ZEBRAFISH
Volume 00, Number 00, 2016

DOI: 10.1089/zeb.2015.1143

Original Article

Trends on the Karyotype Acrocentrization Within Carangidae (Perciformes): A New Phylogenetic Evidence About a Traditional Marine Paradigm

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Abstract

Carangidae is a morphologically diverse family of marine fish, characterized by stable karyotypes, predominantly with $2n = 48$, composed of acrocentric chromosomes (A). This stability is shared with other families of the order Perciformes, which resulted in the hypothesis that 48A is a plesiomorphic karyotype of the group. We tested this hypothesis in the Carangidae family using comparative phylogenetic methods, investigating the evolution of karyotype characters (including chromosome number, morphology, and number of chromosome arms per karyotype [fundamental number, FN]). Our analyses revealed that $2n = 48$ is most likely the ancestral chromosome number for the family. However, an extremely variable number of FNs, always above 48, was observed in basal clades within the family and sister groups. On the other hand, the reduced FN = 48 was consistently observed only in the most derived clades, indicating a tendency for acrocentrization. The number of acrocentric chromosomes apparently was accompanied by a trend of reduction in the genome size (1C-value), suggesting that these changes might be correlated. Our data contradict the marine fish hypothesis that the $2n = 48$ acrocentric karyotype is plesiomorphic, at least for Carangidae, and reveal the importance for the correct interpretation of karyotype in a temporal and phylogenetic context.

Introduction

Understanding the phylogenetic relationships among organisms is a premise of any evolutionary study, which enables the comprehension of how the current species share a common history through their progeny.[1] In this respect, karyotype characteristics have emerged as one of the most powerful genetic tools in taxonomy (cytotaxonomy) and evolutionary analysis.[2,3] Chromosomes are the true genetic material and, therefore, any change in the karyotypes often results in reproductive isolation and, consequently, cladogenetic events.[4] From this perspective, karyotype variation can reveal evidence of a relationship between chromosomal changes and diversification of organism groups.[5] Therefore, groups of species which show wide chromosomal diversity offer an excellent model for the reconstruction of ancestral karyotypes, even for those possessing only basic information such as karyotype chromosomal number ($2n$) and the number of chromosome arms per complement or fundamental number (FN).[6] This approach, has recently been favored by new comparative phylogenetic methods, through new software and algorithms that enable better interpretation of the diversification and karyotype evolution.[7–9]

Among the challenges found in rebuilding the karyotype evolution, through comparative phylogenetic methods, are the groups with stable karyotypes or very low degree of variability. In the marine environment, fish belonging to the order Perciformes are the most diverse group among the Teleostei, with 160 families and $\sim$10,000 species.[10] Despite this huge diversity, the group presents stable karyotypes, in general $2n = 48$ predominantly composed by acrocentric chromosomes (A).[11–13] For this condition, the karyotype $2n = 48$A was suggested to be basal (plesiomorphic) for the order, and the karyotype variants would be considered as derived condition.[13,14]

Among the Perciformes, one of the most morphologically diversified families is Carangidae, comprising 148 species distributed among 13 genera.[15] This family reveals great ecological diversity, being widely distributed in all oceans, occupying a variety of habitats, from rocky environments

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and coral reefs to estuaries.[10] From the karyotype perspective, the carangids are quite stable showing $2n = 48A$ and chromosome evolution related to mainly pericentric inversion events and centric fission/fusion leading to changes in the chromosome morphology from acrocentric to metacentric (M) or submetacentric (SM).[16–19] A molecular phylogeny analysis indicates that this family is monophyletic, although some genera such as *Caranx* and *Carangoides* have been considered paraphyletic.[20,21] Studies performed using a molecular clock, calibrated with a rich fossil record, have shown that the origin of Carangidae as well as the sister families Echeneidae, Coryphaenidae, and Rachycentridae, date back to the late Cretaceous.[21,22]

From a cytogenetic perspective, the Carangidae family already possesses chromosomal data available for representatives of all genera, with data and chromosomal morphology for 32 species, as well as for the sister groups Rachycentridae and Coryphaenidae.[23–25] With such an information volume, along with the availability of recent molecular phylogenies and DNA sequences in the databases for most of the species, Carangidae is an excellent model for studying karyotype evolution trends in a phylogenetic context. These conditions allow to test the hypothesis whether $2n = 48A$ corresponds to the plesiomorphic karyotype of the family, as well as the role of pericentric inversions in the karyotype diversification of this group. In this context, we conducted a phylogenetic reconstruction for the family Carangidae based on the mitochondrial sequences of cytochrome B (*Cyt-b*) and cytochrome oxidase 1 (*COI*). Next, the topology of these trees was used to test the evolution of the karyotype data (number/chromosome morphology and genome size) using reconstruction methods of the ancestral character, with the purpose of elucidating the main mechanisms of chromosomal diversification within this group and the trends between the lineages.

Materials and Methods

Data sampling

The phylogenetic analysis included samples of 34 taxa. DNA sequences of the mitochondrial *Cyt-b* and *COI* were downloaded from GenBank (Table 1). Sequences from the Carangidae genera *Alectis*, *Alepes*, *Atropus*, *Atule*, *Caranx*, *Carangoides*, *Chloroscombrus*, *Megalaspis*, *Oligoplites*,

Table 1. Analyzed Species of Carangidae Family and Outgroups (Rachycentridae and Coryphaenidae) with Their Diploid Chromosome Numbers, Fundamental Number, Metacentric/Submetacentric, Subtelocentric/Acrocentric, and the Genbank Access Numbers

Espécie	2n	*FN*	*M/SM*	*ST/A*	*Cyt-b*	*COI*
Alectis ciliaris	48	48	—	48	AF363739	KF461132
Alepes djedaba	56	56	—	56	EF512295	HQ561009
Alepes melanoptera	48	48	2	46	—	HQ561010
Atropus atropos	48	48	—	48	AY050729	HQ560998
Atule mate	50	64	14	36	AF515737	KC970450
Carangoides armatus	48	48	—	48	NC_004405	KC970373
Carangoides bartholomaei	48	50	—	46	NC_004405	JQ841092
Carangoides equula	48	48	—	48	AY050728	AY541645
Carangoides praeustus	56	56	10	38	—	KC508506
Caranx latus	48	50	2	46	AY050724	JQ365258
Caranx lugubris	48	54	6	42	—	JQ431542
Caranx sansun (ignobilis)	48	50	2	46	KJ464979	KF009574
Caranx sexfasciatus	48	48	—	48	AY050760	KC970458
Chloroscombrus chrysurus	48	48	—	48	AY050752	KF461158
Coryphaena hippurus	48	54	8	40	AY050761	KJ968007
Megalaspis cordyla	50	50	—	50	KJ464986	HQ561011
Oligoplites saliens	48	52	4	44	—	JX124836
Rachycentron canadum	48	50	2	46	AY050759	KF489739
Scomberoides lysan	48	52	8	44	—	JX983494
Selene brownii	48	48	—	48	AF363750	—
Selene setapinnis	46	48	2	44	AF363745	KF461235
Selene vomer	48	50	—	48	AF363746	GU225036
Seriola dumerili	48	50	2	46	AB638328	FJ237922
Seriola dumerili[1]	48	52	2	46	AF143194	FJ237927
Seriola lalandi	48	52	4	44	AB264296	EU752208
Seriola quinqueradiata	48	50	2	46	AB263290	NC_016868
Seriola nigrofasciata	48	48	—	48	DQ197998	KF930429
Trachinotus carolinus	48	56	8	40	AY050756	JX034018
Trachinotus falcatus	48	58	10	38	AY050738	JQ365603
Trachinotus goodei	48	52	4	44	AY050741	GU702385
Trachinotus ovatus	48	54	6	42	DQ198014	KC501748
Trachurus japonicus	48	66	18	30	HM212607	KF930510
Trachurus mediterraneus	48	58	10	38	AY526548	KC501771
Trachurus trachurus	48	50	2	46	AY526533	KJ205232

2*n*, chromosome numbers; *COI*, cytochrome oxidase 1; M/SM, metacentric/submetacentric; FN, fundamental number; ST/A, subtelocentric/acrocentric; *Cyt-b*, cytochrome B.

Scomberoides, *Selene*, *Seriola*, *Trachinotus*, and *Trachurus* were analyzed. Two sister families Rachycentridae (*Rachycentron canadum*) and Coryphaenidae (*Coryphaena hippurus*) were included as outgroups.

Phylogenetic analysis

The resulting partial sequences were prealigned with Geneious 7.0.[26] and manually adjusted. The maximum likelihood (ML) and Bayesian inference (BI) searches were performed only with the *Cyt-b* and *COI* combined data (1140 pb). The best model of sequence evolution for each region was determined using the Akaike Information Criterion as implemented in jModelTest version 3.6.[27] resulting in the same model for both sequence sets GTR+G+I. The ML analysis and bootstrap support calculations (1000 replicates) were performed using the program RaxML,[28] the BI search was performed using Mr. Bayes v3.1.2[29] under a partitioned model as implemented on CIPRES Science Gateway V.3.1 (www.phylo.org). The analysis was conducted for two independent runs for 20,000,000 generations, sampling every 2000 trees. The first one-fourth of the sampled trees was discarded as burn-in. The convergence of the parameters of the models was established from the effective sample size values in Tracer v1.4 software.[30] All effective sample size values were higher than 200. Trees were visualized using FigTree v1.3.1.[31]

Karyotype character reconstruction

The ancestral state reconstruction of the karyotype data (chromosome number [2*n*], FN, metacentric/submetacentric [M/SM], and acrocentric/subtelocentric [A/ST]) were performed in Mesquite v.2.75.[32] The trace character history function was used with the 50% majority-rule consensus tree from the BI analyses. The ancestral state was inferred using ML under the Markov k-state one-parameter (Mk1) model, in which all changes are equally probable. Chromosome data of the species were taken from the literature (Table 1), and they were treated as an unordered, multistate character.

Additionally, the ancestral state of ''number of acrocentric/subtelocentric chromosomes'' along the branches of a tree were estimated using an ML approach as implemented in the package phytools in the R software ver. 3.0.1.[7]

Results

Phylogenetic relationships in Carangidae

The analyses of the mitochondrial gene dataset using both ML and BI produced highly congruent topologies (Fig. 1), which showed carangids as a monophyletic group. Among the Carangidae tribes, only the Scomberoidini was paraphyletic (*Oligoplites* and *Scomberoides*), with the other three tribes remaining monophyletic: Trachinotini (*Trachinotus*), Naucratini (*Seriola*), and the most diverse Carangini (*Trachurus*,

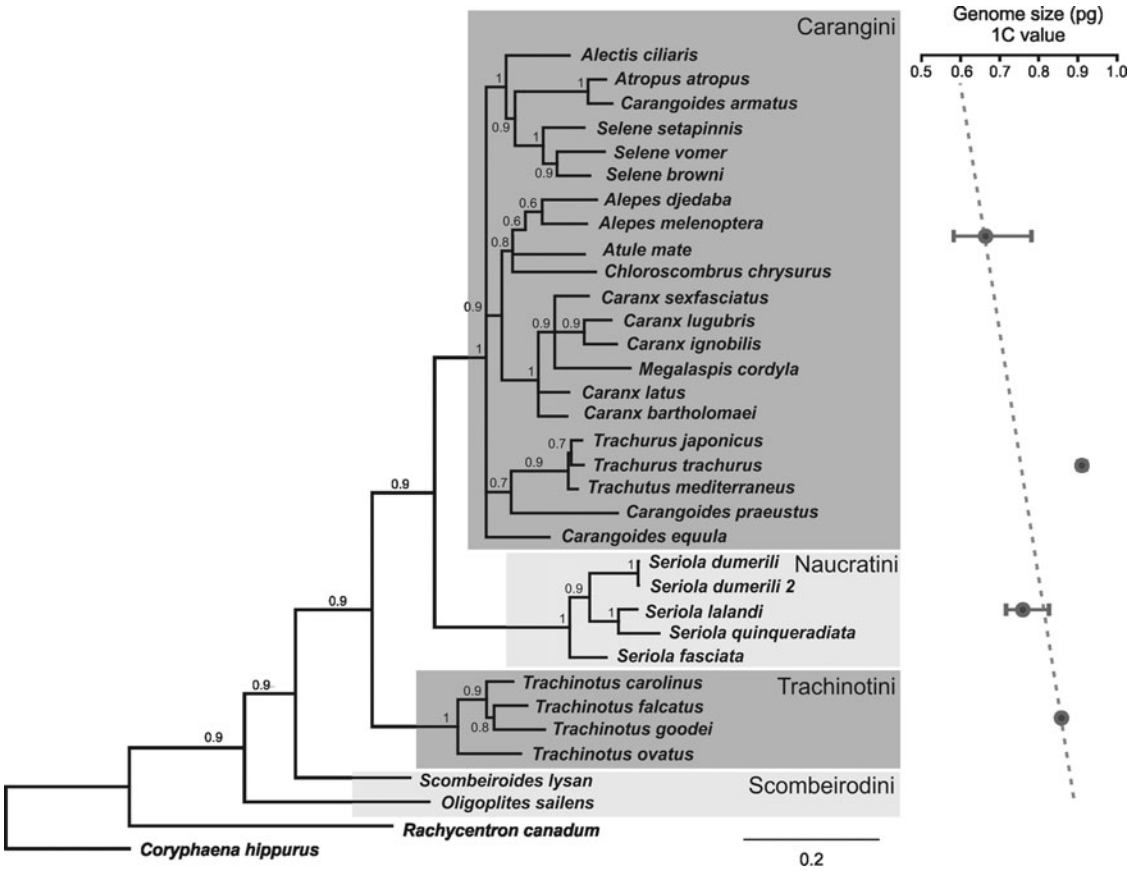

FIG. 1. Bayesian phylogeny of carangoid fish, based on the concatenated dataset analysis with branch length proportional to the number of changes over the branches. Values above the nodes represent the posterior probability of each clade. Featured genome size.

Caranx, *Carangoides*, *Alectis*, *Chloroscombrus*, *Alepes*, *Atule*, *Megalaspis, and Selene*). Representatives of the tribe Scomberoidini (*Oligoplites saliens* + *Scomberoides lysan*, PP = 0.9) appeared to be the most basal lineages in the topology. Naucratini and Carangini formed sister clades and at their base was the Trachinotini clade (PP = 0.9). The Trachinotini and Naucratini clades showed well-defined generic relations, whereas in the clade of Carangini the genus *Carangoides* was polyphyletic, in which the representatives of the genera *Caranx* and *Trachurus* were included (Fig. 1). The time of origin of the main clades comprising the tribes of Carangidae family has been adapted of Santini and Carvenale,[21] allowing interpretation of chromosomal lineage trends in a temporal context (Fig. 2).

Estimation of the ancestral karyotype of the family Carangidae

The estimation of ancestral karyotype using the ML method suggested $2n = 48$ ($p = 99\%$) as the most likely character state for the common ancestor of the clade Carangidae (Fig. 3). Chromosome number changes appeared as autapomorphies ($2n = 46$ and 56) or homoplasies ($2n = 50$) of the lineages of Carangini. On the other hand, ancestral states for the FN were more variable. The nodes that included the most basal tribes of Carangidae along with the sister families Rachycentridae and Coryphaenidae showed a FN = 52 trend with a probability of 44%. The internal probability of FN = 52 increased substantially in the tribes Carangini, Scomberoidini, and Trachinotini ($p = 88\%$). The more derived clades showed a decreased likelihood of the state FN = 52 ($p = 17\%$), whereas the predominant state FN = 48 was observed in Naucratini ($p = 54\%$) and Carangini ($p = 95\%$; Fig. 3).

Reconstruction of the percentage of acrocentric chromosome pairs per karyotype showed a transition of values of 80% over the basal clades, reaching up to 100% of the representatives of the derived groups from the Carangini clade (Fig. 4). On the other hand, the reconstruction analysis revealed that karyotypes harboring a higher number of metacentric/submetacentric (M/SM) chromosomes are predominant in basal clades, followed by a decrease (or complete elimination) of these chromosomal types in more derivative nodes (Supplementary Fig. S1; Supplementary Data are available online at www.liebertpub.com/zeb).

Genome size data (1C-value) were obtained from an online database (www.genomedatasize.com) and were available only for the representatives of the genera of *Carangoides*, *Caranx*, *Chloroscombrus*, *Seriola*, *Trachinotus*, and *Trachurus* (Supplementary Table S1). These data were correlated with the phylogenetic analysis and karyotype formulas. Among the Carangidae, estimates of genome size are available for only a few species, which prevented us from tracing the character history using comparative phylogenetic

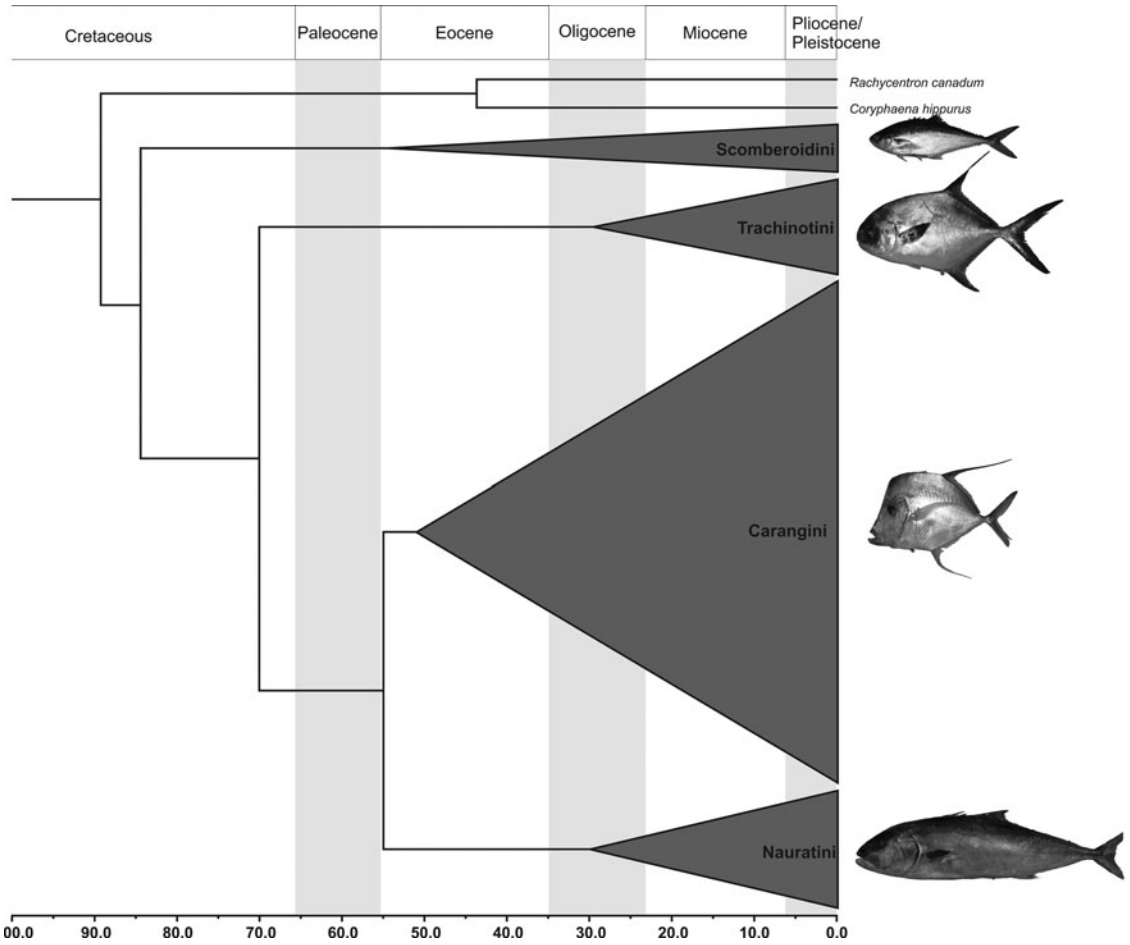

FIG. 2. Timetree of carangoid fishes adapted from Santini and Carvenale.[21]

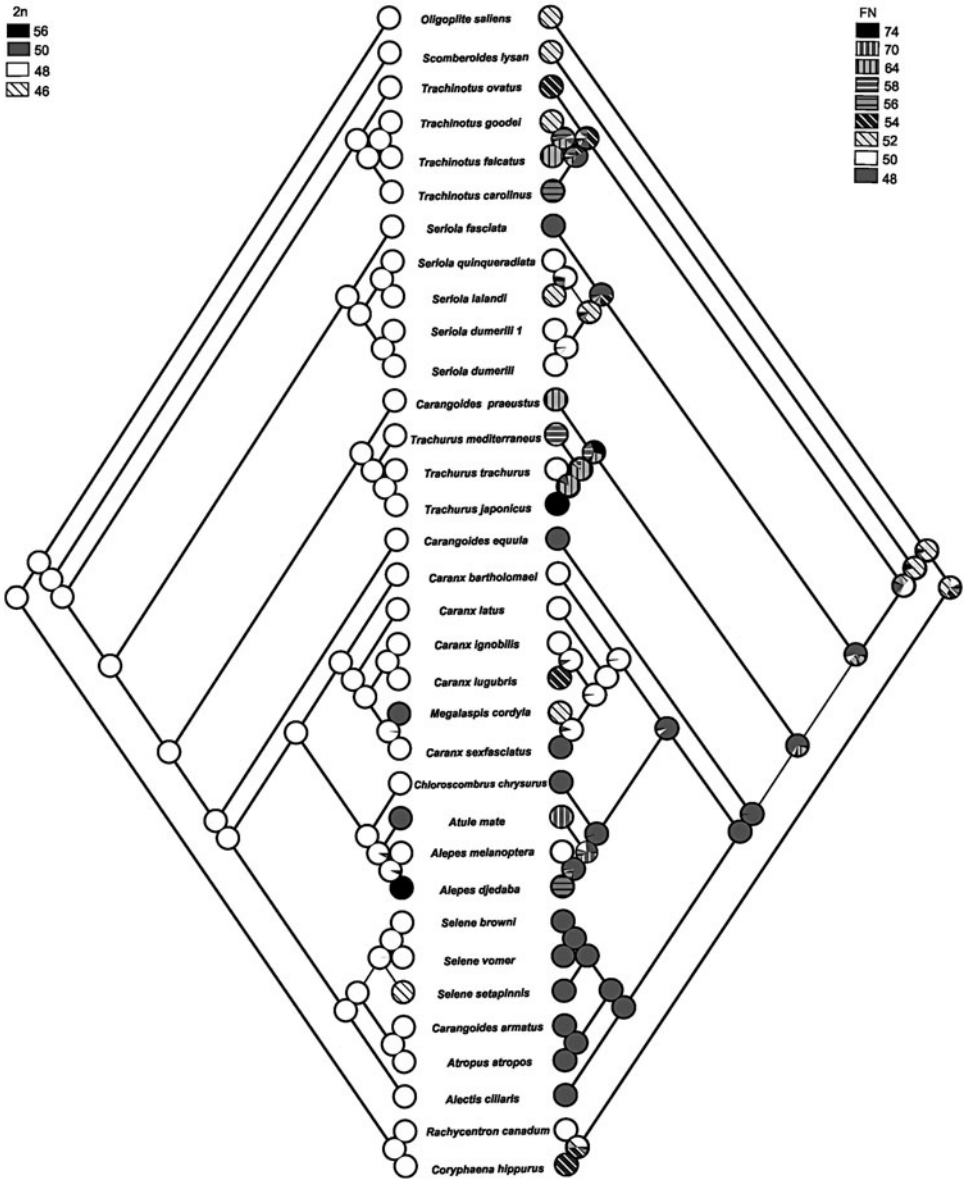

FIG. 3. Reconstruction of the ancestral state of the diploid number and fundamental number of Carangidae, and related families. The reconstruction model was performed with maximum likelihood parameter Markov (Mk1) in Mesquite software.

methods. However, the data allowed us to detect some important trends in the family.

The genome size (1C-value) ranged from 1C = 0.59 pg in *Carangoides gymnostethus* to 1C = 0.92 pg in *Trachurus novaezelandiae*. The results were organized by the average genome size of the main clade of Carangidae. The most basal clades, Trachinotini and Naucratini presented average of 1C = 0.86 and 0.76 pg, respectively. Within the clade Carangini, larger genomes were observed among the species of *Trachurus* (1C $\sim$0.91 pg), while the most derived lineages (*Carangoides, Caranx*, and *Chloroscombrus*) had the smallest genomes in average (1C = 0.66 pg).

Discussion

Karyotype evolution in Carangidae

Our data are the first phylogenetic interpretation of karyotype evolution in a family of marine fish. In the Carangidae family, monophyletism is rarely challenged, and is supported by morphological[33,34] and molecular evidence[20,21] as in the present work. Within the family, the monophyletism of the clades Trachinotini, Naucratini, and Carangini, as well as the paraphyletism of Scomberoidini, have been reported in prior studies.[20,33] Although a nonmonophyletic group, comprising the species of the Scomberoidini tribe (*O. saliens* and *S. lysan*), appear to be the most basal lineage in the family.

The Carangini tribe is the most diverse group, being the only clade that included a polyphyletic genus, *Carangoides*. The controversies surrounding the phylogenetic relationships within the Carangini tribe are widely discussed in the literature.[34–36] However, a monophyletic consensus of all genera has not been achieved yet, probably due to its great morphological and, possibly, diverse homoplasies. Our data support *Carangoides* as polyphyletic, as reported in other studies.[20,21]

About 85% of the species of Carangidae have $2n = 48$ of which 30% have karyotypes composed entirely of acrocentric chromosomes.[37] This indicates the high probability of this

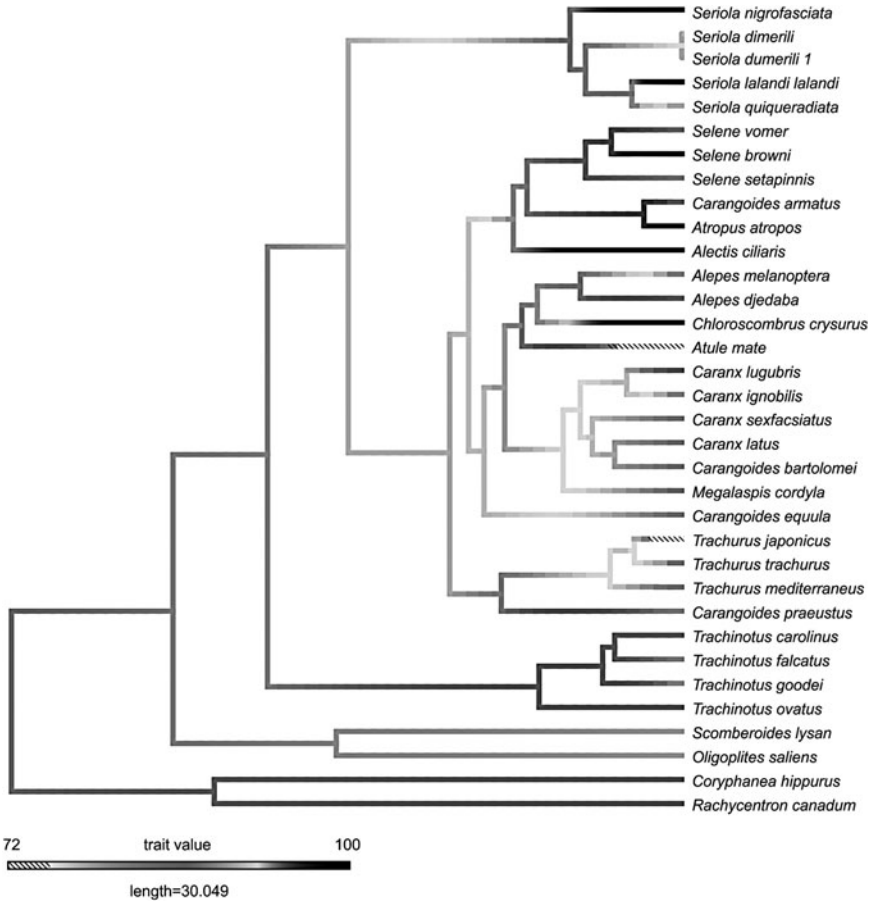

FIG. 4. Estimation of ancestral character percentage of the number of acrocentric (log-transformed maximum count of acrocentric number) along the branches and nodes of the phylogeny of Carangidae. Colors in *black* represent 100% of acrocentrics. The *horizontal bar* is a scale for the lengths of the tree branches.

chromosome number as the ancestral karyotype of this family. The $2n = 48$A has been considered as the basal karyotype, not only for this family, but for the whole order of Perciformes.[14,18,38,39] These conclusions have induced several authors to argue that the presence of bi-armed chromosomes is a phylogenetically derived karyotype feature.[13,38] However, our findings do not support this point of view. Our analyses show, by ancestral karyotype reconstruction analysis that the carangids have karyotypes with a higher proportion of acrocentric chromosomes in the most derived species. On the other hand, the basal groups and representatives of the sister families show a reduced proportion of acrocentric chromosomes per karyotype, with increase in the frequency of bi-armed chromosomes. Our findings contradict the hypothesis that $2n = 48$A would be a plesiomorphic condition in Perciformes. In this scenario, the reconstruction of FN reveals a tendency for the formation of acrocentric chromosomes (acrocentrization) in the derived clades of the family Carangidae, as suggested by previous works.[40] Although the diploid number $2n = 48$ is conserved in the family, the FN 48 varies greatly, especially in the basal groups of the Carangids.[40–42] The acrocentrization hypothesis in Carangidae can be further supported by comparing with the other external groups. The sister species of the Carangidae, *C. hippurus* (FN = 54) and *R. canadum* (FN = 50) also reveals the presence of karyotypes with bi-armed chromosomes, as well as in other basal groups. Thus, the stability of the chromosomal numbers and variation in the FN in Carangidae suggest that the major evolutionary mechanisms in the karyotype evolution of this group are pericentric inversions and in a few cases centric fusions, which are related to the high variability found in the FN of this family.[18]

The high frequency of pericentric inversions found in the karyotypes of Carangidae, as in most Perciformes, has been explained by the hypothesis of centromere drive, where the preference for monobrachial chromosomes in most derived groups seems to have occurred.[43] Indeed, meiotic drive associated with pericentric inversions has been demonstrated in a few cases.[44,45] The centromere drive theory predicts that a large number of species would have either meta-submetacentric chromosomes or acro-telocentric chromosomes, but rarely a mixture of both chromosome types.[44] Hence, our observations that karyotypes in the most derived groups of Carangidae show nonrandom predominance of acrocentrics support the long-term evolutionary trends produced by meiotic drive.

The potential for the occurrence of the preferred rearrangements can also be favored by the presence of repetitive DNA sequences and heterochromatin content, inducing and facilitating the establishment of specific chromosomal rearrangements.[43] Indeed, it is noteworthy that in Carangidae the presence of the single ribosomal site is generally found in one bibrachial chromosome frequently involved in different types of chromosomal rearrangements like inversion, fusion, and fission. This suggests that the nucleolus organizer regions may work as hotspots for chromosomal rearrangements.[16–18]

However, classical banding studies on marine Perciformes demonstrated a certain degree of karyotype stasis with a single ribosomal site and low heterochromatin content.[12]

Although only a few species of Carangidae had their genome size estimated, a slight tendency for genome reduction was observed in the most derived species. Thus, the increase in the number of acrocentric chromosomes might have been accompanied by removal of repetitive DNA, reflecting the genome reduction.[46,47] The correlation between chromosomal rearrangements and variation in genome size is uncertain for fishes. However, the acrocentrization process in Carangidae could lead to a reduction in the recombination rate, and reduce the ability of repetitive sequences to spread throughout the genome.[47]

Estimated temporal diversification in the karyotype of Carangidae

Carangidae originated in the Cretaceous, this period was characterized by tropical climate and an intense continental drift, as well as strong volcanic activity in the Indian and Pacific oceans. During this period, the Carangidae sister groups were established, as well as the most basal clades, which based on our data had most likely a $2n = 48$ karyotype, but with FN >48, formed by the M/SM chromosomes.

The acrocentrization trend began in clade Naucratini (22 Mya) in the genus *Seriola*, and later more sharply in the genera *Caranx* (20 Mya) and *Selene* (17 Mya), all dating from the Miocene.[21] This period was marked by the closure between Africa and Europe and the separation of the Thetis Sea in what is now the Indian Ocean and the Mediterranean Sea from the mid Burdigalian (c. 19.2–17.2 Mya) to Langhiano (c. 15.97–13.65 Ma).[48,49] During this era, large-scale changes in the global ocean circulation occurred, leading to a decrease in the gene flow of the marine biota in several parts of the globe.[50,51] During this time the global climate was tropical, but further decrease in temperature caused instability in the ocean environmental conditions that could have enhanced the speciation process in several lineages.[52] This condition could have allowed the selection of better adapted karyotypes, thus, leading to the acrocentrization process characteristic of this family, accompanied by a trend in genome size reduction.

The rate of chromosomal diversification appears to have been more pronounced in the genus *Trachurus*, which eludes the acrocentrization trend and has larger genomes, with the species *Trachurus japonicus* and *Trachurus mediterraneus* having the most dynamic karyotypes. These species have a more restricted distribution between Carangidae, which seems to indicate that the orogenic movement may have been more intense in this area.

Final considerations

Our data show that the evolution and diversification of Carangidae was mainly modulated by the action of pericentric inversions leading to the formation of acrocentric chromosomes in more derived branches of this family (acrocentrization). However, there is a possibility of repositioning centromere in diversification of acrocentric karyotypes. Although the diploid number 48 is stable in the group and probably the basal number, the FN 48 is most likely not the ancestral state for the family. Hence, the high FN observed in basal Carangidae groups was possibly already present during the origin of the family in the Cretaceous. Our data contradict the hypothesis that $2n = 48A$ would be the plesiomorphic karyotype for marine Perciformes, although has been investigated only in this family, reveals the importance of correct interpretation of the karyotype variability in a phylogenetic context.

Acknowledgments

The authors wish to thank the Brazilian agencies Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq—PAM #200557/2014-9, RAT 306099/2011-0 and 301208/2012-3) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES—PNPD UPJ#1273846) for financial support.

Disclosure Statement

No competing financial interests exist.

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