Cytotaxonomy of 41 Species of Neotropical Cichlidae

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Chromosome morphology for 40 species and diploid counts for 41 species of neotropical Cichlidae were prepared using colchicine treated gill epithelial squashes.

Gross chromosomal evolution among this group appears to have been somewhat conservative with the majority of the species retaining the putative ancestral diploid number of 48. The most parsimonious description of karyotypic evolution among the neotropical Cichlidae indicates a common ancestor with 2N = 48 subtelocentric-telocentric chromosomes which gave rise, probably through pericentric inversions, to the most common present day arrangement which was designated as the 'A' karotype. The rarer 'B' karotype which was dominated by metacentrics was evolved either from the primitive state or from the 'A' by centric fusions.

The karyotypic data does not significantly contradict the generally accepted evolutionary scheme for these fishes. However, an interesting correlation between the probable geographic center of origin and the number of metacentrics within *Cichlasoma* was noted. It was concluded that the South American autochthons (*Cichlasoma* and probable derived genera) showed an evolutionary trend toward the accumulation of metacentrics while Middle American representatives of this group did not.

THE higher relationships among the neotropical Cichlidae have been largely ignored since Regan's review (Regan, 1905a, b, c; 1906a, b). Since that time only a few authors have addressed this speciose assemblage on higher than a generic level (Newsome, 1971; Cichocki, 1976). Additionally there is an account by Hoedeman (1975) which appears to be primarily a reaccounting of the work of Regan although no reference to that work is given. The recent development of simplified techniques for the examination of fish chromosome morphology has stimulated numerous workers to apply cytotaxonomic data to ichthyological investigations. This increased interest can be traced primarily to the work of McPhail and Jones (1966).

Cytotaxonomic data for the neotropical Cichlidae are essentially nonexistent. Nine of the 200 plus species known to taxonomists have been examined karyotypically (Post, 1965; Ohno and Atkin, 1966; Hinegardner and Rosen, 1972; Nishikawa et al., 1973; Michele and Takahashi, 1977). The chromosome morphology of three of these, *Symphysodon aequifasciata* (Ohno and Atkin, 1966), *Cichlasoma citrinellum* (Nishikawa et al., 1973) and *Geophagus brasilien-* sis (Michele and Takahashi, 1977) have been published, the other six are known from haploid numbers only or were presented with marginal morphology from testes squashes. Somatic karyotypes for 40 species and diploid counts for 41 species of neotropical cichlids, including a reexamination of seven of those previously reported, are presented and discussed in this report.

Materials and Methods

With the exception of *Apistogramma agassizi*, *A. borelli*, *Cichlasoma bimaculatum*, *C. labridens*, *C. septemfasciatum* and *Crenicichla lucius* which are in the author's personal collection, identification specimens of all species were deposited in the Texas Natural History Collection of the Texas Memorial Museum in Austin, Texas.

Specimens were collected from their natural habitat when possible but geographic and economic limitations precluded this in most cases. While it is possible that the use of domesticated stock for karyotypic studies might introduce errors, the probability of this is considered to be low. Comparison of wild with domesticated specimens was possible for *Cichlasoma nigrofas-*
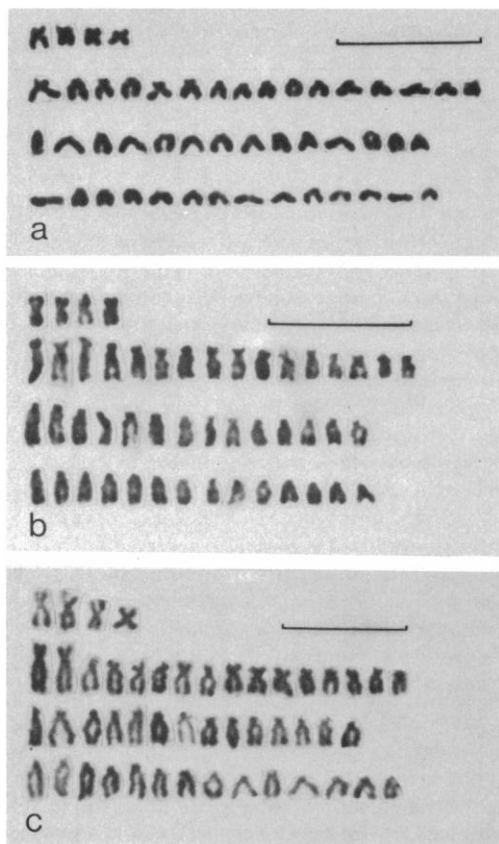
Fig. 1. Karyotypes of *Cichlasoma nigrofasciatum*: a) Male from Laguna Río Cuarto in Costa Rica; b) Female, first generation offspring from Río Cuarto stock; c) Female from aquarium industry. At least two of the top row are metacentrics (r ≈ 1) in each karyotype. Bar = 10 microns.

Ciénegas, Coahuila, México, collected by author and G. L. Powell, 3 specimens from creek at Cueva de Carrizal, near Candela, Coahuila, México, collected by author and G. L. Powell, 2 specimens spring fed pool near San Vicente, Coahuila, México, collected by G. L. Powell and T. C. Scanlon (The original San Marcos R. population was transplanted from the Rio Grande drainage (Buchanan, 1971)).

Cichlasoma sp.: Posos de la Becerra, about 17 km S. Cuatro Ciénegas, Coahuila, México, collected by author and G. L. Powell (morphology indicates this to be the "long head" form of LaBounty (1974); however, all specimens karyotyped were juveniles and allometric growth makes identification of the various morphs uncertain. While LaBounty (1974) indicated 4 endemic species present at this location Sage and Selander (1975) argued that only a single polymorphic species was present).

Somatic C-metaphase karyotypes were prepared from conventional gill epithelial squashes using the techniques described in detail by Thompson (1976) which are essentially the same as those of McPhail and Jones (1966). In brief, the gill epithelial cells were given a hypotonic treatment in deionized water and then stained in orcein and squashed by thumb pressure. Observation and photography were done with phase contrast microscopy and morphology was determined from the photokaryotypes.

In this study, chromosomal nomenclature as suggested by Levan et al. (1964) is used. It provides for two categories, metacentric-submetacentric (msm, $1 \leqslant r \leqslant 3$) and subtelocentric-telocentric (stt, $r \geqslant 3$). Arm ratios (r) were measured from the karyotypes with dial calipers and those equal to three were assigned to a class at the observer's discretion. In most instances the conservative decision was made and these were placed in the stt group. The use of such broad categories may mask some minor differences; however, it is better to lose these than to base phylogenies on conclusions that are the result of preparation artifacts.

High degrees of chromosomal condensation due to colchicine treatment caused increased difficulty in determining the exact point location of the centromere when measuring the arm ratios. Other artifacts of preparation (such as overlaps, twists, losses and breaks) as well as colchicine effects have been indicated by numerous authors as possible sources of error in cytotaxonomic data (Smith, 1965; Bogart, 1969; Mayers and Roberts, 1969; Engmann, 1972; Thorgaard, 1977; Avise and Gold, 1977). Many of the chromosomes in the karyotypes studied have borderline ratios near three and thus, small errors in measurement may lead to apparent but unreal differences in arm number.

When preparing the karyotypes the stt chromosomes could usually be sorted into tentative groups with progressively larger ratios. Each of these groups was arranged in order of descend-

ciatum (Fig. 1) and *Haplochromis burtoni*; no apparent differences were noted. With the exceptions listed below, all specimens were derived from commercial sources.

Cichlasoma beani: third or fourth generation from mixed stock from the Río Mayo near Navojoa and the Río Cuchujachi near Alamos, Sonora, México, collected by M. S. Keasey III.

Cichlasoma dowi: Laguna Río Cuarto, approximately 80 km N. San José, Costa Rica, collected by the author.

Cichlasoma labridens: marsh 10 km S. Ríoverde, San Luis Potosí, México, collected by R. R. Miller.

Cichlasoma salvini: 2 specimens from commercial sources; 9 specimens from fourth or fifth generation from stock taken from roadside ditches 16 km W. Belize City, Belize, collected by N. Aspinwall.

Cichlasoma nigrofasciatum: 1 specimen from commercial source; 5 specimens as for *C. dowi* and 5 offspring of these specimens.

Cichlasoma septemfasciatum: as for *C. dowi* (incorrectly identified as *C. spilurum* in Thompson (1976)).

Cichlasoma cyanoguttatum: 1 specimen North Fork, Llano R. near Junction, Texas, collected by author, 9 specimens offspring of stock from San Marcos R. at Interstate 35 crossing, San Marcos, Texas, collected by author, 2 specimens Laguna Santa Tecla, 25 km S. Cuatro

TABLE 1. DIPLOID NUMBER AND CHROMOSOME MORPHOLOGY FOR NEOTROPICAL CICHLIDAE.

	Species group	2N	Morphology			# of specimens ♂♂/♀♀	Cells counted/ % with modal #
			msm	stt	FN		
Acarichthys heckeli		48	6	42	54	2/–	34/64.7
Aequidens metae		48	6	42	54	3/6	121/84.3
Aequidens paraguayensis		44	26	18	70	6/6	122/54.9
Apistogramma agassizi		46	24	22	70	1/1	26/69.2
Apistogramma borelli		38	22	16	60	1/–	15/100.0
Apistogramma ortmanni		46	24	22	70	4/–	40/60.0
Astronotus ocellatus		48	6	42	54	–/1	13/53.8
Cichla temensis		48	0	48	48	1/1	36/69.4
Cichlasoma citrinellum	Amphilophus	48	8	40	56	10/3	149/67.1
Cichlasoma centrarchus	Archocentrus	48	6	42	54	–/2	38/71.1
Cichlasoma nigrofasciatum	Archocentrus	48	4	44	52	6/5	126/65.1
Cichlasoma octofasciatum	Archocentrus	48	6	42	54	7/4	127/78.7
Cichlasoma septemfasciatum	Archocentrus	48	6	42	54	–/1	17/76.5
Cichlasoma bimaculatum	Cichlasoma	48	6	42	54	1/–	11/63.6
Cichlasoma cyanoguttatum	Herichthys	48	6	42	54	11/7	284/64.1
Cichlasoma sp.	undetermined	48	6	42	54	2/3	76/73.1
Cichlasoma severum	Heros	48	4	44	52	4/6	108/64.8
Cichlasoma festivum	Mesonauta	48	8	40	56	7/3	114/66.7
Cichlasoma beani	Parapetenia	48	6	42	54	5/5	125/75.0
Cichlasoma dowi	Parapetenia	48	8	40	56	7/3	126/73.8
Cichlasoma kraussi	Parapetenia	50	6	44	56	3/10	139/54.7
Cichlasoma labridens	Parapetenia	48	6	42	54	–/1	15/86.7
Cichlasoma managuense	Parapetenia	48	6	42	54	5/6	113/67.3
Cichlasoma salvini	Parapetenia	52	28	24	80	7/4	130/63.8
Cichlasoma trimaculatum	Parapetenia	48	6	42	54	5/5	107/66.4
Cichlasoma coryphaenoides	Section 4	48	6	42	54	4/3	81/67.9
Cichlasoma meeki	Thorichthys	48	6	42	54	8/7	151/66.9
Crenicara filamentosa		46	12	34	58	–/2	14/64.3
Crenicichla lepidota		48	6	42	54	–/1	12/58.3
Crenicichla lucius		48	—	—	–	–/1	10/50.0
Crenicichla notophthalmus		48	6	42	54	–/2	27/63.0
Crenicichla strigata		48	6	42	54	6/4	130/73.1
Geophagus brasiliensis		48	4	44	52	8/8	183/69.9
Geophagus jurupari		48	4	44	52	3/3	71/69.0
Geophagus surinamensis		48	4	44	52	1/–	24/70.8
Herotilapia multispinosa		48	6	42	54	11/6	200/60.5
Nannacara anomala		44	18	26	62	2/2	43/58.1
Neetroplus nematopus		48	8	40	56	10/7	175/66.3
Pterophyllum scalare		48	4	44	52	1/2	49/61.2
Symphysodon aequifasciata		60	58	2	118	1/1	20/50.0
Uaru amphicanthoides		46	8	38	54	3/6	105/73.3

ing length on a separate row of the karyotype. Many of the stt chromosomes on the second row of the karyotypes (Fig. 1) have ratios close to three and could just as easily be considered msm's. In Figure 1 if all the stt chromosomes with ratios of three were placed in the msm class the arm or fundamental number (FN) of 52 (Table 1) would become 55, 57 and 63 re-
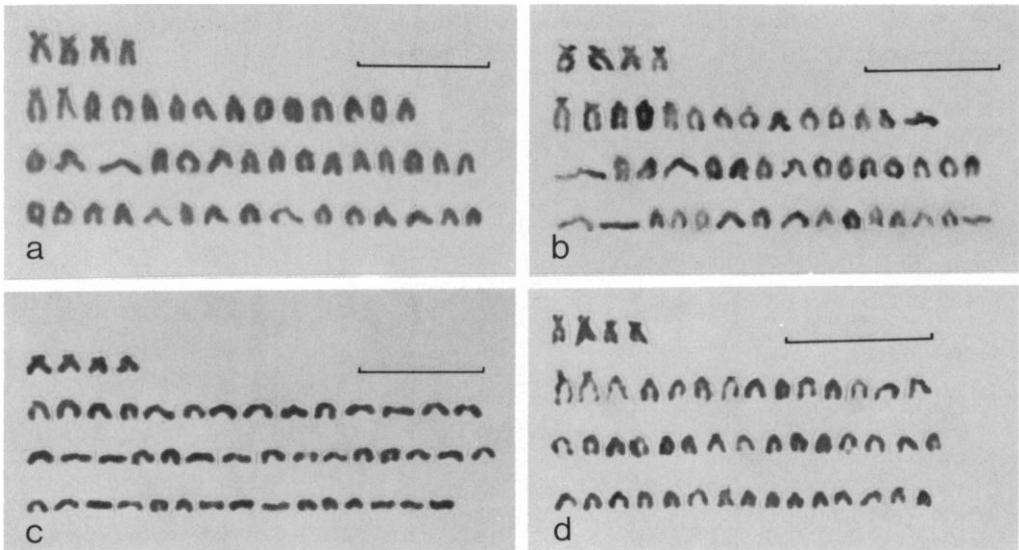
Fig. 2. *Geophagus brasiliensis*: a) Male; b) Female; c) Male; d) Female. Bar = 10 microns.

spectively. Thus most minor differences in FN are best ignored. However, it is possible to recognize chromosomes which have ratios of approximately one (Fig. 1) and are obviously metacentrics compared to those that have ratios closer to three.

RESULTS AND DISCUSSION

It is generally accepted that the ancestral or primitive teleost karyotype consisted of 48 stt chromosomes (FN = 48) (Ohno et al., 1969; Ebeling et al., 1971; Uyeno, 1972; Kirpichnikov, 1973; Ohno, 1974; Arai and Nagaiwa, 1976; Gold, 1977). The evidence for this, as well as for a rather conservative chromosomal evolutionary history, especially within the Perciformes, can be found in recent summaries by Chiarelli and Capanna (1973), Denton (1973), Nikol'skiy and Vasil'yev (1973) and Ojima et al. (1976) which indicate a preponderance of 2N = 48 ± 4 among the more than 120 perciform species included. The conservative nature of chromosomal evolution among teleost fishes is also suggested by the findings of Wilson et al. (1975). The data in Table 1 are consistent with this conclusion. Thirty-one of the 41 species examined have diploid numbers of 48 and only two species have diploid counts outside the above indicated range.

No sexual dimorphism was indicated for any of those species in which both sexes were examined. Michele and Takahashi (1977) presented karyotypes for male *Geophagus brasiliensis* and inferred that this species was male heteromorphic. Karyotypes from two specimens of each sex of *G. brasiliensis* do not indicate heteromorphic sex chromosomes for either sex (Fig. 2). It is probable that the morphology of one submetacentric is obscured by overlap in the photograph presented by Michele and Takahashi (1977).

Hinegardner and Rosen (1972) reported haploid numbers for *Cichlasoma meeki* as did Post (1965) for *C. severum*, *Pterophyllum eimekei* (=*scalare*, Schultz, 1967) and *Nannacara anomala*. With the exception of *N. anomala* these data are in accord with the results of the present study. It is more likely that an error in counting would go undetected when working with haploid material (Kirby et al., 1977), thus it is felt that the error for *N. anomala* is in Post's data. The 2N number determined for this species in the present paper is in agreement with unpublished data of other workers (A. O. Gyldenholm, pers. comm.).

Nishikawa et al. (1973) presents a karyotype for *C. citrinellum* that agrees in diploid number (2N = 48) but not in FN with the results in this paper. Comparison of their figure with the karyotype in the present paper indicates that the differences are not real and are due to clas-

Fig. 3. a) *Cichla temensis*, female; b) *Crenicichla lepidota*, female; c) *C. notophthalmus*, female; d) *C. strigata*, female; e) *Aequidens paraguayensis*, male; f) *A. metae*, female; g) *Nannacara anomala*, female; h) *Crenicara filamentosa*, male. Bar = 10 microns.

sification decisions. This, as well as colchicine induced condensation differences, are undoubtedly responsible for the differences between the arm number reported here and by Ohno and Atkin (1966) for *Symphysodon aequifasciata* (2N = 60).

No single source of phylogenetic information can completely explain the evolution of such a large and varied group of organisms as the Cichlidae. Here the objective is to elucidate chromosomal evolution in light of other sources of evolutionary data, primarily the morphological work of Regan (1906b) and Cichocki (1976). The following discussion is based on the
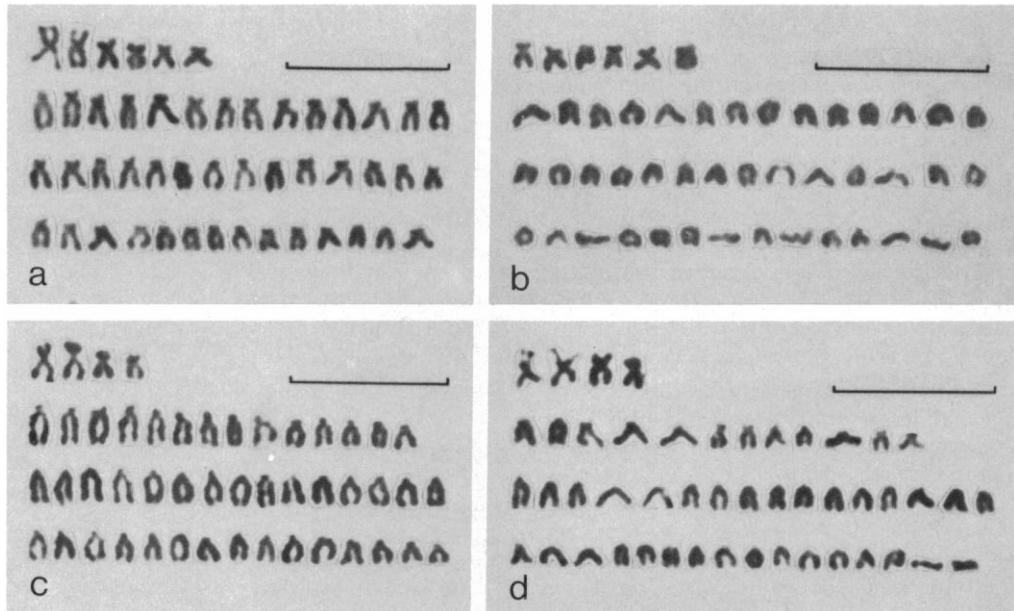
Fig. 4. a) *Astronotus ocellatus*, female; b) *Acarichthys heckeli*, male; c) *Geophagus jurupari*, male; d) *G. suri-namensis*, male. Bar = 10 microns.

premise that the primitive or ancestral diploid karyotype of the Cichlidae consisted of 48 single armed (stt) chromosomes and that any differences in arm number or chromosome number represent derived evolutionary states.

Cichocki (1976) recognized two subfamilies of neotropical Cichlidae, one consisting of the single genus *Cichla* and the other containing all other neotropical cichlids. *Cichla* has been considered the most plesiomorphic of the neotropical cichlids by most authors (Regan, 1906b; Newsome, 1971; Liem, 1973). Cichocki (1976) did not come to a firm conclusion regarding the position of *Cichla* but did concede that it was primitive in many characteristics and placed its point of divergence at the base of the neotropical lineage. The karyotype of *C. temensis* (Fig. 3a) consists of 48 stt chromosomes and appears to have evolved with little detectable karyotypic change from the primitive state.

With the exception of *C. temensis* all species studied were in Cichocki's (1976) second neotropical subfamily and all fell broadly into one of two basic karyotypic arrangements, 'A' or 'B,' a pattern emphasizing the uniqueness of *Cichla*. The first and probably the most primitive of these, 'A,' usually consisted of 48 or more chromosomes most of which were best classified as

stt chromosomes. Obvious metacentrics occurred less frequently than in the 'B' karyotypes. The 'B' karyotype was characterized by numerous metacentrics (r ≈ 1) and in all five species with this type the diploid number was either less than or greater than 48.

The 'A' karyotype could most simply have evolved from the primitive state by a series of pericentric inversions, with various minor rearrangements accounting for present differences. In most of the 'A' karyotypes many of the stt chromosomes on the second row of the figures could just as easily have been placed in the msm class as in the stt class with no significant change in the broad phylogenetic conclusions. In fact, it would tend to reduce the apparent differences somewhat, especially within *Cichlasoma*. The 'B' karyotype could have been derived from the ancestral type or from the 'A' type by an evolutionary step in which all or a large percentage of the chromosomes underwent centric fusions. This would result in numerous metacentrics and reduced diploid numbers. Subsequent minor rearrangements (non-disjunction, inversions, translocations etc.) could then account for increases in the number of chromosomes and the accumulation of stt's.

Cichocki (1976) recognized four tribes within

his second neotropical subfamily. With the exception of that which contained *Chaetobranchus* all were well represented in the present study. For purposes of clarity and brevity each of Cichocki's remaining tribes has been designated numerically. The first of these, tribe 1, contains only *Crenicichla*. Tribe 2 contains all the remaining genera with the exception of *Cichlasoma* and its derivatives (sensu Regan, 1905c). Tribe 3 consists of *Cichlasoma* and the genera thought by Regan (1905c) to have been derived therefrom.

Of the four species of *Crenicichla* (tribe 1) examined, three, *C. lepidota* (Fig. 3b), *C. notophthalmus* (Fig. 3c) and *C. strigata* (Fig. 3d), have 'A' karyotypes and while the material available from the fourth, *C. lucius,* was not sufficient to prepare a karyotype the data are clear enough to class this as an 'A' karyotype. Two metacentrics are evident among the six msm's in the karyotypes of *C. lepidota, C. notophthalmus* and in the preliminary findings for *C. lucius* but not in that of *C. strigata.* This presents a possible correlation with morphological differences among the ctenoid scaled species of *Crenicichla* as defined by Regan (1913). The metacentrics occur in those species with longitudinal series counts of less than 72 but not in those with higher counts.

Considerable variation in both diploid number and chromosome morphology was encountered among the 12 species of tribe 2 that were examined karyotypically. Regan (1906b) felt that *Aequidens* (=*Acara*) was similar to the ancestral type that led to the rest of the neotropical genera with the exception of *Cichla* and *Chaetobranchus.* Two species of this rather large and somewhat ill defined genus were included in this study. Both 'B,' *A. paraguayensis* (Fig. 3e), and 'A,' *A. metae* (Fig. 3f), karyotypes were found. Six other genera from this tribe were examined and all but one had 'A' karyotypes. *Nannacara* (Fig. 3g), *Crenicara* (Fig. 3h) and *Astronotus* (Fig. 4a) all had variations of the 'A' karyotype as did *Acarichthys* and *Geophagus.*

Classically *Acarichthys, Geophagus* and *Apistogramma* have been considered to be closely related on the basis of the occurrence of an epibranchial lobe (Regan, 1906b; Eigenmann, 1912; Lowe-McConnell, 1969). Cichocki (1976) felt that this structure in *Acarichthys* was convergent to that of the others and placed *Acarichthys* in a subtribe with the non-lobed genera. Karyotypically *A. heckeli* (Fig. 4b) and *G. brasiliensis* (Fig. 2), *G. jurupuri* (Fig. 4c) and *G. sur-*
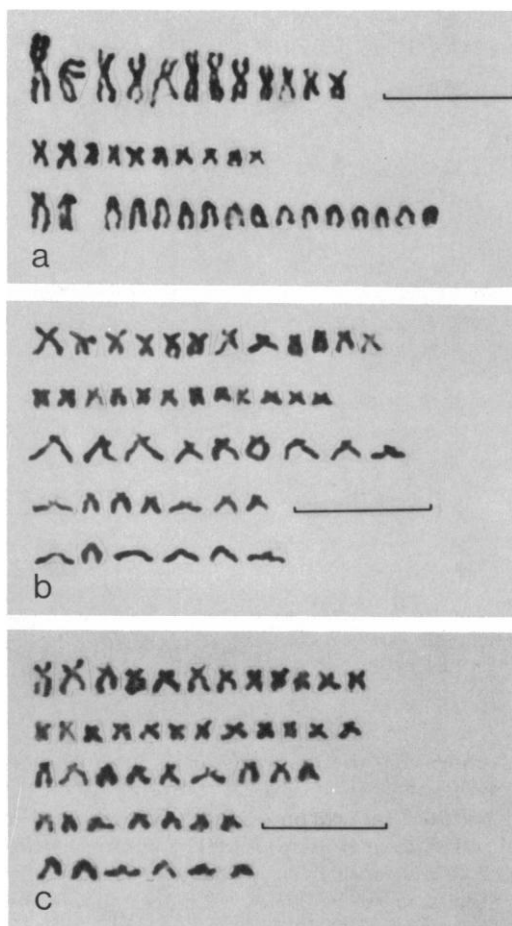
Fig. 5. a) *Apistogramma borelli*, male; b) *A. agassizi*, male; c) *A. ortmanni*, male. Bar = 10 microns.

inamensis (Fig. 4d) show only minor FN differences among their 'A' karyotypes. The possibility of a sattelited pair in *G. surinamensis* could not be verified due to minimal data from a single specimen. In contrast to Cichocki's conclusion regarding these genera the most aberrant chromosomally is *Apistogramma.* Three species of *Apistogramma* were examined and all had 'B' karyotypes with reduced diploid numbers (Fig. 5).

The intrageneric relationships of the large genus, *Cichlasoma,* particularly the Middle American representatives, have attracted the attention of numerous workers. At present the genus is divided into groups of morphologically similar species. Some of these have at various times been given generic or subgeneric status
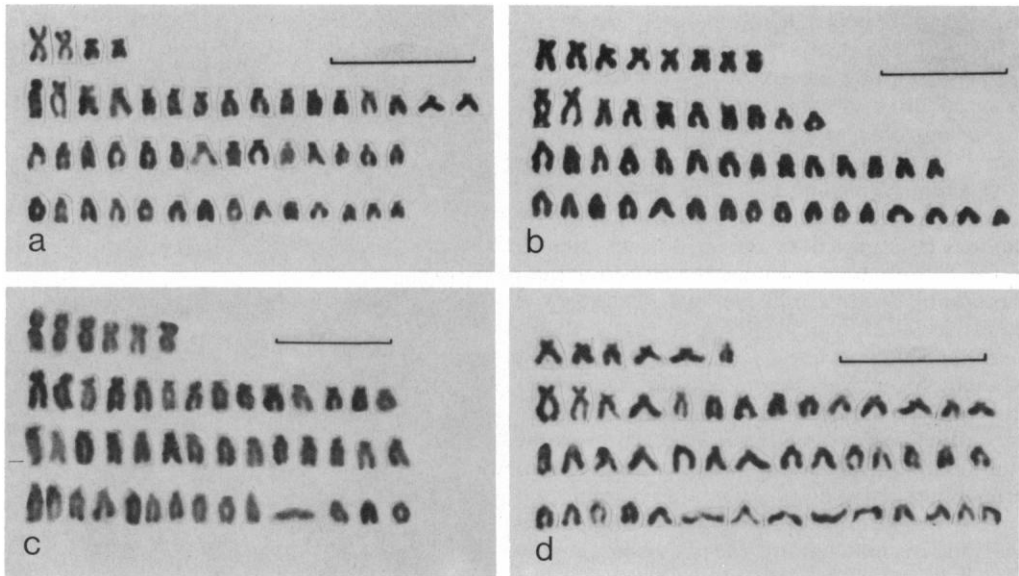
Fig. 6. a) *Cichlasoma severum*, female; b) *C. festivum*, male; c) *C. coryphaenoides*, male; d) *C. bimaculatum*, male. Bar = 10 microns.

by various workers (Meek, 1904; Regan, 1905c; Hubbs, 1936; Schultz, 1944; LaBounty, 1974; Bussing and Martin, 1975). Currently at least 11 groups of species are recognized within *Cichlasoma* (Regan, 1905c; Miller, 1966). Representatives of nine of these species groups or sections were examined karyotypically and the affinities of all are considered to be with the 'A' karyotype group.

The species groups examined that are considered autochthonous to South America (*Heros*, Fig. 6a, *Mesonauta*, Fig. 6b and Regan's section 4, Fig. 6c [Regan, 1905c]) have 'A' karyotypes with some (2–6) of the msm's being obvious metacentrics. The one apparent exception is *C. bimaculatum* (Fig. 6d) which is the single member of Regan's *Cichlasoma* species group and has no obvious metacentrics. Chromosomally it is not significantly different from *Aequidens metae*. Regan considered *C. bimaculatum* to be the most '*Aequidens*-like' of its genus. The possibility that this species may actually represent a morph of *A. portalegrensis* has been noted in the past (Goldstein, 1973). Two of the South American genera that were considered to be closely related to *Cichlasoma* by Regan, *Pterophyllum* (Fig. 7a) and *Uaru* (Fig. 7b), show a similar tendency toward metacentrics. *Sym-*

physodon aequifasciata with 60 chromosomes, most of which are metacentric (NF = 118), would seem to carry this tendency to an extreme and by definition must be classed as a 'B' karyotype. Both Regan (1906b) and Cichocki (1976) indicated that *Symphysodon* was morphologically allied to *Cichlasoma* and it is more parsimonious to postulate that the three genera with 'B' karyotypes represent parallel evolutionary events than to indicate heretofore unimagined relationships transgressing traditional, morphologically based conclusions.

The species groups of *Cichlasoma* examined that are considered to have their centers of origin in Middle America; *Parapetenia* (Fig. 8, 7 species), *Archocentrus* (Figs. 1, 9a–c, 4 species), *Herichthys* (Fig. 9d, e, 2 species probably), *Amphilophus* (Fig. 9f, 1 species) and *Thorichthys* (Fig. 9g, 1 species), all have 'A' karyotypes in which the msm's are all obviously less than metacentric with a single exception. *C. nigrofasciatum* (Fig. 1, *Archocentrus*) with two or four metacentrics shows an interesting similarity to the karyotypes of the South American species groups of this genus. The morphological similarity of this species to the 'primitive' South American species *C. facetum* has been noted (Regan, 1905c). The Middle American deriva-

tives of *Cichlasoma, Neetroplus* (Fig. 10a) and *Herotilapia* (Fig. 10b) have the typical 'A' karyotype without metacentrics.

SUMMARY AND CONCLUSIONS

The data presented indicate that chromosomal evolution among the neotropical Cichlidae has been rather conservative but probably not so conservative as would be predicted using the formula of Wilson et al. (1975). The most probable evolutionary scheme indicates that a common ancestor with a diploid compliment of 48 subtelocentrics gave rise, most probably through pericentric inversions, to the 'A' karyotype which is the most commonly seen thus far among the present day species. Secondarily and probably polyphyletically the 'B' karyotype (*Apistogramma, Symphysodon* and *Aequidens* in part) evolved from the 'A' or the ancestral type with centric fusions being the simplest pathway.

No surprising correlations exist between cytotaxonomic and more conventional data (Regan, 1906b; Cichocki, 1976) with the exception of that seen in *Cichlasoma* and its supposed derivatives. Among the species of and genera derived from this genus a correlation is seen between the number of metacentric chromosomes and their probable geographic center of radiation. Those with Middle American affinities (including the South American *Parapetenia* and excepting *C. nigrofasciatum*) have no obvious metacentric chromosomes while those with South American origins (excepting *C. bimaculatum*) all have an evolutionary tendency toward metacentrics. *C. bimaculatum* probably represents a relict karyotype among South American *Cichlasoma* or it may not be a *Cichlasoma* at all. The South American species with Middle American affinities probably represent a secondary radiation made possible by the reestablishment or near reestablishment of land connections between North and South America during early pliocene (Savage, 1966) while *C. nigrofasciatum* may represent the reciprocal.

Fig. 7. a) *Pterophyllum scalare*, female; b) *Uaru amphiacanthoides*, female; c) *Symphysodon aequifasciata*, female. Bar = 10 microns.
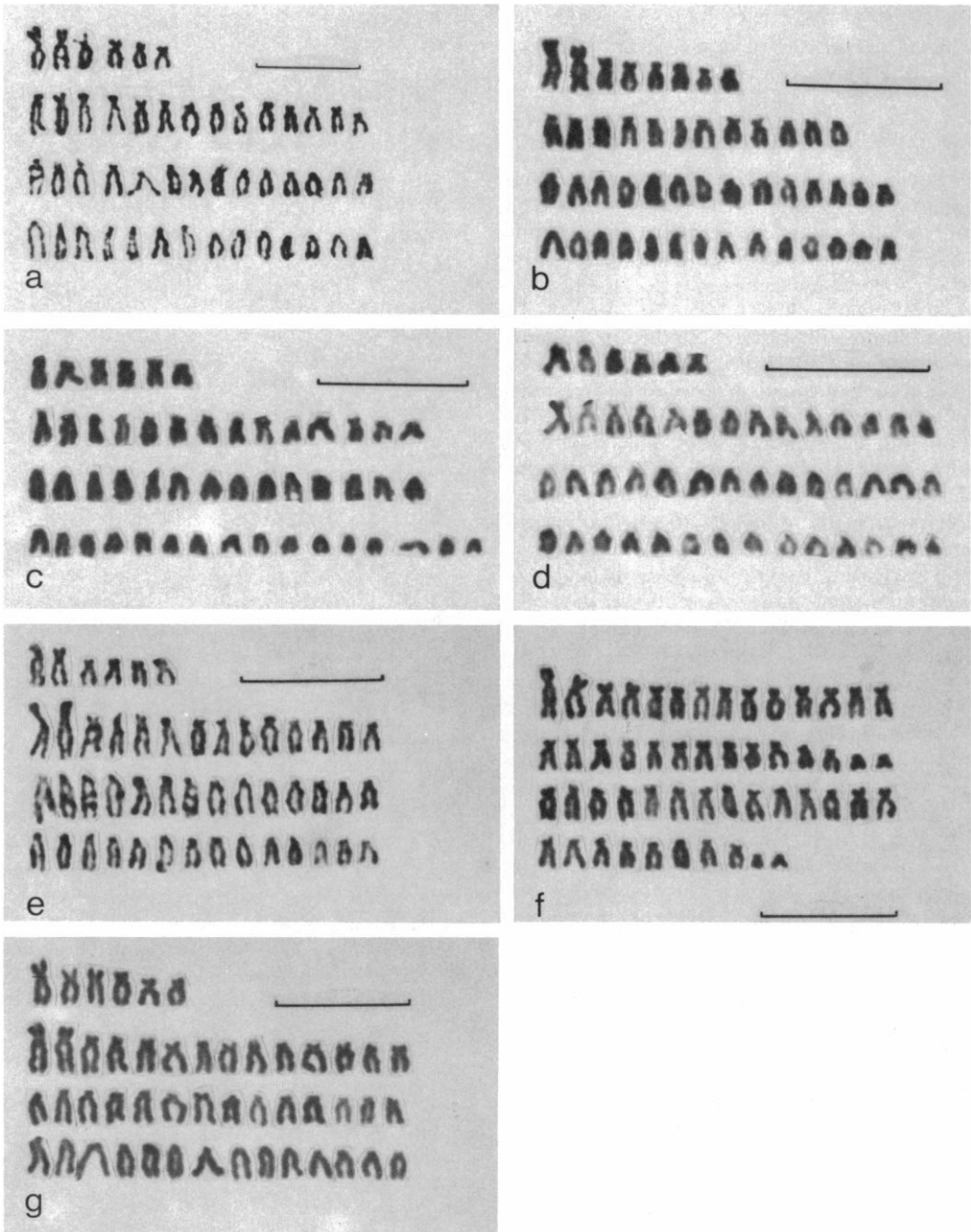
Fig. 8.   a) *Cichlasoma beani*, male; b) *C. dowi*, male; c) *C. kraussi*, male; d) *C. labridens*, female; e) *C. managuense*, male; f) *C. salvini*, female, aquarium stock; g) *C. trimaculatum*, female. Bar = 10 microns.
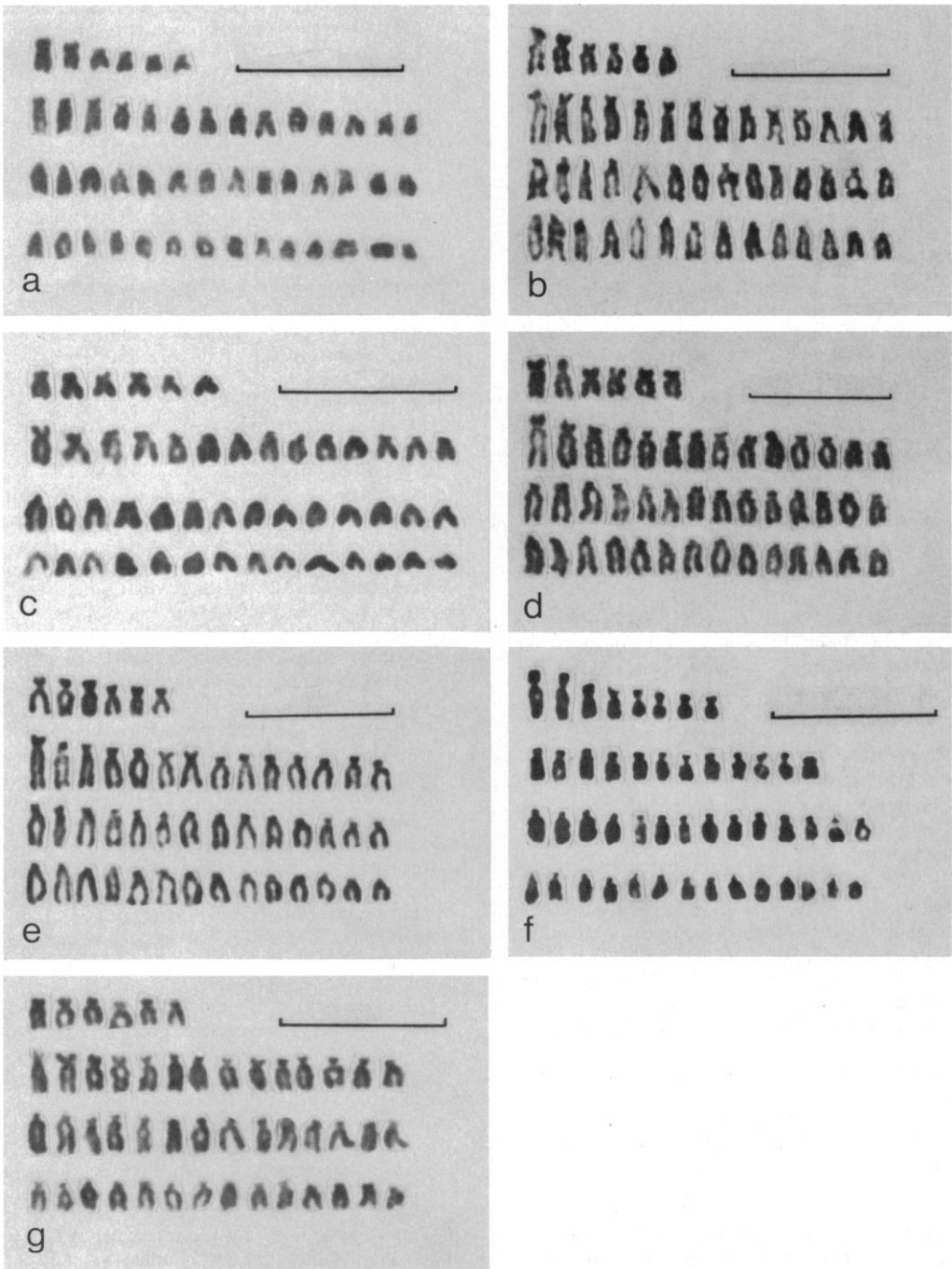
Fig. 9. a) *Cichlasoma centrarchus*, female; b) *C. octofasciatum*, male; c) *C. septemfasciatum*, female; d) *C. cyanoguttatum*, male, Candela, México; e) *Cichlasoma* sp., female, Posos de la Becerra, Cuatro Ciénegas, México; f) *C. citrinellum*, male; g) *C. meeki*, male. Bar = 10 microns.
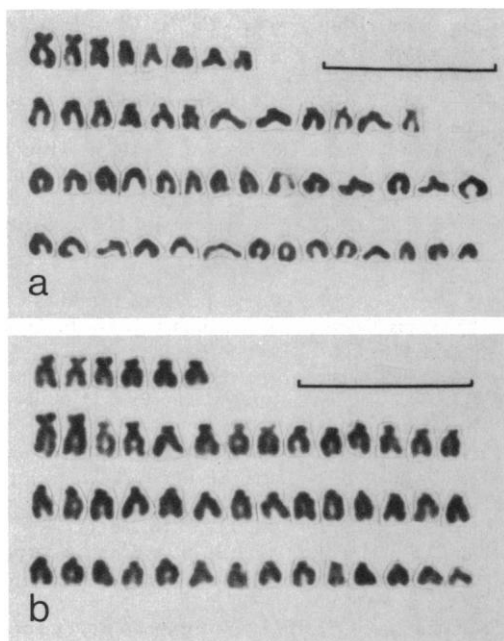
Fig. 10. a) *Neetroplus nematopus*, male, offspring of Costa Rican stock; b) *Herotilapia multispinosa*, male. Bar = 10 microns.

siderations in Texas. This study was supported by a grant from the Smithsonian Institution's TFH Fund.

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