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A STUDY ON THE GUT CONTENTS OF FIVE JUVENILE LOGGERHEAD TURTLES, CARETTA CARETTA (LINNAEUS) (REPTILIA, CHELONIIDAE), FROM THE SOUTH-EASTERN PART OF THE NORTH ATLANTIC OCEAN, WITH EMPHASIS ON COELENTERATE IDENTIFICATION

CANCAP-project, Contributions to the zoology, botany and paleontology of the Canarian – Cape Verdean region of the North Atlantic Ocean, no. 52

by

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Van Nierop M. M. & J. C. den Hartog: A study on the gut contents of five juvenile loggerhead turtles, *Caretta caretta* (Linnaeus) (Reptilia, Cheloniidae), from the south-eastern part of the North Atlantic Ocean, with emphasis on coelenterate identification. CANCAP-project, contributions to the zoology, botany and paleontology of the Canarian-Cape Verdean region of the North Atlantic Ocean, no. 52.

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The gut contents of five juvenile individuals of the loggerhead turtle *Caretta caretta* (L.) from waters around Madeira, Selvagem Grande (Selvagens Islands) and São Miguel (Azores) were analysed macro- and microscopically.

Macroscopic investigations showed that epipelagic salps (e.g., *Pyrosoma atlanticum* Péron) and gastropods (e.g., *lanthina* spp. and *Pterotrachea* spp.) constituted an important part of the food remains present in these loggerheads. To a lesser extent this also holds for organisms such as goose-barnacles (*Lepas* spp.). and *Idotea metallica* Bosc, which live on drifting materials, including algae.

Microscopic examination revealed the presence in all turtles of large numbers of nematocysts, deriving mainly from Siphonophora and to a lesser extent from Scyphomedusae and Hydromedusae, indicating that pelagic coelenterates also formed an important, if not the most important part of the food consumed.

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INTRODUCTION

Knowledge about the food and feeding habits of animal organisms is essential to understand their place and function in the ecosystem. Such knowledge is especially relevant with regard to species which are diminishing in numbers or even threatened with extinction. Marine turtles may be classified as such. In this research one species of turtle has been studied: the loggerhead, Caretta caretta (L.). By means of an analysis of the gut contents of five juvenile loggerheads taken off oceanic islands in the subtropical south-eastern part of the North Atlantic Ocean, additional knowlegde was obtained about the food of this species. Brongersma (1972: 157-162) summarized the results of earlier investigations and concluded that loggerheads on the high seas feed on Scyphomedusae, Physalia physalis (L.) (Siphonophora), Velella velella (L.) (Chondrophora), Salpae, Pteropoda, Ianthina (Gastropoda), squids, Planes (as Nautilograpsus) minutus (L.) (Crustacea, Brachyura), Lepas anatifera (L.) (Crustacea, Cirripedia), syngnathid fishes (Entelurus aequoreus (L.)), and perhaps other fishes. When the loggerhead appears in shallow, coastal waters, bottom dwelling organisms enter into the diet, such as crabs, hermit crabs, conchs, borers, sea urchins, and sponges (Brongersma, 1972: 162). According to Hughes (1974: 16-17) this alteration in diet correlates with the age of the loggerhead. Hughes presumes that juvenile loggerheads at least spend their first four or five years "well away from the littoral zone" and that in this period of their lives they feed on anything that floats. Loggerheads older than four or five years feed on littoral and benthic organisms, mainly molluscs.

In the present study we were primarily interested in the question whether, and especially to what extent, pelagic Coelenterata form part of the diet of juvenile loggerheads. As pelagic coelenterates, with very few exceptions (e.g. *Velella velella*), lack any form of a skeleton and rapidly disintegrate when consumed, it is generally very difficult or impossible to prove their presence in the alimentary canal of sea turtles by macro-morphological features. The tissues of coelenterates, however, invariably contain nematocysts, which are very resistant structures. They occur in a vast variety of types and size-classes, several of which have considerable diagnostic value. Thus it is possible to obtain information on captured coelenterates by means of microscopical investigation of the gut contents (cf. Den Hartog, 1980; Den Hartog & Van Nierop, 1984).

MATERIAL AND METHODS

Of the five turtles studied, three were caught in Madeiran waters, one near Selvagem Grande (Selvagens Islands) and one off the south coast of São Miguel (Azores). An overall examination of the gut contents of these turtles was made with a binocular dissecting microscope, using magnifications of up to 40 \times . In addition squash preparations of samples taken from various parts of the alimentary tract were checked microscopically with Nomarski interference optics for the presence of nematocysts, using magnifications of up to $1000 \times .$ As mentioned in the introduction, nematocysts often have considerable diagnostic value. On the basis of shape, structure, the combination in which they are found, and indirect data (e.g., knowledge about the geographical distribution of species), it is sometimes possible to make accurate identifications of Coelenterata, even up to the species-level. In most cases, however, identifications can only be made with the greatest reserve, and in the present study it often proved impossible to make identifications below the subordinal level. Much depends on the available knowledge of the cnidom of Coelenterata involved. The cnidom of some taxa is relatively well known, while information on other taxa is virtually wanting. Moreover, due to their condition, a reliable indentification of some nematocyst categories derived from the gut of sea turtles may prove very difficult or impossible. Some types may be present mainly in undischarged state, while discharged cnidae tend to become damaged, break or collapse when squash preparations are prepared. Thus it is not always possible to observe relevant details. To indicate tentatively indentified categories of nematocysts, these are put, throughout the text, between quotation marks.

DISCUSSION ON NEMATOCYSTS AND INDENTIFICATION OF CONSUMED COELENTERATA

A survey of the principal categories of nematocysts found in the turtles examined is presented in figs. 1-19. The bulk of these nematocysts derives from Siphonophora and to a lesser extent from Scyphomedusae and Hydromedusae. We have no reason to assume that cubomedusan nematocysts are represented. Detailed studies of the cnidom of only few species of pelagic Coelenterata are available in the literature. Hence accurate identification of the species consumed by the turtles as a rule proved impossible, especially as it was obvious that the gut of each turtle contained a multi-specific mixture of nematocysts. Identifications, as far as these could be made, were mainly based



Figs. 1-19. Caretta caretta. Types and size-classes of nematocysts obtained from the gut of the five turtles examined. Choice of the figured examples more or less arbitrary and identifications partly tentative. All figures on the same scale. (For explanation see caption on next page).



Figs. 1-8a and 14-17. Siphonophora. Figs. 1-8a. Unidentified Calycophorae and Physonectae: 1. "Desmoneme" (round), 2. ditto (pyriform), 3. "ditto" (ovoid), 4. rhopaloneme (discharged and undischarged), 5. anisorhize, 6-7. mastigophore, 8. stenotele (discharged and undischarged), 8a. "stenotele". Figs. 14-15. *Physalia physalis*: 14. Holotrich, 15. stenotele. Figs. 16-17. *Apolemia* uvaria: 16. Birhopaloid, 17. mastigophore.

Figs. 9-12. Scyphozoa: 9-10. Atrich, 11. Holotrich (discharged and undischarged), 12. eurytele. Figs. 13, 18-19. Hydromedusae: 13. "Mastigophore" (*Geryonia proboscidalis*?), 18. "stenotele", 19. "eurytele".

on data presented and summarized by Weill (1934), Russell (1938, 1939, 1940) and Den Hartog & Van Nierop (1984). Weill's nematocyst classification was adopted (cf. also: Werner, 1965), though the full names of a number of nematocyst types were avoided: atrich stands for atrichous isorhize, holotrich of holtrichous isorhize, anisorhize for homotrichous anisorhize, eurytele for microbasic eurytele and mastigophore for microbasic mastigophore.

Nematocysts known to occur in Siphonophora are: Acrophores, anacrophores, desmonemes (all astomocnidae), atrichs, holotrichs, anisorhizes, mastigophores, euryteles, stenoteles and birhopaloids (all stomocnidae). Some of these types are easily recognized, other types may be confused in undischarged condition. Acrophores, anacrophores, anisorhizes and birhopaloids are unique to the order. Anacrophores and acrophores are unique to the suborders Calycophorae and Physonectae, respectively (Weill, 1934: 518, 521), but unfortunately the distinction between these two types (tube without or with a terminal appendix, respectively) cannot be made in undischarged condition. Hence they are here treated as a collective group, rhopalonemes, which have a rather characteristic shape and size (fig. 4). In the smears the anisorhizes were generally found undischarged; their long banana-shaped capsules, however, are highly characteristic (fig. 5). Birhopaloids are exclusively known from a single species of Physonectae, viz., Apolemia *uvaria* (Lesueur). In discharged state this type of nematocyst cannot be confused as the slightly dilated basal part of the tube, the shaft, is characterized by the presence of two distinct bulges. In undischarged condition, especially in the absence of discharged examples of the same, recognition may be difficult. However, the capsules have a characteristic, slightly bilateral symmetry and the two bulges often show up in the capsular contents as spots with different refraction.

Desmonemes have a rather short, thick tube, which everts in a densely coiled spiral, and which, like in rhopalonemes, lacks a terminal orifice. Uneverted and collapsed desmonemes may be confused with hydrozoan and scyphozoan atrichs or holotrichs, and because of this recognition of desmonemes in the smears was sometimes difficult. On the basis of the shape of the desmoneme three varieties were distinguished: globular (fig. 1), more or less ovoid (fig. 3), and pyriform (fig. 2). The latter type is quite characteristic, but identification of globular and ovoid desmonemes was tentative.

Atrichs have rarely been reported from Siphonophora and those records have to be regarded with reserve. Examples are the small, somewhat bananashaped atrichs reported by Russel (1938: 159-161, fig. 88c, d) from *Muggiaea atlantica* Cunningham, and the globular atrichs reported by Weill (1934: 514, fig. 342a, b) from *Physalia physalis* (as *P. arethusa* Browne). The last-named atrichs have since proved to be holotrichs (e.g. Mackie, 1960: 394, pl. 28 figs. 5, 6). Similar holotrichs occur in Scyphozoa and Cubozoa; thus, as far as they were present in the smears, their origin could only be gathered inferentially, in correlation with the presence of other nematocyst types.

Mastigophores are of common occurrence among Hydrozoa. In Siphonophora they often reach considerable dimensions. Their shape is usually long, bilaterally symmetrical, often more or less cigar-shaped (figs. 6, 7). Mastigophores are defined as nematocysts of which the tube has a distinctly dilated, isodiametrical basal shaft. In undischarged cnidae this shaft is generally visible as a straight rod. Mastigophores form part of the cnidom of all species of Calycophorae so far studied in this respect (Weill, 1934: 504-510, 518; Russell, 1938: 159-161), but their presence has also been established in Physonectae, e.g. in *Apolemia uvaria* (Carré & Carré, 1973: 246, figs. 29, 32) and *Agalma elegans* (M. Sars) (Russell, 1939: 356-358). Sizeable mastigophores may also occur in Cubozoa (p. 41).

Although mastigophores generally can be recognized as such in uneverted condition, they may be confused with certain euryteles. An example are the euryteles of the trachymedusa *Geryonia proboscidalis* (Forskål) (Weill, 1934: fig. 66a, b – as *Carmarina hastata* Haeckel). In uneverted state the shaft of these cnidae shows as a straight rod, but when everted it appears that this

shaft gradually increases in diameter distally, thus conforming to the definition of euryteles.

Stenoteles have been reported from representatives of all siphonophoran suborders, with the exception of the Calycophorae (Weill, 1934: 518), but it is not always easy to distinguish them from euryteles, especially not in uneverted or collapsed condition (figs. 8, 8a). Stenoteles and euryteles are both rhopaloids, nematocysts characterized by an anisodiametrically dilated shaft. In euryteles the shaft is distally wider than proximally, in stenoteles it is wider proximally. In addition, the most proximal spines on the shaft of stenoteles are often extremely well developed and known as stylets. The large rhopaloids occuring in Physonectae without exception, though in part erroneously, are referred to by Weill (1934: 510-514, 518) at stenoteles. These rhopaloids have been depicted by Iwanzoff (1896: pl. 5 fig. 22) for Agalma sarsii Leuckart. Iwanzoff's figure leaves no doubt about the true identity of these nematocysts. Their shaft is distally wider than proximally and hence they must be considered euryteles. A study by Russell (1939: 356-358, fig. 4) on the cnidom of Agalma elegans confirms this, though Russell noted that the shaft of these euryteles, in conformity with stenoteles, is characterized by three proximal stylets. Actual transitions between stenoteles and euryteles have been reported by Russell (1940: 521-522, fig. 22) from several individuals of the trachymedusa Aglantha digitalis (O. F. Müller) var. rosea (Forbes).

The number of nematocyst types of Scyphozoa is limited to only three (figs. 9-12) (cf. Den Hartog & Van Nierop, 1984: table 1, pls. 1, 2): more or less ovoid atrichs (often more than one size-class per species), globular to ovoid holotrichs and characteristic, ovoid euryteles, in everted condition with a slightly dilated shaft. A cnidom composed of these three types is present in most Semaeostomeae; atrichs are absent in Coronatae and holotrichs are absent in Rhizostomeae. It is noticeable that in the digestive tract of marine turtles scyphozoan atrichs seem to disintegrate easier than any other type of nematocysts found by us so far.

The cnidom of Cubomedusae (formerly considered an order of Scyphozoa, but recently given the status of a separate class, Cubozoa (Werner, 1973)) is to a large extent similar to that of Scyphozoa, though cubozoan euryteles tend to reach larger dimensions. The cnidom of the class further includes mastigophores (up to a length of at least 100 microns), which, however, are restricted to the members of the family Chirodropidae (e.g., Calder & Peters, 1975; Den Hartog, unpublished notes).

RESULTS

A survey of the results of the study of the gut contents of the individual turtles is presented below and summarized in table 6 (p. 51).

Specimen 1 (RMNH 21635: sex not determined) (table 1). Purchased at Funchal, Madeira (32°45′N, 17°W) by L. D. Brongersma, on 11.vii.1979. Straight carapace length 52 cm.

The oesophagus, intestines and caecum of this turtle were crammed with pieces of Pyrosoma atlanticum Péron, a pelagic colonial tunicate, almost shaped like a hollow cylinder, which generally reaches a size of about 20 \times 3-4 cm (Berrill, 1950: 274-275). From this we inferred that these pieces represented about 10 to 12 of these colonies. In the caecum were also found: some sand (ca. 100 grams), shell fragments of goose-barnacles, Lepas anatifera (L.) (fig. 23), representing the remains of some 20 to 25 individuals, and 20 jellylike "barrels", about 2-3 \times 1 cm in size, ten of which contained remains of the amphipod Phronima sedentaria (Forskål) (fig. 26). Such "barrels" usually derive from salps (Thaliacea: Doliolida, Salpida, Pyrosomida) and less commonly from siphonophores (suborder Calycophorae) (Shih, 1969: 48). They represent the remains of the tunica of the Thaliacea or the mesogloea of the swimming-bells of Calycophorae. They are "constructed" and occupied by the female amphipods, which consume their "host's" organs and body tissues (Huus et al., 1935: 523). Male individuals of Phronima spp. so far have not been reported from these "barrels" (Shih, 1969: 48). The "barrels" found in the caecum of the turtle might derive from salps, but it is more likely that they originate from siphonophores (Dr. R. W. M. van Soest, Amsterdam, in litt.). In addition the following items were found in the intestines of the turtle: one specimen of the shrimp Funchalia villosa (Bouvier) (Penaeidae), length 3 cm; about 40 vertebrae of an unidentified fish, each with a length of 8 mm; a fragment of sea-grass, Cymodocea nodosa (Ucria), 1.5×1 cm; three (commensal) Nematoda, length 6-7 mm; four pieces of glass, up to 2 cm in length; five pieces of transparent, black and blue plastic, up to 5 cm in length (fig. 25); a bit of nylon thread, 4.5 cm. long (fig. 21), and, throughout the alimentary tract, numerous small clots of oil (up to several mm in diameter).

Microscopical analysis of the gut contents revealed the presence of a fairly large number of nematocysts. A detailed survey of the various types and sizeclasses found is presented in table 1. These nematocysts mainly derive from Siphonophora (types 1-9) and to a lesser extent from Scyphozoa (types 10-13). It seems plausible that the bulk of the siphonophoran nematocysts belong to a single species. Four types (3, 5, 6, 7) are rare or sporadic. The other five types

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Nematocyst type	Corresponding figure	Average and range (in parentheses) of length and width of nematocyst capsules in microns	N	Occurrence
1. Rhopaloneme	4	9.8(7.9-10.5) x 2.9(2.6-3.6)	11	uncommon
2."Desmoneme"	1	6.2(4.9- 7.9) in diameter	30	common
3. Do.	2	12.5(9.9-13.8) x 7.5(5.6-8.6)	6	rare
4. Anisorhize	5	52.6(25.0-66.5) x 6.3(4.9-7.9)	25	common
5. Mastigophore	6	83.8(73.7- 95.4) x 16.5(14.5-19.7)	7	rare
6. Do.	7	102.9(102.0-104.6) x 11.0(10.5-11.8)	3	sporadic
7. Do,	6	120.0(118.0-122.0) x 23.0(22.0-24.0)	2	sporadic
8. Do.	6	163.7(141.4-187.5) x 33.9(27.0-38.2)	25	rather common
9. Stenotele	8	71.3(56.6- 92.1) x 29.5(19.1-37.5)	20	ипсоджов
10. Atrich	9	$4.7(4.6-4.9) \times 3.2(3.0-3.3)$	5	rare
11. Do.	10	$10.2(8.6-13.2) \times 6.3(5.6-6.9)$	4	rare
12. Holotrich	11	$13.1(11.8-14.5) \times 12.3(10.5-13.8)$	20	rather common
13. Eurytele	12	10.8(8.6- 13.8) x 8.1(6.9- 9.2)	30	common

Table 1. Caretta caretta, specimen 1 (Madeira, 11.vii.1979). Survey of nematocysts obtained from the gut.

(1, 2, 4, 8, 9), varying in abundance from uncommon to common, more or less correspond to the types reported by Russell (1939: 356-358, fig. 4) from *Agalma elegans* (M. Sars) (Physonectae), although the size ranges do not fully agree and the large rhopaloids (type 9), unlike in that species, are distinct stenoteles. Even if not representing the cnidom of a species of *Agalma*, these nematocysts almost certainly belong to a species of Physonectae.

As to the scyphozoan nematocysts (types 10-13), their combination suggests that they derive from a single species of Semaeostomeae. A more precise identification of this species is impossible. Considering the overall picture of the nematocyst types and size-classes listed in the table, the holotrichs are unlikely to come from a species of Cubozoa or Siphonophora.

Specimen 2 (RMNH 21636: sex not determined) (table 2). Purchased at Funchal, Madeira (32°45'N, 17°W), by L. D. Brongersma on 11.vii.1979. Straight carapace length 27.4 cm.

The intestines and caecum of this turtle contained 700-800 egg capsules (fig. 20), each measuring 4-6 mm in length, of the gastropod *Ianthina pallida* Thompson (Laursen, 1953: 32). Snails of the genus *Ianthina* stay on the surface of the ocean by means of a float, formed by secretion of mucus. To this float the snails may attach hundreds of egg capsules and it is possible, therefore, that the turtle consumed only one such float. In addition were found: remains of probably 10 to 15 specimens of the isopod *Idotea metallica* Bosc (fig. 24) (length about 2 cm each), a species which can be found on drifting materials, including Sargassum weed; two complete beaks originating from the pelagic squids *Japatella* spec. and *Chaunoteuthis mollis* Appellöf, the latter weighing probably 50 grams (Dr. M. R. Clarke, Plymouth, in litt.); several

jelly-like pieces, measuring about 1 cm, possibly originating from Thaliacea; and, found dispersed throughout the alimentary tract, small clots of oil.

Microscopical analysis of the gut contents showed the presence of a considerable number of radula teeth, which were identified as those of a species of *Pterotrachea* (Gastropoda, Heteropoda), a genus commonly occurring in the south-eastern part of the North Atlantic (Van der Spoel, 1976: 185, figs. 242-245), including the surroundings of Madeira (personal observations J. C. den Hartog). The identification was made on the basis of the central tooth of the radula (fig. 22a) (Richter, 1961: 169 fig. 2).

Nematocyst type	Corresponding figure	Average and range (in parentheses) of length and width of nematocyst capsules in microns	N	Occurrence
1. Rhopaloneme	4	12.0(9.2- 15.8) x 4.5(3.3- 5.9)	40	common
2."Desmoneme"	1	5.1(3.9- 6.6) in diameter	15	uncommon
3. Do.	2	14.8(10.5-17.8) x 8.6(6.6-11.2)	20	common
4."Do."	3	11.9(8.6- 15.8) x 6.6(4.6- 9.9)	40	common
5. Anisorhize	5	34.5(21.0-65.8) x 6.3(3.3-9.9)	30	common
Mastigophore	7	93.8(93.4-103.3) x 10.3(8.6-11.8)	20	rather common
7. Do.	7	59.0(48.0-71.0) x 7.8(6.9-7.9)	4	sporadic
8."Stenotele"	8a	20.2(16.5- 21.7) x 14.1(11.2-16.5)	4	sporadic
9. Do.	8	40.5(32.9-47.4) x 26.9(21.7-32.9)	20	rather common
10. Do.	8	57.2(53.3-62.5) x 30.9(27.6-34.9)	3	sporadic
11."Mastigophore"	13	19.4(16.5-21.1) x 6.1(5.6-6.9)	18	uncommon
12."Do,"	13	29.2(28.3-30.3) x 8.0(6.3-9.2)	19	uncommon
13. Atrich	9	5.9(5.3-6.6) x 3.8(3.3-4.3)	17	uncommon
14. Do.	10	12.1(10.5-14.5) x 7.5(6.6-9.2)	9	rare
15. Holotrich	11	12.3(10.5- 14.5) in diameter	12	uncommon
16. Do.	11	21.7(17,1-25.7) in diameter	17	uncommon
17. Eurytele	12	11.9(9.2-14.5) x 8.7(6.3-10.5)	40	rather common

Table 2. Caretta caretta, specimen 2 (Madeira, 11.vii.1979). Survey of nematocysts obtained from the gut.

Furthermore, large numbers of nematocysts were found (table 2), mainly deriving from Siphonophora (types $1-10)^1$) and to a lesser extent from Scyphomedusae (types 13-17) and Hydromedusae (types 11, 12). Considering the presence of three categories of each, desmonemes, mastigophores and stenoteles, it is obvious that more than one species of Siphonophora is involved (Calycophorae and/or Physonectae), but owing to the lack of information in the literature, it is at present impossible to make a more precise identification.

The scyphozoan nematocysts also do not allow an accurate identification. The presence of two size-classes of holotrichs indicates that probably two species of Semaeostomeae are involved. The largest size-class (type 16) matches

¹) The shape and size of certain "stenoteles" (type 8) is reminiscent of cubozoan eutyteles. See, however, footnote 2 (p. 46).

the holotrichs of *Pelagia noctiluca* (Forskål) (Den Hartog & Van Nierop, 1984: table 1), a species common around Madeira (personal observations J. C. den Hartog).

Two size-classes of nematocysts, listed in the table as "mastigophores" (types 11, 12), resemble the euryteles of *Geryonia proboscidalis* (Forskål), a common, cosmopolitan, epipelagic trachymedusa (Kramp, 1959: 60). The bell of this species may reach a diameter of 8 cm. Its (mono)-cnidom, consisting of these euryteles only, has been described and depicted by Weill (1934: 488, fig. 66). According to Weill the size of these euryteles ranges from $20 \times 7 - 35 \times 8$ microns. The resembling mastigophores found in the turtle (seem to) fall apart into two size-classes. Their overall range, however, $16.5 \times 5.6 - 30.3 \times 9.2$ microns, matches the range presented by Weill rather well.

Specimen 3 (RMNH 20218; female) (table 3). Caught one mile south of Selvagem Grande ($30^{\circ}09'N$, $15^{\circ}52'W$; Selvagens Islands) by P. A. Zino on 25. v.1980. Straight carapace length 21.5 cm. Two small crabs, probably *Planes minutus* (L.), were found on the body of this turtle, but unfortunately these were not collected.

The bulk of the gut contents of this turtle was formed by gastropods of the genus *Pterotrachea* (Heteropoda). The stomach alone contained the more or less intact probosces (ca. 1 cm long) of about 35 individuals, while a large number of radula teeth, approximately representing the remains of another 20 individuals, were found in the intestines and caecum (fig. 22). In addition the following items were found: 16 specimens of the isopod *Idotea metallica*

Nematocyst type	Corresponding figure	Average and range (in parentheses) of length and width of nematocyst capsules in microns	N	Occurrence
1. Rhopaloneme	4	13.8(10.5- 15.8) x 4.9(3.6- 5.6)	20	very common
2."Desmoneme"	1	5.6(4.3- 7.9) in diameter	20	rather common
3. Do.	2	13.8(10.5- 16.5) x 7.8(5.9- 9.2)	11	uncommon
4."Do."	3	12.8(9.9-17.1) x 7.1(5.3-8.9)	20	very common
5. Anisorhize	5	40.8(23.0-64.5) x 6.8(4.3-7.9)	40	very common
Holotrich	14	17.4(12.6- 34.2) in diameter	62	uncommon
Mastigophore	6	77.0(72.7- 79.6) x 18.1(14.5-20.4)	10	uncommon
8. Do.	7	96.5(88.8-102.0) x 10.4(9.2-11.2)	11	uncommon
9. Do.	6/7	126.7(118.4-143.4) x 21.8(14.5-28.6)	14	uncommon
10. Do.	6	168.2(154.6-204.0) x 37.3(27.6-52.6)	16	uncommon
11."Stenotele"	8a	20.8(16.5- 26.3) x 14.8(11.2-17.8)	11	uncommon
12. Do.	15	30.4(27.0- 34.2) in diameter	20	uncommon
13. Do.	8	46.9(32.2- 55.9) x 27.1(19.1-40.8)	30	rather common
14. Do.	8	79.2(75.7- 82.3) x 36.6(32.9-39.5)	7	rare
15."Mastigophore"	13	20.4(19.7- 22.4) x 6.5(5.9- 7.9)	20	rather common
16."Do."	13	28.3(26.3- 30.3) x 7.9(6.6- 8.9)	20	rather common
17."Eurytele"	19	12.7(11.8- 13.8) x 7.4(5.9- 8.2)	20	rather common
18."Stenotele"	18	12.8(8.6- 17.0) x 10.0(6.6-14.0)	20	rather common

Table 3. Caretta caretta, specimen 3 (Selvagem Grande, 25.v.1980). Survey of nematocysts obtained from the gut.

(Bosc) (fig. 24); 14 jelly-like "barrels" (p. 42), two of which contained remains of *Phronima sedentaria* (Forskål); a piece of nylon thread, 5 cm long; 5 pieces of firm, transparent plastic, up to 1 cm long; and, dispersed throughout the alimentary tract, clots of oil.

Large numbers of nematocysts were found in all the squash preparations examined (table 3). These derive mainly from Siphonophora (types 1-14) and they represent such a variety of types and size-classes that it is obvious that several species are involved. The large spherical stenoteles (type 12) and holotrichs (type 6) probably originate from *Physalia physalis* (L.) (Cystonectae) (Weill, 1934: figs. 342, 343; Mackie, 1960: pl. 25 fig. 4). The size ranges of these nematocyst types are intermediate between the rather different ranges for this species presented by Weill (1934: 514; stenoteles 35-40 microns, holotrichs 15-40 microns) and Mackie (1960: 395; stenoteles 21-25 microns, holotrichs 9-30 microns). As scyphozoan atrichs and euryteles were not found at all in the turtle's gut, the holotrichs cannot derive from a species of Scyphomedusae²). Considering the variety of types and size-classes listed in the table, the other siphonophoran nematocysts probably belong to three (or more) species of Physonectae (or possibly Physonectae and Calycophorae).

Undischarged nematocysts listed in the table as "mastigophores" (types 15, 16), but much resembling the euryteles of the trachymedusa Geryonia proboscidalis were also found and again we could distinguish two size-classes (cf. turtle specimen 2, p. 45.). The overall range, however, $19.7-30.3 \times 5.9-8.9$ microns, matches their range in Geryonia proboscidalis. Two other types of nematocyst, only observed in undischarged state, and tentatively identified as "stenoteles" (type 18) and "euryteles" (type 17) were also found in considerable numbers. Possibly both types derive from Hydromedusae. The "stenoteles" are reminescent of the stenotele-eurytele of the trachymedusa Aglantha digitalis (O. F. Müller) var. rosea (Forbes) (Russell, 1940: 521-522). This, however, is an arctic-boreal species not reported south of Cape Finisterre in northern Spain (Kramp, 1959: 57). The size-range, moreover, exceeds that presented by Russell (8.6-17 \times 6.6-14 versus 8-13 \times 6-11 microns). The "euryteles" (type 17) deviate from the typical form present in Scyphozoa (figs. 12, 19). Similar euryteles have been reported from the gut contents of a small hawksbill turtle, Eretmochelys imbricata (L.), which, like the turtle here dis-

²) The absence of atrichs also seems to exclude the possibility that Cubomedusae are represented and this further implies that certain "stenoteles" (type 11; fig. 8a), in shape and size reminescent of cubozoan euryteles, also do not derive from Cubozoa. Similar "stenoteles" were also found in turtle nr. 2 (table 2, type 8) and turtle nr. 5 (table 5, type 12). In the absence of cubozoan euryteles, the most characteristic of cubozoan nematocysts, it is self-evident, that also none of the categories of mastigophores found in the turtle(s) can be attributed to Cubozoa.

cussed, was also obtained from waters around the Selvagens Islands (Den Hartog, 1980: 600, pl. 2 fig. 7).

Specimen 4 (RMNH 20219; female) (table 4). Purchased at Funchal, Madeira (32°45'N, 17°W), by J. C. den Hartog on 8.vi.1980. Straight carapace length 28 cm.

An important part of the gut contents of this turtle consisted of the remains of gastropods of the genus *Pterotrachea*. About 20 probosces (measuring about 1 cm each) (fig. 22) of these snails were found in the stomach, while in the intestines and the caecum a large number of radula teeth was found, estimated to represent another 15 to 20 individuals. The caecum also contained: shell fragments, several mm long, representing the remains of 3 to 5 small goose-barnacles, *Lepas* spec.; small shell fragments of an unidentified bivalve; remains of the crab *Planes minutus* (L.), which generally lives on drifting *Sargassum*, but which has also been found on sea turtles; several jellylike pieces, 1-2 cm long, possibly deriving from salps; and, like in the other turtles examined, clots of oil, dispersed throughout the alimentary tract.

Nematocyst type Corresponding Average and range (in paren figure of length and width of nem capsules in microns		responding Average and range (in parentheses) figure of length and width of nematocyst capsules in microns	N	Occurrence
1. Rhopaloneme	4	11.0(9.2-12.5) x 3.6(2.6- 3.9)	20	rather common
2. Desmoneme	2	14.4(11.8- 17.1) x 7.9(5.9-10.5)	20	rather common
Anisorhize	5	43.6(17.1-67.1) x 6.1(3.3-7.9)	20	common
 Mastigophore 	7	51.5(51.0- 52.0) x 7.5(7.0- 8.0)	2	sporadic
5. Do.	7	72.4(65.8-77.6) x 7.8(6.6-9.9)	10	uncommon
6. Do.	6	77.2(72.4- 82.3) x 15.3(13.2-18.4)	10	uncommon
7. Do.	7	102.6(94.8-117.1) x 10.4(9.2-13.2)	20	rather common
8. Do.	6	165.8(160.4-168.3) x 34.0(29.0-35.6)	4	sporadic
9. Atrich	9	6.5(5.3- 6.9) x 3.8(3.3- 4.3)	20	rather common
10. Do.	10	11.6(9.9- 15.8) x 7.2(6.3-9.2)	20	rather common
11. Holotrich	11	23.5(21.1- 26.3) x 22.9(20.4-24.3)	20	common
12. Eurytele	12	13.2(11.2- 16.5) x 9.2(6.6-11.8)	30	very common

Table 4. Caretta caretta, specimen 4 (Madeira, 8.vi.1980). Survey of nematocysts obtained from the gut.

Smears from all parts of the gut revealed the presence of large numbers of nematocysts of both Siphonophora (types 1-8) and Scyphozoa (types 9-12) (table 4). As to the siphonophoran nematocysts, the total absence of euryteles and/or stenoteles and the presence of several size-classes of mastigophores suggests that these all derive from one or more species of Calycophorae.

The scyphozoan nematocyst types (9-12) probably originate from a single species of Semaeostomeae, viz., *Pelagia noctiluca* (Forskål), as mentioned before (p. 45), a species common around Madeira. The range and average size of all four types match those of *Pelagia noctiluca* rather well (Den Hartog & Van Nierop, 1984: table 1).

Specimen 5 (RMNH 21637; sex not determinated) (table 5). Bought from fishermen at Caloura, South coast of São Miguel, Azores (37°33'N, 25°27'W) by J. C. den Hartog on 4.vi.1981. Straight carapace length 26.0 cm.

Intestines and caecum of this turtle contained a considerable number of jelly-like pieces (1-3 cm) presumably deriving from salps. These organisms therefore must have constituted an important part of the food consumed by this loggerhead shortly before it was taken. A large number of shell fragments of the goose-barnacle Lepas anatifera (L.), estimated to represent the remains of some 40 to 60 individuals of about 1-2 cm, was found in the oesophagus and the caecum. In the caecum were also found: remnants of 4-5 shells of the gastropod Ianthina spec., with an estimated size of ca. 2 cm; one specimen of the gastropod Cavolinia tridentata (Niebuhr) (Pteropoda, Thecosomata), its shell measuring 1.5 cm; two otoliths and the spine, 4 cm long, of Ceratoscopelus maderensis (Lowe), a small fish normally occurring in deeper water, but occasionally appearing at the ocean surface by night; two bird's feathers, 2.0 and 5.5 cm long (fig. 21); two fragments of Sargassum vulgare J. G. Agardh (Algae, Phaeophyceae), each 1 cm large; a piece of white paper, 3×3 cm; four pieces of nylon thread, 1 to 3 cm long, and a small ball of the same, measuring $4 \times 1 \times 1$ cm; six pieces of thin, black, white and colourless polyethylene, measuring about $1 \times 1 \times 0.5$ cm. In this turtle, too, clots of oil were found throughout the alimentary tract.

Nematocyst type	Corresponding figure	Average and range (in parentheses) of length and width of nematocyst capsules in microns	N	Occurrence
1. Rhopaloneme	4	$14.2(11.8 - 16.5) \times 5.0(3.9 - 5.9)$	20	very common
2."Desmoneme"	1	5.5(3.9- 7.2) in diameter	20	rather common
3. Do.	2	13 x 7	1	sporadic
4."Do."	3	$12.6(8.6-15.8) \times 6.9(5.3-9.2)$	20	very common
5. Anisorhize	5	36.1(27.0-42.1) x 7.3(4.6-9.2)	20	very common
6. Holotrich	11	15.1(13.8-17.1) x 14.5(13.2-16.5)	20	rather common
7. Mastigophore	17	30.9(28.3- 33.3) x 15.8(13.8-18.0)	10	uncommon
8. Do.	7	72 x 8	1	sporadic
9. Do.	6/7	100.8(96.7-107.9) x 13.7(9.9-18.4)	10	uncommon
10. Stenotele	-	10.9(8.6-13.8) x 8.8(7.2-12.5)	20	uncommon
11. Do.	-	25 x 22.0(20.0-24.0)	3	sporadic
12."Do."	8a	24.6(19.1- 35.5) x 16.5(12.5-24.3)	20	uncommon
13. Do.	8	48.1(39.5-55.8) x 32.1(23.0-41.5)	20	common
14. Do.	8	62.0(59.2-65.8) x 42.4(40.1-44.7)	4	sporadic
15. Birhopaloid	16	14.9(13.2-16.5) x 7.6(6.6-8.6)	5	rare
16. Do.	16	21.1(19.7-23.4) x 12.4(9.9-16.2)	20	rather common
17. Mastigophore	13	28.3(27.6-29.7) x 8.3(7.9-8.6)	3	sporadic
18. Atrich	9	6.5(5.3-7.9) x 4.0(3.3-5.3)	20	uncommon
19. Do.	10	11.3(11.2-11.8) x 6.8(6.6-7.2)	5	rare
20. Holotrich	11	24.6(19.1- 31.5) in diameter	20	uncommon
21. Eurytele	12	6.9(5.9-7.9) x 5.1(4.6-5.9)	20	uncommon
22. Do.	12	12.5(10.5- 14.5) x 7.5(6.6- 9.9)	20	rather common
				1

Table 5. Caretta caretta, specimen 5 (São Miguel, 4.vi.1981). Survey of nematocysts obtained from the gut.

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Large numbers of nematocysts were found in squash preparations from various parts of the gut (table 5). The bulk of these nematocysts derives from Siphonophora (types 1-16) and a minority from Scyphozoa (types 18-22) One type (nr. 17), also found in turtle specimens 2 and 3, may originate from Geryonia proboscidalis (Forskål) (Trachymedusae) or a related species. Considering that only three of these nematocysts were traced, they probably represent contaminations, taken in with a siphonophore or a scyphomedusa. Among the siphonophoran nematocysts are listed two size-classes of a very characteristic type, the birhopaloid (types 15, 16; fig. 16; also: Weill, 1964: pl. 1; Carré & Carré, 1973: 241, fig. 1; Den Hartog, 1980: pl. 5 fig. 9). This nematocyst type is exclusively known from Apolemia uvaria (Lesueur), classified among the Physonectae. This species, however, actually occupies a rather isolated position and its cnidom differs strikingly from that of other representatives of the suborder. The most recent and most complete description of its cnidom has been given by Carré & Carré (1973). It comprises two size-classes of birhopaloids (15 \times 9 and 24 \times 15 microns), two size-classes of stenoteles $(14 \times 12 \text{ and } 26 \times 23 \text{ microns})$, holotrichs (15 microns in diameter), atrichs (7.5 microns in diameter) and mastigophores (32.5 \times 14 microns). In the smears studied, only part of these nematocyst categories were found, and only in small numbers: birhopaloids, in two size classes (types 15, 16) and mastigophores (type 7) (fig. 17). Furthermore, it is possible that part of the stenoteles, which were found in a variety of size-classes, covering a wide range, also derive from Apolemia uvaria (types 10 and 11). The same may apply to the holotrichs (type 6, possibly in part) (figs. 11, 14). The little spherical atrichs occurring in Apolemia uvaria were not found in the smears, but, taking into account the small numbers in which the nematocysts of Apolemia uvaria were found altogether, this negative result is not surprising. The rest of the siphonophoran nematocysts listed in table 5, among which rhopalonemes, "desmonemes", anisorhizes, but also stenoteles dominate, suggests that the turtle had consumed at least one other species of Physonectae in addition to Apolemia uvaria.

The scyphozoan nematocysts found in the turtle (types 18-22) probably derive from more than one species, as can be inferred from the presence of two distinct size-classes of euryteles (types 21, 22). The size of the large holotrichs (type 20) again suggests that *Pelagia noctiluca* (Forskål) is one of these, although the sizes of the other nematocyst categories do not strongly support this possibility. The identity of the second species can only be guessed at. It may belong to the suborder Rhizostomeae (characterized by atrichs and euryteles only), but considering the possibility that (part of) the small holotrichs (type 6) might be of scyphozoan origin, it could also be a species of Semaeostomeae. Cubozoa are unlikely to be represented (cf. p. 46, footnote 2).

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SUMMARY OF THE RESULTS AND DISCUSSION

The results of the present study, summarized in table 6, show that the five loggerheads, examined had fed mainly on pelagic organisms such as siphonophores, jelly-fish, salps and gastropods (*Pterotrachea* spp., *Ianthina* spp.), and to a lesser extent on organisms such as *Lepas* spp. and *Idotea metallica* Bosc that live on drifting objects, including algae. These results support the view of Brongersma (1972: 162), Hughes (1974: 16) and others, that juvenile, oceanic loggerheads feed on "anything that floats". The variety of food items listed in the table agrees with the survey of Brongersma (1972: 157-162). However, the presence of a comparatively large fraction — both in quantity and variety — of pelagic coelenterates, especially siphonophores, in the diet of the turtles here studied is remarkable. Nematocysts of the following taxa were found:



Figs. 20-26. Caretta caretta. A choice of macroscopic items obtained from the gut of the five turtles examined. Fig. 20. Egg-capsules of *Ianthina pallida*; fig. 21. Nylon thread and bird's feathers; fig. 22. Proboscis of *Pterotrachea* spec. and detail of middle tooth of the radula of that species (22a); fig. 23. Fragments of shells of *Lepas anatifera*; fig. 24. *Idotea metallica*; fig. 25. Fragments of plastic and paper; fig. 26. "Barrel" with *Phronima sedentaria*.

Food items		Speci	mens exam	ined:	
	1	2	3	4	5
Coelenterata					
Siphonophora	++	+++	+++	++	+++
Semaeostomeae	++	++		+++	++
Hydromedusae		+	++		
Mollusca					
Pterotrachea spp .		++	+++	+++	
Ianthina spp.		++			+
Cavolinia tridentata					+
Japatella spec.		+			
Chaunoteuthis mollis		+			
Unidentified bivalve				+	
Crustacea					
Idotea metallica		++	++	+	
Lepas spp.	++			+	++
Funchalia villosa	+				
Planes minutus				+	
Phronima sedentaria	+		+		
Tunicata	ļ				
Salpae?: "barrels"	++		++		
Salpae?: jellylike pieces		+		+	++
Pyrosoma atlanticum	+++				
Pisces	1				
Ceratoscopelus maderensis					+
Unidentified vertebrae	+				
Herbivorous matter					
Sargassum vulgare					+
Cymodocea nodosa	+				
Other items					
Nematoda	+				
Feathers					+
Sand	++				
Clots of oil	+ +	+	+	+	+
Plastic	+				+
Glass	+				
Paper					+
Nylon thread	+				+

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Table 6. (cf. figs. 20-26) Caretta caretta, overall survey of food and other items found in the gut of the five turtles examined. The symbols +, + and + + stand, respectively, for: minor, significant and important fraction of the items present.

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Siphonophora: Several unidentified species of Calycophorae and Physonectae, *Apolemia uvaria* (Lesueur) (Physonectae), and *Physalia physalis* (L.) (Cystonectae); Scyphomedusae: *Pelagia noctiluca* (Forskål) and one or two other, unidentified species of Semaeostomeae; Hydromedusae: One or two unidentified species, possibly including the trachymedusa *Geryonia proboscidalis* (Forskål). That no cubozoan nematocysts were found is not unexpected, as Cubomedusae, though also found in the open ocean, are typical inhabitants of shallow, relatively quiet, tropical and subtropical coastal waters (e.g., Hyman, 1940: 515).

With the exception of the large, surface floating *Physalia physalis*, no mention had been made in the literature so far of Siphonophora in the diet of the loggerhead. Hydromedusae had not been reported either, and reports of Scyphomedusae are scarce.

It is obvious that the results here presented are not coincidental, but correlated with the research technique (i.e. the study of squash preparations of samples of the gut contents with high power magnifications). Thus, in our view, there is no doubt that Siphonophora, Scyphomedusae and also sizeable Hydromedusae generally form part of the diet of pelagic feeding, juvenile loggerheads.

The siphonophoran nematocysts found in the turtles in all but one case include stenoteles, which seems to indicate that an important percentage, if not the majority of Siphonophora consumed were Physonectae. Special attention is drawn to this, as representatives of this suborder generally occur in waters below 200 metres depth. In fact, only few species of Siphonophora are normally found at depths less than 50 metres and with few exceptions these are all Calycophorae (Totton, 1965; Pugh, 1974; Kinzer, 1977). This suggests that juvenile, pelagic feeding loggerheads might reach considerable depths in search for food. Bearing in mind that the five turtles examined, without exception, were caugth in the vicinity of oceanic islands, another explanation might be, that turbulence of sea currents around such islands, caused by irregular bottom profiles, carries planktonic organisms from deeper water to the surface layers.

It is interesting to note that small, rather solid clots of oil were found in the gut of all loggerheads examined. These clots must have been swallowed unintentionally while the turtles were feeding on floating organisms and/or garbage. Considering the distant localities where the turtles were caught, the presence of these oil clots gives some indication as to the degree of oil pollution in the south-eastern part of the North Atlantic and one wonders to what extent the regular intake of small amounts of oil, inherent to surface feeding, may affect the organism's physiology and health, especially in the long run.

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The gut of two individuals contained fragments of polyethylene sheets and paper, pieces of hard, floating plastic, and nylon thread. In a recent paper (Den Hartog & Van Nierop, 1984: 21-22) we have already discussed the intake of such materials in relation to the leathery turtle (*Dermochelys coriacea* (L.)). This phenomenon apparently indicates that pelagic feeding turtles are attracted by and consume almost anything that floats, without visually recognizing their prey. The contents of the caecum of one of the turtles, though indicating a pelagic way of feeding, included a considerable amount of sand and some fragments of glass. The glass fragments could have been taken in with some garbage thrown over the side of a ship, but the presence of sand is puzzling and cannot be related to pelagic feeding, unless in heavily disturbed shallow water.

The straight carapace length of the turtles examined varied between 21.5 and 28 cm, while one individual was considerably larger (52 cm). The fact that all these turtles proved to be pelagic feeders is in accordance with results of Hughes (1974: 15), who established that benthic and littoral feeding loggerheads in Tongaland (south-east Sout-Africa) had straight carapace lengths of more than 60 cm.

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REFERENCES

- Berrill, N. J., 1950. The Tunicata, with an account of the British species: i-iii, 1-354, figs. 1-120. London.
- Brongersma, L. D., 1972. European Atlantic Turtles. Zool. Verh. Leiden. 121: 1-318, figs. 1-42, tabs. 1-17, charts 1-8.
- Calder, D. R. & E. C. Peters, 1975. Nematocysts of Chiropsalmus quadrumanus with comments on the systematic status of the Cubomedusae. Helgoländer wiss. Meeresunters. 27: 364-369, fig. 1, table 1.
- Carré, C. & D. Carré, 1973. Étude du cnidome et de la cnidogenèse chez Apolemia uvaria (Lesueur, 1811) (Siphonophore Physonecte). Expl. Cell Res. 81: 237-249, text-figs. 1-4, figs. 1-32.

- Hartog, J. C. den, 1980. Notes on the food of sea turtles: Eretmochelys imbricata (L.) and Dermochelys coriacea (L.). -- Neth. J. Zool. 30(4): 595-610, fig. 1, tabs. 1-3, pls. 1-5.
- Hartog, J. C. den & M. M. van Nierop, 1984. A study on the gut contents of six Leathery Turtles (Dermochelys coriacea (L.)) from British Waters and from the Netherlands. – Zool. Verh. Leiden 209: 1-36, tabs. 1-10, pls. 1-5.
- Hughes, G. R., 1974. The Sea Turtles of South-East Africa. II. The biology of the Tongaland Loggerhead Turtle Caretta caretta L. with comments on the Leatherback Turtle Dermochelys coriacea L. and the Green Turtle Chelonia mydas L. in the study region. – Investl. Rep. Oceanogr. Res. Inst. Durban 36: 1-96, figs. 1-28, tabs. 1-24, pls. 1-7.
- Huus, J., I. E. W. Ihle, H. Lohmann & G. Neumann, 1935. Tunicata. Handb. Zool. Berl. 5, 2te Hälfte: 193-272, figs. 1-59.
- Hyman, L. H., 1940. The Invertebrates: Protozoa through Ctenophora: 1-xii, 1-726, figs. 1-221. New York and London.
- Iwanzoff, N., 1896. Ueber den Bau, die Wirkungsweise und die Entwickelung der Nesselkapseln der Coelenteraten. – Bull. Soc. Nat. Moscou 1896: 95-161, 323-354, pls. 1-6.
- Kinzer, J., 1977. On the vertical distribution of siphonophores in the upwelling area of NW Africa. – Meteor Forsch. Ergebn., Reihe D, 26: 21-27, figs. 1-2, tabs. 1-8.
- Kramp, P., 1959. The Hydromedusae of the Atlantic Ocean and Adjacent waters. Dana Rep. 46: 1-283, figs. 1-335, pls. 1-2.

Laursen, D., 1953. The Genus Ianthina. - Dana Rep. 38: 1-40, figs. 1-41, pl. 1.

Mackie, G. O., 1960. Studies on Physalia physalis (L.). Part 2. Behaviour and histology. – Discovery Rep. 30: 369-408, figs. 1-6, pls. 26-28.

Pugh, P. R., 1974. The vertical distribution of the siphonophores collected during the Sond Cruise, 1965. – J. mar. biol. Ass. U.K. 54(1): 25-90, figs. 1-13, tabs. 1-4.

Richter, G., 1961. Die Radula der Atlantiden (Heteropoda, Prosobranchia) und ihre Bedeutung für die Systematik und Evolution der Familie. – Z. Morph. Ökol. Tiere 50: 163-238, figs. 1-32.

Russell, F. S., 1938. On the nematocysts of Hydromedusae. – J. mar. biol. Ass. U.K. 23: 145-165, figs. 1-88.

Russell, F. S., 1939. On the nematocysts of Hydromedusae. 2. – J. mar. biol. Ass. U.K. 23: 347-359, figs. 1-4.

- Russell, F. S., 1940. On the nematocysts of Hydromedusae. 3. J. mar. biol. Ass. U.K. 24: 515-523, figs. 1-32.
- Shih, C. T., 1969. The systematics and biology of the family Phronimidae (Crustacea: Amphipoda). – Dana Rep. 74: 1-100, figs. 1-22, tabs. 1-3.
- Spoel, S. van der, 1976. Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda): 1-484, figs. 1-246. Utrecht.
- Totton, A. K., 1965. A synopsis of the Siphonophora: 1-230, figs: 1-153, pls. 1-40. London.
- Weil, R., 1934. Contribution à l'étude des cnidaires et de leurs nématocystes. 1. Recherches sur les nématocystes. 2. La valeur taxonomique du cnidome. – Trav. Stn. zool. Wimereux, 10/11: 1-701, figs. 1-432.
- Weill, R., 1964. Une nouvelle catégorie de nématocystes: existence, chez Apolemia uvaria Eschh., de nématocystes birhopaloïdes. – C.R. hebd. Séanc. Acad. Sci., Paris, 258: 4343-4344, pl. 1.
- Werner, B., 1965. Die Nesselkapseln der Cnidaria mit besonderer Berücksichtigung der Hydroida. 1. Klassification und Bedeutung für die Systematik und Evolution. – Helgoländer wiss. Meeresunters. 12: 1-39, figs. 1-23, tabs. 1-9.
- Werner, B., 1973. Spermatozeugmen und Paarungsverhalten bei Tripedalia cystophora (Cubomedusae). – Mar. Biol. Berlin, 18(3): 212-217, figs. 1-2.