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Genome size distribution in phylum Cnidaria

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Abstract Cnidarians are considered ancestral metazoans and, therefore, are important taxa for studying animal evolution. However, little is known about the group's genome size (*C* value), which is an important parameter in whole-genome sequencing. To address this issue, we measured the *C* values of 27 cnidarian species from Japan, using flow cytometry, and found that they ranged from 0.26 to 3.56 pg. Excluding the results for *Agalma elegans* and *Physalia physalis* (order Siphonophorae), which had the highest *C* values among the species included in the present study, the *C* values for the cnidarians were 0.26–1.49 pg. In particular, we found that hydrozoans possessed relatively large and wide-ranging *C* values, indicating that evolution within the group involved considerable gains or losses of genomic content. Overall, the *C* values reported in the present study could be valuable for whole-genome sequencing, using next-generation sequencers, and for future research in cytogenetics.

Keywords Jellyfish · Coral · Sea anemone · DNA content · *C* value enigma

Introduction

Genome size, which has been termed *C* value by Swift [1], describes the total amount of DNA included a haploid nucleus, and an adequate understanding of *C* values and karyotypes are important for the advancement of cytogenetics, molecular biology, and phylogenetics. In the animal kingdom, *C* values are highly diverse, ranging from 18.8 Mbp (~0.02 pg) in the banana root nematode *Pratylenchus coffeae* [2] to 132.83 pg in the African lungfish *Protopterus aethiopicus* [3] (Gregory, TR. Animal Genome Size Database: http://www.genomesize.com, accessed 14 May 2016), and variation in *C* value differs widely between different phyla. For example, *C* value variation of each phylum in the animal kingdom reported 125-fold in nematodes, 130-fold in annelids, 18-fold in mollusks, and 1.5-fold in brachiopods [4], and, furthermore, no broad correlation between *C* value and organismal complexity has been reported, a phenomenon that has been coined the "*C* value paradox" [5].

Recently, it has been suggested that the paradox is caused by interspecific differences in the amount of non-coding DNA; however, it remains unclear why some species possess a high amount of non-coding DNA, while others have a very low amount, or why the patterns of *C* value distribution among taxa exist [6]. Furthermore, relationships between *C* value and cell characteristics, such as cell and nucleus size and the duration of cell cycles and development, have been reported [7].

These gaps in knowledge are commonly referred to as the "*C* value enigma" [8], and elucidating such issues will improve our understanding of the process of genome evolution. For example, in vertebrates, three consecutive whole-genome duplications (WGDs) are thought to have played an important role in vertebrate evolution [9–11], but little is known about the potential occurrence of genome duplication in ancestral taxonomic groups. Therefore, it is important to investigate *C* values and their diversity in ancestral taxonomic groups, such as the phylum Cnidaria.

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Cnidaria comprises five classes (Anthozoa, Scyphozoa, Staurozoa, Cubozoa, and Hydrozoa) and more than 11,000 species [12]. The cnidarians are widely distributed in a variety of environments, including fresh, continental, deep-sea, tropical, and Arctic waters [13–17], and cnidarian taxa from different environments exhibit a variety of life cycles and morphologies, including species that harbor symbiotic algae. In addition, some cnidarians have value to human society. For example, many basic scientific and medical research projects use a fluorescence protein from cnidarians, and hard corals (Madreporaria) constitute coral reefs and are economically valuable as tourism resources. However, jellyfish blooms, especially blooms of larger species like *Stomolophus nomurai* and poisonous species, cause damage to the fishing and tourist industries [18, 19]. Thus, ecological, molecular biological, and cytogenetic studies of cnidarians are important. Recently, the whole genome sequence of the coral *Acropora digitifera* [20] was reported. However, the development of cytogenetics in the group is less advanced than that of molecular biology, and *C* values have only been reported from 9 species in 3 classes: *Acropora digitifera,* 420 Mb (~0.43 pg) [20]; *Cassiopeia* sp., 0.33 pg; *Aurelia aurita,* 0.73 pg; *Hydra viridissima,* 0.40 pg; *H. circumcincta,* 1.15 pg; *H. vulgaris,* 1.29 pg; *H. oligactis,* 1.48 pg; *H. attenuata,* 1.85 pg; and *H. carnea,* 1.38 pg [21–23] (Gregory, TR. Animal Genome Size Database: http://www.genomesize.com, accessed 14 May 2016), with most of the reported species belonging to the genus *Hydra*. This bias in reported taxa inhibits the investigation of *C* value variation in cnidarians. Therefore, we measured the *C* values of 27 species from four classes of cnidarians, in order to investigate the evolutionary dynamics of genome size in Cnidaria. Our results could be valuable for whole-genome sequencing, since we included species like *Turritopsis* sp. (North Japan type), in which rejuvenation has been reported [24], and for future research in cytogenetics.

Materials and methods

Most of the jellyfish samples used in the present study were collected using a dipper with a long handle or a 0.22-mm mesh plankton net from quays in two areas (Ofunato and Okirai Bay) of Iwate Prefecture, Japan, from 2009 to 2010 (Table 1). However, *Sanderia malayensis* and *Cassiopea ornata* were collected from Kagoshima Bay, Kagoshima Prefecture, Japan, in September 2009; *Turritopsis* sp. (North Japan type) was collected from Otsu Port, Ibaraki Prefecture, Japan, in February 2010; and *Physalia physalis* was collected from the coast of the Miura Peninsula in Sagami Bay, Kanagawa Prefecture, Japan, in June 2016 (Table 1). Meanwhile, several corals (*Catalaphyllia jardinei*, *Physogyra lichtensteini*, *Euphyllia divisa,* and *Euphyllia ancora*) and a tropical sea anemone (*Entacmaea quadricolor*) were purchased from an aquarium shop in September 2013 and June 2015, and three other sea anemones (*Anthopleura japonica*, *Anthopleura fuscoviridis*, and *Actinia equina*) were collected in Okirai Bay (Table 1).

Either tentacle tissue or the whole bodies of smaller organisms were used to determine *C* values. To prepare the samples for flow cytometry, either tentacle tissue or whole organisms were placed in 1.5-ml microcentrifuge tubes with 2 or 3 drops of solution A (CyStain DNA 2-step extraction buffer; Partec GmbH, Görlitz, Germany), macerated with scissors, and incubated at room temperature (~21 °C) for 5 min. Next, the resulting cell suspensions were supplemented with 700 ml staining buffer (Partec) and then filtered through a 50-mm mesh filter (CellTrics; Partec). Afterward, 1.5 µl RNase A and 3 µl propidium iodide solution (Partec) were added to the filtered cell suspensions, and the stained samples were kept in the dark at 4 °C for 30 min before analysis.

Subsequently, the samples were analyzed using a PA model flow cytometer (Partec) that had been modified to measure the fluorescence of propidium iodide [25]. At least 5000 nuclei were measured per sample, and displayed modes of histograms were accepted as fluorescence intensity (FL) (Fig. 1). The *C* value of each sample was then calculated from the fluorescence intensity, according to Rees et al. [26]: *C* value (pg) = (sample FL/standard FL) × standard *C* value; and the cephalic tentacles cells of abalone (*Haliotis discus hannai*) reared at a facility of Kitasato University (Kanagawa prefecture, Japan) were used as a standard, since the species' *C* value had been reported previously (1.84 pg) [25]. In addition, the individual *C* values were converted to genome sizes (bp), according to Doležel et al. [27]: Genome size (bp) = $(0.978 \times 10^9) \times C$ value.

In order to estimate the population mean of *C* values for each species, we used the D'Agostino-Pearson normality test, which is based on skewness (*s*) and kurtosis values (*k*), to determine whether the *C* values fit to a Gaussian distribution, and then calculated 95% confidence intervals of the mean *C* values, according to a Gaussian distribution. In addition, we also compared the mean *C* values of symbiotic and non-symbiotic species, using the Mann–Whitney *U* test and the *t*-test. Statistical analyses were conducted using Prism6 for Windows (Graphpad Software, Inc., La Jolla, CA, USA).

Results

The *C* values of the 27 examined cnidarian species ranged from 0.26 pg in *Sanderia malayensis* to 3.56 pg in *Agalma elegans*, thus exhibiting a 13.69-fold variation in genome size (Table 1). The *C* values of the eight anthozoan species

Table 1 Taxonomic positions, *C* values, and collection locality for Cnidaria

Taxa				Symbiotic or non-symbiotic	*N*	C value ± SE (pg)	Genome size ± SE (Mbp)	Collected locality	Reference
Class	Order	Family	Species						
Anthozoa	Scleractinia	Acroporidae	*Acropora digitifera*	S	N/A	0.44	420	N/A	[20]
	Alcyonacea	Alcyoniidae	*Sarcophyton* sp.	S	3	0.64 ± 0.01	629 ± 7.99	Aquarium shop	Current
	Actiniaria	Actiniidae	*Anthopleura japonica*	N-S	1	0.48	467	Okirai Bay	Current
			Anthopleura fuscoviridis	N-S	4	0.51 ± 0.00	494 ± 4.23	Okirai Bay	Current
			Actinia equina	N-S	2	0.52 ± 0.00	503 ± 0.00	Okirai Bay	Current
		Stichodactylidae	*Entacmaea quadricolor*	S	10	0.88 ± 0.01	863 ± 8.44	Aquarium shop	Current
	Scleractinia	Caryophylliidae	*Catalaphyllia jardinei*	S	1	0.90	881	Aquarium shop	Current
			Physogyra lichtensteini	S	1	0.98	958	Aquarium shop	Current
			Euphyllia divisa	S	1	0.72	702	Aquarium shop	Current
			Euphyllia ancora	N-S	1	0.64	630	Aquarium shop	Current
Scyphozoa	Semaeostomeae	Pelagiidae	*Sanderia malayensis*	N-S	3	0.26 ± 0.00	251.93 ± 8.48	Kagoshima Bay	Current
		Cyaneidae	*Cyanea capillata*	N-S	1	0.39	378	Okirai Bay	Current
		Ulmaridae	*Aurelia aurita* s.l.	N-S	3	0.71 ± 0.01	695 ± 9.80	Ofunato Bay	Current
			Aurelia limbata	N-S	7	0.70 ± 0.01	681 ± 11.16	Okirai Bay	Current
	Rhizostomeae	Rhizostomatidae	*Nemopilema nomurai*	N-S	2	0.29 ± 0.01	287 ± 12.72	Okirai Bay	Current
		Cassiopeidae	*Cassiopea ornata*	S	2	0.40 ± 0.00	386 ± 6.36	Kagoshima Bay	Current
Cubozoa	Cubomedusae	Carybdeidae	*Carybdea brevipedalia*	N-S	1	0.77	756	Okirai Bay	
Hydrozoa	Anthomedusae	Corynidae	*Sarsia tubulosa*	N-S	7	0.70 ± 0.01	681 ± 13.81	Okirai Bay	Current
		Corymorphidae	*Hydrocoryne miurensh*	N-S	2	0.33 ± 0.00	323 ± 0.00	Okirai Bay	Current
		Cladonematidae	*Cladonema pacifica*	N-S	2	0.61 ± 0.01	593 ± 12.72	Okirai Bay	Current
		Oceanidae	*Turritopsis* sp. (North Japan type)	N-S	3	0.39 ± 0.00	383 ± 4.90	Otsu Port	Current
		Hydridae	*Hydra circumcincta*	N-S	N/A	1.15		N/A	[23]
			Hydra vulgaris	N-S	N/A	1.29		N/A	[23]
			Hydra oligactis	N-S	N/A	1.48		N/A	[23]
			Hydra viridissima	S	N/A	0.39		N/A	[23]
			Hydra attenuata	N-S	N/A	1.85		N/A	[23]
			Hydra carnea	N-S	N/A	1.38		N/A	[23]

Table 1 continued

Taxa				Symbiotic or non-symbiotic	*N*	C value ± SE (pg)	Genome size ± SE (Mbp)	Collected locality	Reference
Class	Order	Family	Species						
		Bougainvilliidae	*Nemopsis dofleini*	N-S	9	0.75 ± 0.00	737 ± 4.50	Okirai Bay	Current
	Leptomedusae	Abylidae	*Eutima japonica*	N-S	2	0.28 ± 0.01	269 ± 12.72	Okirai Bay	Current
		Aequoreidae	*Aequorea coerulescens*	N-S	2	0.54 ± 0.02	530 ± 31.81	Okirai Bay	Current
	Limnomedusae	Olindiasidae	*Gonionema vertens*	N-S	3	1.25 ± 0.01	1223 ± 14.69	Ofunato Bay	Current
	Trachy medusae	Rhopalonematidae	*Aglantha digitale*	N-S	1	1.49	1458	Okirai Bay	Current
	Siphonophorae	Physaliidae	*Physalia physalis*	N-S	1	3.32	3247	Sagami Bay	Current
		Agalmatidae	*Agalma elegans,*	N-S	2	3.56 ± 0.02	3482 ± 19.09	Okirai Bay	Current

S symbiotic, *N-S* non-symbiotic, *N/A* not available

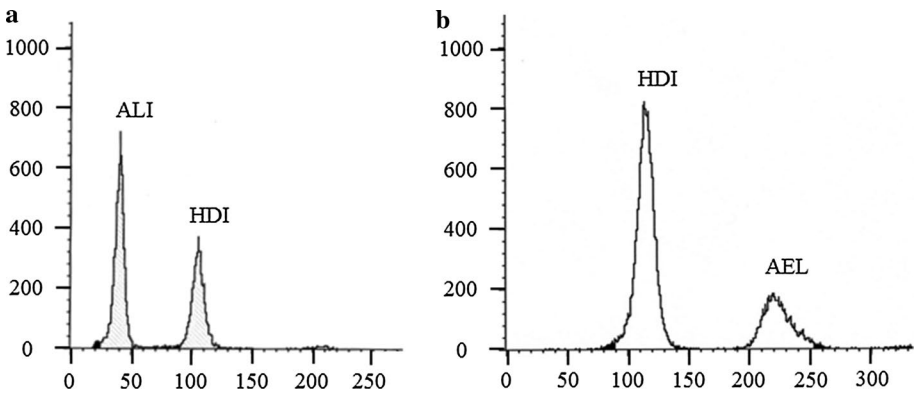

Fig. 1 Typical flow cytometry histograms of *Haliotis discus hannai* as standard cells (HDI) and *Aurelia limbata* (ALI) (**a**). Flow cytometry histograms of *Agalma elegans* (AEL) by using *H. discus hannai* (HDI) as standard cells (**b**). The *horizontal* and *vertical axes* are relative fluorescence intensities (FL) of propidium iodide and cell number, respectively

ranged from 0.48 pg in *Anthopleura fuscoviridis* to 0.98 pg in *Physogyra lichtensteini*, which constituted a 2.04-fold difference; the *C* values of in the six scyphozoan species ranged from 0.26 pg in *S. malayensis* to 0.71 pg in *Aurelia aurita* s.l., which constituted a 2.73-fold difference; and the *C* values of the nine hydrozoan species ranged from 0.28 pg in *Eutima japonica* to 3.56 pg in *A. elegans*, which constituted a 12.71-fold difference. In addition, the mean *C* values of species from Anthozoa, Scyphozoa, and Hydrozoa were 0.70, 0.46, and 1.20 pg, respectively, whereas the only species representing Cubuzoa, *Carybdea brevipedalia*, provided a *C* value of 0.77 pg. The *C* values of *Physalia physalis* (3.32 pg) and *A. elegans* (3.56 pg) (Hydrozoa, Siphonophorae) were both high.

Discussion

Investigating the variation of *C* values in Cnidaria is important for understanding genome evolution in the animal kingdom, especially since changes in genome size, such as polyploid events, expansions of retrotransposon elements, and chromosome deletions, could play an important role in animal evolution. Therefore, we measured the *C* values of 27 cnidarian species, which represent an ancestral taxonomic group in the animal kingdom.

The observed *C* values ranged from 0.26 (*Sanderia malayensis*) to 3.56 pg (*Agalma elegans*) (Table 1) and exhibited a multimodal distribution (Fig. 2). Since the *C* values of hydrozoan species were relatively large and widely distributed, we examined the normality of the distribution of *C* values from the 16 non-hydrozoan species and found that the data were normal, at the 5% significance level ($s = 0.02$, $k = -1.06$, Omnibus K^2 statistic $= 0.433$, $p = 0.8052$). Therefore, the C-values of the anthozoan and scyphozoan species were expected to range from 0.55 to 0.75 pg ($p < 0.05$). However, although most chromosome numbers reported for non-hydrozoan species are $2n = 28$ or $2n = 32$ [28–30], one previous study reported that the chromosome number of an *Aurelia aurita* s.l.

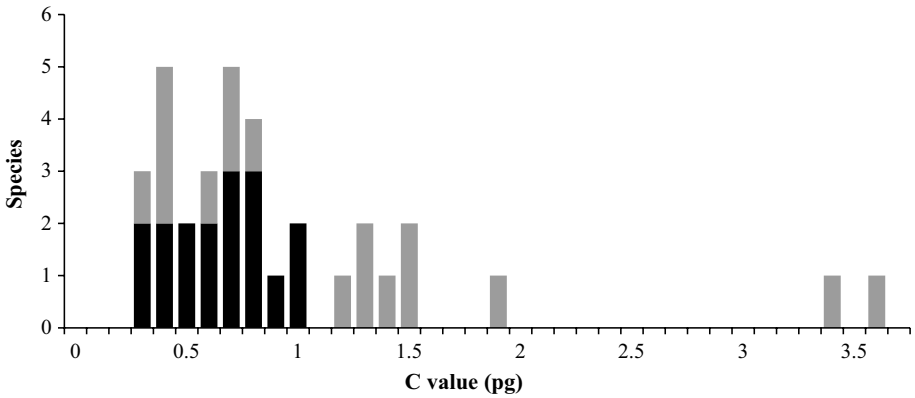

Fig. 2 Distribution of genome size in the phylum Cnidaria, based on flow cytometry data and publicly available information from the Animal Genome Database (http://www.genomesize.com, accessed 14 May 2016). The *gray* and *black bars* indicate the *C* values of Hydrozoan and non-Hydrozoan (i.e., Anthozoan, Scyphozoan, and Cubozoan) taxa, respectively ($n = 34$)

(non-hydrozoan species) specimen collected in the Gulf of Mexico was $2n = 44$ [31]. Interestingly, despite the species' much greater number of chromosomes, we found that the *C* value of *A. aurita* s.l. was similar to the values reported for other non-hydrozoan species. Therefore, the possibility that an evolutionary event, such as genome duplication, increased both the genome size and chromosome number of *A. aurita* s.l. is unlikely, which is probably also the case for other non-hydrozoan cnidarians, based on the low diversity in reported chromosome number, normal distribution of *C* values, and narrow range of expected *C* values (~0.5–0.7 pg).

On the other hand, the high variability of *C* values in Hydrozoa suggests the occurrence of an evolutionary event that increased the group's genome size. For example, the presence of multiple copies of a *Tol2* transposable element were reported in the *Hydra magnipapillata* genome [32], and the amplification of numerous transposable elements could result in an increased genome size. In contrast to the Anthozoa, Scyphozoa, and Cubozoa, class Hydrozoa is composed of species with simple body construction and high variability. It has been assumed that the group's diverse life-history stages and morphology were caused by this simple body construction [33]. Consequently, the complex evolution of such simple body construction would require considerable gains or losses in genomic content.

The association of high *C* value variation and complex evolution in Hydrozoa was previously suggested for six *Hydra* spp., of which the symbiotic *H. viridissima* was reported to have a genome that was about threefold smaller (0.40 pg) than those of five other non-symbiotic species (*H. circumcincta,* 1.15 pg; *H. vulgaris,* 1.29 pg; *H. oligactis,* 1.48 pg; *H. attenuate,* 1.85 pg; and *H. carnea* 1.38 pg) [23]. The previous study also demonstrated a relationship between *C* value and cell cycle or metabolic rate, which suggested that the presence of symbiotic algae, which influences the metabolic rate of its host, might be responsible for the lower *C* value of *H. viridissima* [23]. Since some cnidarian species harbor photosynthetic algae, such as coral and the mangrove jellyfish *Cassiopea*, we compared the *C* values of both symbiotic and non-symbiotic species shown in Table 1, from the present study, as well as from previous studies [20–23]. However, no significant differences were observed ($p = 0.08$, excluding Hydrozoa, *t*-test; $p = 0.71$, including Hydrozoa, Mann–Whitney *U* test), and the relationship between algal symbiosis and cnidarian *C* values could not be supported. The most probable explanation for the aberrant *C* value of *H. viridissima* is that it actually falls within the expected range of *C* values in the genus, since 1.6-fold differences in *C* value occur even among non-symbiotic *Hydra* (e.g., *H. circumcincta,* 1.15 pg; *H. attenuate,* 1.85 pg), and thus is not actually aberrant.

On the other hand, this study reports the high *C* values of two species (*Physalia physalis* 3.32 pg; *A. elegans* 3.56 pg) in Siphonophorae. Individual colonies of these species consist of highly specialized zooids. Although the relationship between the complex colony structure and high *C* values of siphonophores was not confirmed, this fact is interesting because genome duplication might be involved.

The extensive variation in *C* values within Hydrozoa could be supported by additional cytogenetic studies in the group. The present study provides a comprehensive examination of genome size in the phylum Cnidaria. The reported *C* values provide basic information that is necessary to plan whole-genome sequencing and are valuable for studying the evolution of animal genomes.

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