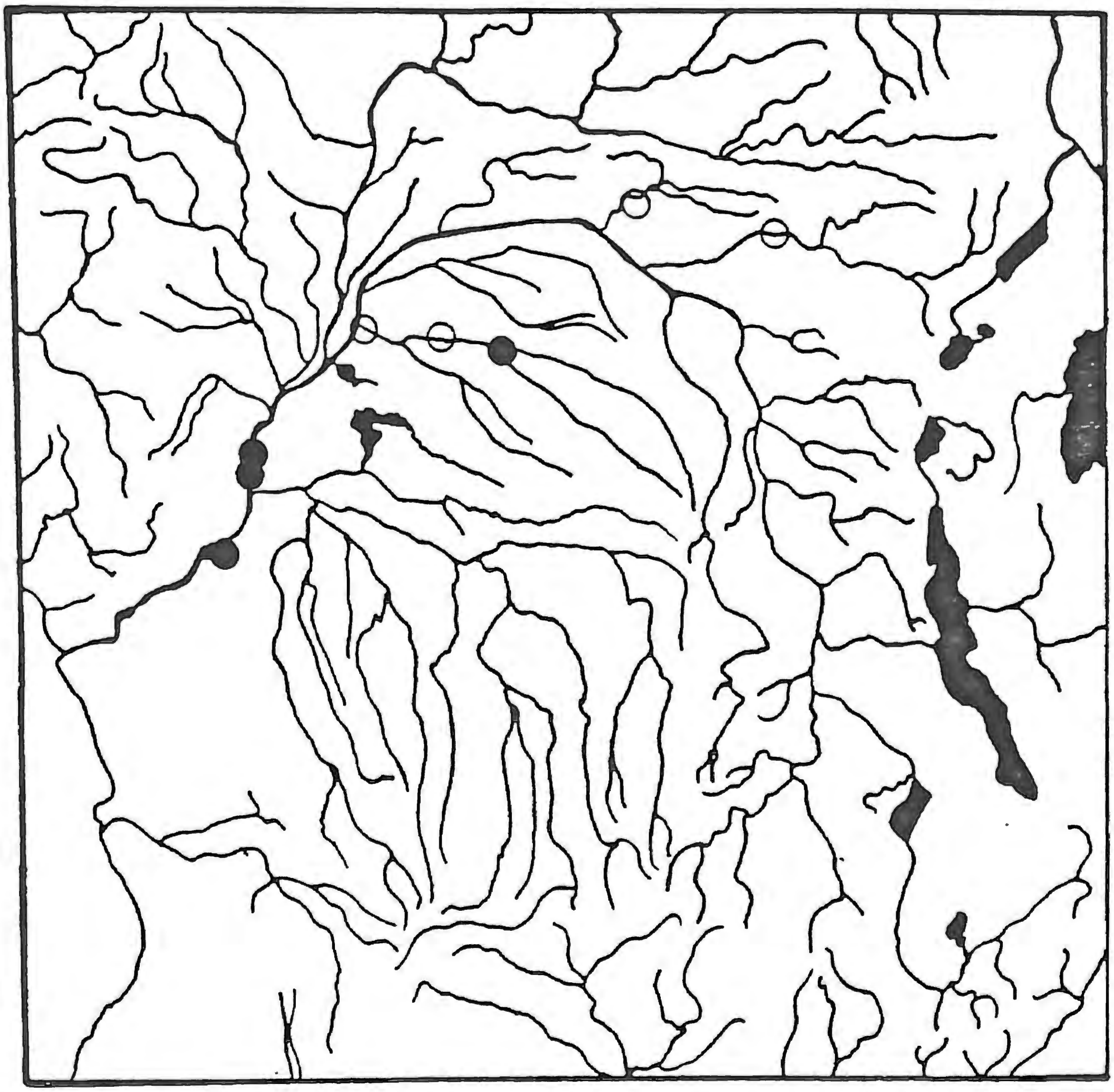
Distribution. See Figure 35. *Ctenopoma ocellatum* is endemic to the Zaire River basin and confined to the *cuvette centrale*.

Comments. *Ctenopoma ocellatum* is less common in museum collections than *C. acutirostre*. The only near complete key to *Ctenopoma* is that provided by Boulenger (1916). Since Boulenger confounded *C. acutirostre* under *C. ocellatum*, both species key to the latter name and in museum collections the name *C. ocellatum* is not uncommonly found on specimens of *C. acutirostre*.



△: type ○: confirmed locations
(solid figures = specimens examined)

Figure 34. Distribution of *C. acutirostre*.



△ : type ○ :confirmed locations
(solid figures = specimens examined)

Figure 35. Distribution of *C. ocellatum*.

Ctenopoma maculatum Thominot, 1886

Synonyms. *Ctenopoma multifasciata* Thominot, 1886
Synonymy by Boulenger (1916)

Anabas pleurostigma Boulenger, 1903
Synonymy by Boulenger (1916)

Distribution. See Figure 36. *Ctenopoma maculatum* is restricted to waters in southern Cameroun and northern Gabon. This includes the westward flowing rivers (from south to north) Benito, Ntem, Nyong and Sanaga. It also inhabits the closely associated headwaters of the Dja River (Zaire basin) and the Ivindo River (Ogooue River). This is the most compact distribution shown by any *Ctenopoma* except *C. damasi* which is endemic to the margins of Lake Edward.

Comments. This species has occasionally been confused with *C. oxyrhynchum* (e.g. Gosse, 1963), though the two have very distint distributions and color patterns. Boulenger (1916) erroneously synonymized *C. weeksii* Boulenger to this form. The two syntypes of *C. weeksii* are clearly *C. oxyrhynchum*; the collection locality for the types is noted with a "w" on Figure 36.

△: type ○: confirmed locations
(solid figures = specimens examined)

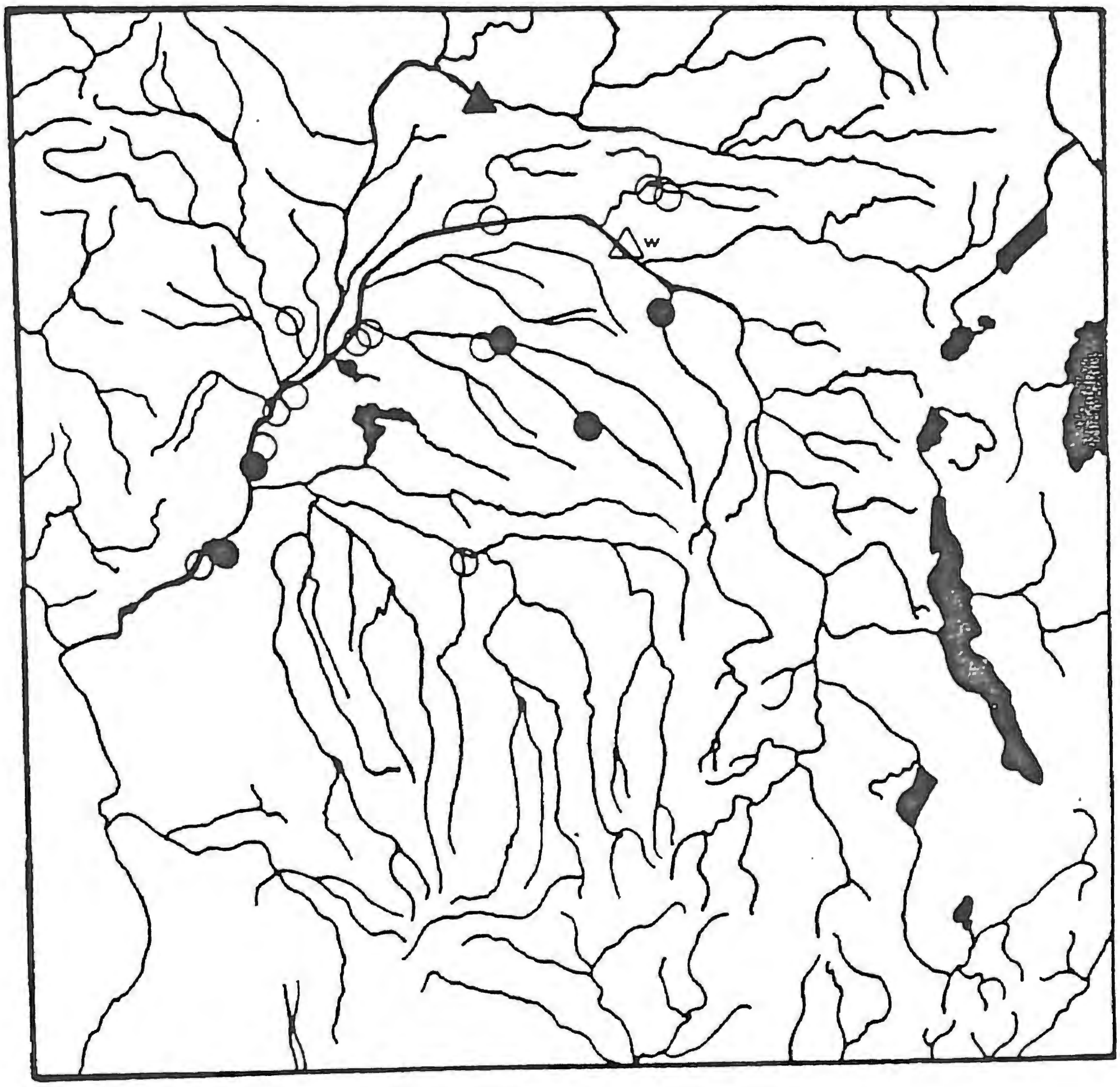
Figure 36. Distribution of C. maculatum.

Ctenopoma oxyrhynchum (Boulenger, 1902)

Synonymy. *Ctenopoma weeksii* Boulenger, 1896
(*syn. nov.*)

Distribution. See Figure 37. *Ctenopoma oxyrhynchum* is another species confined almost exclusively to the *cuvette centrale*. It is known from the lower reaches of the Sangha River (a tributary to the lower Zaire); whereas *C. maculatum* occurs in the headwaters of the Sanagha (Dja River). There does not appear to be any sympatry between the two species. *Ctenopoma oxyrhynchum* also occurs at one locality beyond the *cuvette centrale* on the middle Kasai River.

Comments. In 1896 Boulenger described *C. weeksii* based on two specimens from the "upper Congo" (Zaire). Twenty years later, he synonymized *C. weeksii* to *C. maculatum* without making comment. The syntypes of *C. weeksii* are *C. oxyrhynchum*, not *C. maculatum*. The description of *C. weeksii* preceeds that of *C. oxyrhynchum* by six years and thus has clear priority. In order to avoid the confusion that would result from resurrecting the name *weeksii* (which has been out of use since 1916, and until that time had only rarely been used correctly), the International Commission of Zoological Nomenclature has been petitioned to use its Plenary Powers under Art. 79 of the Code and supress the name *weeksii* with regard to *Ctenopoma* (S. Norris, in submission).



△ : type ○ : confirmed locations
w: type of C. weeksii
(solid figures = specimens examined)

Figure 37. Distribution of *C. oxyrhynchum*.

Ctenopoma kingsleyae Gunther, 1896

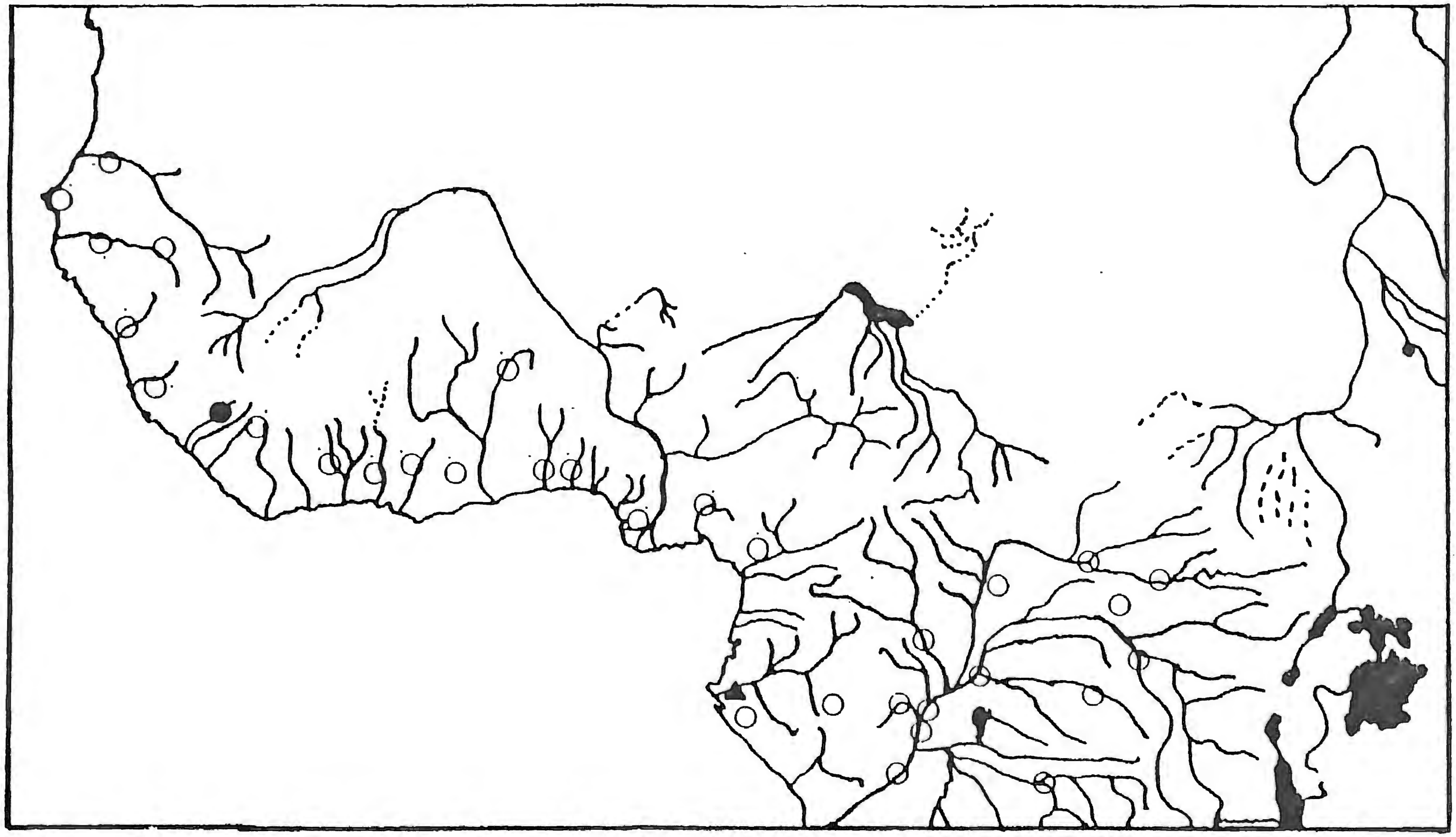
Synonymy. *Anabas argentoventer* Ahl, *IN* Schreitmuller and Ahl,
1922 (*syn. nov.*)

Anabas breviventralis Pellegrin, 1938
(*syn. nov.*)

Anabas togoensis Ahl, 1928
Synonymy by Daget (1958)

Distribution. See Figure 38. *Ctenopoma kingsleyae* is found throughout the *cuvette centrale* of the Zaire basin and in the some of the associated west coast drainages. Daget (1958) also records it from most of the west African rivers draining into the Atlantic. I have confirmed several sites in Liberia, but some other west African specimens assigned to *C. kingslyae* by Daget appear to be *C. petherici*. Until more specimens can be examined and distinguishing characters found for this species and *C. petherici*, the west African distribution of both forms will be problematic.

Comments. Daget (1958) listed *A. togoensis* in his *C. kingsleyae* synonymy without having examined the holotype (and only known specimen) which has been lost. I tentatively list *A. argentoventer* and *A. breviventralis* (the types of which I have seen) in my synonymy and await further analyses and clarification of the distributional pattern to make a final determination.



△ :type

○ : confirmed locations

○˙: literature records

Figure 38. Distribution of C. kingsleyae.

Ctenopoma pethérici Gunther, 1864

Synonymy. *Anabas petherici chadensis* Fowler, 1936
Synonymy by Blanche, et al. (1964)

Anabas caudomaculatus Ahl, 1927
Synonymy by Blanche, et al. (1964)

Anabas riggenbachi Ahl, 1927 (*syn. nov.*)

Anabas weesksii (non-Boulenger) Pellegrin, 1907

Distribution. See Figure 39. *Ctenopoma petherici* is almost exclusively a Nilo-Sudanic species. It is known from the White Nile and the Lake Chad basin. It is widespread in Nilo-Sudanic waters in west Africa, particularly in the Niger River basin. It is apparently present in some of the rivers draining into the Atlantic (e.g., the Volta River). Daget (1958) excluded *C. petherici* from these drainages, and as with *C. kingsleyae* the west African distribution of this species is unclear.

Comments. Blanche *et al.* (1964) listed *A. petherici chadensis* and *A. caudomaculatus* in their synonymy of *C. petherici* without having examined the types. After examining the types, I agree with them The *Anabas riggenbachi* holotype is a terrible specimen, but represents *C. petherici*. In the absence of figures of specimens or the specimens themselves, the superficial descriptions of *Ctenopoma* given by early workers are often of little use in specimen identification, and frequently incorrect names were applied to specimens by researchers working with these descriptions. This is the case of the "*A. weeksii*" reported by Pellegrin (1907) from Lake Chad.

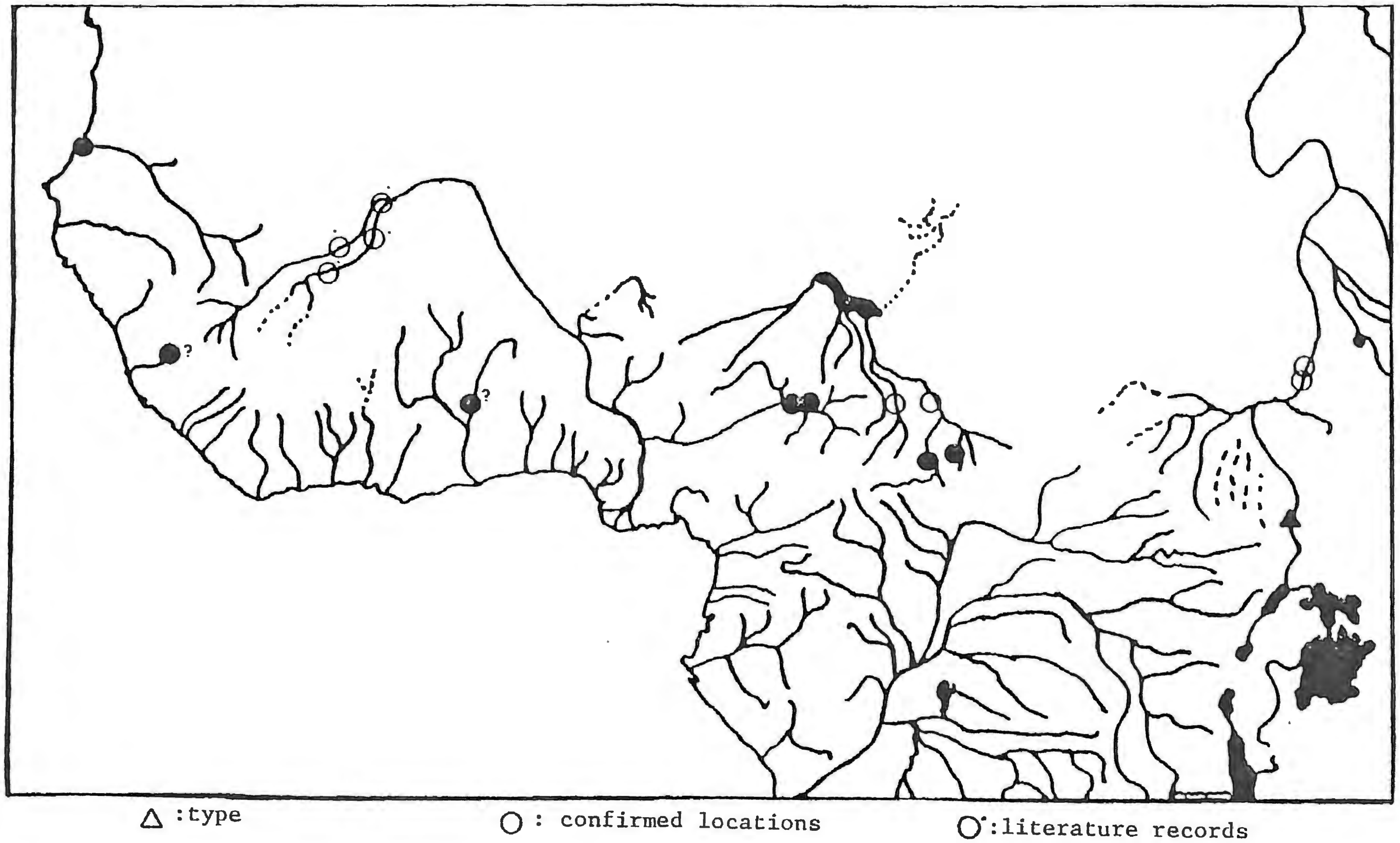


Figure 39. Distribution of C. petherici.

Ctenopoma muriei (Boulenger, 1906)

Synonymy. *Anabas ctenotis* Boulenger, 1919 (*syn. nov.*)

Anabas houyi Ahl, 1927
Synonymy by Blanche et al., 1954

Distribution. See Figure 40. *Ctenopoma muriei* is found in eastern Nilo-Sudanic waters: the Nile River up to Lakes Edward and Victoria, the Lake Chad basin, and the closely associated headwaters of the Benue River (Niger River system). It is also found in the upper Zaire basin: the Lake Tanganyika basin and the Lualaba River.

Comments. Since the 1920s the name *C. ctenotis* has been applied to a species of the "*Nana*" clade, soon to be known as *C. intermedium*. It was first noted by Skelton *et al.* (1985) that the types of *A. ctenotis* did not match the taxon to which the name had been applied. I subsequently examined the types, and identified them as *C. muriei* (S.M. Norris et al., in prep.). Synonymy for *A. houyi* and *C. muriei* was originally suggested by Blanche, et al. (1964). My examination of the types verified this. *Anabas muriei ocellifer* Nichols, 1928 is *C. intermedium* not *C. muriei*.

Ctenopoma muriei demonstrates a rare, if not unique, distribution. It is most common and widespread in Nilo-Sudanic waters, but it is also found in some elements of the upper Zaire River. Poll (1963) used the presence of *C. muriei* and several other reputed Nilo-Sudanic species in the upper Zaire basin as evidence for a hypothesized historical (c. Miocene) connection between the upper Zaire River basin and the Nile. Specifically he suggested that the Lualaba River was once a tributary of the Nile, and was captured by the Zaire basin when extensive rifting occured in east Africa in the Miocene. Thus eight or so Nilo-Sudanic forms were isolated in the upper Zaire. Banister and Bailey (1979), among others, argued strongly against this hypothesis by noting that the geology simply does not support any connection and that the reputed Nilo-Sudanic forms in the Lualaba were included in the Lualaba fauna as results of errors in identification or labeling or that they really were not Nilo-Sudanic forms but rather Pan-African in distribution. They felt that the only record of *C. muriei* in the upper Zaire was the type series of *A. muriei ocellifer* which they correctly identified as "*C. ctenotis*" (= *C. intermedium*) . They however missed numerous other records of *C. muriei* from the upper Zaire. Poll (1948) and Marlier (1952) recorded numerous specimens (verified by me) from the shores of Lake Tanganyika which faunistically is part of the Zaire basin and I have identified a single juvenile specimen of *C. muriei* from the Lualaba River (an upper tributary of the Zaire. The types of *A. ctenotis* (= *C. muriei*) are from the west shore of Lake Tanganika. Banister (pers. comm.) feels strongly that no true Nilo-Sudanic species should be found in the upper Zaire basin and if *C. muriei* is indeed found in the upper Zaire basin, it would be the only one to have penetrated upper Zairean waters. There is little doubt that *C. muriei* should be condidered a Nilo-Sudanic species. Besides the Upper Zairean specimens, it is restricted to Nilo-Sudanic waters. There is no evidence suggesting that it is archaic enough to have remnant populations in the two regions (e.g., have be pan-African in distribution). An attempt was made to differentiate the Zairean *C. muriei* from the Nilotic populations. A clear degree of differentiation could indicate that _C. muriei_ is more archaic than thought previously. No differences could be found and we are forced to conclude that _C. muriei_ is a Nilo-Sudanic fish with spotty representation in upper Zairean waters. In a discussion followings Poll's 1963 paper suggesting the Nile/Lualaba connection, M. Symoens states that the separation between the southern Lake Victoria drainage (Nilotic) and the Malagarisi River (a tributary of Lake Tanganyika, Zairean) is not great, and that Nilotic forms in Lake Victoria could gain access to the Zaire basin (via Lake Tanganyika) across this watershed. An air-breathing fish such as _C. muriei_ would have an even easier time with such a migration. This is an attractive hypothesis to account for the presence of _C. muriei_ in both systems, though it is not supported by any additional species known to have made the migration in either direction.

△ : type ○ : confirmed locations
(solid figures = specimens examined)

Figure 40. Distribution of C. muriei.

THE SUBGENUS NANA

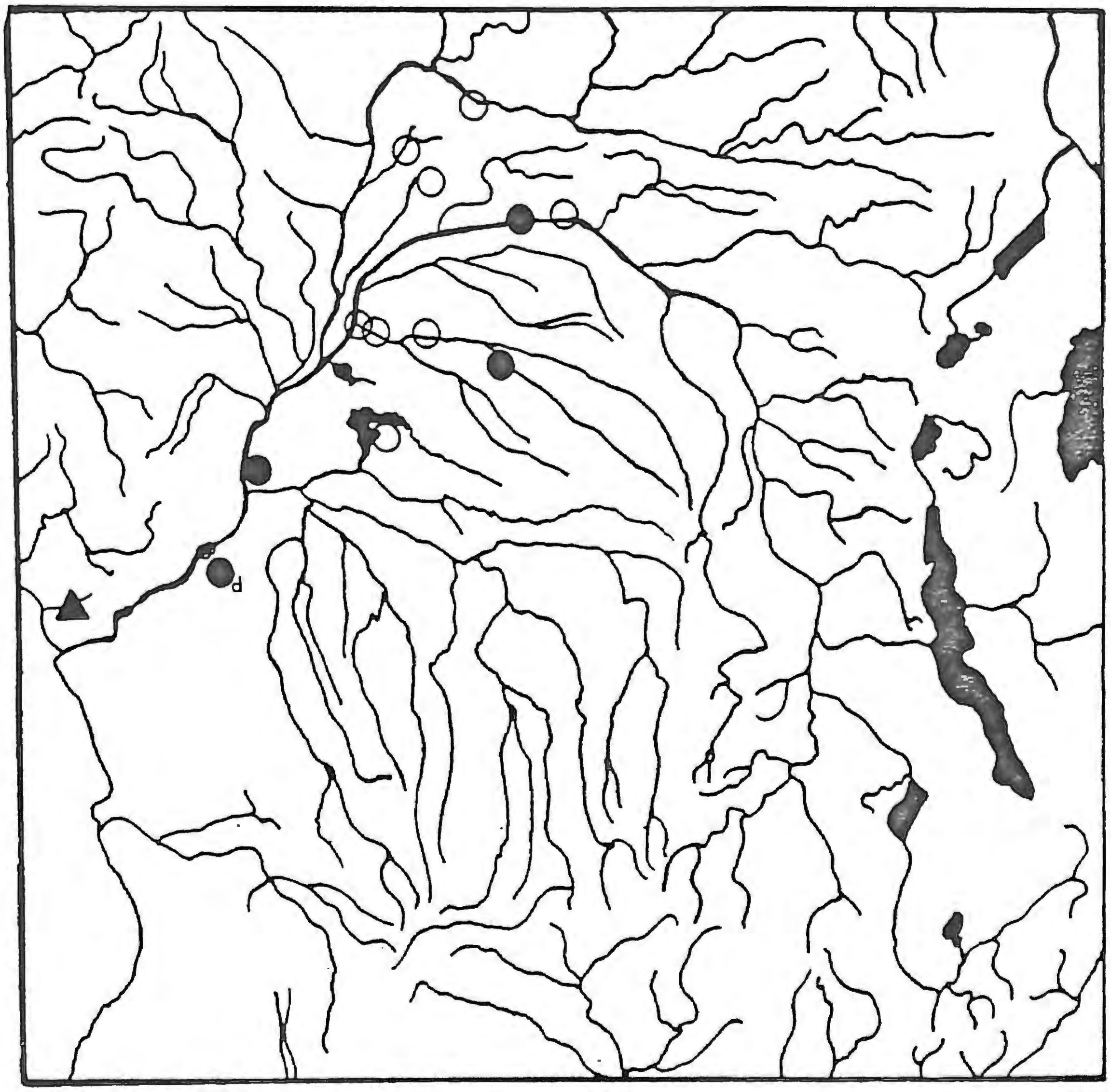
Ctenopoma ansorgei (Boulenger, 1912)

Synonymy. *Anabas davidae* Poll, 1939 (*syn. nov.*)

Distribution. See Figure 41. *Ctenopoma ansorgei* is restricted to the lower and middle reaches of the *cuvette centrale* and to the Chiloango River.

Comments. As noted in the discussion, there are no clear differences between *C. ansorgei* and *C. davidae*.

Nomenclatural Note. This species was named by Boulenger in honor of its original collector, Dr. W.J. Ansorge. The spelling used by Boulenger throughout his description (and in subsequent works) is *ansorgii*. The International Code of Zoological Nomenclature (Third Edition, 1985) (Art. 31) recommends that masculine patronyms be formed by the addition of a single "i" to the end name of the person being honored--without otherwise changing the spelling of the name. "*Ansorgei*" is clearly the patronym which Boulenger should have formed. There is a problem as to how the rules are to be interpreted with regard to a malformed patronym. Arguments can be made for the retention of either spelling. To maintain stability of nomenclature, I would prefer to use the correct form--instead of "original spelling"--when the original spelling is clearly in error (R. Bailey, pers. comm., provided the above insights into and interpretations of the rule on zoological nomenclature).



△: type ○: confirmed locations
d: type of *Anabas davidae*
(solid figures = specimens examined)

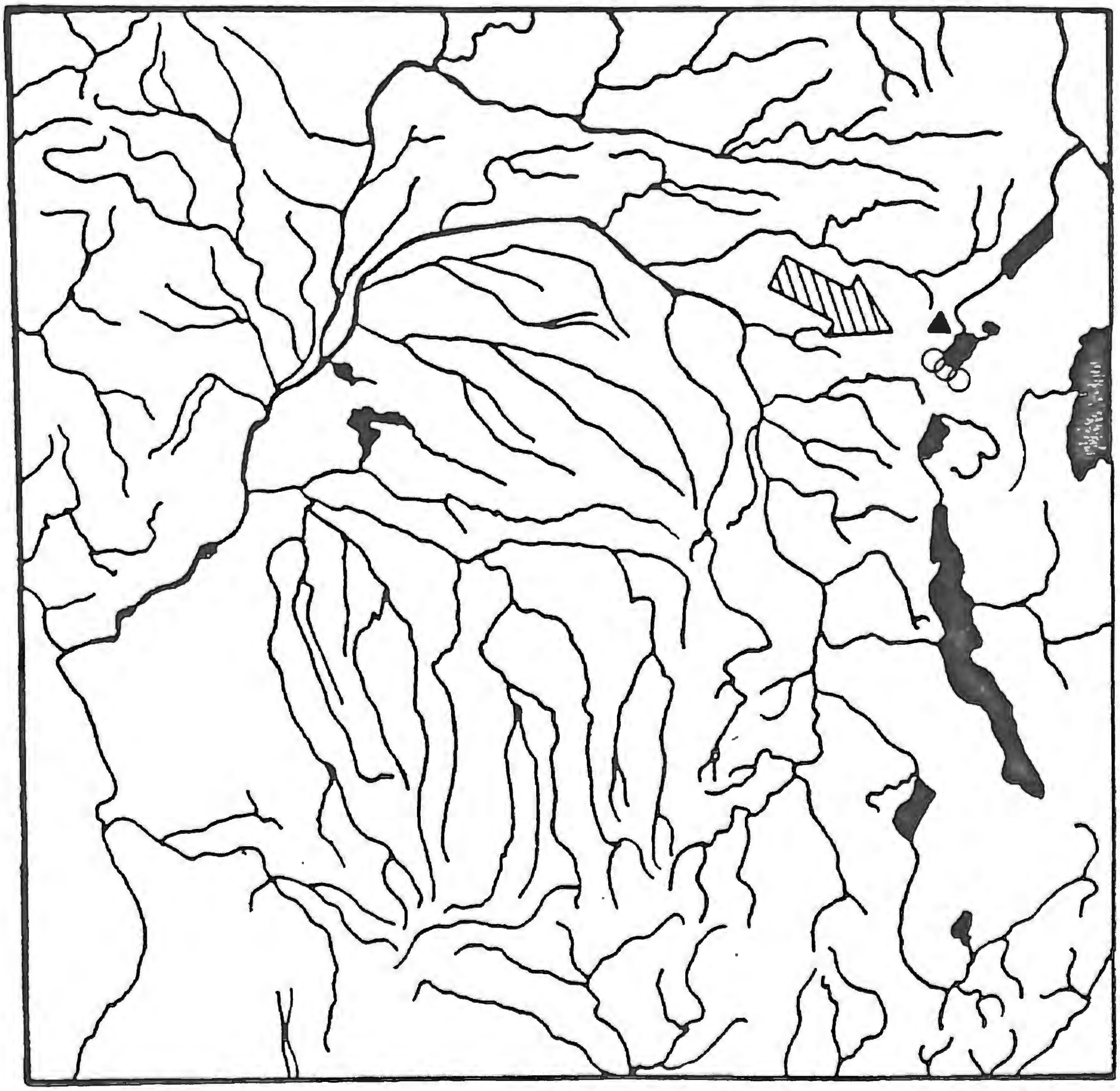
Figure 41. Distribution of *C. ansorgei*.

Ctenopoma damasi (Poll, 1939)

Synonymy. None

Distribution. See Figure 42. *Ctenopoma damasi* is endemic to the borders of Lakes Edward and George on the Headwaters of the Albert Nile.

Comments. Almost all specimens of *C. damasi* which I have seen were taken in a seven month period in 1934-35, and possibly represent a single cohort. They are fairly uniform in size. Berns and Peters (1969) imported live specimens to Germany, and the specimens subsequently circulated amoung German aquarists.



△ : type ○ : confirmed locations
(solid figures = specimens examined)

Figure 42. Distribution of C. damasi.

Ctenopoma congicum Boulenger, 1887

Synonymy. *Anabas pekkolai* Rendahl, 1939 (*syn. nov.*)

?*Ctenopoma congicum longipinnis* Fowler, 1949
Synonymy suggested by Matthes (1964)

Distribution. See Figure 43. *Ctenopoma congicum* is common in the *cuvette centrale* and is also represented in the Chiloango and Ogooue River. This species is also found in the headwaters of the Lake Chad basin, and is represented by several series of specimens (including the holotype of *A. pekkolai*) from the White Nile.

Comments. The populations in the Lake Chad and Nile systems probably crossed from headwaters of Zairean tributaries into the Nilotic systems in a manner similar to that described by Bell-Cross (1965) for a region of exchange between the Zaire and Zambesi Rivers.

△ : type ○ : confirmed locations
p: holotype of *C. pekkolai*
(solid figures = specimens examined)

Figure 43. Distribtution of *C. congicum*.

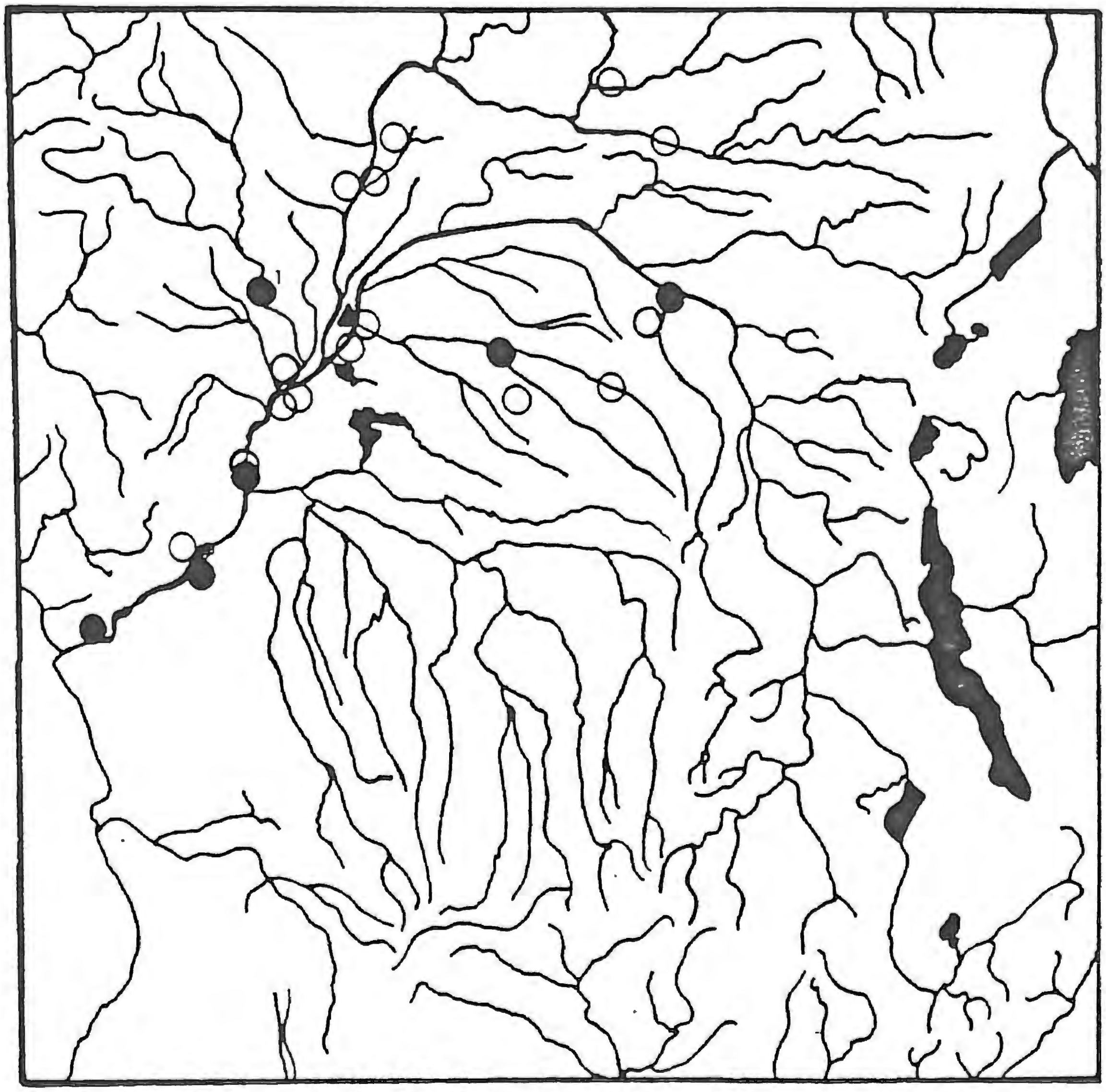
Ctenopoma fasciolatum Boulenger, 1899

Synonymy. *Anabas fasciolatus filamentosa* Pellegrin, 1925
Synonymy by Matthes (1964)

?*Ctenopoma congicum longipinnis* Fowler, 1949
Synonymy suggested by present study

Distribution. See Figure 44. *Ctenopoma fasciolatum* is confined to the forested regions of the *cuvette centrale*. It is not known beyond the Zaire basin.

Comments. The type series of *C. c. longipinnis* probably represents *C. fasciolatum*.



△: type ○: confirmed locations
1: type of *A. f. filamentosa*
(solid figures = specimens examined)

Figure 44. Distribution of *C. fasciolatum*.

Ctenopoma intermedium (Pellegrin, 1920)

Synonymy. *Anabas ctenotis* (non-Boulenger)

Used by numerous authors e.g., Ricardo-Bertram (1940)

Anabas muriei ocellifer Nichols, 1928
Synonymy suggested by Banister and Bailey (1979)

Ctenopoma nanum (non-Gunther)

Used by various authors, e.g., Poll (1967)

Distribution. See Figure 45. *Ctenopoma intermedium* inhabits the upper reaches of all Zaire River basin tributaries and the waters of the Zambesi River and Okavango Swamp drainages. It is also reported from east coast drainages south of the Zambesi to northern South Africa.

Comments. The taxonomy of this form is confused; it is reviewed in the main text. P.H. Skelton (in prep.) will formally make the nomenclatural changes outlined in this thesis.

△ : type ○ : confirmed locations
o: A. muriei ocellier
(solid figures = specimens examined)

Figure 45. Distribution of C. intermedium.

Ctenopoma nanum Gunther, 1896

Synonymy. *Anabas lineatus* Nichols, 1923
Synonymy suggested by Matthes (1964)

?*Anabas brunneus* Ahl, 1927
Synonymy by Holly (1930)

Anabas garuanus Ahl, 1927 (*syn. nov.*)

Anabas multifasciatus (non-Thominot)
Used by Pellegrin (1899; 1907A; 1908; 1908A; 1908B)

Distribution. See Figure 46. *Ctenopoma nanum* is the most wide-spread species of *Nana*. It is found throughout the Zaire River basin, except in the southern tributaries where it is replaced by *C. intermedium*, in the smaller drainages of the west coast of Africa (e.g., Chilogango, Ogooue, Ntem and Nyong Rivers), and in the Upper White Nile. It is apparently absent from the Lake Chad basin and the Sanaga River (in central Cameroun).

Comments. The holotype of *A. garuanus* is a gravid female *C. nanum*. As noted in the discussion the syntypes of *A. brunneus* are a possible varient of *C. nanum* or a distinct taxon. Pellegrin and authors following him confused *C. multifasciatum* (= *C. maculatum*) with *C. nanum*. This is another case of early workers making mistakes while trying to distinguish species based on descriptions only, without having specimens or figures to which to refer.

△ : type ○ : confirmed locations
b: type of A. brunneus
(solid figures = specimens examined)

Figure 46. Distribution of C. nanum.

APPENDIX B

SPECIMENS EXAMINED

All specimens included in the morphometric analyses are included in this list. Some other significant specimens which were examined but not used in the multivariate analyses are also listed. Specimens examined just to verify distribution records are not listed here.

Abbreviations used: AMNH, The American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, The British Musum, (Natural History); CAS, California Acadamy of Sciences; FMNH, Field Museum of Natural History; JFBM, University of Minnesota, J.F. Bell Museum of Zoology; MNHN, National Museum of Natural History (Paris); MRAC, Royal Museum of Central Africa; MZB, Zoological Museum of Berlin; RMNH, Royal Museum of Natural History (Lieden); UMMZ, Univeristy of Michigan Museum of Zoology; UTMZ, University of Turku (Finland) Museum of Zoology; USNM, United States National Museum; ZMUB, University of Bergen Museum of Zoology (Norway).

CTENOPOMA ACUTIRIOSTRE

Zaire River Basin.

CAS 24171 (1).
MNHN 1886-473, 1897-813 (syntypes); 1890-36 (holotype of *C. denticulatum*

CTENOPOMA ACUTIROSTRE (continued).

MRAC 14922 (1); 48692 (1); 68424-426 (3); 78600 (1); 87943-944 (2) 93834-835 (2); 99405-418 (14); 73-22-P-4971 (1); 73-23-P-426 (3).

CTENOPOMA ANSORGEI

Chiloango River.

ANSP 38655-658 (4) (syntypes).
BMNH 1912-4-1-480-487 (4) (syntypes).
MRAC 1703-1704 (1) (syntype); 1705-1708 (3) (syntypes).

Zaire River Basin.

MRAC 43971 (1) (syntype of Anabas daviadae); 47710 (1); 47413-415 (3); 57562-57583 (9); 62408-62457 (26); 118201-118214 (17).

CTENOPOMA ASHBYSMITHI

Upper Zaire River Basin.

BMNH 1976-10-21-2 (holotype); 1976-10-21-3-11 (paratypes); 1976-10-21-21-61.

CTENOPOMA CONGICUM

Chiloango River.

ANSP 38736-38 (3).
MRAC 1699-702 (3).

Zaire River Basin.

ANSP 67225-29 (5).
BMNH 1887-1-13-11 (holotype)
MRAC 71539-540 (2); 71640-641 (2); 74310-312 (4); 75731-758 (24) 94917-919 (2); 103325-331 (3)

White Nile.

UTMZ HT3 (1) (holotye of Anabas pekkolai)

CTENOPOMA CONGICUM LONGIPINNIS

Zaire River Basin.

ANSP 71925-71936 (7) (holotype and paratypes).

CTENOPOMA DAMASI

Lake Edward Drainage.

MRAC 66003-66024 (4) ("cotypes"); 66011-012 (8) ("types").

CTENOPOMA FASCIOLATUM

Zaire River Drainage.

BMNH 1898-7-9-6-8 (3) (syntypes).
MNHN 1925-155 (holotype of *Anabas fasciolatum filamentosa*).
MRAC 19070; 47903-904 (2); 62531-549 (6); 102116-117 (1); 105350-383 (10); 118168-175 (4); 118178-187 (10); 137333 (3); 137334-339 (6); 182560 (1).

CTENOPOMA INTERMEDIUM

Zambesi River System.

BMNH 1932-12-16-317-320 (2).
MNHN 1920-102-103 (4) (syntypes of *Anabas intermedius*); 1980-1328 (5).
MRAC 118636-651 (6); 164081-085 (4); 164086-094 (8).
UMMZ 200148 (18).

Lualaba River Drainage (Zaire basin).

AMNH 9253 (1) (holotype of *Anabas muriei ocellifer*); 9259 (3) (paratypes of *A. muriei ocellifer*).
BMNH 1943-7-27-429-433 (3).
MRAC 88676 (1); 164589-611 (5); 164620-630 (4); 164631-635 (4); 164631-635 (4); 79-1-P-6292-300 (2); 79-1-P-6301-317 (17).

CTENOPOMA INTERMEDIUM (CONTINUED)

Kasai River System (Zaire basin).

AMNH 12389 (5).
MRAC 87160-167 (3); 98656-658 (3); 101981 (1); 101982 (1); 104317-331 (12); 153441-446 (4); 153523-527 (4); 164073-074 (2); 164097-138 (17); 164139-140 (2); 164142-152 (11); 164153-159 (8); 164160 (1); 164161-162 (2) 164163-172 (7).

CTENOPOMA KINGSLEYAE

Central Africa.

BMNH 1896-5-5-30-32 (1) (syntype of *Ctenopoma kingsleyae*).
MNHN 1938-31 (1) (holotype of *Anabas breviventralis*).

West Africa.

AMNH 32756 (16).
MNHN 1963-526 (5); 1979-465 (1).
USNM 114769 (5); 118836 (2); 118837 (3); 118839 (4).
ZMB 20636 (1) (holotype of *Anabas argentoventer*).

CTENOPOMA MACHADOI

Cuanza River.

ANSP 51800-51855 (34) (holotype and paratypes of *Anabas machadoi*

Kasai River System. (Zaire Basin).

MRAC 164180-195 (8).

CTENOPOMA MACULATUM

Dja River (Zaire Basin).

MRAC 75-56-P-1096-100 (2).

CTEMOPOMA MACULATUM (CONTINUED)

West Coast Atlantic Drainages.

AMNH 11747 (1).
BMNH 1902-11-12-150 (1) and 1903-7-38-59-63 (3) (types of *Anabas pleurostigma*).
CAS 15783 (1)
JFBM 1528 (1); 1544 (2); 1558 (1).
MNHN 1885-423 (1) (holotype of *Ctenopoma maculatum*); 1885-424 (1) (holotype of *Ctenopoma multifasciatum*).
MRAC 73-02-P2184 (2); 73-02-P-2188 (1); 73-02-P-2195 (1); 73-18-P-3243-253 (4); 73-32-P-97-103 (2).

CTENOPOMA MULTISPINE

Zambesi River System.

MNHN 2239 (1) (syntype of *Ctenopoma multispinis*).
UMMZ 200062 (30).

Zaire River System.

AMNH 12368 (4).
MRAC 31951-31965 (15); 36385-36417; 152131-138 (8); 76-3-18-P-2472.

CTENOPOMA MURIEI

Lake Chad and Niger River Basins.

MNHN 1959-430 (2).
MRAC 73-15-P-11642-657 (16).

Nile River Drainage.

BMNH 1907-12-2-2884-2903 (4) (syntypes of *Anabas muriei*).
CAS 51361 (7).
MNHN 1907-240-242 (2) (syntypes of *A. muriei*).
USNM 61335 (2).

CTENOPOMA MURIEI (CONTINUED)

Upper Zaire River and Lake Tanganyika.

BMNH 1919-7-24-33-34 (2) (syntypes of *Anabas ctenotis*);
1971-6-22-139-144 (4).
MRAC 38878 (1); 38990-991 (2); 66009 (1); 182474-476 (1);
79-07-P-231-233 (2).
USNM 191604 (1).

CTENOPOMA NANUM

West Coast Atlantic Drainage.

BMNH 1868-8-16-9-10 (2) (syntypes of C. nanum);
1967-10-12-31-40 (7).
CAS 53622 (2) ("*brunneus*-like" specimens).
JFBM 1558 (1); 2144 (2).
MNHN 1906-328 (2); 1908-247-250 (4).);
MRAC 73-18-P-3272 (1); 73-18-P-3273-276 (4); 75-04-P-175-190 (12
76-32-P-696-698 (2); 76-32-P-742-750 (1); 76-32-P-751 (1);
76-32-P-753-757 (1); 76-32-P-773 (1); 76-32-P-791 (1);
76-64-P-60-61 (2); 77-17-P-1284-1290 (6); 77-25-P-551-552 (2).

Zaire River System.

AMNH 6110 (18); 6111 (25); 6113 (5); 8108 (1) (holotype of
Anabas lineatus).
ANSP 66798-812 (1); 66823-29 (7); 66876-888 (13); 67230-35 (2).
MNHN 1977-443 (1); 1979-278(1); 1978-12 (1); 1978-13 (1).
MRAC 1794 (1); 1801 (1); 1840-1841 (2); 1870-1871 (1); 2841 (1);
22564 (1); 37117-119 (3); 37120-121 (2); 62408-457 (3);
67619-627 (3); 75888 (1); 75889-890 (2); 79393-398 (6); ;
90994-001 (4); 91093-101 (2); 96842-853 (11); 98462-463 (2)
101981 (1); 101982 (1); 102467-470 (4); 105353-355 (3);
118218-230(12); 137291-293 (1); 137295-302 (2);
153441-446 (4); 167953-959 (1); 167960-984 (8); 174209-212
(3); 182450-451 (2); 182462 (3); 73-16-P-6132-138 (4); ;
73-16-P-6347 (1); 73-23-P-661-620 (3); 73-23-P-6477-553 (6)
75-56-P-368-692 (6); 76-32-P-783-790; 105356-369 (7).
ZMB 31538 (2) (syntypes of *A. brunneus*).

CTENOPOMA NIGROPANNOSUM

West Coast Drainages.

BMNH 1868-8-16-11 (1) (type of *C. gabonense*).
MZB 9131 (1) (syntype of *C. nigropannosum*).

Zaire River System.

AMNH 5969 (4); 19694 (3).
CAS 64609 (1).
MRAC 39465; 56397; 57541-57552; 94916.

CTENOPOMA OCELLATUM

Zaire River System.

CAS 64756 (1).
MNHN 1886-472 (1) (holotype of *C. ocellatum*).
MRAC 19030-031 (2); 30638 (1); 52513 (1); 98940 (1); 99439-440 (1); 103192-195 (2); 118232 (1); 182443-444 (2) 182559 (1).

CTENOPOMA OXYRHYNCHUM

Zaire River System.

CAS 66269 (1).
BMNH 1896-3-9-16 (type of *C. weeksii*).
MRAC 1164 (holotype of *A. oxyrhynchum*); 78482-484 (3); 118237-238 (2); 137352 (1); 137345 (1); 137346 (1); 182478 (1); 73-23-P-6348 (1); 76-27-P-70 (1).

CTENOPOMA PELLEGRINI

West Coast Drainages.

MRAC 173859-861.

CTENOPOMA PELLEGRINI (CONTINUED)

Zaire River System.

BMNH 1901-12-26-59 (1) (syntype of *C. pellegrini*).
MRAC 1276 (1) (syntype of *C. pellegrini*); 1831 (1); 22795 (1); 46785-786 (1); 94914-915 (2); 131318-320 (2); 167988 (1).

CTENOPOMA PETHERICI

Nile River System.

BMNH 1863-3-9-17 (1) (holotype of *C. petherici*).
MNHN 1959-152 (6); 1961-805 (4); 1961-807 (2).
USNM 72845 (2).

West Africa.

ANSP 66126 (1) (holotype of *C. p. chadensis*); 67222 (1) (paratypes); 66127-30 (1) (paratypes).
MNHN 1961-796 (2); 1961-795 (3); 1968-72 (3); 1969-179 (1); 1978-308 (2); 1984-571 (2).
MRAC 154017 (1); 154170 (1); 73-14-P-516 (3); 73-15-P-1587 (1); 73-15-P-1660-666 (2); 73-15-P-1665-1666 (2); 73-15-P-1667-1668.

SANDELIA CAPENSIS

MNHN A-365 (syntypes of *Spirobranchus capensis*).
1980 1335 (5).
USNM 232692 (3).

ANABAS TESTUDINEUS

Thailand

CAS 45004 (2); 53077 (2); 53144 (1).

VITA

Steven Mark Norris

Candidate for the Degree of

Master of Science

Thesis: SUPERSPECIFIC RELATIONSHIPS WITHIN THE GENUS CTENOPOMA (PERCIFORMES, ANABANTOIDEI): A MORPHOMETRIC ANALYSIS AND PRELIMINARY PHYLOGENY

Major Field: Zoology

Biographical:

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