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Extensive chromosomal rearrangements and nuclear DNA content changes in the evolution of the armoured catfishes genus *Corydoras* (Pisces, Siluriformes, Callichthyidae)

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Karyotypes and nuclear DNA content were studied in 11 species of the genus *Corydoras* from rivers in South America: *C.* sp. from Caripi river $2n=60$, *C.* cf. *simulatus* $2n=62$, *C. simulatus* $2n=62$, *C. reticulatus* $2n=74$, *C.* sp. from Galheiro river $2n=84$, *C.* aff. *punctatus* from Negro river $2n=102$, *C. flaveolus* $2n=58$, *C. arcuatus* $2n=46$, *C. trilineatus* $2n=46$, *C. schwartzi* $2n=46$, and *C. metae* $2n=92$. Extensive chromosome diversity and differences in DNA content were detected among species. The high variability in chromosome counts was not exclusively related to chromosomal structural rearrangements, but also to large changes in DNA content. Species could be grouped using their shared cytogenetic characteristics, suggesting that within the genus *Corydoras* different groups of species followed distinct evolutionary trends. Chromosomal rearrangements in *Corydoras* are, apparently, more frequent that morphological modifications, so cytogenetic data may be very useful for species delimitation and for the understanding of interrelationships among species.

Key words: Callichthyidae; chromosome number; karyotype; NOR; C band; DNA content.

I. INTRODUCTION

About 115 species and subspecies of the genus *Corydoras* have been described in South America; their distribution includes the eastern part of the Andes from north of Argentina through Colombia, including the island of Trinidad (Nijssen & Isbruker, 1986). According to Strauss (1985), the systematic relationships within this genus have been very difficult to elucidate mainly due to the occurrence of similar body forms among species, lack of discrete morphological features, and uncertain homologies of pigmentation patterns.

Cytogenetic studies carried out by Scheel *et al.* (1972) and Hinegardner & Rosen (1972) showed that karyotypic variability in the genus *Corydoras* is among the highest for fishes; this led Strauss (1985) to suggest cytogenetics as the most promising area for future phylogenetic work in the genus. In this paper we present a cytogenetic analysis of 11 species of *Corydoras* from different localities in South America.

II. MATERIALS AND METHODS

Eleven species belonging to the genus *Corydoras* were collected from rivers in South America (Fig. 1). Table I lists the species analysed and the numbers and sexes of the

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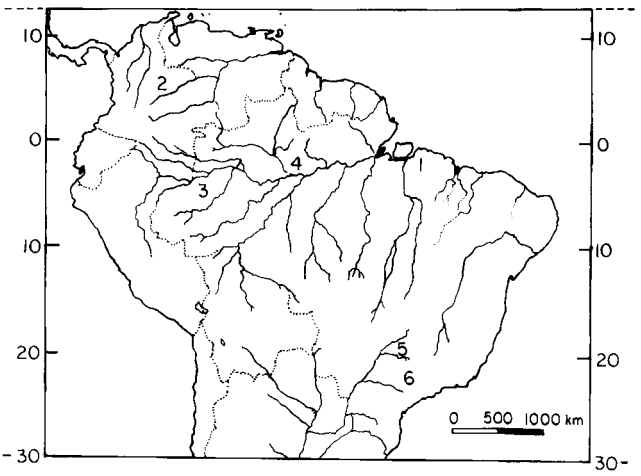

FIG. 1. Collecting localities of *Corydoras* species in South America. (1) Caripi river, Igarapé-Açu, State of Pará, Brazil: *C.* sp., and *C. trilineatus*. (2) Colombia: *C.* cf. *simulatus*, *C. simulatus*, and *C. metae*. (3) Tabatinga river, Leticia, the frontier between Brazil and Peru: *C. arcuatus*. (4) Negro river, Manaus, State of Amozonas, Brazil: *C. reticulatus*, *C.* aff. *punctatus*, and *C. schwartzi*. (5) Galheiro river, Araxá, State of Minas Gerais, Brazil: *C.* sp. (6) Alambari river, Botucatu, State of São Paulo, Brazil: *C. flaveolus*.

specimens investigated at each locality. Specimens of all species were identified and deposited in the Museu de Zoologia of the Universidade de São Paulo (MZUSP), São Paulo, Brazil.

Chromosome spreads, silver staining of nucleolus organizer regions (NORs) and C-banding were made as described in Oliveira *et al.* (1988). Chromosome preparations were made from gill and kidney tissues and at least 30 metaphases were examined for each specimen. Chromosomes were classified as metacentrics (M), submetacentrics (SM), subtelocentrics (ST) and acrocentrics (A); NF (chromosome arm number) was determined considering M/SM chromosomes as having two arms and ST/A chromosomes one arm. For DNA content determination, blood was collected by caudal vein puncture, spread over slides and air dried. The spreads were then fixed in Carnoy solution, hydrolysed for 10 min at 60° C in 2 N HCl, and stained by the Feulgen method for 1·5 h. Nuclear DNA content was determined with a Zeiss Scanning Cytophotometer at 540 nm light, using off-line computation with automatic scanning steps of 0·5 nm. Forty nuclei were scanned for each specimen. *Bufo*, *Gallo* or *Homo* blood or *Homo* fibroblast with known DNA contents were utilized as controls.

The DNA data were submitted to descriptive statistical analysis which included generation of sample means, variances and ranges. Homogeneity of variances was tested by Bartlett's method. Since the variances were not homogeneous, non-parametric techniques of comparisons among groups (the Kruskal–Wallis test) were used. Tukey's test of multiple comparisons was used for identifying the groups responsible for statistical significance (Zar, 1984).

III. RESULTS

Figures 2–5 show the karyotypes of the 11 species investigated. The karyotypes are similar for males and females in the species where both sexes were analyzed. Diploid numbers, chromosome formulae, numbers of pairs with NORs and diploid DNA contents are summarized in Table I.

TABLE I. Species and numbers of specimens analysed and cytogenetic data obtained from blood cells of *Corydoras* catfish

Species	Number of specimens ♂♂/♀♀	2*n* DNA content (in picograms) mean ± S.E.	2*n*	Karyotype* M	SM	ST	A	NF†	Pairs with NORs‡
C. cf. *simulatus*	1/0	1·04 ± 0·09	62	34	22	6		118	1
C. sp. Caripi river	3/0	1·28 ± 0·17	60	38	16	6		114	1
C. simulatus	2/0	1·29 ± 0·17	62	32	18	6	6	112	2
C. reticulatus	1/1	1·95 ± 0·26	74	16	20	12	26	110	1
C. sp. Galheiro river	1/2	2·37 ± 0·34	84	4	2	18	60	90	5
C. aff. *punctatus* Negro river	0/1	ND	102	10	14	20	58	126	1
C. flaveolus	2/5	3·04 ± 0·94	58	18	26	14		102	2
C. arcuatus	2/0	4·53 ± 0·41	46	28	18			92	1
C. schwartzi	1/5	4·78 ± 0·83	46	32	14			92	1
C. trilineatus	4/0	4·90 ± 0·65	46	28	18			92	1
C. metae	2/1	8·75 ± 1·50	92	40	36	6	10	168	3

*M = metacentrics, SM = submetacentrics, ST = subtelocentrics and A = acrocentrics.
†NF = diploid chromosome arm number.
‡Nucleolus organizer region.
ND = not determined.

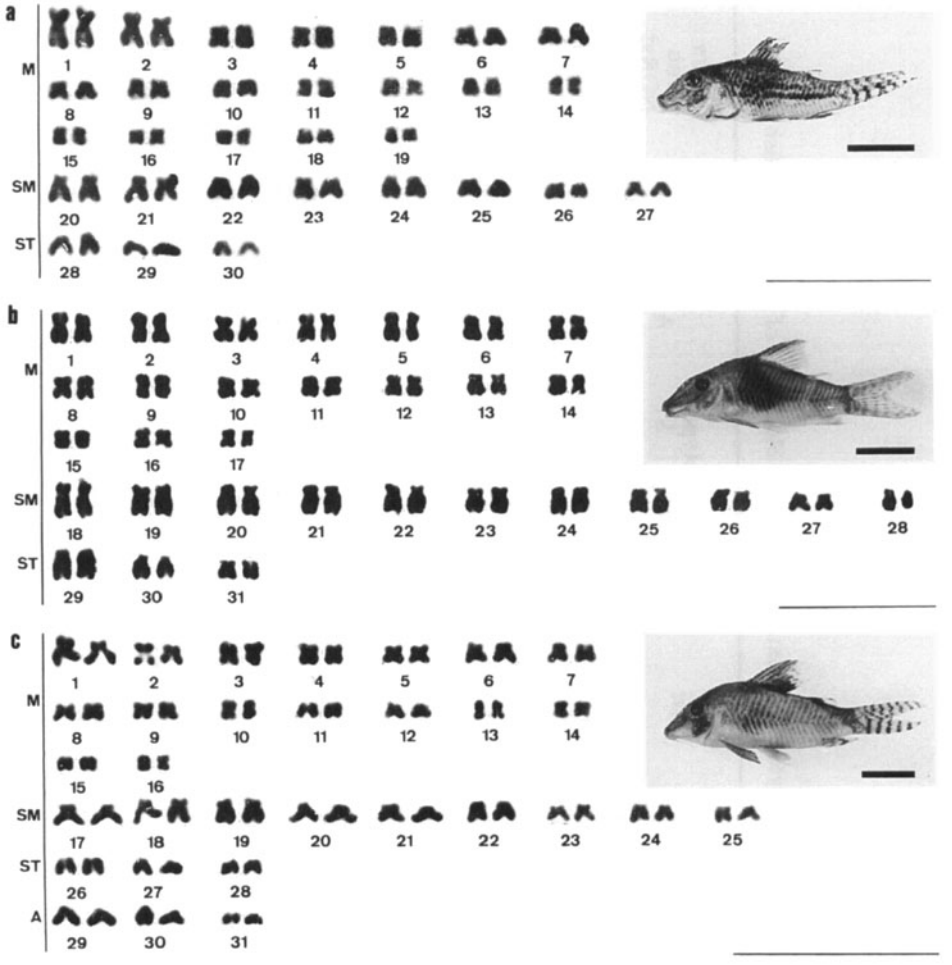

FIG. 2. Karyotypes and examples of: (a) *C.* sp. from Caripi river ($2n = 60$); (b) *C.* cf. *simulatus* ($2n = 62$); (c) *C. simulatus* ($2n = 62$). Thick bar = 1 cm and thin bar = 10 μm.

The chromosome numbers ranged from $2n = 46$ in *C. arcuatus*, *C. schwartzi* and *C. trilineatus*, to $2n = 102$ in *C.* aff. *punctatus* (Table I).

The numbers of chromosome pairs with NORs ranged from 1 to 5 (Fig. 6 and Table I) and intraspecific variability of NORs was observed. The NORs were present in telomeric position in the short arm of *C.* cf. *simulatus* (in one large SM pair), *C.* sp. from Galheiro river [in four medium-sized ST pairs and in one large A pair, Fig. 6(b)], *C.* aff. *punctatus* from Negro river (in one large SM pair), *C. flaveolus* [in one medium-sized M pair and in one medium-sized ST pair, Fig. 6(c)], *C. schwartzi* (in one large M pair) and *C. trilineatus* [in one large M pair, Fig. 6(d)]; and in telomeric position in the long arm of *C.* sp. from Caripi river [in one large M pair, Fig. 6(a)], *C. reticulatus* (in one large A pair), *C. arcuatus* (in one medium-sized M pair) and *C. metae* [in one large M pair, in one large SM pair and in one large A pair, Fig. 6(e)]. The species *C. simulatus* has an interstitial NOR in a large metacentric chromosome pair as evidenced by the presence of a secondary constriction [pair 2, Fig. 2(c)].

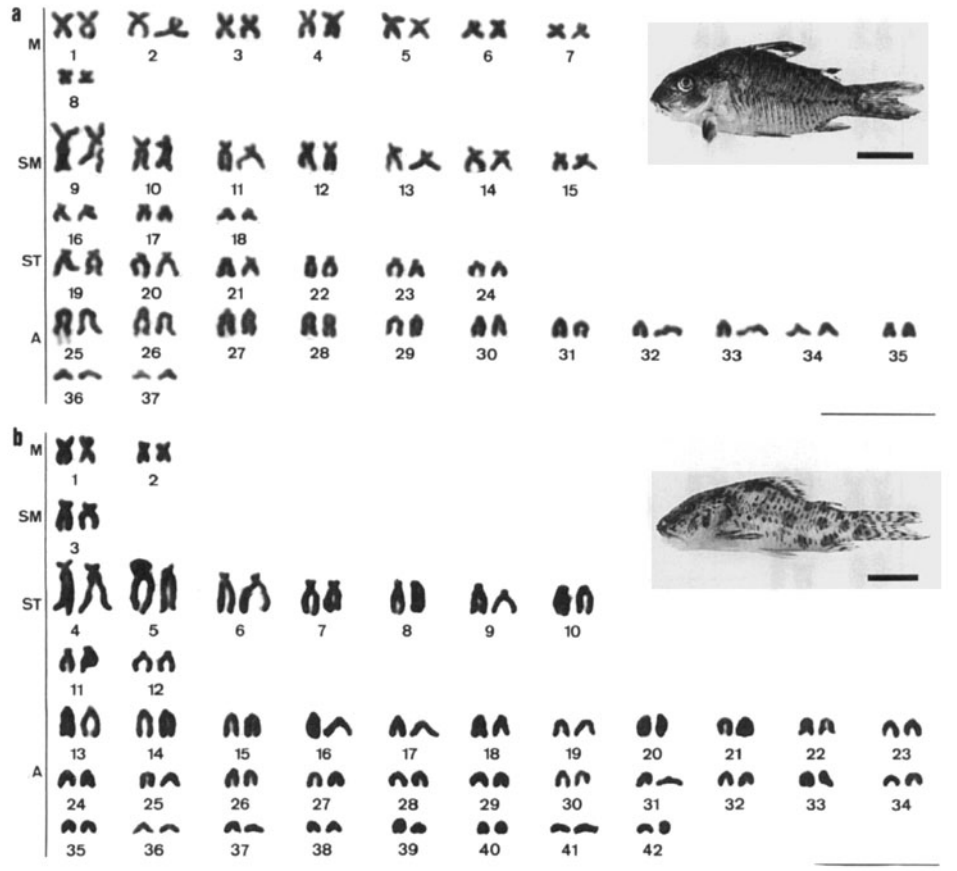

FIG. 3. Karyotypes and examples of: (a) *C. reticulatus* ($2n = 74$); (b) *C.* sp. from Galheiro river ($2n = 84$). Thick bar = 1 cm and thin bar = 10 μm.

Constitutive heterochromatin was pericentromeric and/or interstitial in *C. arcuatus* [Fig. 7(d)], *C. schwartzi*, *C. trilineatus* and *C. metae* [Fig. 7(e)]. The species *C.* cf. *simulatus* [Fig. 7(a)], *C.* sp. from Caripi river, *C.* sp. from Galheiro river [Fig. 7(b)], *C. reticulatus*, *C.* aff. *punctatus* from Negro river and *C. flaveolus* [Fig. 7(c)] had some chromosome pairs with heterochromatic blocks in pericentromeric and/or interstitial regions, and several chromosome pairs with heterochromatic short arms. The quantity of heterochromatin was apparently not related to the amount of nuclear DNA content; species with higher nuclear DNA contents did not present proportionally more heterochromatin than species with small nuclear DNA content.

The statistical parameters from the distributions of all DNA values for all individuals of each species are shown in Table I. Diploid DNA content ranged from $1{\cdot}04 \pm 0{\cdot}09$ picograms/nucleus in *C.* cf. *simulatus* to $8{\cdot}75 \pm 1{\cdot}50$ picograms/nucleus in *C. metae*. Bartlett's test revealed significant heterogeneity ($\chi^2_{[9]} = 810{\cdot}9169$, $P < 0.05$) among species variances. The Kruskal–Wallis test revealed a significant difference in DNA content among species ($H = 736{\cdot}377$, d.f. = 9, $P < 0{\cdot}05$). The Tukey test of multiple comparisons showed that the DNA values for *C.* cf. *simulatus*, *C. simulatus* and *C.* sp. from Caripi river, for *C. reticulatus* and *C.* sp.

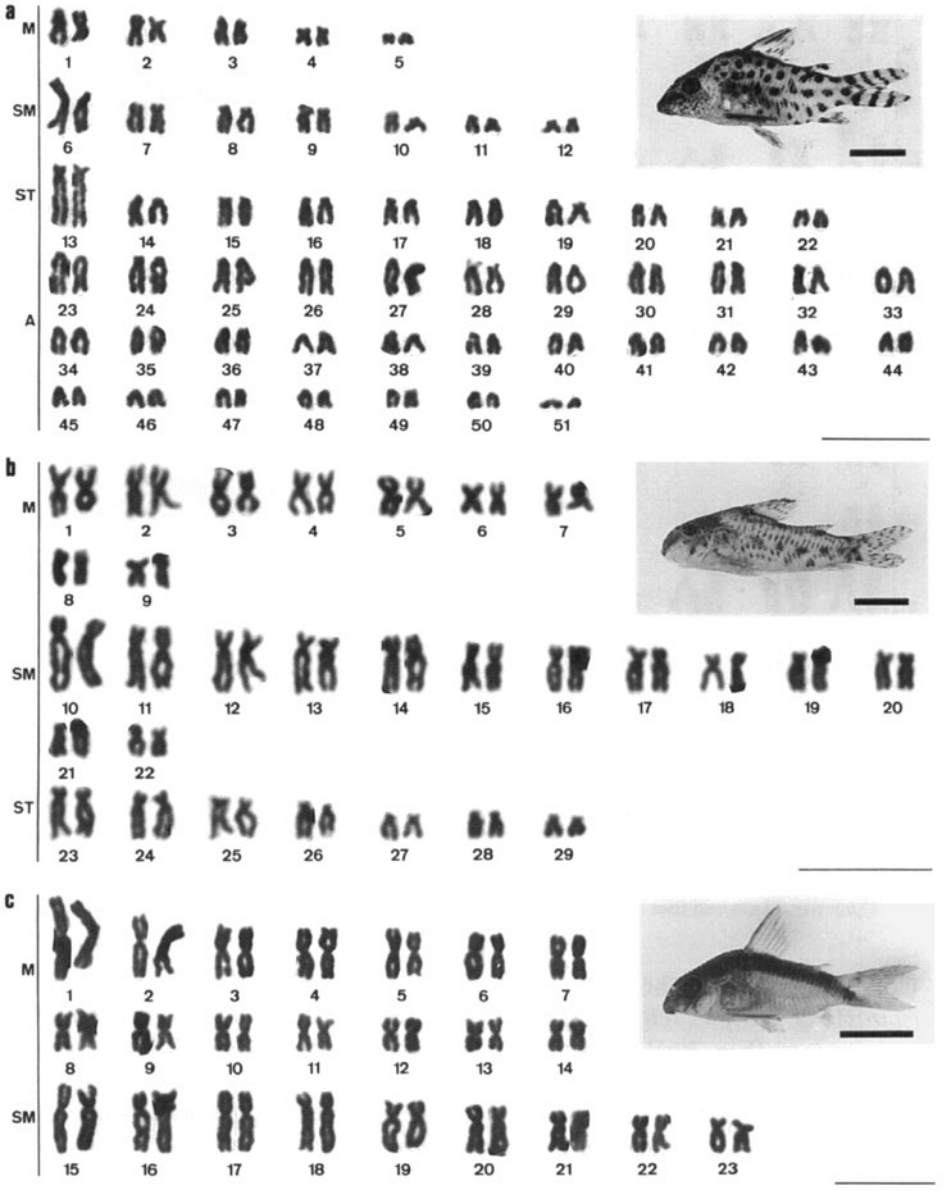

FIG. 4. Karyotypes and examples of: (a) *C.* aff. *punctatus* from Negro river ($2n = 102$); (b) *C. flaveolus* ($2n = 58$); (c) *C. arcuatus* ($2n = 46$). Thick bar = 1 cm and thin bar = 10 μm.

from Galheiro river, for *C.* sp. from Galheiro river and *C. flaveolus*, for *C. arcuatus*, *C. schwartzi* and *C. trilineatus* did not differ significantly while all other comparisons among species were significant at the 0·05 level.

Using chromosome morphology, diploid number, and DNA contents we tentatively divided the species studied in five groups (Table II).

Group 1 includes species with chromosome numbers ranging from $2n = 60$ to $2n = 86$, with an average diploid DNA content of $1{\cdot}39 \pm 0{\cdot}26$ pg/nucleus; most of the chromosomes are metacentrics and submetacentrics, containing one or more

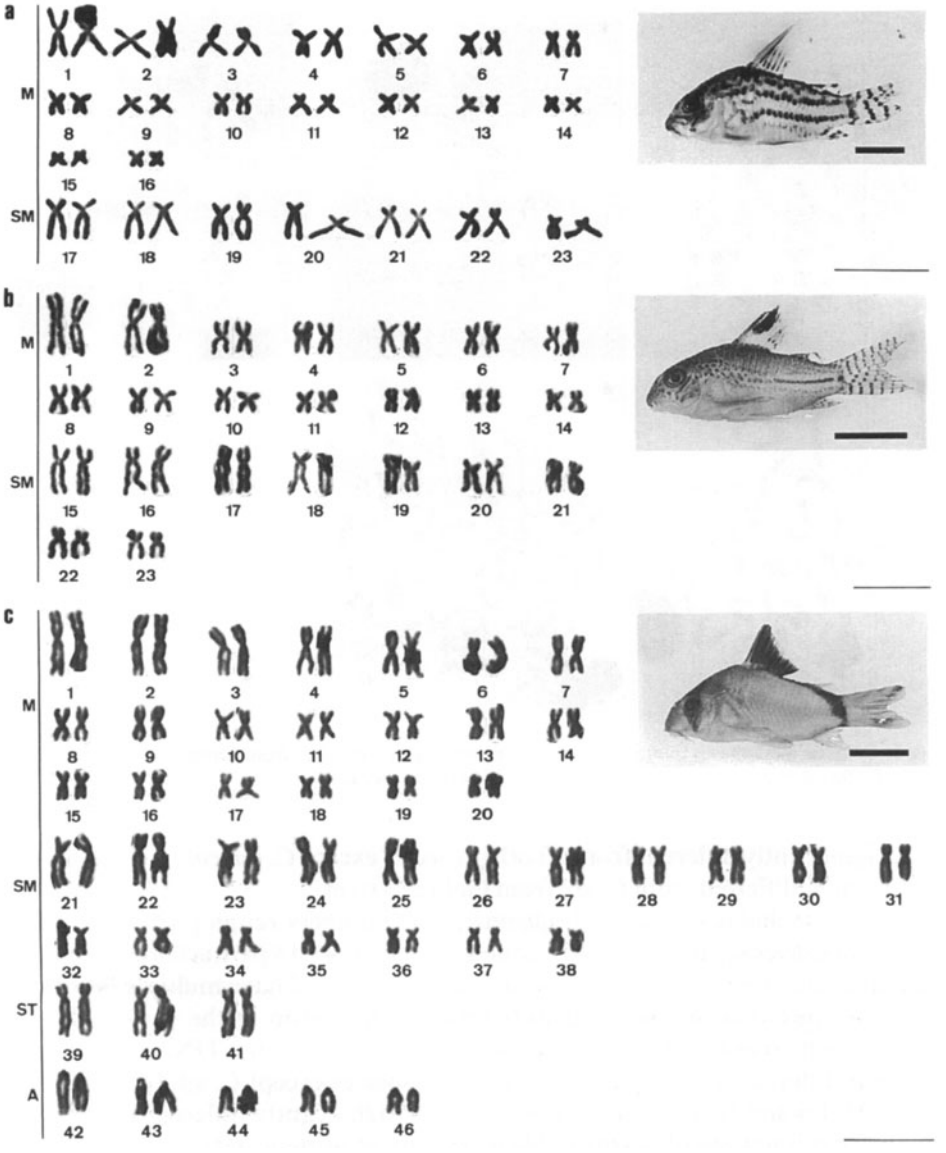

FIG. 5. Karyotypes and examples of: (a) *C. schwartzi* ($2n=46$); (b) *C. trilineatus* ($2n=46$); (c) *C. metae* ($2n=92$). Thick bar = 1 cm and thin bar = 10 μm.

NORs, and sometimes have heterochromatic arms. The three species we examined from group 1 were not significantly different in DNA content ($P>0{\cdot}05$) from each other, but were significantly different from all other species we studied.

Group 2 includes species with chromosome numbers ranging from $2n=74$ to $2n=102$, with an average diploid DNA content of $2{\cdot}16\pm0{\cdot}21$ pg/nucleus; most of the chromosomes are acrocentrics, and containing one or more NORs and constitutive heterochromatin distributed mainly in the pericentromeric region, but there are also telomeric and interstitial blocks. The two species we examined from group 2 were not significantly different in DNA content ($P>0{\cdot}05$) from each other, but

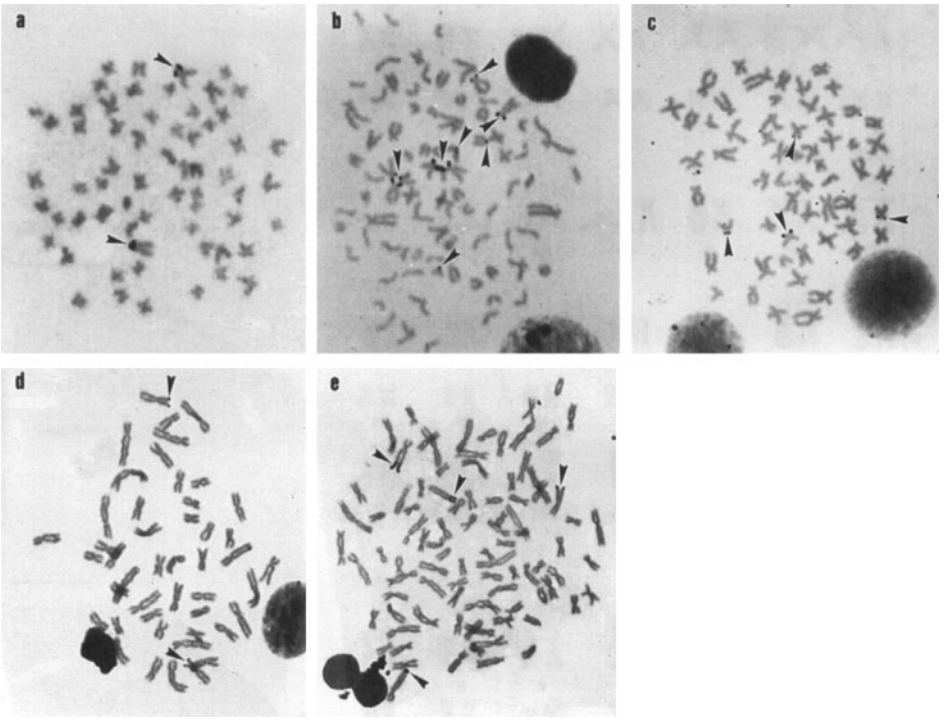

FIG. 6. Somatic metaphases treated with Ag-NOR techniques. (a) *C.* sp. from Caripi river; (b) *C.* sp. from Galheiro river; (c) *C. flaveolus*; (d) *C. trilineatus*; (e) *C. metae.*

were significantly different from all other species except *C. flaveolus* which was not significantly different from *C.* sp. from Galheiro river.

Group 3 includes species with chromosome numbers ranging from $2n=56$ to $2n=60$ and average diploid DNA contents of $2{\cdot}91 \pm 0{\cdot}14$ pg/nucleus; most of the chromosomes are metacentrics and submetacentrics and have multiple NORs; the chromosomes also contain constitutive heterochromatin in the pericentromeric and telomeric regions or occupying entire chromosome arms. DNA content of *C. flaveolus* differ significantly from those of all species except *C.* sp. from Galheiro river. Males and females of *C. flaveolus* were significantly different ($P>0{\cdot}05$), a finding that is not readily explainable from our cytogenetic data and could be due to intraspecific variability as also was found in cyprinid fishes (Gold & Amemiya, 1987; Gold *et al.*, 1990) and in the genus *Lepomis* (Ragland & Gold, 1989).

Group 4 includes species with chromosome numbers ranging from $2n=40$ to $2n=52$, with an average diploid DNA content of $4{\cdot}38 \pm 0{\cdot}49$ pg/nucleus; some of these chromosomes are very large and they are exclusively metacentrics or submetacentrics, containing one or more NORs; the chromosomes also contain constitutive heterochromatin in pericentromeric regions, extending to the proximal portions of some long or short arms. The three species we examined from group 4 were not significantly different in DNA content ($P>0{\cdot}05$) from each other, but were significantly different from all other species we studied.

Group 5 is composed of species having $2n=92$ chromosomes and high DNA contents of about $8{\cdot}75 \pm 0{\cdot}00$ pg/nucleus; the chromosomes are about the same

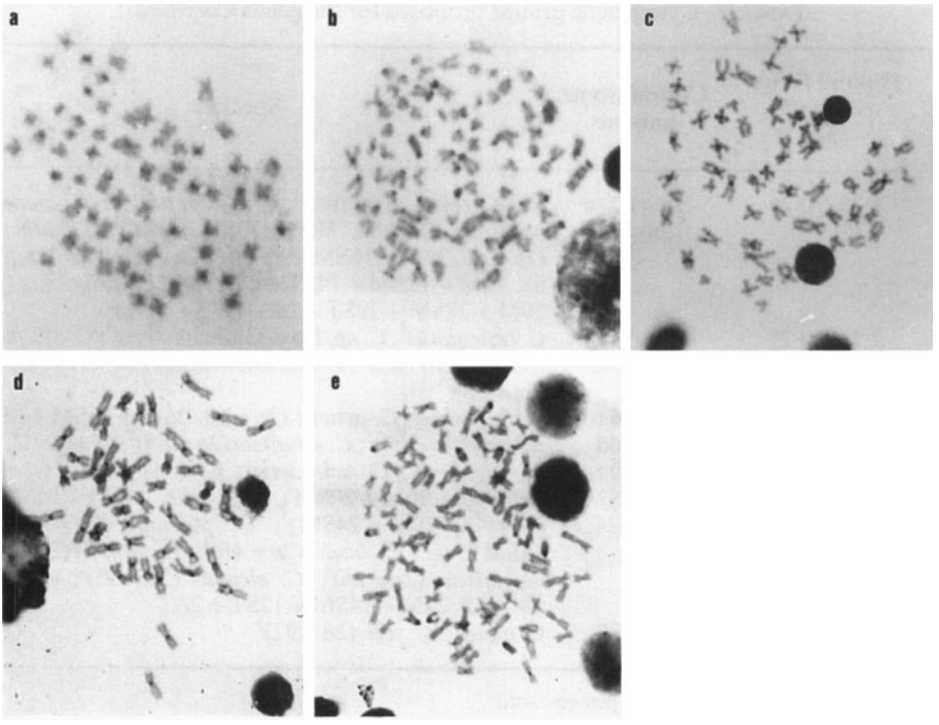

FIG. 7. Somatic metaphases treated with C-banding techniques. (a) *C.* cf. *simulatus*; (b) *C.* sp. from Galheiro river; (c) *C. flaveolus*; (d) *C. arcuatus*; (e) *C. metae*.

sizes as detected in group 4, and are almost exclusively metacentrics and submetacentrics, showing multiple NORs and constitutive heterochromatin distributed in the pericentromeric region, sometimes extending to the proximal regions of some arms. DNA content of *C. metae* was significantly different from all other species we examined (0·05 level).

Comparison of DNA contents among the five groups by the Kruskal–Wallis test indicates significant differences ($H = 723{\cdot}547$, d.f. $= 4$, $P < 0{\cdot}05$). A comparison by Tukey's test showed that all differ among themselves significantly ($P > 0{\cdot}05$).

IV. DISCUSSION

The wide range of chromosome numbers present in the species of *Corydoras* we analysed reinforce the findings of Scheel *et al.* (1972) and Hinegardner & Rosen (1972) that extensive karyotypic diversity occurs in this genus. Among the 11 species analysed in this paper, three of them, *C. arcuatus* $2n = 46$, *C. schwartzi* $2n = 46$ and *C. metae* $2n = 92$, had previously known diploid chromosome numbers (Scheel *et al.*, 1972). The present study increases the number of *Corydoras* species with known karyotypic constitution to 30 (Table II).

This paper shows that there are at least five groups of species sharing similar chromosome morphology, diploid numbers, and DNA contents (Table II). The five groups include all except one of the species of *Corydoras* for which chromosome number is known. The exception is *C. aeneus* a species reported to have

TABLE II. Cytogenetic groups proposed for the genus *Corydoras*

Group	Diploid DNA content* (pg)	Chromosome number	Species†
1	1·39 ± 0·26	$2n = 60$ to $2n = 86$	*C.* sp. from Caripi river[1]; *C.* cf. *simulatus*[1]; *C. simulatus*[1]; *C. barbatus* ($2n = 64$, 38M + 20SM + 6ST)[2]; *C. macropterus* ($2n = 66$, 28M + 16SM + 8ST + 14A)[2]; *C.* cf. *prionotos* ($2n = 68$, 14M + 12SM + 14ST + 28A)[2]; *C.* cf. *prionotos* ($2n = 86$, 20M + 28SM + 20ST + 18A)[2]
2	2·16 ± 0·21	$2n = 74$ to $2n = 102$	*C. reticulatus*[1]; *C.* sp. from Galheiro river[1]; *C.* aff. *punctatus* from Negro river[1]; *C.* aff. *osteocardus* ($2n = 76$)[3]; *C. agassizi* ($2n = 98$)[3]
3	2·91 ± 0·14	$2n = 56$ to $2n = 60$	*C. flaveolus*[1]; *C. aeneus* ($2n = 60$, 26M + 26SM + 8ST)[4]; *C. rabauti* ($2n = 58$)[3]; *C. schultzei* ($2n = 58$)[3]; *C. myersi* ($n = 28$)[5]
4	4·38 ± 0·49	$2n = 40$ to $2n = 52$	*C. arcuatus*[1]; *C. schwartzi*[1]; *C. trilineatus*[1]; *C. nattereri* ($2n = 40$, 20M + 20SM), ($2n = 42$, 18M + 24SM) and ($2n = 44$, 20M + 24SM)[7]; *C. paleatus* ($2n = 44$, 20M + 24SM)[2]; *C. axelrodi* ($2n = 46$)[3]; *C. bondi* ($2n = 46$)[3]; *C. melanistus* ($2n = 46$)[3]; *C. elegans* ($2n = 50$)[3]; *C. undulatus* ($2n = 52$, 24M + 14SM + 12ST + 2A)[6]
5	8·75 ± 0·00	$2n = 92$	*C. metae*[1]; *C. julii* ($2n = 92$)[3]

*Only the data obtained in the present paper were used.

†Diploid number and chromosome formulae were included for species that were not analysed in the present paper. M = metacentrics, SM = submetacentrics, ST = subtelocentrics and A = acrocentrics.

1 = Present paper; 2 = Oliveira, 1987; 3 = Scheel *et al.*, 1972; 4 = Oliveira *et al.*, 1988; 5 = Dunham *et al.*, 1980; 6 = Calcagnoto *et al.*, 1986; 7 = Oliveira *et al.*, 1990.

$2n = \pm 132$ (Scheel *et al.*, 1972) and $n = 60$ (Hinegardner & Rosen, 1972). The *C. aeneus* specimens analyzed by these authors were aquarium specimens from unknown localities. Because *C. aeneus* from São Paulo, Brazil has $2n = 60/61$ with 0 to 3 supernumerary chromosomes (Oliveira *et al.*, 1988), the above mentioned *C. aeneus* with $n = 60$ chromosomes could represent a tetraploid form and could belong to a sixth group. An analysis of more species will allow identification of new groups or divide some of the five groups proposed into subgroups.

Apparently the number of NORs is not related to the diploid number nor to the nuclear DNA content (Table I). The NORs position is very different among the species studied and is probably not related to the species groups. The presence of different numbers of chromosome pairs with NORs indicates that some events of inactivation may have occurred during the process of divergence among species.

In the genus *Corydoras* there are species with C-band positive NORs (like *C.* cf. *simulatus*), species with C-band negative NORs (like *C. flaveolus*) and species with one chromosome pair with C-band positive NORs and one chromosome pair with C-band negative NORs (like *C. nattereri*, Oliveira *et al.*, 1990). This phenomenon is common among fishes and was previously described from other groups like the Gymnotoidei (Almeida Toledo *et al.*, 1981).

The distribution of constitutive heterochromatin reinforces the idea of a possible interrelationship between groups 4 and 5 whose species have no heterochromatic arms and among groups 1, 2 and 3 which have several chromosome pairs with

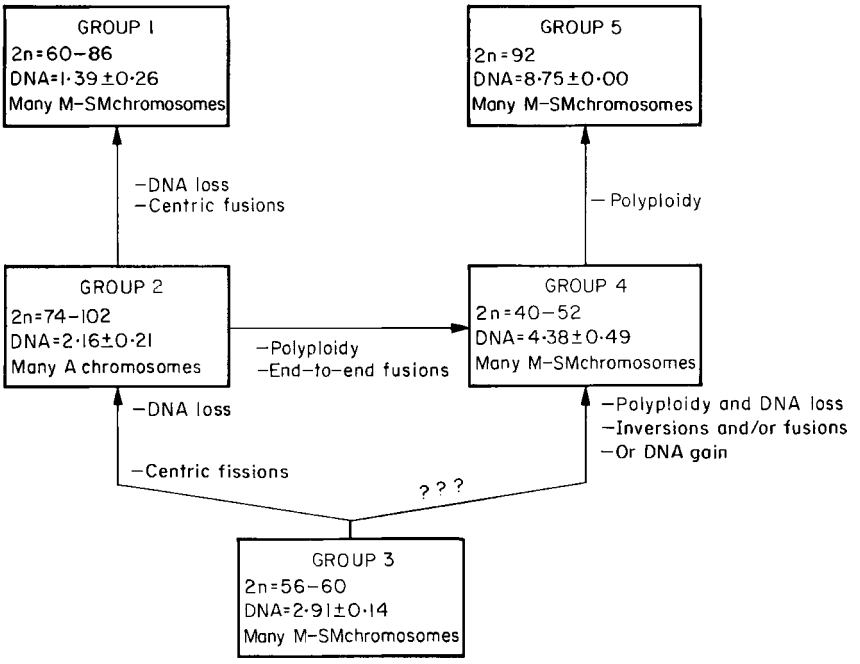

FIG. 8. Diagram indicating cytogenetic interrelationships in the genus *Corydoras*.

heterochromatic arms. On the other hand, the presence of different quantities of heterochromatin among the groups reinforces the idea proposed by Olmo *et al.* (1981) that variation in genome size depends also on single-copy DNA.

Gold & Amemiya (1987), working with 20 species of cyprinids, suggested that changes in DNA quantities both at the population and specific level are small, involving both gains and losses of DNA, and are cumulative and independent in effect. According to Gold & Amemiya (1987) similar conclusions were reached by Johnson & Utter (1986) for salmonids and by Ragland & Gold (1986) for centrarchids. The present data for *Corydoras* species show, on the other hand, that among fishes there are groups which had great changes in genome size during their evolutionary history.

A comparison of the cytogenetic data from *Corydoras* with those for other genera of the family Callichthyidae (unpublished data) shows that species belonging to group 3 are more similar to species belonging to the genera *Callichthys*, *Hoplosternum* and *Dianema* which, according to Gosline (1940) probably represent the most primitive genera in the family. This allows insight into chromosome relationships among the five groups of *Corydoras* (Fig. 8). Species in group 5, *C. metae* and *C. julii* ($2n = 92$), could represent tetraploid forms derived from a $2n = 46$ ancestral (group 4) as proposed by Scheel *et al.* (1972). DNA contents of groups 4 and 5 (Table I) are consistent with this hypothesis. The similarities between the diploid and tetraploid complements suggest that group 5 probably originated more recently in the evolutionary history of the genus *Corydoras*. This indicates that recent rearrangements have occurred because in *C. metae* we find ST and A chromosomes, usually not present in forms belonging to group 4.

Group 4 could have originated from an ancestral species belonging to groups 2 or 3 by polyploidization followed by reduction of DNA content and diploid numbers. In fact, species of group 4 have approximately double the DNA content of species belonging to group 2 (Table II), but group 4 species have about half of the diploid numbers of those species. Studies on DNA reassociation kinetics of some species of selachians (Olmo *et al.*, 1982), showed that the phenomenon of polyploidization would often be followed by wide chromosomal rearrangements and progressive divergence of various repetitive DNA sequences. According to this view, species belonging to group 4 could represent forms in which a series of chromosome rearrangements (end-to-end fusions) has reduced the diploid numbers without significant loss of chromatin.

Species of group 2 probably originated from group 3 by reduction in DNA content and a series of centric fissions. Group 1 might have originated from ancestral species belonging to group 2 where many events of centric fusions and DNA loss occurred.

Nijssen (1970) and Nijssen & Isbrucker (1980) proposed dividing the genus *Corydoras* in five groups of species based on colour pattern, morphometric, and meristic characters. However, Strauss (1985), found that four of these five groups cannot be discriminated properly because they overlap widely in body form and meristics. The distribution of the genus *Corydoras* based on cytogenetic characteristics seems to be an alternative way of identification for groups presenting distinct evolutionary histories.

The cytogenetic data for the genus *Corydoras* also reveal a number of instances where cryptic species may be grouped taxonomically under a single species name. For example, the different cytotypes of *C. nattereri* ($2n=40$, $2n=42$ and $2n=44$, Oliveira *et al.*, 1990) and specially those of *C.* cf. *prionotos* ($2n=68$ and $2n=86$, Oliveira, 1987) probably are genetically isolated.

Chromosome rearrangements and changes of DNA content in the genus *Corydoras* probably were very important in the evolutionary history of this group. The evolutionary importance of chromosome rearrangements seems to be different in various groups of fish, and could probably be related to the population structure of different groups.

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