

RÉVISION CARYOLOGIQUE DES BARBINÉS ET HYPOTHÈSES CONCERNANT LA PLÉSIOMORPHIE POSSIBLE DE L'ÉTAT POLYPLOÏDE CHEZ LES CYPRINIDÉS.

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RÉSUMÉ

Le modèle d'évolution caryologique des Cyprinidés, selon lequel le nombre polyploïde $2n=100$ doit être considéré comme plésiomorphe pour la famille, en opposition à la théorie orthodoxe, semble se vérifier par la publication récente de nouvelles données concernant les nombres chromosomiques de Cyprinidés d'Afrique et d'Asie du sud. L'hypothèse d'un ancêtre de type Cyprinidé, appartenant probablement à une lignée proche des Barbinés, ainsi que l'existence d'une polyplôïdie fonctionnant comme un «système-ouvert» est suggérée sur la base de caractères caryoévolutifs. L'importance de ce phénomène dans le processus évolutif de quelques lignées justifie un appel à l'inclusion future de l'information caryologique dans les travaux de systématique évolutive. En effet, les progrès actuels en cytogénétique moléculaire, en rendant possible la reconnaissance d'homologies chromosomiques interspécifiques, permettront probablement de clarifier les relations phylogénétiques au sein même des Cypriniformes.

Mots-clés : Polyplôïdie, évolution caryologique, Cyprinidés, Cyprinidés, *Barbus*.

THE KARYOLOGY OF BARBINS AND THE POSSIBLE PLESIOMORPHIC CONDITION OF POLYPLOÏDY IN CYPRINIDAE.

ABSTRACT

The new model of karyological evolution of Cyprinidae which proposes that the polyploid value $2n=100$ should be regarded as plesiomorphic for the family, contrary to the orthodox theory, seems to be reinforced by some new data on chromosome numbers of African and South-Asian cyprinids. So, the hypothesis of a cyprinid-like ancestor, probably close to the barbin lineage, with polyploidy acting as an «open-system» in the karyoevolution of cyprinids, is suggested. The important role of this phenomenon in the evolutionary process of some lineages seems to be unquestionable and, in this sense, it is proposed that systematists should give more attention to karyological data in the establishment of their classification schemes. Besides, technological advances in molecular cytogenetics will provide important tools for the revision of the hierarchical levels used in the classification of Cyprinidae and, possibly, for the recognition of phylogenetic relationships within cypriniforms.

Key-words : Polyploidy, karyological evolution, Cyprinidae, Cyprinidae, *Barbus*.

INTRODUCTION

In Cyprinidae, phylogenetic schemes have been based on anatomical / morphological characters, specially through comparative osteological approaches (see general revisions such as CHEN *et al.*, 1984 ; HOWES, 1987 ; BOGUTSKAYA, 1992 for the Old World taxa, and MAYDEN, 1989 for the New World taxa). More recently, indeed, the trend has been to erect classifications based on phylogenetic systematics, and as correctly pointed out by RAINBOTH (1991), the reliability of the characters which have been defined as synapomorphies may be questionable.

Moreover, according to HOWES (1991), this family is divided into seven subfamilies, among which only some have demonstrated monophyly - Gobioninae, Cultrinae, Alburninae and Acheilognatinae - the others (Cyprininae, Rasborinae and Leuciscinae) being considered as «categories of taxonomic convenience». As yet, the whole family Cyprinidae is not shown to be monophyletic, and the revision of hierarchical levels must be paralleled with the remaining cypriniforms. Such a co-ordination, as defended by the author himself, would perhaps raise the family status to superfamily (Cyprinoidea), and to elevate to family rank all the presently recognized subfamilies.

Very few authors have used karyological data to establish phylogenetic relationships within the family Cyprinidae, accepting the possibility of uniting several species or species-groups into putatively monophyletic lineages based on chromosome numbers (e.g. ARAI, 1982 ; ZAN *et al.*, 1986 ; YU *et al.*, 1987). Besides, such proposals have even been disregarded as clearly demonstrated in the systematic review papers recently edited by WINFIELD and NELSON (1991) (see BANARESCU and COAD · HOWES ; RAINBOTH).

However, the obvious existence of multiple genomes in several cyprinid taxa, included in the subfamilies Cyprininae, Rasborinae and Leuciscinae (Table I), and the discovery of a very high number of chromosomes ($2n=446$) in the schizothoracin *Diptychus dipogon* (YU and YU, 1990) suggests, as already stated by RAB and COLLARES-PEREIRA (*in press*), that the occurrence of polyploidy in the family may correspond to evolutionary mechanisms much more complex than expected. Furthermore, such a phenomenon may be much less exceptional in fish evolution than previously considered - see the recent description of a sturgeon *Acipenser mikadoi* with a DNA content corresponding to a chromosome number of around 500, i.e. a tetraploid derivative of octaploid level (BIRNSTEIN *et al.*, 1993).

The aim of the present review is simply to emphasize that current ideas on the barbin lineage and on the classification of the subfamily Cyprininae, must be regarded as provisional, and subject to further information on chromosome numbers, particularly of South-Asian and African taxa. Moreover, the role of karyological data (both chromosome form and structure allowing to ascertain interspecific chromosomal homologies) should be reinforced in the establishment of a revised concept of «cyprinids» (*sensu* HOWES, 1991) and in the definition of their relationships with the remaining cypriniforms.

THE BARBINS AND THE GENUS *BARBUS STRICTO SENSU*

The barbin lineage comprises the genus *Barbus s.s.*, the genus *Aulopyge*, and other barbines as *Varicorhinus*, *Capoeta*, *Cyprinus*, *Carassius*, *Carassioides*, *Procypris* and *Probarbus* (see HOWES, 1991 ; BANARESCU, 1990). It ranges throughout North-Africa and Eurasia being limited at East by the Urals and in the South by the Tien Shan.

As defined by HOWES (1987), the genus *Barbus s.s.* is distributed in Europe, North-Africa and South-West Asia and has only 21 species out of the 800 described nominal species. Of these nominal species, a significant fraction inhabits Africa, and have been included in two distinct groups: the so-called large-barbels (SL > 15 cm) representing 20-25 % of the taxa, and the small-barbels (SL < 15 cm) much more frequent (80-75 %). Only the former group was considered close to the European taxa by ALMAÇA (1988) and HOWES (*op.cit.*), with the exception of the large-barbel species *B. andrewi* Barnard 1937 and *B. serra* Peters 1864 from Western Cape, which need to be more carefully analysed (SKELTON *et al.*, 1991).

Tableau I : Nombres diploïdes de chromosomes signalés chez les différentes sous-familles de Cyprinidés, telles qu'elles ont été définies par HOWES (1991) (entre parenthèses, leurs principales distributions géographiques).

Table I : Diploid chromosome numbers observed in the distinct Cyprinidae subfamilies defined by HOWES (1991) (in brackets, the main distributional areas).

	2n=48-446
(Europe, W Asia, Africa, India, SE Asia)	
Barbin lineage	2n=96-206
Schizothoracin lineage	2n=92-446
Labein lineage	2n=48-50
Squaliobarbin lineage	2n=48-50
Cyprinion-Onychostoma lineage	2n=48-50
RASBORINAE	2n=50-78
(Africa, India, SE Asia, marginally W and E Asia)	
LEUCISCINAE	2n=48-75
(Europe, NE Asia and N America)	
GOBIONINAE	2n=50-52
(Holartic Asia)	
ALBURNINAE	2n=48-50
(Europe, W and E Asia, upper part of SE Asia)	
CULTRINAE	2n=48
(E Asia)	
ACHEILOGNATHINAE	2n=42-48
(Holarctic Asia)	

The relationship between European *Barbus* and the group of African large-barbels was also documented through the comparative genetic analyses of AGNESE *et al.* (1990) and BERREBI *et al.* (1990), who proposed that large African *Barbus* should be «tetraploïds», in contrast to the remaining African small-barbels which were also analysed, and classified as «diploïds».

In fact, the European barbels so far karyotyped represent almost 40% of *Barbus s.s.* and have 2n=100 (Table II). Unfortunately, there are very few karyological studies of African barbels and they showed that some are in fact «tetraploïds» (2n=100), some are «diploïds» (2n=50), and a fraction of the analysed taxa from Eastern and Southern Africa, also reproducing bisexually, have been interpreted as «hexaploïds» (2n=148-150) (see GOLUBTSOV and KRYSANOV, 1993 ; OELLERMANN and SKELTON, 1991, respectively). More recently, GUEGAN *et al.* (*in press*) suggested a panAfrican distribution of the evolutionary «hexaploïds» based on the karyotypes of three more large-*Barbus* species from Western Africa.

Although its monophyly was not demonstrated, all the barbin genera cytogenetically analysed, excluding *Capoeta*, have polyploid karyotypes, which suggests that this condition is plesiomorphic for the lineage. As proposed by COLLARES-PEREIRA and COELHO (1989), such an ancient condition has been retained to some extant genera (the ancestral karyotype 2n=100 - Fig.1A), while others entered a progressive reduction of chromosome number by successive fusion events towards the lower basic number 2n=50 (although for some species the reduction has extended at least until 2n=42). In fact, primary tetraploïds have an important fraction of subtelocentric-telocentric chromosomes (30 %-60 %), when compared with «diploïds» (most frequently with 10%-15 %).

Tableau II : Liste des espèces de Cyprinines polyploïdes (d'après ARAI, 1982 ; VASIL'IEV, 1985 ; SUZUKI et TAKI, 1986,1988 ; YU *et al.*, 1987, 1989 ; MAZIK *et al.*, 1989 ; COLLARES-PEREIRA et MADEIRA, 1990 ; OELLERMANN et SKELTON, 1990 ; TOKTOSUNOV et MAZIK, 1991 ; GOLUBTSOV et KRYSANOV, 1993 ; GUEGAN *et al.*, sous presse - avec (*) les *Barbus s.s.*).

Table II : List of known polyploïd cyprinins (see ARAI, 1982 ; VASIL'IEV, 1985 ; SUZUKI and TAKI, 1986,1988 ; YU *et al.*, 1987, 1989 ; MAZIK *et al.*, 1989 ; COLLARES-PEREIRA and MADEIRA, 1990 ; OELLERMANN and SKELTON, 1990 ; TOKTOSUNOV and MAZIK, 1991 ; GOLUBTSOV and KRYSANOV, 1993 ; GUEGAN *et al.*, in press - with (*) the *Barbus s.s.*).

BARBIN LINEAGE			
Acrossocheilus hexagonolepis	2n=100	C. auratus gibelio	2n=100,156
A. (Neolissocheilus) sumatranus	2n=98	C. auratus buergeri	2n=100,156
Aulopyge hugeli	2n=100	C. auratus cuvieri	2n=100
Barbodes (Spinibarbus) sinensis	2n=100	C. auratus grandoculis	2n=100
B. (Spinibarbus) caldwelli	2n=100	C. auratus langsdorfi	2n=100,156,206
B. (Spinibarbus) denticulatus	2n=100	Cyprinus carpio	2n=100
Barbus barbus (*)	2n=100	C. carpio haematopterus	2n=100
B. bocagei (*)	2n=100	C. carpio chilia	2n=100,150
B. corniza (*)	2n=100	C. carpio rubrofuscus	2n=100
B. meridionalis (*)	2n=100	C. longipectoralis	2n=100
B. meridionalis petenyi (*)	2n=100	C. megalophthalmus	2n=100
B. microcephalus (*)	2n=100	C. pellegrini pellegrini	2n=100
B. plebejus (*)	2n=100	C. pellegrini barbatus	2n=100
B. sclateri (*)	2n=100	C. yunnanensis dalliensis	2n=100
B. steindachneri (*)	2n=100	C. micristius fuxianensis	2n=100
B. tauricus cubanicus	2n=100	Procypris rabaudi	2n=100
B. bynni bynni	2n=150		
B. bynni occidentalis	2n=148	SCHIZOTHORACIN LINEAGE	
B. intermedius	2n=150	Chuanchia labiosa	2n=92
B. ethiopicus	2n=150	Diptychus sp.	2n=98
B. aeneus	2n=148	D. micromaculatus	2n=98
B. capensis	2n=150	D. sewerzowi	2n=98
B. kimberleyensis	2n=148	D. dybowski	2n=98
B. natalensis	2n=150	D. dybowski lansdelli	2n=98
B. polylepis	2n=150	D. gymnogaster microcephalus	2n=100
B. marequensis	2n=150	D. gymnogaster oschanini	2n=100
B. brachycephalus	2n=100	D. (Phycobarus) dipogon	2n=446
B. wurzi	2n=148	Platypharodon extremus	2n=90
B. petitjeani	2n=150	Gymnocypris eckloni	2n=94
Catlocarpio siammensis	2n=98	Gymnodiptychus pachycheilus	2n=90-98
Percocypris pingi pingi	2n=98	Oxygymnocypris stewarti	2n=92
P. pingi regani	2n=98	Schizothorax sp.	2n=148
Probarbus jullieni	2n=98	S. lissolabiatu	2n=148
Sinocyclocheilus grahami grahami	2n=96	S. grahami	2n=148
S. grahami tingi	2n=96	S. prenanti	2n=148
S. maculatus	2n=96	S. intermedius	2n=98-100
Tor tor	2n=100	S. pseudaksaiensis issykkuli	2n=98-100
T. sinensis	2n=100	S. niger	2n=98
T. douronensis	2n=100	S. yunnanensis	2n=148
T. khudree	2n=100	S. (Racoma) waltoni	2n=92
T. mosal mahanadicus	2n=100	S. (Racoma) macropogon	2n=90-98
T. putitora	2n=100	S. (Schizopyge) taliensis	2n=148
Varicorhinus nelspruitensis	2n=150	S. (Schizopyge) davidi	2n=98
V. beso	2n=150	S. (Schizopyge) oconnori	2n=92
Pseudobarbus	2n=96	Schizopygopsis pylzovi	2n=92
Carassioides cantonensis	2n=100	S. younghusbandi younghusbandi	2n=90
Carassius auratus	2n=100	Schizothoraichthys progastus	2n=98

Moreover, such a process is apparently reversible which may explain the existence of secondary polyploidy in modern Leuciscinae as represented in Fig.1B (see COLLARES-PEREIRA, 1989). Also the description of higher levels of polyploidization in cyprinins suggests that the complex phenomenon of polyploidy should be reanalysed. In fact, the possibility of occurrence of both auto- and allopolyploidization processes in the genesis of the so-called «hexaploid» barbin group, was already considered by OELLERMANN and SKELTON (1990), starting from a «diploid» karyotype with $2n=50$. However, these taxa with $2n=148-150$ can be easily produced by the fertilization of an unreduced egg with $2n=100$, and such a triploid may endure a unisexual mode of reproduction during a transition period, before the progressive «diploidization» and the return to bisexuality.

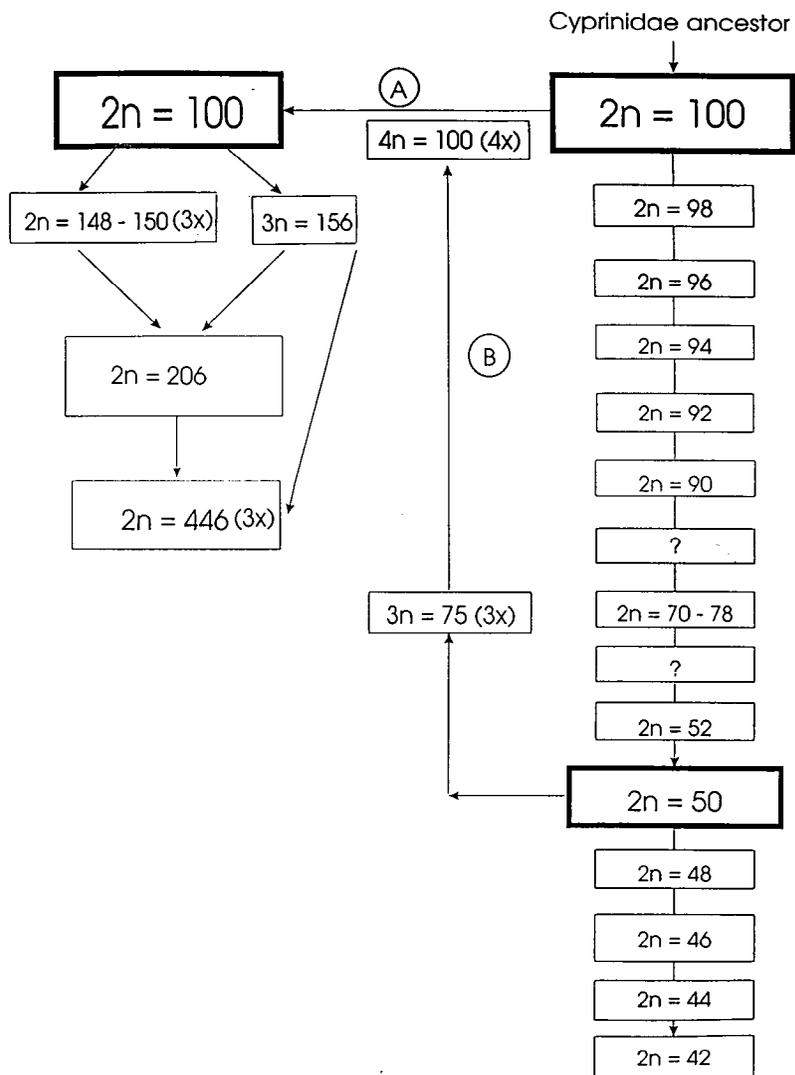


Figure 1 : Représentation schématique d'un nouveau modèle caryoévolutif pour la famille des Cyprinidés, proposé par COLLARES-PEREIRA et COELHO (1989) : évolution par polyploïdie primaire (A) et secondaire (B).

Figure 1 : Schematic representation of the new model of karyological evolution proposed by COLLARES - PEREIRA and COELHO (1989) for the family Cyprinidae : primary polyploidy (A) and secondary polyploidy (B).

Effectively, some populations of the Eurasian crucian carp *Carassius auratus gibelio*, have triploïds with $3n=156$, which if «normal» meiosis occurs may become diploïd in behaviour and return to a bisexual normal reproduction (see ZAN *et al.*, 1986 ; FAN and LIU, 1990 ; FAN and SHEN, 1990). According to these authors, unisexual species might revert directly into bisexuality if males of their own species are available in the populations. Besides, the revision of the taxonomy of this genus seems to be also necessary, with the possibility of elevating to species rank some of the extant known subspecies.

CYPRININAE LINEAGES AND POLYPLÖIDY

Assuming that in cyprinid evolution two major branches differentiated — Cyprininae and Leuciscinae — as referred to by HOWES (1987), the ancestral-type would have been polyploïd and close to the former branch accepting the new model of karyological evolution proposed by COLLARES-PEREIRA and COELHO (1989). This model reopened the discussion about the primitive chromosome number in the family and assumed that «diploïdy» should be considered as an apomorphic state conversely to the orthodox theory, that points out that the derived stage is the $2n=100$ karyotype (see BUTH *et al.*, 1991).

Fossil representatives of those two phyletic groups dating to the early Oligocene have been recorded (see CAVENDER, 1991), and the fact that the oldest cyprinid fossil record assigned to the extinct genus *Parabarb* is known from Asia (middle Eocene fauna from Kazakhstan), seems remarkable. Effectively, South-East Asia has been considered the center of origin and radiation of the family, and relying on geographic evidence GOSLINE (1978) suggested a «cyprininae rather than a leuciscin-like ancestor».

Moreover, early Tertiary deposits from Northern and Central Asia contain both cyprinids and catostomids (a cypriniform group entirely polyploïd) proving that they were both already present there, the latter being widespread in Western North-America also by late Eocene times. However, cyprinids living in Eastern Asia at similar latitudes during the Paleogene have only reached the American continent 20 MY later (CAVENDER, *op.cit.*). The fact that only the Leuciscinae group, which is clearly polyphyletic, had apparent success in the colonization process, suggests that the «diploïd» state was already achieved at that time very probably by a cyprinid(?) -diploïd group.

Effectively, during the Cenozoic, South-East Asia had a high tectonic activity, altering significantly its hydrography by producing elevation and gradient changes (see RAINBOTH, 1991), which could have affected chromosomal rearrangements such as the Robertsonian translocations hypothesized in the new model of karyological evolution (COLLARES-PEREIRA and COELHO, 1989). In fact, the rapidly fragmenting and populations dispersing, might have allowed the fixation of negatively heterotic rearrangements, and, consequently, an unimpeded differentiation due to disruption of gene flow.

At about the same time (early Miocene), the colonization of the African continent by both «diploïd» and «polyploïd» cyprinins started, aided by the apparent absence of competition, with successful radiations of barbines, labeins and barilins groups (CAVENDER, 1991), three clades that share their distributional pattern with South-East Asia. GOLUBTSOV and KRYSANOV (1993), based on the geographic distribution of «large» *Barbus* species with $2n=148-150$ in Africa, hypothesized the occurrence of an «hexaploïdic» event before their dispersal over this continent, which can be perfectly adjusted to a «triploïdic» event, as stated previously. After analysing both karyological and morphological data, these authors suggested an independent origin for the «large» and «small» *Barbus* of Africa.

According to HOWES (1991), there are five distinct lineages in Cyprininae occurring presently in Europe and Western Asia but principally in Africa, Central and High Asia, and South-East Asia including Indonesia. In addition to the barbines, there is another lineage completely polyploïd - the Schizothoracin - which is a dominant group living in Central and High Asia almost all endemic (see RAINBOTH, 1991), and some other taxa including *Barbus sensu lato*, *Tor*, and *Pseudobarbus*. The remaining three lineages already analysed, including the most widespread lineage which is predominantly South-East Asiatic — the labein — seem to be at least almost exclusively «diploïd» ($2n=48-50$). Such a chromosome number may be considered as synapomorphic for those distinct lineages, the process of reduction being probably achieved by successive centric fusions.

This is suggested by the chromosome sets of some already known extant barbines and schizothoracines, exhibiting karyotypes with reductions until at least $2n=90$ and also by some «rasborines» *sensu* HOWES (1991). Effectively, the South-East Asiatic species already karyotyped *Opsariichthys uncirostris* ($2n=74 - 76$), *Zacco platypus* ($2n= 78$) and *Perilampus atpar* ($2n=70$) (see YU *et al.*, 1987 and TRIPATHI and SHARMA, 1987) may also be considered as relicts of that process. Interestingly, all these species were assigned to the large assemblage of Rasborinae «subfamily» (HOWES 1991), which is characterized by taxa with barbel peculiar morphotype, and assumed by that author as having «...derived independently from that of cyprinins and other barbelled groups».

However, if our hypothesis is consistent, then the suggestion by ARAI (1982) of a plesiomorphic status for barbelled cyprinids is correct, in spite of one of the arguments used by cladistic methodology referring to the commonality principle (see HOWES, 1991). Besides, such an argument has been also used to refute the hypothesis of a primitive polyploidy in the family (see BUTH *et al.*, 1991), but is it valid enough ?

The cytogenetic patterns of Barbin and Schizothoracin lead MAZIK *et al.* (1989) to suggest a splitting of the latter from the *Barbus* lineage after a tetraploidization event for the whole group. However, such a phenomenon can be regarded as having occurred prior to the origin of Cyprinidae, and not as a secondary evolutionary event.

In conclusion and because many important cyprinid lineages have not been thoroughly studied from the karyological viewpoint, the phylogenetic systematists should pay more attention to these data and include them, whenever available, in their tentative classification schemes.

In the near future, by using the most modern cytogenetic technology, which will resolve interspecific chromosome homologies, the revision of the hierarchical levels in cyprinid classification and the definition of their phylogenetic relationships with the cypriniforms as suggested by HOWES (1991), will be more reliable. In fact, diploid-polyploid relationships are also known in the two larger lineages — the catostomids and the cobitids — and this suggests that polyploidy may be acting as an «open-system», not only in the evolution of cyprinids but also within the cypriniforms.

Finally, a deeper insight into the plesiomorphic condition of polyploidy in Cyprinidae will be probably achieved by both accurate nuclear DNA measurements and molecular analysis of the duplicate loci of the «diploids» *versus* «tetraploids» extant taxa. Moreover, it is also anticipated that a more complete knowledge of the karyology of the genus *Barbus s.l.* (a polyphyletic assemblage that requires «taxonomic reorganization» - see SKELTON *et al.*, 1991), together with the remaining cyprinins, especially from Africa and South-East Asia including Indonesia, will contribute to a better understanding of patterns and processes of evolution of the entire Cyprinidae.

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