

Chromosomal complements of some Atlantic Blennioidei and Gobioidei species (Perciformes)

Tatiana Barbosa Galvão¹, Luiz Antonio Carlos Bertollo²,
Wagner Franco Molina¹

1 Department of Cell Biology and Genetics, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59078 – 970, Natal, RN, Brazil **2** Department of Genetics and Evolution, Universidade Federal de São Carlos, Via Washington Luiz, Km 235, 13565 – 905, São Carlos, São Paulo, Brazil

Corresponding author: Wagner Franco Molina (molinawf@yahoo.com.br)

Academic editor: V. Gokhman | Received 20 July 2011 | Accepted 13 September 2011 | Published 9 November 2011

Citation: Galvão TB, Bertollo LAC, Molina WF (2011) Chromosomal complements of some Atlantic Blennioidei and Gobioidei species (Perciformes). Comparative Cytogenetics 5(4): 259–275. doi: 10.3897/CompCytogen.v5i4.1834

Abstract

A remarkable degree of chromosomal conservatism ($2n=48$, FN=48) has been identified in several families of Perciformes. However, some families exhibit greater karyotypic diversity, although there is still scant information on the Atlantic species. In addition to a review of karyotypic data available for representatives of the suborders Blennioidei and Gobioidei, we have performed chromosomal analyses on Atlantic species of the families Blenniidae, *Ophioblennius trinitatis* Miranda-Ribeiro, 1919 ($2n=46$; FN=64) and *Scartella cristata* (Linnaeus, 1758) ($2n=48$; FN=50), Labrisomidae, *Labrisomus nuchipinnis* (Quoy & Gaimard, 1824) ($2n=48$; FN=50) and Gobiidae, *Bathygobius soporator* (Valenciennes, 1837) ($2n=48$; FN=56). Besides variations in chromosome number and karyotype formulas, Ag-NOR sites, albeit unique, were located in different positions and/or chromosome pairs for the species analyzed. On the other hand, the heterochromatic pattern was more conservative, distributed predominantly in the centromeric/pericentromeric regions of the four species. Data already available for Gobiidae, Blenniidae and Labrisomidae show greater intra- and interspecific karyotypic diversification when compared to other groups of Perciformes, where higher uniformity is found for various chromosome characteristics. Evolutionary dynamism displayed by these two families is likely associated with population fractionation resulting from unique biological characteristics, such as lower mobility and/or specific environmental requirements.

Keywords

Chromosomal evolution, marine fish, Blenniidae, Gobiidae, Labrisomidae

Introduction

Although karyotypic characteristics for some families of marine fish are already known, information on groups of Perciformes is still significantly disproportionate. Among these, suborders Blennioidei and Gobioidei stand out because of the large number of species they represent.

Suborders Gobioidei, with 2,121 species, and Blennioidei with 732 species, are spread throughout the tropical zone, typically represented by small specimens with low mobility and the ability to withstand changes in temperature and salinity (Nelson 2006).

Species of Blennioidei and Gobioidei investigated (e.g. Cataudela et al. 1973; Garcia et al. 1987; Ene 2003) have shown sufficient chromosomal peculiarities for species discrimination and understanding of their evolutionary aspects. In some families, such as Blenniidae, Labrisomidae and Gobiidae, sharing cryptic morphological characteristics combined with poor knowledge of the biological characteristics for many species, contributes to the relative taxonomic inaccuracy of this group. As such, cytogenetic markers (Garcia et al. 1987; Caputo 1998; Caputo et al. 2001) and phylogenetic analyses based on molecular data (Wang et al. 2001; Thacker 2003; Gysels et al. 2004; Almada et al. 2005) have been increasingly used when assessing their kinship relations. Indeed, it has been suggested that phylogenetic analyses combine molecular and morphological data (Thacker 2003), as well as cytogenetic information. However, in light of the diversity in these groups, solid chromosome data are not yet sufficiently available, with only 7.5% of Blenniidae species and 4.5% of Gobioidei was karyotyped (Table 1). Despite the scarcity of data, a high degree of chromosomal polymorphism has been characterized among Gobiidae, primarily Robertsonian rearrangements (Caputo et al. 1999, Ene 2003), along with others such as tandem fusions and pericentric inversions (Giles et al. 1985; Thode et al. 1985; Amores et al. 1990).

The present study focuses on the karyotypic characterization of some Atlantic species of the families Blenniidae, *Ophioblennius trinitatis* Miranda-Ribeiro, 1919 and *Scartella cristata* (Linnaeus, 1758), Labrisomidae, *Labrisomus nuchipinnis* (Quoy & Gaimard, 1824) and Gobiidae, *Bathygobius soporator* (Valenciennes, 1837), through conventional chromosomal analysis, characterization of nucleolar organizer regions (Ag-NORs) and the distribution pattern of C-positive heterochromatin (C-banding) in chromosomes, discussing evolutionary aspects.

Material and methods

A total of 25 specimens of *Ophioblennius trinitatis* (7♂, 4♀ and 14 indeterminate), 11 specimens of *Scartella cristata* (4♂, 5♀ and 2 indeterminate), 13 specimens of *Labrisomus nuchipinnis* (4♂, 4♀ and 5 indeterminate) and 12 specimens of *Bathygobius soporator*, (5♂, 5♀ and 2 indeterminate) were used for chromosome analysis. *Ophioblennius trinitatis* specimens came from the coast of Rio Grande do Norte

Table I. Cytogenetic data for Blennioidei and Gobioidei (Perciformes).

Suborder/ Family	Species	2n	Karyotype formula	FN	References
Blennioidei					
Blenniidae	<i>Aidablennius sphyinx</i>	48	4m+4sm+40a	56	Cano et al. (1982)
	<i>A. sphyinx</i>	48	2st+46a	50	Cataudella and Civitelli (1975)
	<i>Atrosalarias fuscus</i>	48	48a	48	Arai and Shiotsuki (1973)
	<i>Blennius ocellaris</i>	48	2m+2st+44a	52	Vitturi et al. (1986)
	<i>B. ponticus</i>	48	16sm+10st+22a	74	Garcia et al. (1987)
	<i>B. yatabei</i>	48	6sm+12st+30a	66	Arai and Shiotsuki (1974)
	<i>Coryphoblennius galerita</i>	48	2m+12sm+34a	62	Garcia et al. (1973)
	<i>Dasson trossulus</i>	40	8m+32st/a	48	Arai and Shiotsuki (1974)
	<i>Istiblennius enoshimae</i>	48	2m+46a	50	Arai and Shiotsuki (1973)
	<i>I. lineatus</i>	48	48st/a	48	Arai and Shiotsuki (1974)
	<i>Lipophrys canevai</i>	48	8st+40a	56	Cataudella and Civitelli (1975)
	<i>L. pholis</i>	46	8m+8sm+30a	62	Garcia et al. (1987)
	<i>L. trigloides</i>	46	4m+4sm+10st+28a	64	Cano et al. (1982)
	<i>L. trigloides</i>	48	2m+6sm+18st+22a	74	Cataudella and Civitelli (1975)
	<i>L. trigloides</i>	48	2m+22sm+2st+22a	74	Garcia et al. (1987)
	<i>L. trigloides</i>	48	2m+6sm+18st+22a	74	Vitturi et al. (1986)
	<i>Omobranchus elegans</i>	42	10m+2sm+6st+24a	60	Arai and Shiotsuki (1974)
	<i>O. punctatus</i>	44	4m+40a	48	Arai (1984)
	<i>Ophioblennius trinitatis</i>	46	6m+12st+28a	64	Present study
	<i>Parablennius incognitus</i> (= <i>Blennius incognitus</i>)	48	4st+44a	52	Cano et al. (1982)
	<i>P. pilicornis</i> (= <i>Blennius pilicornis</i>)	48	8st+40a	56	Catalano et al. (1985)
	<i>P. gattorugine</i>	48	2m+4sm+42a	54	Vitturi et al. (1986)
	<i>P. pilicornis</i>	48	48a	48	Brum et al. (1992)
	<i>P. sanguinolentus</i>	48	12st+36a	60	Cataudella et al. (1973)
	<i>P. sanguinolentus</i>	48	20sm+10st+18a	78	Garcia et al. (1987)
	<i>P. tentacularis</i>	48	48st/a	48	Vasil'ev (1985)
	<i>P. tentacularis</i>	48	1st+47a	49	Carbone et al. (1987)
	<i>P. tentacularis</i>	47	1sm+46a	48	Carbone et al. (1987)
	<i>Salaria fluviatilis</i>	48	48st/a	48	Cataudella and Civitelli (1975)
	<i>S. pavo</i>	48	8st+40a	56	Cataudella et al. (1973)
	<i>S. pavo</i>	48	16sm+14st+18a	78	Garcia et al. (1987)
	<i>S. pavo</i>	48	2st+46a	50	Vasil'ev (1980)
	<i>Salarias faciatus</i>	48	48a	48	Arai and Shiotsuki (1973)
	<i>S. luctuosus</i>	48	48st/a	48	Arai and Shiotsuki (1974)
	<i>Scartella cristata</i> (= <i>Blennius cristatus</i>)	48	2st+46a	50	Vitturi et al. (1986)
	<i>S. cristata</i>	48	2sm+46st/a	50	Brum et al. (1995)
	<i>S. cristata</i>	48	4st+44a	52	Present study
Gobioidei					
Clinidae	<i>Clinithracus argentatus</i>	48	2st+46a	50	Vitturi et al. (1986)
Labrisomidae	<i>Labrisomus nuchipinnis</i>	48	2sm+46a	50	Affonso (2000)
	<i>L. nuchipinnis</i>	48	2st+46a	50	Present study

Suborder/ Family	Species	2n	Karyotype formula	FN	References
Eleotridae	<i>Dormitator latifrons</i>	46	44m/sm+2st/a	90	Uribe-Alcocer et al. (1983)
	<i>D. maculatus</i>	46	34m/sm+12st/a	80	Maldonado-Monroy et al. (1985)
	<i>D. maculatus</i>	46	40m/sm+6st/a	86	Molina (2005)
	<i>D. maculatus</i>	46	14m+28sm+2st+2a(φ) 13m+28sm+3st+2a(δ)	90	Oliveira and Almeida-Toledo (2006)
	<i>Eleotrioides strigatus</i>	44	2m+42st/a	46	Arai and Sawada (1974)
	<i>Eleotris acanthopomus</i>	46	46st/a	46	Arai and Sawada (1974)
	<i>E. picta</i>	52	52a	52	Uribe-Alcocer and Diaz-James (1996)
	<i>E. pisonis</i>	46	2m/sm+42st/a	46	Uribe-Alcocer and Diaz-James (1996)
	<i>E. pisonis</i>	46	46a	46	Rocon-Stange (1992)
	<i>E. pisonis</i>	46	46a	46	Molina (2005)
	<i>E. muralis</i>	46	46a	46	Khuda-Bukhsh and Nayak (1990)
	<i>Mogurnda mogurnda</i>	46	6sm+40st/a	52	Arai et al. (1974)
	<i>M. obscura</i>	62	-	-	Nogusa (1960)
	<i>Ophiocara porocephala</i>	48	48a	48	Arai and Fujiki (1979)
	<i>Oxyeleotris marmorata</i>	46	2m+2sm+42a	50	Arai and Fujiki (1979)
Gobiidae	<i>Aboma latipes</i>	40	40a	40	Arai and Sawada (1974)
	<i>Acanthogobius flavimanus</i>	44	44st/a	44	Arai and Sawada (1974)
	<i>A. flavimanus</i>	44	36st+8a	80	Arai and Kobayashi (1973)
	<i>A. flavimanus</i>	44	10m/sm/st+34a	54	Arai and Sawada (1975)
	<i>Acentrogobius pflaumi</i>	50	48m/sm+2st/a	98	Nogusa (1960)
	<i>Amblygobius albimaculatus</i>	44	2m+42st/a	46	Nishikawa et al. (1974)
	<i>Aphia minuta</i>	44	44a	44	Caputo et al. (1999)
	<i>A. minuta</i>	43	42a+1st	42	Caputo et al. (1999)
	<i>A. minuta</i>	42	1m+1st+40a	44	Caputo et al. (1999)
	<i>A. minuta</i>	42	1M+1m+40a	44	Caputo et al. (1999)
	<i>A. minuta</i>	41	2M+1st+38a	44	Caputo et al. (1999)
	<i>Apocryptes bato</i>	46	24m+10sm+12a	80	Nayak and Khuda-Bukhsh (1987)
	<i>A. lanceolatus</i>	38	14m+22sm+2st	76	Nayak and Khuda-Bukhsh (1987)
	<i>Awaous grammepomus</i>	46	46st/a	46	Khuda-Bukhsh and Barat (1987)
	<i>A. tajasica</i>	46	46a	46	Stange and Passamani (1986)
	<i>Bathygobius fuscus</i>	48	48a	48	Arai and Sawada (1975)
	<i>B. soporator</i>	48	2m+46a	50	Brum et al. (1996)
	<i>B. soporator</i>	48	2m/sm+46a	50	Cipriano et al. (2002)
	<i>B. soporator</i>	48	2m+6st+40a	56	Present study
	<i>B. stellatus</i>	46	2st+44a	48	Vasil'ev (1985)
	<i>B. stellatus</i>	47	1sm+2st+43a	49	Vasil'ev (1985)
	<i>Boleophthalmus boddaerty</i>	46	46m/sm	92	Subrahmanyam (1969)
	<i>B. glaucus</i>	46	12m+20sm+2st+12a	80	Manna and Prasad (1974)
	<i>B. pectinirostrus</i>	46	46st/a	46	Arai and Sawada (1975)
	<i>Bostrichthys sinensis</i>	48	4m/sm+44a	52	Arai et al. (1974)
	<i>Chaenogobius annularis</i>	44	18sm+26st/a	62	Arai and Sawada (1975)
	<i>C. annularis</i>	44	36m/sm+8a	80	Arai et al. (1974)
	<i>C. annularis</i>	44	44a	44	Nogusa (1960)
	<i>C. castaneus</i>	44	36m/sm/st+8a	80	Nishikawa et al. (1974)
	<i>C. isaza</i>	44	12sm+32st/a	56	Arai and Sawada (1975)
	<i>C. urotaenia</i>	44	-	-	Nogusa (1960)

Suborder/ Family	Species	2n	Karyotype formula	FN	References
	<i>C. urotaenia</i>	42	14sm+28a	56	Yamada (1967)
	<i>Chasmichthys dolichognathus</i>	44	44st/a	44	Arai and Sawada (1975)
	<i>C. gulosus</i>	44	44st/a	44	Arai and Sawada (1975)
	<i>C. gulosus</i>	44	16m/sm/st+28a	60	Nishikawa et al. (1974)
	<i>Ctenogobius criniger</i>	50	34m/sm+6st+10a	90	Arai and Sawada (1974)
	<i>Gilllichthys mirabilis</i>	44	12sm+32a	56	Chen and Ebeling (1971)
	<i>G. seta</i>	44	6m+14sm+24a	64	Chen and Ebeling (1971)
	<i>Glossogobius fasciatopunctatus</i>	44	10m+28sm+2st+4a	84	Fei and Tao (1987)
	<i>G. giuris</i>	46	46a	46	Rishi and Singh (1982)
	<i>Gobiodon citrinus</i>	44	2m+42st/a	46	Arai and Sawada (1974)
	<i>G. citrinus</i>	43	1m+42st/a	44	Arai and Sawada (1974)
	<i>G. quinquestrigatus</i>	44	44a	44	Arai and Fujiki (1979)
	<i>G. rivulatus</i>	44	44a	44	Arai and Fujiki (1979)
	<i>Gobiooides rubicundus</i>	46	2m+26sm+10st+8a	84	Manna and Prasad (1974)
	<i>Gobionellus shufeldti</i>	48	48a (♀)	48	Pezold (1984)
	<i>G. shufeldti</i>	47	46a+1m (♂)	48	Pezold (1984)
	<i>Gobiosoma macrodon</i>	38	38a	38	Musamil (1974)
	<i>G. zebrella</i>	38	38a	38	Musamil (1974)
	<i>Gobius abei</i>	46	-	-	Nogusa (1960)
	<i>G. buccichi</i>	44	2sm+42a	46	Thode and Alvarez (1983)
	<i>G. cobitis</i>	46	46a	46	Caputo et al. (1997)
	<i>G. cruentatus</i>	46	2st+44a	48	Thode and Alvarez (1983)
	<i>G. fallax</i>	38	8m/sm+30a	46	Thode et al. (1988)
	<i>G. fallax</i>	39	7m/sm+32a	46	Thode et al. (1988)
	<i>G. fallax</i>	40	6m/sm+34a	46	Thode et al. (1988)
	<i>G. fallax</i>	40	7m/sm+33a	47	Thode et al. (1988)
	<i>G. fallax</i>	41	5m/sm+36a	46	Thode et al. (1988)
	<i>G. fallax</i>	42	4m/sm+38a	46	Thode et al. (1988)
	<i>G. fallax</i>	43	3m/sm+40a	46	Thode et al. (1988)
	<i>G. niger</i>	52	2m+4sm+16st+30a	74	Vitturi and Catalano (1989)
	<i>G. niger</i>	51	3m+4sm+16st+28a	74	Caputo et al. (1997)
	<i>G. niger</i>	50	4m+4sm+16st+26a	74	Caputo et al. (1997)
	<i>G. niger</i>	49	5m+4sm+16st+24a	74	Caputo et al. (1997)
	<i>G. paganelius</i>	48	2sm+46a	50	Caputo et al. (1997)
	<i>G. similis</i>	44	?		Nogusa (1960)
	<i>Gobiusculus flavescens</i>	46	6m/sm+40a	52	Klinkhardt (1992)
	<i>Luciogobius grandis</i>	44	?		Arai (1981)
	<i>L. guttatus</i>	44	?		Arai and Kobayashi (1973)
	<i>Mesogobius batrachocephalus</i>	30	16m+14a	46	Ivanov (1975)
	<i>Neogobius cephalarges</i>	46	46a	46	Vasil'ev (1985)
	<i>N. constructor</i>	42	4m/sm+38a	46	Vasil'ev and Vasil'yeva (1994)
	<i>N. cyrius</i>	36	structural polymorphism		Vasil'ev and Vasil'yeva (1994)
	<i>N. fluviatilis</i>	46	46a	46	Vasil'ev (1985)
	<i>N. eurycephalus</i>	32	12m+2sm+18a	46	Ene (2003)

Suborder/ Family	Species	2n	Karyotype formula	FN	References
	<i>N. eurycephalus</i>	31	13m+2sm+16a	46	Ene (2003)
	<i>N. eurycephalus</i>	30	14m+2sm+14a	46	Ene (2003)
	<i>N. gymnotrachelus</i>	46	46a	46	Vasil'ev and Grigoryan (1992)
	<i>N. kessleri</i>	46	46a	46	Vasil'ev (1985)
	<i>N. melanostomus</i>	46	46a	46	Vasil'ev (1985)
	<i>N. rhodionovi</i>	46	46a	46	Vasil'ev and Vasil'yeva (1994)
	<i>Odontamblyops rubicundus</i>	46	4m+16sm+26st/a	66	Arai and Sawada (1975)
	<i>Padogobius martensi</i>	46	1m+3sm+2st+40a	52	Cataudella et al. (1973)
	<i>Parioglossus raoi</i>	46	46st/a	46	Webb (1986)
	<i>Periophthalmodon cantonensis</i>	46	18m+12sm+16st/a	76	Arai and Sawada (1975)
	<i>Pomatoschistus lozanoi</i>	37	3m+12sm+10st+12a	62	Webb (1980)
	<i>P. microps</i>	46	4m+16sm+20st+6a	86	Klinkhardt (1989)
	<i>P. minutus</i>	46	4m+16sm+16st+10a	82	Klinkhardt (1989)
	<i>P. minutus</i>	46	18sm+18st+10a	82	Klinkhardt (1992)
	<i>P. norvegicus</i>	32	10m+10sm+8st+4a	60	Webb (1980)
	<i>P. pictus</i>	46	22m/sm+12st+12a	80	Klinkhardt (1992)
	<i>Proterorhinus marmoratus</i>	46	46a	46	Rab (1985)
	<i>Pterogobius elapoides</i>	44	14sm+30st	88	Arai and Kobayashi (1973)
	<i>P. zonoleucus</i>	44	14sm+30st	88	Arai and Sawada (1975)
	<i>Quietula guaymasiae</i>	42	6m+4sm+32a	52	Cook (1978)
	<i>Q. y-cauda</i>	42	42a	42	Cook (1978)
	<i>Rhinogobius brunneus</i>	44	44a	44	Nishikawa et al. (1974)
	<i>R. flumineus</i>	44	44a	44	Arai and Kobayashi (1973)
	<i>R. giurinus</i>	44	44a	44	Nishikawa et al. (1974)
	<i>Rhodonichthys laevis</i>	42	16m/sm+26st	84	Arai et al. (1974)
	<i>Sicyopterus japonicus</i>	44	10m+10sm+24a	64	Arai and Fujiki (1979)
	<i>Synechogobius hasta</i>	44	2m+42st/a	46	Arai and Sawada (1975)
	<i>Tridentiger obscurus</i>	44	10m/sm+34a	54	Arai et al. (1974)
	<i>T. trigonocephalus</i>	44	28m/sm/st+16a	72	Arai et al. (1973)
	<i>T. trigonocephalus</i>	46	16sm+6st+24a	68	Fei and Tao (1987)
	<i>Trypauchen vagina</i>	46	12m+6sm+10st+18a	74	Khuda-Bukhsh (1978)
	<i>Tukugobius flumineus</i>	44	44a	44	Nadamitsu (1974)
	<i>Zosterisessor ophiocephalus</i> (= <i>Gobius ophiocephalus</i>)	46	46a	46	Vasil'ev (1985)
	<i>Zosterisessor ophiocephalus</i> (= <i>Gobius ophiocephalus</i>)	45	1st+45a	47	Vasil'ev (1985)
	<i>Zosterisessor ophiocephalus</i>	46	2m/sm+44a	48	Caputo et al. (1996)

(5°13'1.73"S; 35°9'57.85"W), northeastern Brazil (n=1), and the Saint Peter and Saint Paul (n=8) (00°55'02"N; 29°20'42"W) and Fernando de Noronha (n=16) (3°52'11"S; 32°26'13"W) archipelagos. The remaining specimens were collected on the coast of Rio Grande do Norte. Individuals were previously submitted to mitotic stimulation with compound attenuated antigens, for 24 to 48 hours (Molina 2001, Molina et al. 2010), anesthetized with clove oil (Eugenol) and sacrificed for the removal of anterior kidney fragments. Sexing of specimens was performed by macroscopic and microscopic examination of the gonads. Chromosome preparations were obtained from kidney

cells (Gold et al. 1990). Nucleolar organizer regions (NORs) were identified by stain with silver nitrate - Ag-NORs (Howell and Black 1980) and C-positive heterochromatin sites through C-banding (Sumner 1972).

Metaphase preparations were examined and photographed on an Olympus BX50 photomicroscope, using an Olympus DP70 digital camera system. Chromosomes were classified according to the position of the centromere in metacentrics (m), submetacentrics (sm), subtelocentrics (st) and acrocentrics (a) (Levan et al. 1964) and organized in order of decreasing size. The chromosome formula and FN (fundamental number or number of chromosomal arms) were established for each species, considering acrocentric chromosomes with a single arm and the remaining chromosomes exhibiting two arms.

Results

Cytogenetic analyses of Blenniidae species (Blennioidei)

Ophioblennius trinitatis showed 2n=46, with a chromosome formula equal to 6m+12st+28a (FN=64), irrespective of sex. Although chromosomes showed a gradual decline in size, the smallest acrocentric pairs corresponded to approximately one-third of the largest metacentric pairs. Nucleolar organizer regions are located in the terminal portions of the short arm on pair 9, the smallest subtelocentric pair. C-positive heterochromatin is discretely located in the centromeric/pericentromeric region of the chromosomes (Fig. 1a, b).

Scartella cristata showed 2n=48 chromosomes, with a chromosome formula equal to 4st+44a (FN=52). The karyotype also displays a gradual reduction in chromosome size. However, the largest chromosome pair exhibits only double the size in relation to the smallest karyotype pair. Ribosomal sites are located on the terminal portions of the short arms on chromosome pair 1. C-positive heterochromatin is also reduced and located in the centromeric regions of chromosomes (Fig. 1c, d).

Cytogenetic analyses of Labrisomidae and Gobiidae species (Gobioidei)

Labrisomus nuchipinnis (Labrisomidae) showed 2n=48 chromosomes with a chromosome formula of 2st+46a (FN=50), showing relatively more differentiated size between the largest and smallest chromosomes of the karyotype. Nucleolar organizer regions are in the terminal portions of the long arms on pair 2, corresponding to the largest pair of acrocentric chromosomes. C-positive heterochromatin was showed in the centromeric/pericentromeric region of all chromosome pairs, in relatively conspicuous blocks (Fig. 1e, f).

Bathygobius soporator (Gobiidae) also displayed the karyotype composed of 2n=48 chromosomes, but with the chromosome formula distinct from that of *L. nuchipinnis*, specifically, 2m+6st+40a (FN=56). Size difference between the largest and smallest

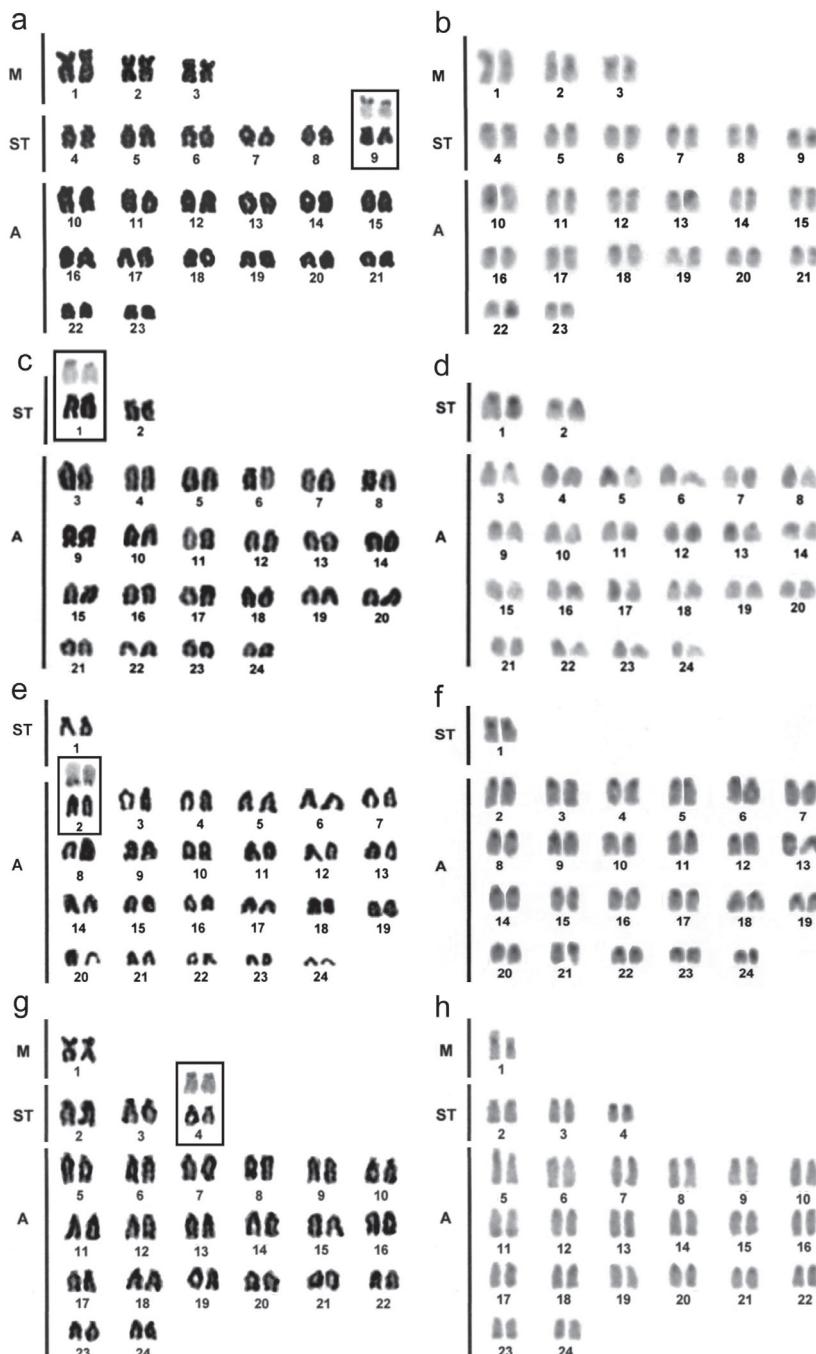


Figure 1. Karyotypes under Giemsa staining **a, c, e, g** and C-banding **b, d, f, h** of *Ophioblennius trinitatis*; **a, b** *Scartella cristata*; **c, d** *Labrisomus nuchipinnis*; **e, f** and *Bathygobius soporator*; **g, h** Ag-NOR-bearing chromosome pairs are highlighted.

chromosomes of the karyotype was far less pronounced. Ribosomal sites were on the terminal portions of the short arms on chromosome pair 4. C-banding showed discrete heterochromatic regions in the centromeric regions of most chromosomes and telomeric regions of some acrocentric pairs (Fig. 1g, h).

Discussion

Though many perciform families display a conserved karyotype pattern, with $2n=48$ acrocentric chromosomes, some groups demonstrate dynamic tendencies in relation to chromosome evolution (Molina 2007). Much of identifiable chromosome diversity is attributed to pericentric inversions, the most common mechanism of chromosome evolution in this order (Galetti et al. 2000, 2006).

Representatives of the suborder Blennioidei (e.g., Carbone et al. 1987) and Gobioidei (e.g., Arai and Sawada 1974, 1975; Thode et al. 1988; Oliveira and Almeida-Toledo 2006) stand out for their greater karyotype variability and diversity. This includes species with conserved karyotypes and those that are highly diversified.

Within the Blennioidei, the Blenniidae, a monophyletic family, is divided into six tribes including Salariini and Parablenniini which, in turn, include the Atlantic species *O. trinitatis* and *S. cristata* respectively (Nelson 2006). Comparisons of mitochondrial DNA sequences in samples of *Ophioblennius* Gill, 1860 collected throughout the Atlantic suggest that the genus consists of six distinct lineages. One of these corresponds to species found in the Pacific, while the rest are recorded in the biogeographic provinces of the Atlantic: Brazilian, Caribbean, Mid-Atlantic, Sao Tome and Azores/Cape Verde (Muss et al. 2001). Chromosome characteristics reported here for *O. trinitatis* are the first for the genus, exhibiting $2n=46$, $6m+12st+28a$ and $FN=64$. The relatively low diploid number and higher fundamental number in relation to the mean of other species of Blenniidae (Table 1), as well as the presence of large metacentric chromosomes, suggests pericentric inversion events and the occurrence of Robertsonian translocation involving two of its chromosome pairs. In turn, *S. cristata*, while also belonging to the family Blenniidae, has a distinct karyotype of $2n=48$, $4st+44a$ and $FN=52$. Thus, *S. cristata* differs from *O. trinitatis* in that it contains an extra pair of chromosomes, lacks metacentric chromosomes and has different numbers of subtelocentric and acrocentric chromosomes in the karyotype. The karyotype of the *S. cristata* population studied here differs from the karyotypes previously described for the coastal population of Rio de Janeiro (SE Brazil), with $2sm+46st/a$ (Brum et al. 1994), and the Mediterranean population, with $2st+46a$ (Vitturi et al. 1986). Nevertheless, despite the growing number of discordant karyotype descriptions between populations on the NE and SE coasts of Brazil, one cannot rule out that these differences may arise from the difficulty in precisely defining types of cryptic chromosomes in the karyotype of this species.

In spite of displaying relative diversity in chromosome structure, only 18.5% of Blennioidei species exhibit differences in the basal diploid number, $2n=48$ chromosomes. As shown in table 1, diploid numbers for representatives of this suborder vary

between $2n=40$, found in *Dasson trossulus* (Jordan & Snyder, 1902) (Arai and Shiot-suki 1974) and $2n=52$ in *Gobius niger* Linnaeus, 1758 (Vitturi and Catalano 1989), but with a conspicuous modal value of $2n=48$.

In contrast to Blennioidei, suborder Gobioidei shows much more dynamic karyotype evolution, demonstrating highly variable karyotype patterns, where the diploid number ranges from $2n=30$ for *Neogobius eurycephalus* (Kessler, 1874) (Ene 2003), to $2n=62$ in *Mogurnda mogurnda* (Richardson, 1844) (Nogusa 1960). Cytogenetic data for 95 species show that only 9.6% have $2n=48$ chromosomes, whereas the highest frequencies observed correspond to $2n=46$ in 40% of species investigated, and $2n=44$ in 32% (Table 1). As such, both Gobioidei species studied here are included in the group showing $2n=48$ chromosomes, *L. nuchipinnis* with $2st+46a$ and FN=50 and *B. soporator* with $2m+6st+40a$ and FN=56. Thus, *B. soporator* differs from *L. nuchipinnis* in the presence of metacentric chromosomes and different numbers of subtelocentric and acrocentric chromosomes in the karyotype.

Among chromosome rearrangements involved in karyotypic differentiation of Gobiidae, Robertsonian fusions stand out, and are likely the most common event in this group (Amores et al. 1990; Galetti et al. 2000). However, other more complex changes in karyotypic structure (Thode et al. 1988; Vitturi and Catalano 1989; Caputo et al. 1997; Caputo et al. 1999), as well as the presence of different sex chromosomes (e.g., Pezold 1984; Baroiller et al. 1999), can also be observed, corroborating the high dynamic evolution that characterizes suborder Gobioidei. It has been suggested that the baseline/ancestral karyotype for Gobiidae would consist of $2n=46$ acrocentric chromosomes (Vasil'ev and Grigoryan 1993), from which an increase in bi-brachial chromosomes would characterize more derived karyotypes. Based on this proposal, *B. soporator* (FN=56) would experience a greater number of structural rearrangements during its karyotypic evolution process in relation to *L. nuchipinnis* (FN=50).

Location and frequency of Ag-NOR sites are efficient cytotaxonomic markers in many groups of fish (Caputo 1998). Among species of Gobiidae, at least six different arrangement patterns for nucleolar organizer regions have been identified (Fig. 2), which supports the occurrence of intense karyotypic diversification mechanisms in this group. Thus, Ag-NOR sites can be found (a) in the telomeric region on the short arm of a single pair of acrocentric chromosomes, as in *Gobius fallax* Sarato, 1889 (Thode et al. 1983) and *Gobius paganellus* Linnaeus, 1758 (Caputo 1998); (b) in the telomeric region on the long arm of a single pair of acrocentrics, such as in *Zosterisessor ophiocephalus* (Pallas, 1814) (Caputo 1998); (c) in the interstitial/pericentromeric region on the long arm of a single pair of acrocentric chromosomes, as seen in *Proterorhinus marmoratus* (Pallas, 1814) (Ráb 1985) and *Gobius cobitis* Pallas, 1814 (Caputo 1998); (d) in the telomeric region on the short arm of a single subtelocentric pair, described in *B. soporator*; (e) in the interstitial/pericentromeric region on the long arm of a single metacentric pair, observed in *N. eurycephalus* (Ene 2003); and (f) in the telomeric regions on the short arms of two acrocentric chromosome pairs, recorded in *Gobiusculus flavescens* (Fabricius, 1779) (Klinkhardt 1992).

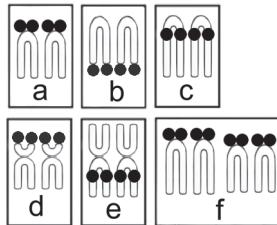


Figure 2. Ag-NOR phenotypes **a–f** described in species of Gobiidae. Ag-NORs sites described in the karyotypes of Gobiidae species were found **a** in the telomeric region on the short arm of a single pair of acrocentric chromosomes **b** in the telomeric region on the long arm of a single pair of acrocentrics **c** in the interstitial/peri centromeric region on the long arm of a single pair of acrocentric chromosomes **d** in the telomeric region on the short arm of a single subtelocentric pair **e** in the interstitial/peri centromeric region on the long arm of a single metacentric pair and **f** in the telomeric regions on the short arms of two acrocentric chromosome pairs.

Few data are available on ribosomal sites for Labrisomidae. Ag-NORs in *L. nuchipinnis* exhibit the phenotype (b) described above, in addition to both species of Blenniidae, *O. trinitatis* and *S. cristata*, which may suggest an ancestral condition for this location.

In contrast, other chromosome characteristics, such as C-positive heterochromatin distribution, may be more conserved. This occurs in several species of Perciformes where discrete blocks are preferentially located in the centromeric/peri centromeric regions of chromosomes (Molina 2007). This pattern is repeated in *S. cristata*, *O. trinitatis* and *L. nuchipinnis*, as well as in some Gobiidae, such as *G. cobitis*, *Z. ophiocephalus* and *N. eurycephalus* (e.g. Caputo et al. 1997; Ene 2003). In *B. soporator*, in addition to centromeric/peri centromeric regions, heterochromatic sites are also observed in terminal regions of some chromosomes. This arrangement has already been described for other Gobiidae, including *G. paganellus* and *G. niger*, where peri centromeric and telomeric heterochromatic regions are distributed among almost all chromosomes (Amores et al. 1990; Caputo et al. 1997).

Moreover, karyotypic diversity present in Gobioidei is increased by the occurrence of chromosome polymorphisms frequently observed in this group. This is particularly evident in several examples of intraspecific karyotypic variability, as well as polymorphisms involving different types of chromosome rearrangements, such as in *G. niger* (Vitturi and Catalano 1989; Caputo et al. 1997) and *G. fallax* (Thode et al. 1988). Data obtained for the paedomorphic Gobiidae *Aphia minuta* (Risso, 1810) also show variations in the diploid number and chromosome formula, resulting in five different cytotypes ($2n=41-44$ and $FN=42-44$) (Caputo et al. 1999). Similar karyotypic variability was reported in *N. eurycephalus*, where three specific cytotypes ($2n=30$, 31 and 32) were associated to the occurrence of centric fusions (Ene 2003). All these examples demonstrate clear chromosomal dynamism, with possible transitions to new karyotype patterns.

In fact, karyotypic diversity among Blennioidei and Gobioidei seems to accompany phyletic diversification of these groups. This is a result of vicariant factors (Pampoulie et al. 2004) and could be favored by their low dispersive potential (Fanta 1997), as well as ecological specificities that favor population fractionation in this family (Huyse et al. 2004). The present study also highlight the importance of ribosomal sites as effective chromosomal markers in the further cytogenetic studies in gobiids species.

Acknowledgements

We are grateful to the National Council of Technological and Scientific Development (CNPq) for its financial support (Project 556793/2009-9) and to José Garcia Júnior for taxonomic identification of species.

References

- Affonso PRAM (2000) Caracterização citogenética de peixes de recifes de corais da família Pomacanthidae (Perciformes). Master thesis, Universidade Federal de São Carlos, São Carlos, SP, Brasil. [in Portuguese]
- Affonso PRAM, Guedes W, Pauls E, Galetti Jr PM (2001) Cytogenetic analysis of coral reef fishes from Brazil (families Pomacanthidae and Chaetodontidae). *Cytologia* 66: 379–384.
- Akihito, Iwata A, Kobayashi T, Ieko K, Imanishi T, Ono H, Umehara Y, Hamamatsu C, Sugiyama K, Ikeda Y, Sakamoto K, Fumihito A, Ohno S, Gojobori T (2000) Evolutionary aspects of gobioid fishes based upon a phylogenetic analysis of mitochondrial cytochrome *b* genes. *Gene* 259: 5–15.
- Almada F, Almada VC, Guillemaud T, Wirtz P (2005) Phylogenetic relationships of the north-eastern Atlantic and Mediterranean blenniids. *Biological Journal of the Linnean Society* 86: 283–295.
- Amores A, Giles V, Thode G, Alvarez MC (1990) Adaptive character of a Robertsonian fusion in chromosomes of the fish *Gobius paganellus* (Pisces, Perciformes). *Heredity* 65: 151–155.
- Arai R (1981) Fishes of the genus *Luciogobius* and *Inu* (Gobiidae) from peninsula Idzu, Central Japan. *Memoirs of National Science Museum* 14: 151–166.
- Arai R (1984) Karyotypes of a mugiloidid, *Parapercis kamoharai*, and a blenniid, *Omobranchus punctatus* (Pisces, Perciformes). *Bulletin of National Science Museum* 10: 209–213.
- Arai R, Fujiki S (1979) Chromosomes of Japanese gobioid fishes (IV). *Bulletin of National Science Museum* 5: 153–159.
- Arai R, Katsuyama I, Sawada Y (1974) Chromosomes of Japanese gobioid fishes (II). *Bulletin of National Science Museum* 17: 269–279.
- Arai R, Kobayashi H (1973) A chromosome study on thirteen species of Japanese gobiid fishes. *Jap. J. Ichthyol.* 20: 1–6.

- Arai R, Sawada Y (1974) Chromosomes of Japanese gobioid fishes (II). Bulletin of National Science Museum 17: 97–102.
- Arai R, Sawada Y (1975) Chromosomes of Japanese gobioid fishes (III). Bulletin of National Science Museum 1: 225–232.
- Arai R, Shiotsuki K (1973) A chromosome study on three species of the tribe Salariini from Japan (Pisces, Blenniidae). Bulletin of National Science Museum 16: 581–584.
- Arai R, Shiotsuki K (1974) Chromosomes of six species of Japanese blennioid fishes Bulletin of National Science Museum 17: 261–268.
- Brum MJI, Aguilar CT, Correa MM, Oliveira C, Galetti Jr PM (1992) Estudos citogenéticos em peixes marinhos, análises cromossômicas nas famílias Clupeidae (Clupeiformes), Serranidae, Pomadasytidae and Blenniidae. Proceedings of the IV. Simpósio de Citogenética Evolutiva e Aplicada de Peixes Neotropicais, Rio de Janeiro, 1992, Rio de Janeiro, 43.
- Brum MJI, Galetti Jr PM (1997) Teleostei ground plan karyotype. Journal of Computational Biology 2: 91–102.
- Brum MJI, Oliveira C, Correa MM, Oliveira CC, Galetti Jr PM (1995) Cytogenetic studies on the Perciformes *Orthopristis ruber* (Haemulidae) and *Scartella cristata* (Blenniidae). Caryologia 48: 309–318.
- Cano J, Alvarez MC, Thode G, Munoz E (1982) Phylogenetic interpretation of chromosomal and nuclear-DNA-content data in the genus *Blennius* (Blenniidae: Perciformes). Genetica 58: 11–16.
- Caputo V (1998) Nucleolar organizer (NOR) and cytotaxonomic implications in six species of gobiid fishes (Perciformes, Gobiidae). Italian Journal of Zoology 65: 93–99.
- Caputo V, Caniglia ML, Machella N (1999) The chromosomal complement of *Aphia minuta*, a paedomorphic goby. Journal of Fish Biology 55: 455–458.
- Caputo V, Machella N, Cerioni-Nisi P, Olmo E (2001) Cytogenetics of nine species of Mediterranean blennies and additional evidence for an unusual multiple sex-chromosome system in *Parablennius tentacularis* (Perciformes, Blenniidae). Chromosome Research 9: 3–12.
- Caputo V, Marchegiani F, Sorice M, Olmo E (1997) Heterochromatin heterogeneity and chromosome variability in four species of gobiid fishes (Perciformes: Gobiidae). Cytogenetics and Cell Genetics 79: 266–271. doi: 10.1159/000134739
- Caputo V, Vitturi R, Odierna G, Cano J, Olmo E, Colombe MS (1996) Characterization of mitotic chromosomes in the gobiid fish *Zosterisessor ophiocephalus* (Pallas, 1811) (Perciformes, Gobiidae). Biologisches Zentralblatt 115: 328–336.
- Carbone P, Vitturi R, Catalano E, Macaluso M (1987) Chromosome sex determination and Y-autosom fusion in *Blennius tentacularis* (Brunnich, 1765) (Pisces, Blenniidae). Journal of Fish Biology 31: 597–602. doi: 10.1111/j.1095-8649.1987.tb05264.x
- Catalano E, Vitturi R, Zava B, Macaluso M (1985) Ritrovamento di *Parablennius pilicornis* (Cuvier, 1829) nelle acque italiane e suo cariotipo (Pisces, Blenniidae). Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 126: 155–164.
- Cataudella S, Civitelli MV (1975) Cytotaxonomical consideration of the genus *Blennius* (Pisces: Perciformes). Experientia 31: 167–169.

- Cataudella S, Civitelli MV, Capanna E (1973) The chromosomes of some mediterranean teleosts: Scorpaenidae, Serranidae, Labridae, Blenniidae, Gobiidae (Pisces: Scorpaeniformes, Perciformes). *Bulletino di Zoologia* 40: 385–389.
- Chen TR, Ebeling AW (1971) Chromosomes of the goby fishes in the genus *Gillichthys*. *Copeia* 1971: 171–174.
- Cook PC (1978) Karyotypic analysis of the gobiid fish genus *Quietula* Jordan and Evermann. *Journal of Fish Biology* 12: 173–179.
- Ene AC (2003) Chromosomal polymorphism in the goby *Neogobius eurycephalus* (Perciformes: Gobiidae). *Marine Biology* 142: 583–588. doi: 10.1007/s00227-002-0978-3
- Fanta E (1997) Behaviour and circadian rhythm of the fish *Bathygobius soporator* Valenciennes (Gobiidae) under the influence of environmental salinity and temperature. *Revista Brasileira de Zoologia* 14: 221–224.
- Fei Z, Tao R (1987) Studies on the karyotypes of four species in Gobioidei and compared with other fishes in there. *Journal of Zhejiang College of Fisheries* 6: 127–131.
- Floeter SR, Gasparini JL (2000) The southwestern Atlantic reef fish fauna: composition and zoogeographic patterns. *Journal of Fish Biology* 56: 1099–1114. doi: 10.1111/j.1095-8649.2000.tb02126.x
- Garcia E, Alvarez MC, Thode G (1987) Chromosome relationships in the genus *Blennius* (Blenniidae, Perciformes) C-banding patterns suggest two karyoevolutional pathways. *Genetica* 72: 27–36.
- Galetti Jr PM, Aguilar CT, Molina WF (2000) An overview on marine fish cytogenetics. *Hydrobiologia* 420: 55–62.
- Galetti Jr PM, Molina WF, Affonso PRAM, Aguilar CT (2006) Assessing genetic diversity of Brazilian reef fishes by chromosomal and DNA markers. *Genetica* 126: 161–177.
- Giles V, Thode G, Alvarez MC (1985) A new Robertsonian fusion in the multiple chromosome polymorphism of a Mediterranean population of *Gobius paganellus* (Gobiidae, Perciformes). *Heredity* 55: 255–260.
- Gold JR, Li C, Shipley NS, Powers PK (1990) Improved methods for working with fish chromosomes with a review of metaphase chromosome banding. *Journal of Fish Biology* 37: 563–575.
- Gysels ES, Hellemans B, Pampoulie C, Volckaert AM (2004) Phylogeography of the common goby, *Pomatoschistus microps*, with particular emphasis on the colonization of the Mediterranean and the North Sea. *Molecular Ecology* 33: 403–417.
- Howell WM, Black DA (1980) Controlled silver staining of nucleolus organizer region with protective colloidal developer: a 1-step method. *Experientia* 36: 1014–1015.
- Huyse T, Houdt JV, Volckaert FA (2004) Paleoclimatic history and vicariant speciation in the “sand goby” group (Gobiidae, Teleoste). *Molecular Phylogenetics and Evolution* 32: 324–36.
- Ivanov VN (1975) Chromosomes of the Black sea Gobiidae - *Gobius melanostomus* (Pallas) and *Gobius batrachcephalus* (Pallas). *Tsitologiya i Genetika* 9: 551–552.
- Khuda-Bukhsh AR (1978) Somatic chromosomes of an estuarine fish, *Trypauchen vagina* (Fam.: Gobiidae) from Sagar Island, West Bengal, India. *Current Science* 47: 137–138.

- Khuda-Bukhsh AR, Barat A (1987) Chromosomes in fifteen species of Indian teleost (Pisces). *Caryologia* 40: 131–144.
- Khuda-Bukhsh AR, Nayak K (1990) Karyotypic studies in six species of brackish water fishes from India. *Kromosomo* 2: 1955–1960.
- Klinkhardt MB (1989) Untersuchungen zur Karyologie und Fruchtbarkeit von *Pomatoschistus microps* (Kroyer) und *P. minutus* (Pallas) (Teleostei, Gobiidae). Aus einem inneren Küstengewässer der südwestlichen Ostsee. *Zoologischer Anzeiger* 222: 177–190.
- Klinkhardt MB (1992) Chromosome structures of four Norwegian gobies (Gobiidae, Teleostei) and a hypothetical model of their karyo-evolution. *Chromatin* 3: 169–183.
- Levan A, Fredga K, Sandberg AA (1964) Nomenclature for centromeric position on chromosomes. *Hereditas* 52: 201–220.
- Maldonado-Monroy MC, Uribe-Alcocer M, Arreguin Spinoza J, Castro Perez A (1985) Karyotypical studies on *Dormitator maculatus* Bloch and *Gobiomorus maculatus* Lacepede (Gobiidae, Perciformes). *Cytologia* 50: 15–21.
- Manna GK, Prasad R (1974) Chromosome analysis in three species of fishes belonging to family Gobiidae. *Cytologia* 39: 609–618.
- Molina WF (2005) Intraspecific karyotypical diversity in brackish water fishes of the Eleotridae family (Pisces, Perciformes). *Cytologia* 70: 39–45.
- Molina WF, Galetti Jr PM (2004) Karyotypic changes associated to the dispersive potential on Pomacentridae (Pisces, Perciformes). *Journal of Experimental Marine Biology and Ecology* 309: 109–119. doi: 10.1016/j.jembe.2004.03.011
- Musammil A (1974) A chromosome study of two species of *Gobiosoma* from Venezuela (Gobiidae, Teleostei). *Boletim del Instituto Oceanografico da Universidad do Oriente* 13: 11–16.
- Muss A, Robertson DR, Stepien CA, Wirtz P, Bowen BW (2001) Phylogeography of *Ophioblennius*: The role of ocean currents and geography in reef fish evolution. *Evolution* 55: 561–572. doi: 10.1111/j.0014-3820.2001.tb00789.x
- Nadamitsu S (1974) Karyological studies of two types of Gobiod fish, “Yoshinobori”. *Bulletin of Hiroshima Women’s University* 9: 3–9.
- Nayak K, Khuda-Bukhsh AR (1987) Chromosomes of two species of fishes *Apocryptes* (Gobiidae: Pisces). *Environment and Ecology* 5: 371–373.
- Nelson JS (2006) Fishes of the world, 4 ed, New York, 601 pp.
- Nishikawa S, Amaoka K, Nakanishi K (1974) A comparative study of chromosomes of twelve species of gobioid fish in Japan. *Japanese Journal of Ichthyology* 21: 61–71.
- Nogusa S (1960) A comparative study of the chromosomes of fishes with particular considerations on taxonomy and evolution. *Memoirs of the Hyogo University of Agriculture* 3: 1–62.
- Oliveira C, Almeida-Toledo LF (2006) Evidence of an XX/XY sex chromosome system in the fish *Dormitator maculatus* (Teleostei, Eleotrididae). *Genetics and Molecular Biology* 29(4): 653–655.
- Pampoulie C, Gysels ES, Maes GE, Hellemans B, Lentjes V, Jones AG, Volckaert FAM (2004) Evidence for fine-scale genetic structure and estuarine colonization in a potential high gene flow marine goby (*Pomatoschistus minutus*). *Heredity* 92: 434–445.

- Pezold F (1984) Evidence for multiple sex chromosomes in the freshwater goby, *Gobionellus shufeldti* (Pisces: Gobiidae). *Copeia* 1984: 235–238.
- Rab P (1985) Karyotype of the Danube goby, *Proterorhinus marmoratus* (Pisces, Gobiidae). *Folia Zoologica (Brno)* 34: 329–334.
- Rishi KK, Singh J (1982) Karyological studies on five estuarine fishes. *Nucleus* 25: 178–180.
- Rocon-Stange EA (1992) Caracterização cromossômica de *Eleotris pisonis* (Perciformes, Eleotrididae). Proceedings of the IV Simpósio de Citogenética Evolutiva e Aplicada de Peixes Neotropicais, Rio de Janeiro, 1992, Rio de Janeiro, 45.
- Stange EAR, Passamani M (1986) Caracterização cromossômica de *Awaous tajasica* (Lichtenstein, 1822) (Pisces, Gobiidae). Proceedings of the I Simpósio de Citogenética Evolutiva e Aplicada de Peixes Neotropicais. São Carlos, 1986, São Carlos, 59.
- Subrahmanyam K (1969) A karyotypic study of the estuarine fish *Boleophthalmus boddaerti* (Pallas) with calcium treatment. *Current Science* 38: 437–439.
- Sumner AT (1972) A simple technique for demonstrating centromeric heterochromatin. *Experimental Cell Research* 75: 304.
- Tavolga WN (1950) Pattern variability among populations of the gobiid fish, *Bathygobius soporator*. *Copeia* 182–194.
- Thacker CE (2003) Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). *Molecular Phylogenetics and Evolution* 26: 354–368. doi: 10.1016/S1055-7903(02)00361-5
- Thode G, Alvarez MC (1983) The chromosome complements of two species of *Gobius* (Teleostei, Perciformes). *Experientia* 39: 1312–1314.
- Thode G, Giles V, Alvarez MC (1985) Multiple chromosome polymorphism in *Gobius paganelius* (Teleostei, Perciformes). *Heredity* 54: 3–7. doi: 10.1038/hdy.1985.2
- Thode G, Martinez G, Ruiz JL, Lopez JR (1988) A complex chromosomal polymorphism in *Gobius fallax* (Gobiidae, Perciformes). *Genetica* 76: 65–71.
- Uribe-Alcocer M, Arreguin JA, Padilla AT, Perez AC (1983) The chromosomes of *Dormitator latifrons* (Pisces: Gobiidae). Anales del Instituto de Biología, Universidad Nacional Autónoma de Mexico, Serie Zoología 10: 23–30.
- Uribe-Alcocer M, Diaz-Jaimes P (1996) Chromosome complements of *Gobionellus microdon* and *Eleotris picta* collected in Mexico. *Journal of Fish Biology* 48: 796–798. doi: 10.1111/j.1095-8649.1996.tb01473.x
- Vasil'ev VP (1985) The evolutionary karyology of fishes (=Evoljuzionnaja kariologiya ryb). Nauka, Moscow, 300 pp.
- Vasil'ev VP, Grigoryan KA (1992) Karyology of fishes from the family Gobiidae. *Voprosy Ikhtiolozii* 32: 27–40.
- Vasil'ev VP, Grigoryan KA (1993) Karyology of the Gobiidae. *Journal of Ichthyology* 33: 1–16.
- Vasil'ev VP, Vasil'yeva ED (1994) The new systematics of freshwater Caucasian gobies: three distinct species within former *N. platyrostris constructor* (Gobiidae). Proceedings of the VIII European Society Congress of Ichthyology. Oviedo, 1994, Oviedo, 66.
- Vitturi R, Carbone P, Catalano E, Macaluso M (1986) Karyotypes of five species of Blennioidea (Pisces, Perciformes). *Caryologia* 39: 273–279.

- Vitturi R, Catalano E (1989) Multiple chromosome polymorphism in the gobiid fish *Gobius niger joso* L. 1758 (Pisces, Gobiidae). Cytologia 54: 231–235.
- Wang HY, Tsai MP, Dean J, Lee SC (2001) Molecular phylogeny of gobioid fishes (Perciformes: Gobioidei) based on mitochondrial 12S rRNA sequences. Molecular Phylogenetics and Evolution 20: 309–408. doi: 10.1006/mpev.2001.0957
- Webb CJ (1986) Karyology of the Indo-Pacific *Parioglossus raoi* (Herre) (Teleostei: Gobioidae) from Fiji. Australian Journal of Marine and Freshwater Research 37: 347–351. doi: org/10.1071/MF9870777
- Wirth T, Bernatchez L (2001) Genetic evidence against panmixia in European eel. Nature 409: 1037–1040. doi: 10.1038/35059079
- Yamada J (1967) An observation of the chromosomes in the embryonic cells of a goby, *Chænogobius urotaenia* (Hilgendorf). Bulletin of the Faculty of Fisheries Hokkaido University 18: 183–187.