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Cytogenetic and DNA content in six genera of the family Callichthyidae (Pisces, Siluriformes)

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SUMMARY — Cytogenetic studies involving conventional Giemsa staining, C-banding analysis and silver staining of NORs were performed on nine species belonging to six genera of the family Callichthyidae. The diploid number ranged from $2n = 44$ to $2n = 100$, the number of chromosomal pairs with NORs ranged from 1 to 4 and constitutive heterochromatin was mainly distributed in the centromeric and/or pericentromeric position of the chromosomes. The DNA content of erythrocytes from six species studied ranged from 1.18 ± 0.07 to 2.77 ± 0.22 pg/nucleus. The extensive variability in karyotypes and in nuclear DNA content detected are in accordance with the initial hypothesis that chromosome rearrangements and polyploidy have played a significant role in the evolutionary history of Callichthyidae.

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

INTRODUCTION

The family Callichthyidae comprises eight genera: *Aspidoras*, *Brochis*, *Callichthys*, *Cascadura*, *Cataphractops*, *Corydoras*, *Dianema* and *Hoplosternum* (GOSLINE 1940). *Cascadura* and *Cataphractops* have only one species described each and may not constitute valid genera (HOEDEMAN 1957). An interesting peculiarity of this family is the discrepancy in the number of species belonging to each genus, with the occurrence of genera comprising many species such as the genus *Corydoras* with about 115 species and subspecies described (NIJSEN and ISBRUCKER 1986) and of genera such as *Callichthys*, with a very reduced number of species described (GOSLINE 1940).

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The cytogenetic data available for the family Callichthyidae are basically restricted to the genus *Corydoras* of which about 30 species have already been analysed cytogenetically (OLIVEIRA *et al.* 1992). For *Brochis splendens* (cited as *B. coelureus* by SCHEEL 1973) and for *Dianema longibarbis* (HUDSON 1976 according to LEGRANDE 1981) haploid and/or diploid numbers have been described. The karyotype constitution and position of nucleolus organizer regions (NORs) have been described for *Callichthys callichthys* (CALCAGNOTO 1988; PORTO and FELDBERG 1988; PORTO and FELDBERG 1992b), *Hoplosternum littorale* and *H. thoracatum* (PORTO and FELDBERG 1992a and 1992b) and *Hoplosternum* sp. from São Paulo (VENERE and GALETTI Jr. 1986). Nuclear DNA content has been described for some species of *Corydoras* (HINEGARDNER and ROSEN 1972; OLIVEIRA *et al.* 1992) and for *Callichthys callichthys* (HINEGARDNER and ROSEN 1972). The lack of more complete karyotypic data, information about NORs, C-banding patterns and nuclear DNA content has limited the discussion of chromosomal evolution in this group.

The present paper describes the cytogenetic and/or nuclear DNA content data of ten species belonging to six genera of Callichthyidae with the purpose of evaluating the extent, frequency and importance of chromosomal rearrangements in their evolutionary process.

MATERIALS AND METHODS

The species used in this study were: *Aspidoras fuscoguttatus*: 1 male and 2 females from Monte Alto and 1 male from Mirassolândia, SP, Brazil; *Brochis britskii*: 1 female; *Brochis splendens*: 2 males; *Callichthys callichthys*: 2 males and 1 female from Itanhaém and 2 males and 1 female from Guarulhos, SP, Brazil; *Corydoras aeneus*: 6 males and 5 females from Botucatu, SP, Brazil; *Corydoras panda*: 1 male and 1 female; *Corydoras rabauti*: 1 male and 2 females; *Dianema urostriata*: 5 males and 1 female; *Hoplosternum littorale*: 2 females from an experimental aquaculture station, Pirassununga, SP, Brazil; and *Hoplosternum* sp.: 2 males and 2 females from Mirassolândia, SP, Brazil. All samples whose site of origin is not mentioned were bought from tropical fish dealers. Specimens were identified and deposited in the fish collections of Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre, RS, Brazil or in the Museu de Zoologia, Universidade de São Paulo (MZUSP), São Paulo, SP, Brazil.

Chromosome spreads, silver staining of Nucleolus Organizer Regions (NORs) and C-banding were done as described by OLIVEIRA *et al.* (1988b). Chromosome preparations were obtained from gill and kidney tissues and about 30 metaphases were examined for each specimen. Chromosome morphology was determined on the basis of arm ratios as proposed by LEVAN *et al.* (1964) and the chromosomes were classified as metacentrics (M), submetacentrics (SM), subtelocentrics (ST) and acrocentrics (A); NF (chromosome arm number) was determined considering M/SM chromosomes to have two arms and ST/A chromosomes to have one arm. Nuclear DNA content was determined from erythrocytes as described by OLIVEIRA *et al.* (1992).

RESULTS

Analysis of Giemsa-stained karyotypes showed that *Aspidoras fuscoguttatus* has $2n=44$ (28M + 12SM + 4ST, Fig. 1a), with the two local populations analysed presenting no karyotypic differences, *Brochis britskii* has $2n=90$ (4M + 10SM + 22ST + 54A, Fig. 2a), *B. splendens* has $2n=100$ (18M + 18SM + 20ST + 44A, Fig. 2c), *Callichthys callichthys* has $2n=58$ (22M + 22SM + 14ST, Fig. 3a) and the specimens from Itanhaém have a variable number of supernumerary microchromosomes (0 to 5, Fig. 8A), *Corydoras panda* has $2n=46$ (24M + 22SM, Fig. 4a), *C. rabauti* has $2n=58$ (20M + 22SM + 10ST + 6A, Fig. 4c), *Dianema urostriata* has $2n=62$ (8M + 4SM + 4ST + 46A, Fig. 5a), *Hoplosternum littorale* has $2n=60$ (4M + 4SM + 52A, Fig. 6a) and *Hoplosternum* sp. has $2n=60$ (6M + 2SM + 52A, Fig. 6c). Karyotypic differences between sexes were not found.

The number and position of NORs, visualized by silver-staining, were highly variable. The eight species karyotyped here have only one chromosome pair with NORs and the NORs are located in different positions: a) in the interstitial position on the long arm of a large SM pair (*A. fuscoguttatus*, Fig. 1b), b) in the terminal position on the short arm of a small ST pair (*C. callichthys*, Fig. 3b), c) in the terminal position on the long arm of a medium-sized M pair (*C. panda*, Fig. 4b), d) in the terminal position on the short arm of



Fig. 1. — Karyotype of an *Aspidoras fuscoguttatus* female with $2n=44$ (a), and, in the inset, the chromosome pair with NORs (b). Bar = 10 μ m.

a small SM pair (*C. rabauti*, Fig. 4d) and e) in the terminal position on the short arm of a large A pair (*B. britskii* Fig. 2b, *D. urostriata* Fig. 5b, *H. littorale* Fig. 6b and *H. sp.* Fig. 6d). One species, *B. splendens*, has two ST pairs with NORs, one in a medium-sized pair and the other in a small-sized pair, both in the terminal position on the short arms (Fig. 2d). Several species presented highly polymorphic NORs (Figs. 1b, 2b, 3b and 6d).

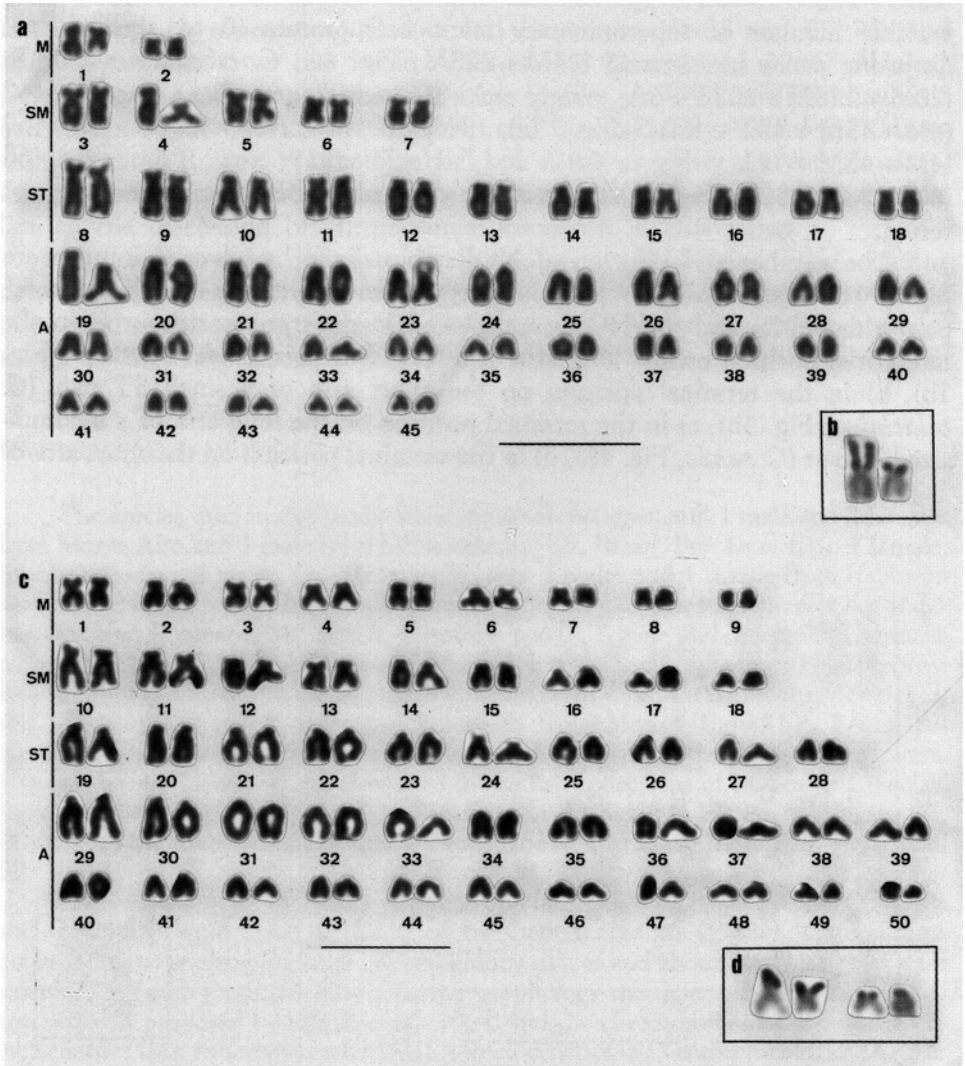


Fig. 2. — Karyotype of a *Brochis britskii* female with $2n=90$ (a), and, in the inset, the chromosome pair with NORs (b); karyotype of a *Brochis splendens* female with $2n=100$ (c), and, in the inset, the chromosome pairs with NORs (d). Bars = 10 µm.



Fig. 3. — Karyotype of a *Callichthys callichthys* female with $2n=58$ (a), and, in the inset, the chromosome pair with NORs (b). Bar = 10 μm .

Analysis of heterochromatin distribution showed that some species such as *C. panda* have a small quantity of heterochromatin limited to the centromeric position of a few chromosome pairs (Fig. 7D), and others, such as *A. fuscoguttatus* (Fig. 7A), *B. britskii* (Fig. 7B) and *B. splendens* (Fig. 7C), have large heterochromatin blocks in almost all chromosome pairs. The species *C. rabauti* has some chromosomes with heterochromatic short arms and small heterochromatin blocks in the pericentromeric position of some chromosomes (Fig. 7E); heterochromatic arms are also present in *C. callichthys* (Fig. 8A), *H. littorale* (Fig. 8D) and *H. sp.* (Fig. 8E). The species *D. urostriata* (Fig. 8C), *H. littorale* (Fig. 8D) and *H. sp.* (Fig. 8E) have many heterochromatin blocks adjacent to the centromere in the interstitial position.

C. callichthys from Itanhaém presents a centromeric heterochromatin in block in pair 12 (Fig. 8Ba); the same pair in the sample from Guarulhos has an heterochromatic short arm (Fig. 8Bb, 8Bc and 8 Bd). One *C. callichthys* male from Guarulhos has heteromorphism of the heterochromatic short arm of pair 12 (Fig. 8Bc), not found in another male of the same population (Fig. 8Bb). Thus, this heteromorphism is possibly not sex related.

The nuclear DNA content ranged from 1.18 ± 0.07 pg/nucleus for *D. urostriata* ($2n=62$) to 2.77 ± 0.22 pg/nucleus for *C. aeneus* ($2n=60/63$) (Table 1).

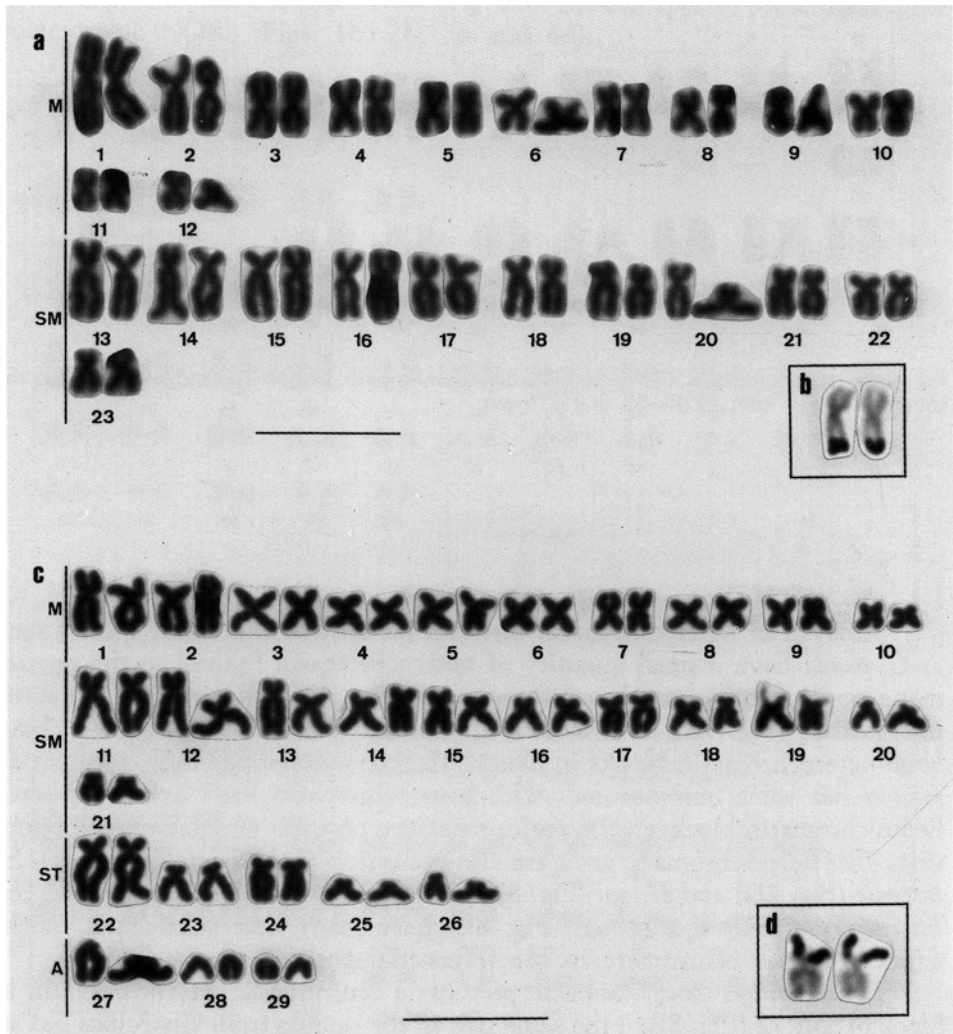


Fig. 4. — Karyotype of a *Corydoras panda* female with $2n=46$ (a), and, in the inset, the chromosome pair with NORs (b); karyotype of a *Corydoras rabauti* female with $2n=58$ (c), and, in the inset, the chromosome pair with NORs (d). Bars = 10 μm .

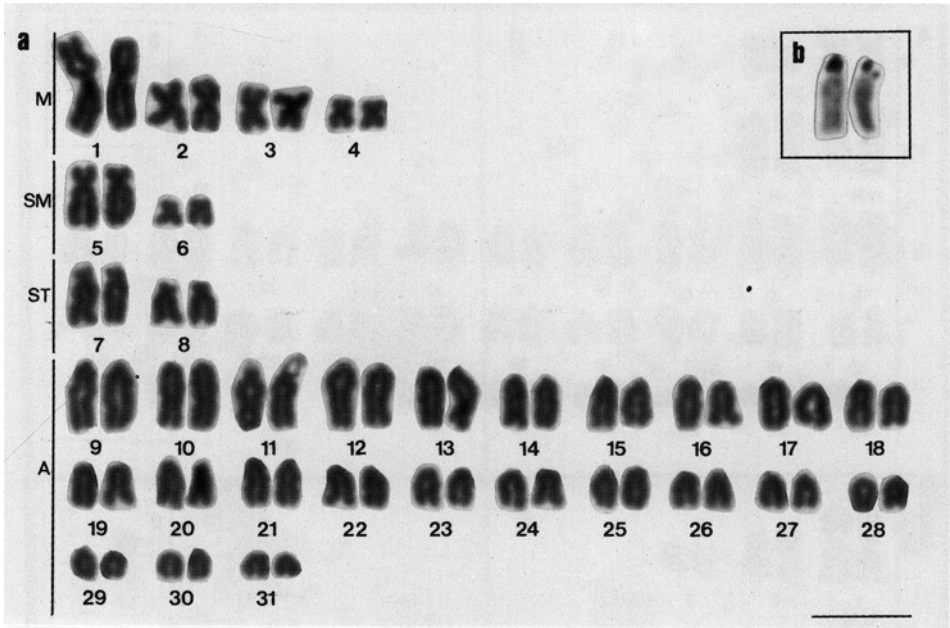


Fig. 5. — Karyotype of a *Dianema urostriata* female with $2n = 62$ (a), and, in the inset, the chromosome pair with NORs (b). Bar = 10 μm .

DISCUSSION

Karyotypic variability among Callichthyidae genera.

In the genus *Aspidoras* only one species was studied cytogenetically and this fact limits the discussion about chromosome structure in this genus since it includes 14 described species (Nijssen and Isbrucker 1980). The diploid number of *A. fuscoguttatus*, $2n = 44$ (Table 1), is small when compared to the chromosome numbers usually found in Siluriformes, which are $2n = 56 \pm 2$ (Fitzsimons *et al.* 1988; Oliveira *et al.* 1988a). If we consider this chromosome number as representative of this genus, several chromosome rearrangements causing a reduction in chromosome number, such as end-to-end fusions, must have occurred in the evolutionary history of *Aspidoras*.

The presence of interstitial NORs, as found in *A. fuscoguttatus* (Fig. 1b), is unusual for Siluriformes, having been found thus far only in the genus *Corydoras* (Oliveira *et al.* 1990; Oliveira *et al.* 1992) and in the subfamily Hypoptopomatinae (Andreati 1991). *A. fuscoguttatus* has a small nuclear DNA content when compared to other Siluriformes (Hinegardner and Rosen

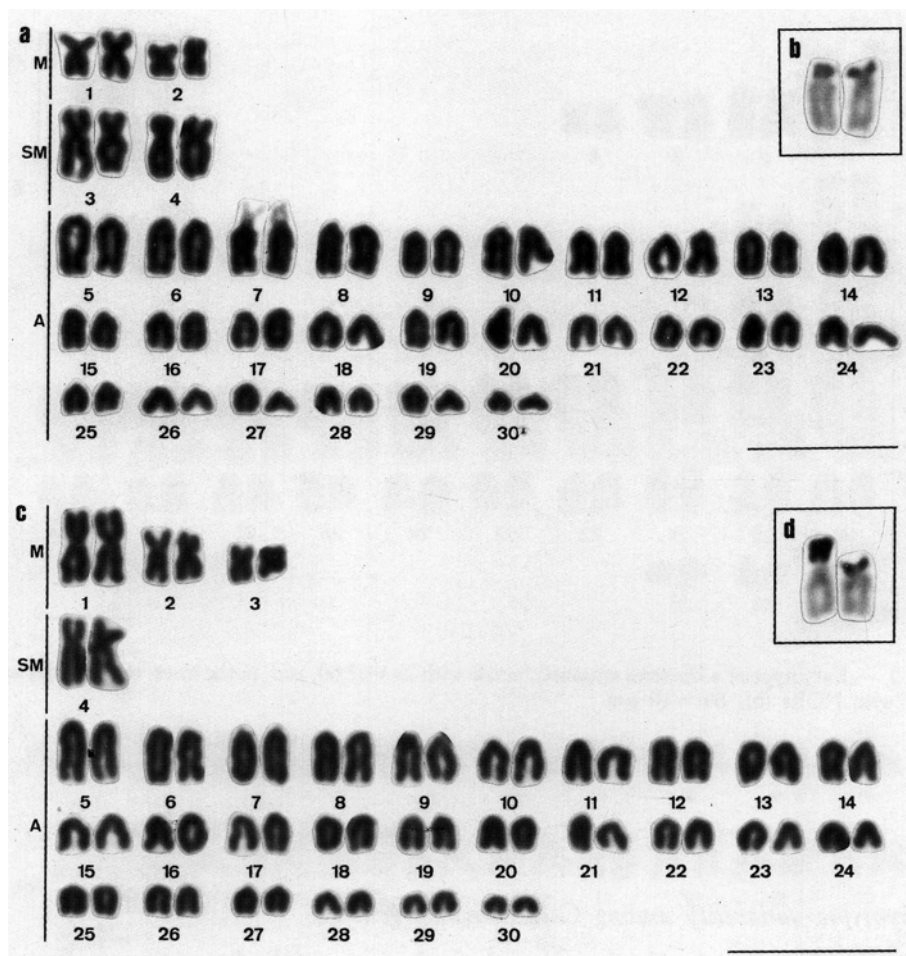


Fig. 6. — Karyotype of a *Hoplosternum littorale* female with $2n=60$ (a), and, in the inset, the chromosome pair with NORs (b); karyotype of a *Hoplosternum* sp. female with $2n=60$ (c), and, in the inset, the chromosome pair with NORs (d). Bars = 10 μm .

Fig. 7. — Somatic metaphases of *Aspidoras fuscoguttatus* from Monte Alto (A), *Brochis britskii* (B), *Brochis splendens* (C), *Corydoras panda* (D) and *Corydoras rabauti* (E) treated by the C-banding technique.

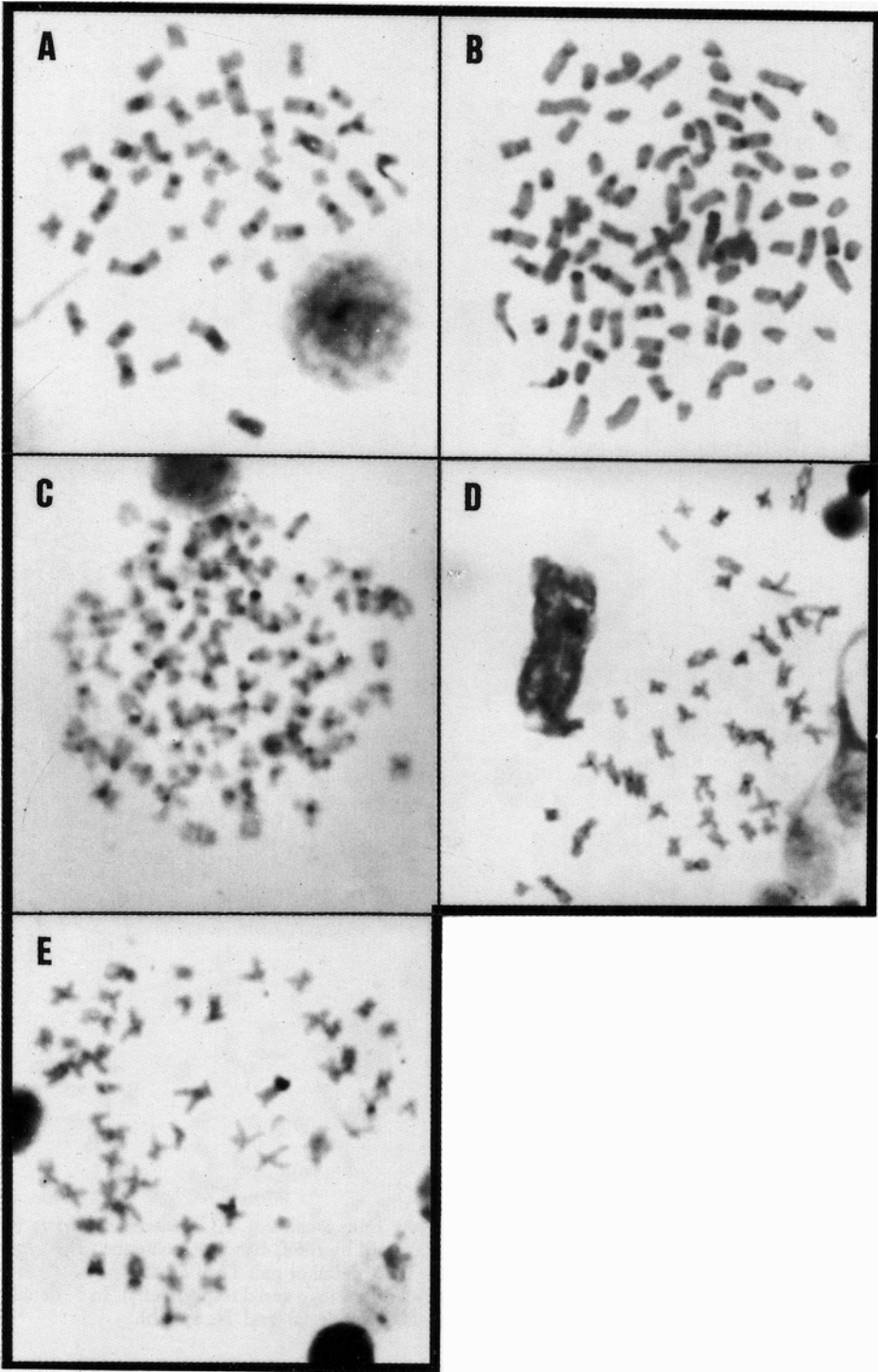
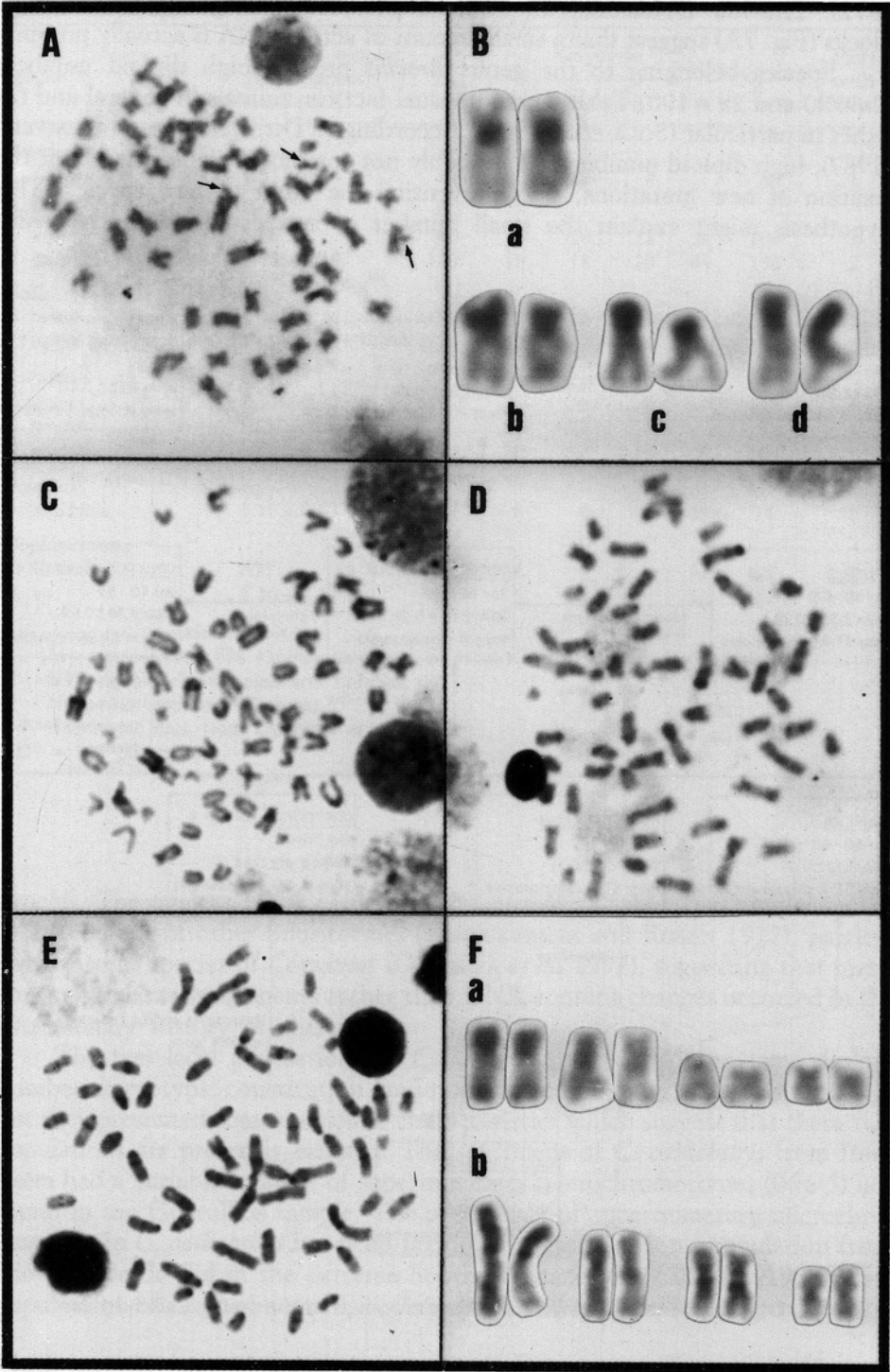


Fig. 8. — Somatic metaphases of *Callichthys callichthys* from Itanhaém (A), *Dianema urostriata* (C), *Hoplosternum littorale* (D) and *Hoplosternum* sp. (E) treated by the C-banding technique. The arrows in A indicate the supernumerary microchromosomes. In B, detail of pair 12 of *C. callichthys* male from Itanhaém (a) and of two males and one female from Guarulhos (b, c and d respectively). In F, detail of the four metacentric and submetacentric pairs of *H. littorale* (a) and *H. sp.* (b).



1972). The low DNA content, and the presence of large heterochromatin blocks (Fig. 7A) suggest that a small amount of active DNA is actually present.

Species belonging to the genus *Brochis* present high diploid numbers ($2n=90$ and $2n=100$, Table 1), an unusual fact for animals in general and for fishes in particular (SOLA *et al.* 1981). According to DUTRILLAUX and RUMPLER (1987), high diploid numbers are probably not common because they limit the fixation of new mutations, thus preventing the onset of new species. This hypothesis might explain the small number of species found in the genus

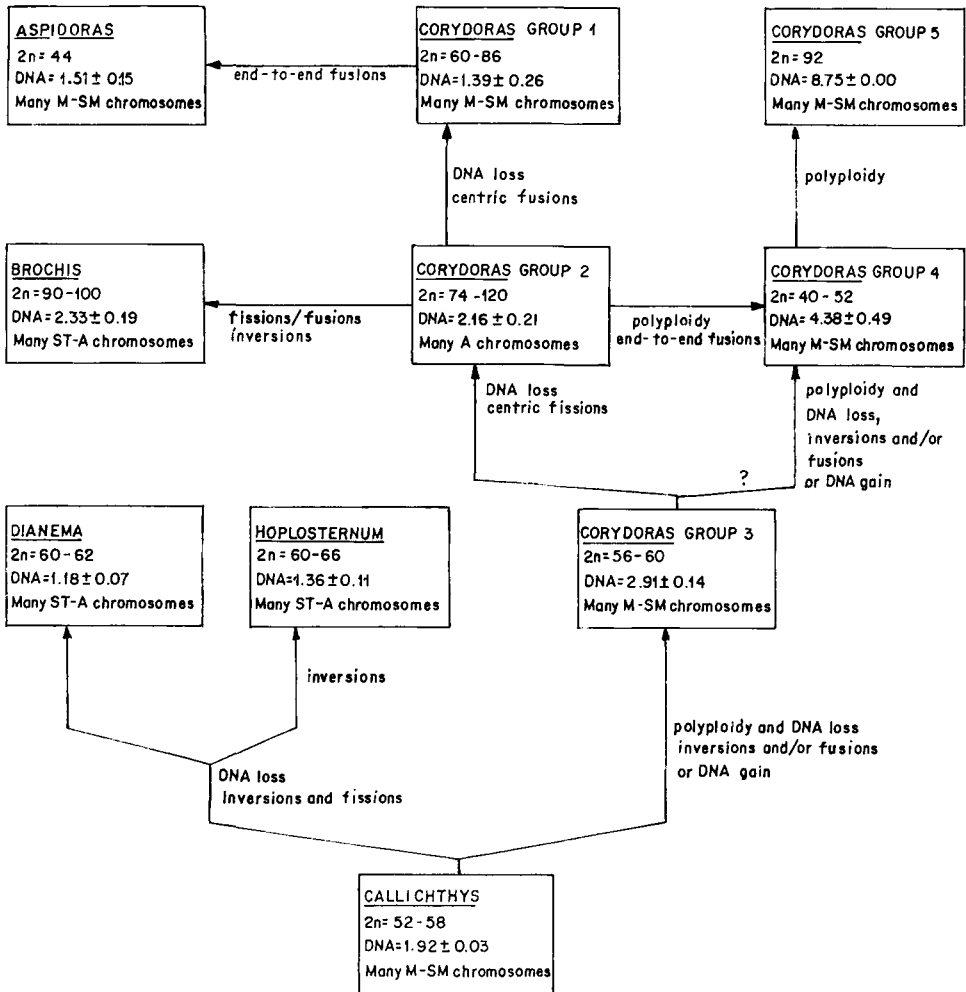


Fig. 9. — Diagram indicating cytogenetic interrelationships in the family Callichthyidae.

TABLE 1 - Cytogenetic and DNA content data obtained for the species analysed.

Species	2n DNA content (in picograms) mean $\pm$ S.E.	2n	Karyotype *				NF **	Pairs with NORs +
			M	SM	ST	A		
Aspidoras								
<i>A. fuscoguttatus</i>	1.51 $\pm$ 0.15	44	28	12	4		84	1
Brochis								
<i>B. britskii</i>	ND	90	4	10	22	54	104	1
<i>B. splendens</i>	2.33 $\pm$ 0.19	100	18	18	20	44	136	2
Callichthys								
<i>C. callichthys</i> Itanhaén	1.94 $\pm$ 0.15	58	22	22	14		102	1
<i>C. callichthys</i> Guarulhos	1.89 $\pm$ 0.24	58	22	22	14		102	1
Corydoras								
<i>C. aeneus</i> + +	2.77 $\pm$ 0.22	60/63	26	26	8		112	4
<i>C. panda</i>	ND	46	24	22			92	1
<i>C. rabauti</i>	ND	58	20	22	10	6	104	1
Dianema								
<i>D. urostriata</i>	1.18 $\pm$ 0.07	62	8	4	4	46	74	1
Hoplosternum								
<i>H. littorale</i>	ND	60	4	4		52	68	1
<i>H. sp.</i>	1.36 $\pm$ 0.11	60	6	2		52	68	1

* M = metacentrics, SM = submetacentrics, ST = subtelocentrics and A = acrocentrics;
 ** NF = diploid chromosome arm number;
 + Nucleolus Organizer Regions;
 + + Karyotypic data from OLIVEIRA *et al.* (1988b);
 ND = not determined.

Brochis. The nuclear DNA content of *B. splendens* (Table 1) is similar to the DNA content of other Siluriformes (HINEGARDNER and ROSEN 1972), particularly of some species of *Corydoras* (OLIVEIRA *et al.* 1992), suggesting that many chromosome rearrangements rather than DNA content changes occurred in the evolutionary history of this genus.

The two local populations of *Callichthys* studied had the same diploid number, karyotypic constitution, and number and position of NORs (Table 1) but they presented some particular characteristics which suggest that these two populations are presently isolated. The specimens of *C. callichthys* from Itanhaém had a variable number of supernumerary microchromosomes (0 to 5) not found in the Guarulhos sample. The occurrence of supernumerary microchromosomes in *C. callichthys* has been previously described for a population from Rio Grande do Sul in the extreme South of Brazil (CALCAGNOTO 1988). The populations of Itanhaém and Rio Grande do Sul were collected from coastal

ivers that drain into the Atlantic Ocean. Thus, although these populations are now geographically isolated they could be descendents of the same ancestral stock. The presence of supernumerary microchromosomes is relatively common among Neotropical freshwater fishes (SALVADOR and MOREIRA-FILHO 1992) and, for the family Callichthyidae, the occurrence of supernumerary chromosomes has been previously reported for *Corydoras aeneus* (OLIVEIRA *et al.* 1988b).

A comparative analysis of C-banding pattern between the two populations of *C. callichthys* studied here shows that they differ by the fact that in the Itanhaém population pair 12 has a heterochromatin block restricted to the centromeric position (Fig. 8Ba) while in the Guarulhos population, pair 12 has a heterochromatic short arm (Figs. 8Bb, 8Bc and 8Bd). One male from the Guarulhos population presented heteromorphism of pair 12 (Fig. 8Bc) which was not observed in another male (Fig. 8Bb) and in the female analysed (Fig. 8Bd). Thus, this heteromorphism is probably an autosomal polymorphism.

The occurrence of local populations of *C. callichthys* with $2n=52$, $2n=54$ and $2n=58$ in the Amazon region (PORTO and FELDBERG 1988; PORTO and FELDBERG 1992b) and the differences found among the local populations studied here indicates the necessity of a taxonomic revision of this genus which has been considered thus far to be monotypic.

The species *Corydoras panda* has $2n=46$ (Table 1) and a karyotype similar to those found in several species of *Corydoras* from the Amazon region (OLIVEIRA *et al.* 1992), suggesting that all of these species may belong to the same cytogenetic group (group 4 according to OLIVEIRA *et al.* 1992).

The diploid number of *Corydoras rabauti*, $2n=58$ (Table 1), has been previously described by SCHEEL *et al.* (1972). The diploid number, karyotype and C-banding pattern of this species are similar to those described for *Corydoras aeneus* (OLIVEIRA *et al.* 1988b) and *C. flaveolus* (OLIVEIRA *et al.* 1992), suggesting that all of these species may belong to the same cytogenetic group of *Corydoras* (group 3 according to OLIVEIRA *et al.* 1992).

Dianema urostriata presents $2n=62$ chromosomes (Table 1), a diploid number similar to that described for *D. longibarbis* ($2n=60$) by HUDSON (1976, in LEGRANDE 1981). A particular characteristic found in *D. urostriata* is the presence of many heterochromatin blocks adjacent to the centromere in many chromosome pairs (Fig. 8C). A similar pattern of C-band distribution has also been found in *Hoplosternum littorale* and *H. sp.* (Figs. 8D and 8E).

Hoplosternum littorale and *H. sp.* presented the same diploid number of $2n=60$ (Table 1) but differed in karyotype structure. Thus, while *H. littorale* has 2 metacentric and 2 submetacentric chromosome pairs (Fig. 6a), *H. sp.* presents 3 metacentric pairs and 1 submetacentric pair (Fig. 6c). *Hoplosternum littorale* presented the short arm of the largest SM pair entirely heterochromatic and homogeneously stained by the C-banding technique (Fig. 8Fa) while in *Hoplosternum sp.* the short arm of the largest M pair was entirely heterochro-

matic but two regions differently stained by the C-banding technique were observed (Fig. 8Fb), suggesting a different molecular constitution in these two regions. This difference is probably due to the addition or deletion of a heterochromatin block in pair 1 of *H. sp.* when compared with the largest pair of *H. littorale*.

Another *Hoplosternum* species, *H. thoracatum*, had local populations with $2n=62$, $2n=64$ and $2n=66$ chromosomes in the Amazon region (PORTO and FELDBERG 1992a and 1992b) which are diploid numbers similar to those found for the other species cited above. Thus, this genus possibly has little variation in diploid number. The occurrence of many M/SM chromosomes in *H. thoracatum* (PORTO and FELDBERG 1992a) suggests that many chromosome rearrangements, such as inversions, may have occurred during the differentiation process of this group.

The nuclear DNA content of Callichthyidae ranges from 1.04 ± 0.09 pg/nucleus in *Corydoras cf. simulatus* to 8.75 ± 1.50 pg/nucleus in *Corydoras metae* (OLIVEIRA *et al.* 1992), an eight-fold variation. The lack of expressive morphological differences among Callichthyidae, mainly among *Corydoras* species, is in accordance with the idea of HINEGARDNER and ROSEN (1972) that an appreciable amount of DNA can be lost or added without causing any important changes in fish morphology. In the family Callichthyidae there is no correlation between nuclear DNA content and diploid number or chromosome formulae (Table 1), as already suggested by data from several other fish groups (HINEGARDNER and ROSEN 1972; CUI *et al.*, 1991).

Chromosome evolution in Callichthyidae.

Many fish groups such as several families of Cypriniformes (GOLD 1979; YU *et al.* 1987) and Characiformes (OLIVEIRA *et al.* 1988a; AREFJEV 1990) present a characteristic diploid chromosome number with small variations among species. Other fish groups such as Siluroidei (LEGRANDE 1981; OLIVEIRA *et al.* 1988a) and Gymnotoidei (OLIVEIRA *et al.* 1988a), present a high rate of variation in diploid number and/or karyotype structure among species. The family Callichthyidae is included in this second group.

A comparison of the cytogenetic data from the different Callichthyidae genera and those described for other species of Siluroidei (HINEGARDNER and ROSEN 1972; LEGRANDE 1981; OLIVEIRA *et al.* 1988a) shows that fishes belonging to the genus *Callichthys* share a large number of characteristics with other Siluroidei species, suggesting that their karyotypes with $2n=52-58$, many M-SM chromosomes, one or two chromosome pairs with NORs and about 1.92 pg of DNA/nucleus might represent the most primitive karyotype condition for the family Callichthyidae (Fig. 9). This assumption is in accordance with the proposition of GOSLINE (1940) who placed the genus *Callichthys* close to the

genus *Cascadura* on the basis of the phylogeny he proposed for the family Callichthyidae.

The karyotype structure and DNA content of *Callichthys* are more similar to those present in some *Corydoras* species such as *C. rabauti* (Fig. 3c), *C. aeneus* (OLIVEIRA *et al.* 1988) and *C. flaveolus* (OLIVEIRA *et al.* 1992) than to those found in other species and genera of Callichthyidae (Table 1). This fact suggests that *Callichthys* is more related to this species group (group 3 of OLIVEIRA *et al.* (1992) classification). Differences in DNA content may be due to an increase in DNA by duplication events or to a DNA loss after polyploidy (Fig. 9).

Possible relationships among different *Corydoras* groups were discussed by OLIVEIRA *et al.* (1992) and are summarized in Figure 9.

The genera *Dianema* and *Hoplosternum* present several cytogenetic characteristics in common, such as diploid number, presence of many ST-A chromosomes, one chromosome pair with NOR, distribution of C-banded blocks and about 1.27 pg of DNA/nucleus. These genera are probably more related to the genus *Callichthys* than to others in the family Callichthyidae (GOSLINE 1940). They could have originated from an ancestral form similar to *Callichthys*, and pericentromeric inversions and fissions with simultaneous reduction of DNA content may have occurred later (Fig. 9).

GOSLINE (1940) suggests that the genera *Aspidoras*, *Brochis* and *Corydoras* are closely related. The present cytogenetic data for *A. fuscoguttatus* show that this species has a small DNA content which, as also observed in *Corydoras* species belonging to group 1 from the classification of OLIVEIRA *et al.* (1992). However, their karyotype constitution is different. A probable derivation can be done only if the occurrence of several end-to-end fusions is assumed (Fig. 9).

The cytogenetic characteristics of species belonging to the genus *Brochis* are very similar to those found in *Corydoras* species belonging to group 2 in the classification of OLIVEIRA *et al.* (1992). This suggests that these two groups may be related, assuming that rearrangements such as fusions/fissions and/or inversions have occurred (Fig. 9).

Among the Callichthyidae studied, we can observe that while a few karyotypic differences are found among species of the genera *Brochis*, *Dianema*, *Callichthys* and *Hoplosternum* (Table 1), species from the genus *Corydoras* present a karyotypic diversity which is among the highest described for fishes (OLIVEIRA *et al.* 1992; present paper). These data are positively related to the number of species described for each genus; thus, while the genus *Corydoras* comprises a large number of species, the other genera cited comprise only a few described species. This relationship suggests that chromosome rearrangements and alterations in DNA content may have been very important in the evolution of fishes belonging to the genus *Corydoras*.

The cytogenetic data obtained for the family Callichthyidae, and the possible pattern of relationship proposed (Fig. 9) show that, for at least two groups of *Corydoras* species, polyploidy may have been the main event in their

speciation process. For the other *Corydoras* groups and for the possible ancestor of the genera *Dianema* and *Hoplosternum*, the main evolutionary event was probably a decrease in DNA content, which seems to be a common phenomenon in fish evolution (HINEGARDNER and ROSEN 1972; CUI *et al.* 1991). For the genera *Aspidoras*, *Callichthys*, *Brochis*, *Dianema* and *Hoplosternum* the occurrence of chromosome rearrangements seems to have been a basic step in the speciation process, rather than great changes in DNA content.

According to a review by ALLENDORF and THORGAARD (1984), many examples of diplo-tetraploid relationships among fish species of several families have been described and there are two cases of polyploidy in fishes giving rise to entire families (Catostomidae and Salmonidae). The family Callichthyidae represents a particular example of evolution among fishes since some species groups in this family have apparently arisen by polyploidy while the differentiation of other groups was followed by chromosomal rearrangements and the basic DNA content of the family was preserved.

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