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THE IMPORTANCE OF THE INDIAN OCEAN AS ORIGIN OF THE SPECIES AND BIOLOGICAL LINK UNITING THE PACIFIC AND ATLANTIC OCEANS*

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ABSTRACT

The tropico-equatorial species of Chaetognatha and Siphonophorae in the Indian Ocean and adjacent waters are analysed. Particular attention is devoted to the species composition in the various regions, their abundance, spatial distribution, and to the taxonomic and ecological relationships of sympatric species and with their cognates inhabiting adjacent and farther allopatric localities. These studies will attempt to analyse the relative importance of the species producing centers, and the mechanisms involved in the processes of dispersal, spatial permanence of the populations and zoogeographical boundaries.

INTRODUCTION

THE epiplanktonic Chaetognatha and Siphonophorae of the Indian Ocean can be grouped into the following zoogeographic categories : Indo-Pacific-Atlantic ; Tropico-equatorial Indo-Pacific ; SE Asia ; Indian Ocean ; Subantarctic.

The data presented in this article are based on the analyses of the plankton material from the world oceans, collected during one hundred Expeditions and Cruises along a span of about twenty years, and the revision of the pertinent literature, most of which appears reviewed in Alvariño, 1965, 1967, 1969, 1971.

The world distribution of the Chaetognatha is fairly well known at present. The data on the distribution of the siphonophores are not as definitive as for the chaetognaths, because a higher number of studies on siphonophores had been concentrated on the tropico-equatorial belt than in any other oceanic region. This fact could mislead to consider some species restricted only to the tropico-equatorial regions when their domain may actually extend into adjacent temperate areas and into other oceans. Therefore, in the present work, emphasis will be applied mainly to the Chaetognatha.

The Siphonophorae are not so distinctly restricted to water masses as are most of the Chaetognatha. The morphological stability of the group is also noteworthy and species separated in time and space maintain exactly the same morphological characteristics. Although in general the tropico-equatorial siphonophores inhabit the tropico-equatorial belt continuously, interrupted only by the continents ; the

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highest number of species occur in the SE Asia-Indonesian Seas and the tropico-equatorial Indian Ocean (Table 1).

TABLE 1. *Tropico-equatorial Chaetognatha and Siphonophorae*

Region	Chaetognatha	Siphonophorae
INDIAN OCEAN	*Krohnitta pacifica* (Aida) 1897 *Sagitta bedfordii* Doncaster 1903 *S. bedoti* Béraneck 1895 *S. bombayensis* Lele and Gae 1936 *S. ferox* Doncaster 1903 *S. neglecta* Aida 1897 *S. pacifica* Tokioka 1940 *S. pulchra* Doncaster 1903 *S. regularis* Aida 1897 *S. robusta* Doncaster 1903 *S. septata* Doncaster 1903	*Muggiaea delsmani* Totton 1954 *Diphyes bojani* (Eschscholtz) 1829 *D. chamissonis* Huxley 1859 *D. dispar* Chamisso & Eysenhardt 1821 *Diphyopsis mitra* (Huxley) 1859 *Chelophyes contorta* (Lens & Riemsdijk) 1908 *Eudoxia macra* Totton 1954 *Lensia campanella* (Moser) 1925 *L. cossack* Totton 1941* *L. hotspur* Totton 1941* *L. hunter* Totton 1941 *L. meteori* (Leloup) 1934 *L. reticulata* Totton 1954 *L. tottoni* A. and R. Daniel 1963 *Sulculeolaria angusta* Totton 1954 *S. chuni* (Lens & Riemsdijk) 1908 *S. turgida* (Gegenbaur) 1853 *Abyla bicarinata* Moser 1925 *A. brownia* Sears 1953 *A. carina* Haeckel 1888 *A. haeckeli* Lens & Riemsdijk 1908 *A. ingeborgae* Sears 1953 *A. schmidti* Sears 1953 *A. trigona* Quoy & Gaimard 1827 *Ceratocymba dentata* (Bigelow) 1918 *C. intermedia* Sears 1953 *C. leuckarti* (Huxley) 1859 *Chuniphyes moserae* Totton 1954 *Maresearsia preclara* Totton 1954 *Melophysa melo* (Quoy & Gaimard) 1827 *Nectopyramis natans* (Bigelow) 1911 *N. spinosa* Sears 1952* *Bargmannia elongata* Totton 1954 *Amphicaryon ernesti* Totton 1954 *A. peltifera* (Haeckel) 1888
SOUTH-EAST ASIA AND INDONESIAN SEAS	*Krohnitta pacifica* *S. bedfordii* *S. bedoti* *S. bruuni* Alvarino 1967 *S. ferox* *S. johorensis* Pathansali & Tokioka 1963 *S. nagae* Alvarino 1967 *S. neglecta* *S. oceania* Grey 1930 *S. pacifica* *S. pulchra* *S. regularis* *S. robusta* *S. septata* *S. tokiokai* Alvarino 1967	Includes the species mentioned for the Indian Ocean, plus *Sulculeolaria bigelowi* Sears 1953 *S. brintoni* Alvarino 1968 *Enneagonum searsae* Alvarino 1968 and except of *Sulculeolaria turgida* *L. tottoni* *Eudoxia macra* *Maresearsia preclara*

* Tropico-equatorial species, except for the observations off Scotland, Fraser 1961, 1967.

TABLE 1 (*Contd.*)

Region	Chaetognatha	Siphonophorae
INDIAN AND PACIFIC OCEANS	*Krohnitta pacifica* *Sagitta bedoti* *S. ferox* *S. neglecta* *S. pacifica* *S. pulchra* *S. regularis* *S. robusta*	Includes the species mentioned for the Indian Ocean, except *Eudoxia macra* *Lensia tottoni* *Amphicaryon peltifera* *Maresearsia preclara* *Muggiaea delsmani* *Diphyes chamissonis*
ATLANTIC OCEAN	*Krohnitta mutabbii* Alvarino 1969 *Sagitta helenae* Ritter-Zahony 1910 *S. hispida* Conant 1895 *S. serratodentata* Krohn 1853 *S. tenuis* Conant 1896	Includes the species mentioned for the Indian Ocean plus *Lensia leloupi* Totton 1954 *L. lelouveteau* Totton 1941 *Vogtia kuruae* Alvarino 1967 and except of *M. delsmani* *D. chamissonis* *A. brownia*
EASTERN PACIFIC OCEAN	*Krohnitta pacifica* *Sagitta bedoti* *S. ferox* *S. pacifica* *S. peruviana* Sund 1961 *S. popovicii* Sund 1961 *S. pulchra* *S. regularis* *S. robusta*	Includes the species mentioned for the Indian and Pacific Oceans, plus *Abyla peruana* Sears 1953 *L. lelouveteau* *V. kuruae*

The populations of the species common to both the Pacific and Indian Oceans are connected by two routes : The Indonesian paths and along the South Australia and Tasmania. The tropico-equatorial species will follow almost exclusively the Indonesian passages, the temperate species, the two mentioned routes, and the Sub-antarctic species (extending into the southernmost part of the three oceans) the Australian and Tasmanian Seas.

The tropico-equatorial species can be grouped, considering their main spatial distribution into :

(1) Indo-Pacific.

(2) SE Asia and Indonesian.

(3) SE Asia and Indian.

(4) Atlantic.

(5) Eastern Pacific.

Except for the last category, the other four are represented in variable degree in the Indian Ocean.

The SE Asia and Indonesian Seas encompass the highest number of species. This fact could be due to the topographic complexity of the region (great number of islands, peninsulas, bays, inlets) and the subsequent dynamics of currents, eddies,

etc., favoured by the particular meteorological regime of that region. Populations can be stranded into partially locked areas and remain periodically or permanently isolated from the main population. The migrant population, established in confined localities, adapt to the environmental conditions, diverging from the parent population. There, the probability of extinction, emigration and competition may appear diminished, while immigration could be increased. However, it appears evident that some of these species restricted to small geographic areas may progressively invade adjacent regions. The SE Asia-Indonesian Seas and adjacent Indian Ocean regions appear as a species producing center, where the highest number of closely related species was observed. Those species occupy restricted allopatric regions. Some of the species centered in the SE Asia regions reached neighbouring locations in the Indian Ocean and Indonesian Seas and farther into the western tropico-equatorial Pacific. Attention should be devoted to the fluctuations in those populations both in magnitude, space and time. The more rigorous living conditions at bordering areas in the northern part of the South China Sea and into the tropico-equatorial Pacific band, will restrict the establishment of populations towards other latitudinal and longitudinal areas in that region, as compared to the successful settlement of the populations into localities in the Indian Ocean. The plankton studies in the Indian Ocean will provide valuable information to complete the patterns of distribution of some species, which up to now are only known from a few localities.

Temperate epiplanktonic Chaetognatha and Siphonophorae extend roughly from 40°N to 40°S in the Pacific ; from 40°N in the west and 58° N in the east and 40°S in the Atlantic, and in the Indian Ocean from the Asiatic continent to the Subtropical convergence in the south. The general picture of the distribution of the species of Chaetognatha and Siphonophorae in this category may be represented by that of *Sagitta hexaptera* (Fig. 1).

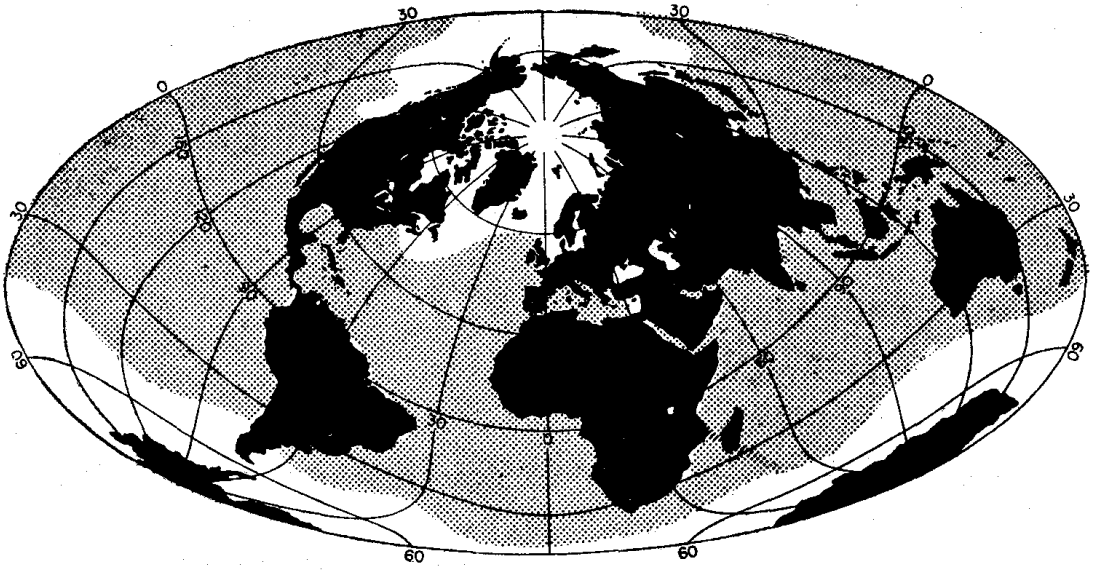

Fig. 1. General distribution of the epiplanktonic species common to the Atlantic, Indian and Pacific Oceans.

The distributional pattern of the Subantarctic species could be represented by *Sagitta tasmanica* (Fig. 2). This oceanic species inhabits the Subantarctic region

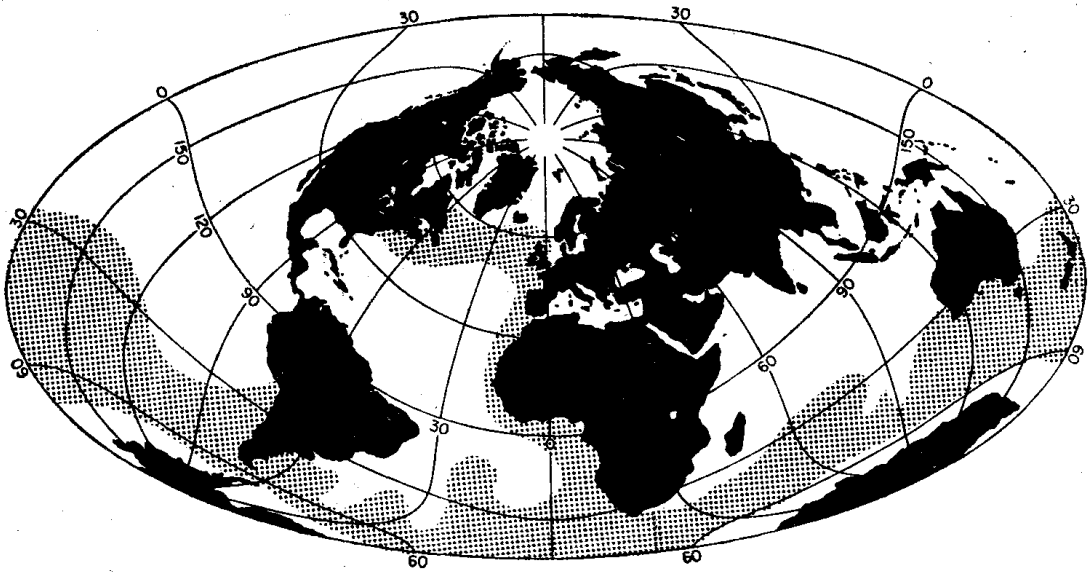

Fig. 2. Distribution of a Subantarctic species, *Sagitta tasmanica*.

and the southernmost parts of the Indian and Pacific Oceans, and in the Atlantic extends also along the southernmost region and progresses with the Benguela Current into the Gulf of Guinea continuing farther towards the northern cold Atlantic regions.

Sagitta lyra inhabits the warm and temperate regions of the Atlantic, Indian Ocean and the SE Asia, Indonesian waters progressing farther into the Kuroshio region (Fig. 3).

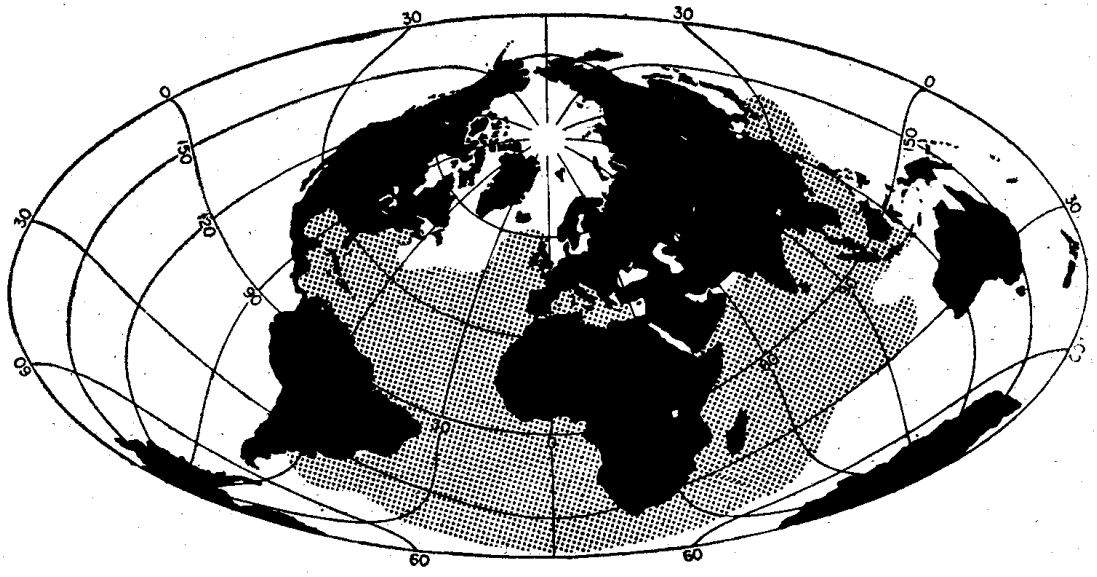

Fig. 3. Distribution of *Sagitta lyra*.

Some of the tropico-equatorial Indo-Pacific Chaetognatha extend into the Atlantic only to the southernmost part off Africa, via the Agulhas Current. These species are : *Sagitta neglecta*, *S. pacifica*, *S. pulchra*, *S. regularis*, *S. robusta* (Alvariño, 1965, 1969 ; Heydorn, 1959). The distribution of *S. robusta* might be used (Fig. 4) to represent the distributional domain of the other species in the group.

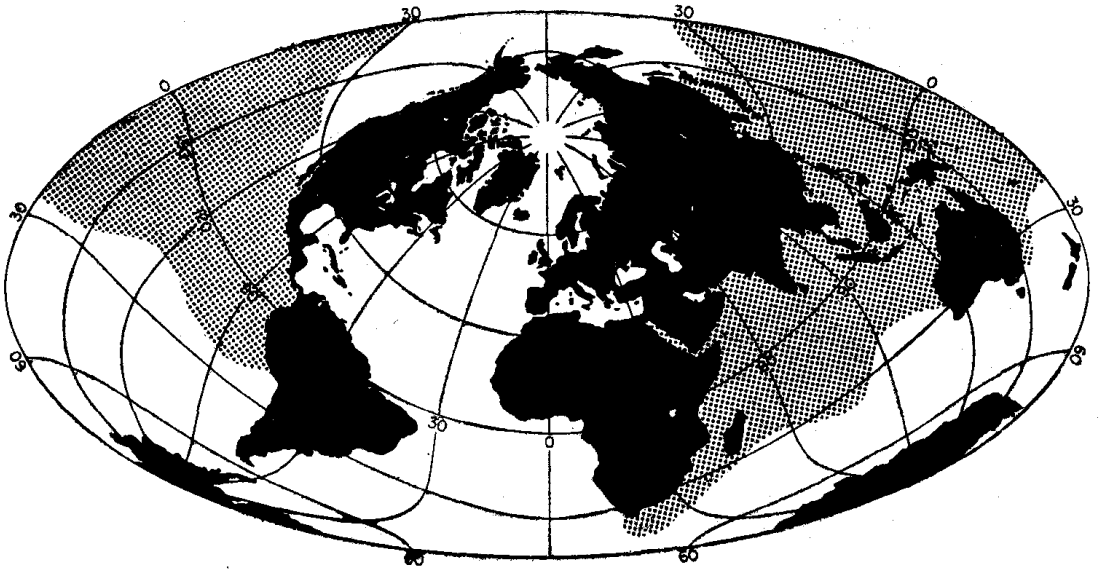

Fig. 4. General distribution of the tropico-equatorial Indo-Pacific species reaching the region off South Africa.

Most of the tropico-equatorial Indo-Pacific Siphonophorae are also common to the Atlantic (Table 1).

The Atlantic Ocean enjoys the lowest number of tropico-equatorial Chaetognatha (*Krohnitta mutabbii*, *Sagitta helenae*, *S. hispida*, *S. serratodentata*, *S. tenuis*). These species appear restricted to that Ocean, although *S. serratodentata* merits particular attention. *S. serratodentata* extends along the tropico-equatorial Atlantic and into the adjacent temperate regions, reaching to about 36°S off South Africa. The analysis of the material from the MONSOON Expedition proved that (Alvariño, 1969) specimens of *S. serratodentata* appeared distributed along the southern central part of the Indian Ocean and the Pacific as follows : 42°03′S-70°39′E, 37°40′S-41°41′E, 39°50′S-75°03′E, 37°49′S-85°21′E, 36°18′S-98°41′E, 39°18′S-119°51′E, 36°29′S-163°09′W, 34°04′S-161°54′W, 26°28′S-156°29′W. Clusters of *S. serratodentata* specimens dislocated from the Atlantic populations progressed eastward with the West wind Drift. The numerical data showed that although the travelling population may be maintained by reproduction and recruitment, it appears decimated along the extent of the route. Some specimens obviously reach the Juan Fernandez Islands region, where the species appears relatively successfully established. The genetic continuity of the identity of this population may be maintained by the periodic flow of new recruits from the west. The progression and reproduction of the Altantic *S. serratodentata* along the Indian and Pacific Oceans may result in a pulsating trend. The clusters of this population may appear along the southern route changing in both magnitude and rhythm with season and longitudinal position.

Several authors (Burfield and Harvey, 1926 ; Furnestin and Radiguet, 1964 ; Furnestin and Codaccioni, 1968 ; George, 1952 ; Ghirardelli, 1947 ; Rao, 1958a; Rao and Ganapati, 1958 ; Silas and Srinivasan , 1968 ; Subramanian, 1937 mentioned *S. hispida* (tropico-equatorial Atlantic species) in the Indian Ocean. In every case the morphological characteristics and illustrations of this *S. hispida* were

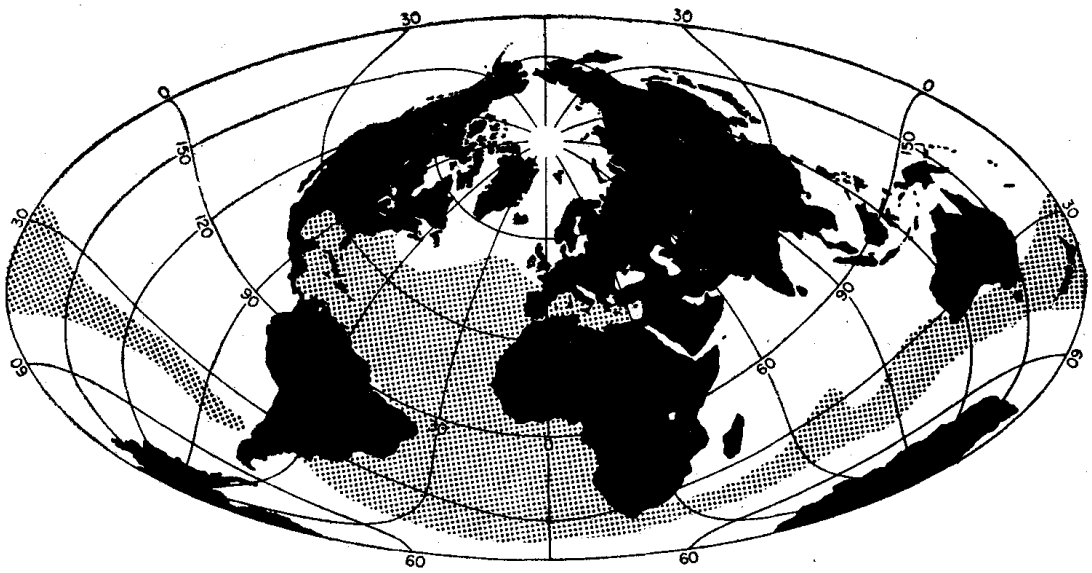

Fig. 5. Distribution of *Sagitta serratodentata* in the Atlantic and along the southernmost part of the Indian Ocean and the Pacific to the Juan Fernandez islands region.

included, it would appear that the specimens were erroneously identified as *S. hispida*. For instance, in some cases, these specimens were described with ova in the ovaries arranged in one line. *S. hispida* Conant has the ova in the ovaries arranged in two dorsoventral rows. George (1952) reported *S. hispida* from the Malabar coast, but his description corresponded to *S. bipunctata* in that the posterior fin 'never reached the seminal vesicles ' and no information was included on the intestinal diverticula. Ghirardelli (1947) mentioned *S. hispida* in one location in the Red Sea, in three locations in the Gulf of Aden and in several localities in the Indian Ocean. The description and photographs he included permit to properly identify those specimens as *S. ferox* Doncaster (anterior fins longer or equal in length to posterior fins). It appears that in most cases, the identifications of *S. hispida* from the Indian Ocean are based entirely on the ' hispida ' appearance of the specimens, without realizing that several species of Chaetognatha present this characteristic in common. Therefore, it could be conditionally stated that the *S. hispida* reported from the Indian Ocean could apply to a closely related species, either *Sagitta neglecta, S. septata* or *S. oceania.*

Reports of *Sagitta tenuis* (neritic species of the tropico-equatorial Atlantic) from the Indian Ocean (Chacko, 1950, Furnestin and Codaccioni, 1968 ; George, 1949, 1952 ; John, 1933 ; Sudarsan, 1963) could be a misidentification of a well known species or an undescribed species. No data obtained up to now would properly indicate the presence of *S. tenuis* in the Indian Ocean.

The SE Asia-Indonesian regions include the highest number of tropico-

equatorial Chaetognatha (Table 1), of which eight species reach the American Pacific, while ten or more progress into the Indian Ocean. *Sagitta bombayensis* is a typical species in the neritic Indian regions. Five species appear restricted to the SE Asia regions : *Sagitta bruuni* (neritic in the Gulf of Thailand, Alvariño, 1967) ; *S. johorensis* (South China Sea and Malay regions, Alvariño 1967 ; Pathansali and Tokioka, 1963) ; *S. nagae* (Alvariño, 1967, Omori, 1969) ; *S. oceania* (Alvariño, 1963, 1967 ; Grey, 1930 ; Hamon, 1956 ; Tokioka, 1942) ; *S. tokiokai* (Alvariño, 1967).

The tropico-equatorial Chaetognatha restricted to either the SE Asia-Indonesian and/or Indian Ocean (*S. bedfordii, S. bombayensis, S. bruuni, S. johorensis, S. nagae, S. oceania, S. septata, S. tokiokai*) belong to four taxonomic groups. *S. bedfordii, S. johorensis, S. oceania, S. septata,* are closely related species integrants of the group ' oceania ' (Alvariño, 1967). *S. bruuni,* and *S. bombayensis* are neritic species, allopatric in distribution with the other neritic chaetognaths. *S. nagae* is the closely related species of *S. bedoti.* The former inhabits the SE Asia waters progressing into the Kuroshio region, and *S. bedoti* extends along the tropico-equatorial Indo-Pacific (Alvariño, 1967, 1969).

Sagitta tokiokai belongs to the ' hispida ' group (Alvariño, 1967, 1969) which also includes *S. ferox, S. robusta, S. hispida.* The first two species of the Indian and Pacific Oceans, the later of the tropico-equatorial Atlantic, and *S. tokiokai* inhabiting the SE Asia waters. *Sagitta ferox* and *S. robusta* appear sympatric in the latitudinal and longitudinal parameters, but allopatric in their respective depth distribution ; and both are allopatric with *S. hispida* and at least partially also with *S. tokiokai.*

The tropico-equatorial Siphonophorae present about the same number of species in the SE Asia and the Indian Ocean, and the number appears to be higher that for any other oceanic region (Table 1). *Diphyes chamissonis* and *Muggiaea delsmani* are only observed in the SE Asia-Indonesian and the Indian Ocean ; and *Sulculeolaria bigelowi, S. brintoni, Enneagonum searsae* appear confined to the SE Asia region.

Other species of the genus *Muggiaea,* are also neritic in distribution, *Muggiaea atlantica* Cunningham 1892, *M. kochi* (Will) 1844, *M. bargmannae* Totton 1954. *M. atlantica* inhabits the neritic temperate Atlantic, the American Pacific and the Japanese region. *M. kochi* inhabits the warm neritic regions in the Atlantic and the eastern Pacific. *M. atlantica* appears to be the dominant neritic siphonophore off Central America in the Pacific, while *M. kochi* is the dominant species in the Caribbean, and also along the neritic regions off Ecuador and Peru. *M. bargmannae* is a cold water species inhabiting the neritic regions of the high latitudes, although Totton (1954) reported it from east of Crozet (47°22.5'S-56°19.5'E). *M. atlantica* was also observed in the Gulf of Aden, Alayu, Red Sea (Totton, 1954), and *M. kochi* around the Chagos and Amirante islands (Browne, 1926).

The present outlines and information establish the importance of the Indian Ocean in the origin of species and uniting the populations in both the Atlantic and Pacific Oceans.

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