A STUDY ON THE GUT CONTENTS OF SIX LEATHERY TURTLES *DERMOCHELYS CORIACEA* (LINNAEUS) (REPTILIA: TESTUDINES: DERMOCHELYIDAE) FROM BRITISH WATERS AND FROM THE NETHERLANDS

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Hartog, J. C. den & M. M. van Nierop: A study on the gut contents of six Leathery Turtles *Dermochelys coriacea* (Linnaeus) (Reptilia, Testudines, Dermochelyidae) from British waters and from The Netherlands.

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Key words: Scyphozoa; Leptomedusae; Siphonophora; Testudines; *Dermochelys*; nematocysts; British Isles, Netherlands; food; digestive tract; anatomy; functional morphology.

Microscopical investigations of the gut contents of six individuals of *Dermochelys coriacea* from southern England and the North Sea revealed the presence in all of these of numerous nematocysts, mainly scyphozoan. Only six species of Scyphozoa occur in British shallow waters and in the North Sea, viz., *Pelagia noctiluca* (Forskål), *Chrysaora hysoscella* (L.), *Aurelia aurita* (L.), *Cyanea capillata* (L.), *C. lamarckii* (L.) and *Rhizostoma octopus* (L.). For the purpose of comparison and identification an inventory was made of the cnidom of these six species (based on preserved material). Nematocysts of one or more of these species appeared to be present in each of the turtles, all six species being represented. One of the turtles in addition appeared to have foraged upon the leptomedusa *Aequorea* spec. Small numbers of siphonophoran nematocysts were also found, but these may represent contaminations taken in with Scyphozoa, many of which feed upon other coelenterates.

As the extremely watery diet of leathery turtles implicates the intake of large amounts of excess sea-water, speculations are put forward about the way in which this water is removed. In our view this is mainly done by oral expulsion and not primarily by renal and lachrymal gland excretion.

Basing ourselves on the sparse and very rough data available in the literature, we conclude that the amount of organic matter taken in per day by a fully grown leathery turtle (in its eastern North Atlantic seasonal quarters) may be in the order of 2.5 kg per day (not 8–10 kg as suggested by Duron, 1978), standing for an energy intake of about 11.000–16.000 k.cal.

The intake of plastics and other indigestable matters, a phenomenon frequently reported for this species, indicates that it apparently is indiscriminately attracted by all slow moving or floating objects of some size. The fact in itself that it takes such materials proves that the shape of its food items is of little or no relevance. The anthropomorphic interpretation therefore that the leathery turtle (and the same holds for other sea turtles) would mistake plastics for jelly-fish as has repeatedly been suggested in the literature, cannot be taken seriously.

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INTRODUCTION

A review of the literature up to 1969 concerning the diet of the leathery turtle has been given by Brongersma (1969: 83-96). This survey reveals a striking discrepancy between the data often presented in the general literature and the facts derived from actual investigations (Brongersma, l.c.: tables 1 and 2). In the general literature the leathery turtle is often regarded omnivorous, though primarily a predator on fish, crustaceans and molluscs; an idea frequently deduced from its strong, deeply notched jaws. Actual evidence, however, based on investigations of the alimentary tract or of the stomach alone, revealed that the species feeds mainly upon soft-bodied pelagic organisms like jelly-fish and salpae (Brongersma, 1969: table 2). Recent information confirms this[1]. Even the actual intake of jelly-fish has now been observed (e.g. Duron, 1978: 89-94, 99-100, pl. 1; Duguy, Duron & Alzieu, 1980; Duron & Duron, 1980).

On the whole, exact identifications of coelenterates taken in by the leathery turtle, or by sea turtles in general, are scarce. Once taken in, these organisms rapidly disintegrate and therefore a conclusive identification of the remains

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[1] There is one exception. Glüsing (1973) reported gastropods, bivalve shells, fragments of crabs and disintegrated holothurians from the stomach of a leathery turtle taken by a fishing boat off western Ireland and Scotland (11/12-ix-1966). As such a diet is most unusual for a leathery turtle, we look upon this report with the greatest reserve. In our view this diet — resulting from bottom foraging activties — rather indicates that another species of turtle has been involved in this case, probably a loggerhead *Caretta caretta*. Glüsing, who obtained the stomach contents by intervention of others and apparently did not himself see the turtle, possibly was wrongly informed about the specific identity. Another possibility is that the identification in fact was correct but that Glüsing obtained the incorrectly labelled stomach contents of a different turtle. In this connection it may be noted that the distribution of several of the molluscs listed by Glüsing is restricted to tropical and sub-tropical waters (*Strombus, Conus, Murex*).

often can only be achieved microscopically (presence or absence of nematocysts). Such studies, however, so far have hardly been performed (e.g. Den Hartog, 1980), although substances suspected to be the remains of coelenterates have repeatedly been reported from the gut of leathery turtles (Brongersma, 1969: 94). The present study, apart from presenting additional information on the diet of the leathery turtle, aims to be an example of such a detailed microscopical study.

MATERIAL AND METHODS

The present study is based on an examination of the contents of the alimentary canal of six leathery turtles obtained from the south-west coast of England and from the North Sea. Of two individuals we only had at our disposal preserved samples of gut contents. The gut of the four other turtles — one of which had been dissected on a previous occasion — were examined and sampled by ourselves. For each turtle a general inventory of the samples was made, followed by an extensive microscopical investigation of squash preparations, under magnifications up to 1000 ×. The nematocyst typology and terminology used in the present paper is after Weill (1934). For the sake of convenience the full names of certain nematocyst types are not employed here; eurytele stands for microbasic eurytele, mastigophore stands for microbasic mastigophore and the term anisorhize is used instead of homotrichous anisorhize.

IDENTIFICATION

Judging from the nematocysts encountered in the squash preparations, it soon appeared — not quite unexpectedly — that the main bulk of the food taken in by the turtles examined consisted of Scyphozoa. Taking into account the region where the animals were found or taken, only a few species of Scyphozoa were to be considered (Russell, 1970): *Pelagia noctiluca* (Forskål), *Chrysaora hysoscella* (L.), *Aurelia aurita* (L.), *Cyanea capillata* (L.), *C. lamarckii* (L.) (all order Semaeostomeae) and *Rhizostoma octopus* (L.) (order Rhizostomeae). Representatives of the order Coronatae, although reported from British waters (Russell, l.c.: 27-69) beforehand, were not likely to be involved because these occur in deep water — mesopelagial and bathypelagial — only. Even if it is assumed that the leathery turtle may reach a depth of several hundred metres in search of food, it seems unlikely that it will do so in the presence of an abundance of other, considerably larger, palatable species of Scyphozoa occuring near the surface, which require much less effort to be caught. This of course does not exclude the possibility that species of Coronatae may occasionally be taken in.

The nematocysts of the six species mentioned above have been studied by Weill (1934: 535-546) and partly by Papenfuss (1936: 5-22). Unfortunately Weill only presents rough data concerning range, average or maximal size. The data given by Papenfuss (averages) were exclusively based on nematocysts from the tentacles, which tend to be slightly larger than those from other parts of the medusan body. Consequent upon this state of affairs, we have once more studied the cnidom of the six species concerned. The results of this study are presented in table 1.

Species Nematocyst type	Average and range (in parentheses) of length and width of nematocyst capsules in microns	Number of capsules measured	Occurrence
Cyanea capillata (cf. pl.1)			
1. Atrich	9.4(5.9-12.6) x 5.2(3.9- 5.9)	71	very common
2. Do.[3]	17.1(12.5-26.1) x 11.1(6.3-18.9)	54	rather common
3. Eurytele	13.9(10.2-18.0) x 8.7(6.3-10.5)	70	very common
4. Holotrich	15.2(12.5-17.8) x 13.5(10.8-15.3)	67	rather common
Cyanea lamarckii (cf. pl.1)			
1. Atrich	8.3(5.3- 9.9) x 5.1(4.1- 5.9)	40	very common
2. Do.	12.8(10.4-15.8) x 8.3(6.3-11.7)	40	common
3. Eurytele	15.0(12.6-20.7) x 9.2(7.2-12.2)	40	common
4. Holotrich	11.7(9.9-13.5) x 10.0(9.0-10.8)	40	rather common
Chrysaora hysoscella (cf. pl.2)			
1. Atrich	5.9(4.6- 7.2) x 3.8(3.0- 4.6)	120	very common
2. Do.	12.7(10.2-15.8) x 8.0(5.9-10.5)	60	rather common
3. Eurytele	11.0(8.6-13.2) x 6.9(5.3- 9.2)	100	very common
4. Holotrich	14.5(12.2-17.8) x 13.4(10.0-16.8)	111	rather common
Pelagia noctiluca (cf. pl.2)			
1. Atrich	7.0(5.4- 8.1) x 4.4(3.6- 5.4)	31	common
2. Do.	13.7(11.7-16.2) x 8.3(7.2- 9.9)	25	common
3. Eurytele	13.2(11.3-15.3) x 9.7(8.1-11.7)	42	common
4. Holotrich	23.1(16.7-28.8) in diameter	41	common
Aurelia aurita (cf. pl.1)			
1. Atrich	7.9(5.9-10.4) x 4.5(4.1- 5.0)	50	very common
2. Eurytele	10.2(8.6-12.2) x 7.0(5.4- 9.0)	55	very common
Rhizostoma octopus (cf. pl.1)			
1. Atrich	4.9(4.0- 5.6) x 3.2(2.6- 4.0)	80	very common
2. Eurytele	8.1(6.7- 9.5) x 5.9(4.6- 7.6)	146	very common

Table 1 (cf. plates 1, 2). Survey of the cnidom of the six species of epipelagic Scyphozoa occurring in the North Sea and in the English Channel[1, 2]

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[1] Nematocyst data in table 1 were obtained from the following material: *Cyanea capillata*, RMNH s.n., Bergen, Norway and Kristineberg, Sweden, viii–ix-1981, 5 specimens, bell diameter 10–15 cm; *Cyanea lamarckii*, RMNH 5358, Kristineberg, Sweden, v-1937, 2 specimens, bell diameter 7 and 10 cm; *Chrysaora hysoscella*, RMNH 5258, Noordwijk, Netherlands, x-1922, 2 specimens, bell diameter 5 and 10 cm; *Pelagia noctiluca*, RMNH 6925, Mediterranean, no date, 1 spe-

cimen, bell diameter 8 cm, and RMNH s.n. (CANCAP-I, sta. 136), off Cape Blanc, 33°14'N — 9°15'W, iii-1976, 1 specimen, bell diameter 6 cm; *Aurelia aurita*, RMNH s.n., Bergen, Norway and Kristineberg, Sweden, viii-ix-1981, 2 specimens, bell diameter 5 and 20 cm; *Rhizostoma octopus*, RMNH 7006, Den Helder, Netherlands, viii-1929, 2 specimens, bell diameter 11 and 25 cm, and RMNH 7009, Katwijk-Noordwijk, Netherlands, ix-1926, 1 specimen, bell diameter 9 cm. Measurements are based on undischarged nematocysts from various parts of the medusae; exumbrella (bell), subumbrella, oral arms and marginal tentacles. The nematocysts in these parts may show slight differences in size and therefore the best way to study the nematocysts would have been on the basis of random samples of complete, homogenized jelly-fish. This, however, could not be done with registered museum-specimens.

[2] The most relevant literature data on the size (in microns) of the nematocysts of the species listed in table 1 are as follows [W = Weill, 1934: 535—546; P = Papenfuss, 1936: 5—22 (always averages); Wid = Widersten, 1973: 149, fig. 2a, b]: *Cyanea capillata*: 1. Atrich — 10 × 6 (W), 9.8 × 5.6 (P), length 5—9.5 (Wid); 2. Atrich — max. 35 × 25 (W), 20.8 × 14.2 (P), length 12—17, 17—23 (Wid); 3. Eurytele — 15 × 8—22 × 12 (W), 17.6 × 10.6 (P); 4. Holotrich — diam. 15—20 (W), 17 × 14.4 (P). *Cyanea lamarckii*: 1. Atrich — 9 × 5 (W), 9.0 × 5.6 (P), length 6—10.5 (Wid); 2. Atrich — max. 15 × 11 (W), 15.6 × 9.8 (P), length 14—20 (Wid); 3. Eurytele — length 12—17 (W), 14.6 × 8.2 (P); 4. Holotrichs — diam. 11—15 (W), 12.6 × 10.4 (P). *Chrysaora hysoscella*: 1. Atrich — length 7—9 (W), 8 × 3.8 (P); 2. Atrich — length 11—14 (W), 16.2 × 9.2 (P); 3. Eurytele — length 10—13 (W), 12 × 7.0 (P); 4. Holotrich — diam. 15—17 (W), 13.8 × 12.0 (P). *Pelagia noctiluca*: 1. Atrich — 7 × 3 (W); 2. Atrich — 17 × 12 (W); 3. Eurytele — 20 × 14 (W); 4. Holotrich — 30 × 29 (W). *Aurelia aurita*: 1. Atrich — length ca. 8 (W); 2. Eurytele — length 9—14 (W). *Rhizostoma octopus*: 1. Atrich — length 7—8 (W); 2. Eurytele — 8 × 5—11 × 6 (W). 1.

[3] This size-class can arbitrarily be split up into two categories (2^1 and 2^2), with a length of 12.5—20 and 20—26.1 microns, respectively.

This table demonstrates that all species of Semaeostomeae, with the exception of *Aurelia aurita*, are characterized by a cnidom consisting of atrichs (two size-classes), euryteles and holotrichs. The cnidom of *Aurelia aurita* consists of small atrichs and euryteles only, and in this respect the species agrees with *Rhizostoma octopus* (order Rhizostomeae). This remarkable fact has already been indicated by Weill (1934: 549) and by Russell (1970: 152). A remark may further be made with regard to *Cyanea lamarckii* and *C. capillata*. Unlike the other four species which can easily be distinguished in the field, these two species have often been confused and their specific identity doubted. However, especially as a result of the studies by Thiel (1960, 1962), their specific status is now widely accepted. A survey of the characters distinguishing these species is given by Russell (1970: 105, 111, figs. 58, 130, fig. 68). Russell does not include nematocyst data in his survey, although in the text (Russell, l.c.: 115, 133) he refers to data given by Weill (1934: 535-539, 551) and Papenfuss (1936: 5), which strongly support their specific status. The inventory of the cnidom of the two species presented in table 1 fully confirms this. In addition, a remarkable difference was found to exist in the distribution of nematocysts in the oral arms. In *Cyanea capillata* the armament of these oral arms includes clusters entirely consisting of relatively large holotrichs. In *Cyanea lamarckii* similar clusters occur, consisting of relatively large euryteles. Whether or not this is an absolute difference seems worthwhile to be further investigated.

With the aid of the data presented in table 1 (and to a lesser degree with those from the literature; cf. table 1 footnote 2) specific identification of the remains of Scyphozoa derived from the various turtles examined appeared possible in a number of cases. Of diagnostic value are, e.g., the maximal size of the atrichs in *Cyanea capillata* and the large size of the holotrichs of *Pelagia noctiluca*. Most useful for identification are also the small size of the holotrichs of *Cyanea lamarckii* and the small size of both atrichs and euryteles in *Rhizostoma octopus*. In other cases, even after a balanced consideration of all available data (average size, range, maximal and minimal size, ratio, combination and abundance of the various types of cnidae) such conclusive identifications could not be made. Difficulties resulted especially from the fact that the turtles had invariably taken in more than one species of jelly-fish, and taking into account the relatively small differences between the cnidom of some species, this proved to be most confusing.

Species Nematocyst type	Average and range (in parentheses) of length and width of nematocyst capsules in microns	Number of capsules measured	Occurrence
Aequorea forskalea			
1. Basitrich	14.9(13.5-16.2) x 4.2(3.6- 5.0)	25	very common
2. Atrich	17.7(17.1-18.5) x 9.4(9.0-10.4)	15	rather common
Aequorea vitrina			
1. Basitrich	12.0(9.0-13.5) x 3.2(2.7- 3.6)	25	very common
2. Atrich	19.9(18.0-21.6) x 8.2(7.2- 9.5)	20	common

Table 2 (cf. plate 2). Survey of the cnidom of species of *Aequorea* (Leptomedusae) recorded from the North Sea and the English Channel.[1], [2]

[1] Nematocyst data in the table are based on the following material: *Aequorea forskalea*, RMNH 3264, Den Helder, Netherlands, viii-1924, 1 specimen, bell diameter 7 cm; *Aequorea vitrina*, RMNH 3446, "Texel" lightvessel, 53°01'N4°22'E, vii-1961, 1 specimen, bell diameter 9 cm.

[2] Data on the cnidom of species of *Aequorea* from the same area listed in the literature are [W = Weill, 1934: 458; R = Russell, 1939: 348—355]: *Aequorea forskalea*: 1. Basitrich — length 15 (W), 12—18 × 2.5—4 (R); 2. Atrich — length 15—20 (W), 17—34 × 7—17 (R). *Aequorea vitrina*: 1. Basitrich — 10—15 × 2.5—3 and 12—13 × 3 (R); 2. Atrich — 19—22 × 17.5—8.5 and 18—20 × 7.5—8 (R). *Aequorea pensilis*: 1. Basitrich — 9—13 × 2.5—3 (R); 2. Atrich — absent (R).

Apart from scyphozoan nematocysts we ascertained the presence of nematocysts of Siphonophora (notably in the turtles from south-west England) and also of some types which we suspect to be of hydromedusan origin. The cnidom of Siphonophora is only poorly known. Hence, species identifications as a rule are not possible on the basis of nematocysts. The principal papers dealing with the cnidom of Siphonophora here used are those of Iwanzoff (1896: 334-348, pls. 5-6), Weill (1934: 504-521) and Russell (1938: 159-161; 1939:

356-358). As regards the intake of Hydromedusae, it may be remarked that only a few species are here worthy of consideration, viz., those species attaining substantial dimensions. The size of the majority of species is so insignificant that effective manipulation and intake by a "clumsy" giant as a full-grown leathery turtle may be assumed to be most unlikely (unless these medusae would occur in extremely high densities). Drawing the arbitrary size limit at a bell diameter of about 5 cm, representatives of the genus *Aequorea* Péron & Lesueur (Leptomedusae) in particular have to be considered as possible food items. Three species of *Aequorea, viz., A. pensilis* (Haeckel), *A. forskalea* Péron & Lesueur and *A. vitrina* Gosse have been reported from British waters and from the North Sea. In the two last-mentioned species the diameter of the bell may reach 17 cm (Russell, 1953: 337-358). For data on the nematocysts of the three species of *Aequorea* we refer to table 2.

DETAILED RESULTS OF THE INVENTORY OF THE INTESTINAL TRACTS OF THE VARIOUS INDIVIDUALS OF *DERMOCHELYS CORIACEA* (LINNAEUS)

Specimen 1 (table 3). — A carcase of a fully grown male (RMNH 14914) washed ashore on the beach of the island of Ameland (km 5), Netherlands, on 4-viii-1968. Total length 244 cm. Carapace heavily damaged, apparently by the blow of a ship's propeller. Weight 485 kg.

This individual has been described extensively by Brongersma (1969: 76-83; 1972: 63-64). Its complete alimentary tract still turned out to be present in the RMNH-collection. The anterior part of the oesophagus contained considerable amounts of sand, presumably taken in during its death-struggle in shallow water before having been washed up on the beach. The rest of the gut was all but empty. The turtle apparently had not taken in any food for some time, possibly as a result of its bad condition. Traces of an amorphous, greyish to blackish substance (possibly produced by the disintegration of the lining of the gut) containing small quantities of nematocysts were all that could be found. The results of the study of these nematocysts are presented in table 3. All nematocysts listed in this table, with the exception of the anisorhizes (7), are of scyphozoan origin and a comparison with table 1 (p. 6) reveals that most probably two species of Scyphozoa are involved: *Cyanea capillata* and *Rhizostoma octopus*. The smallest category of euryteles (4) can only be attributed to *Rhizostoma octopus*; as a consequence at least part of the smallest size-class of atrichs (1) also originates from this species. The large atrichs (3) can only originate from *Cyanea capillata*; the maximal size of the atrichs ocurring

Nematocyst type	Corresponding figure(s) in plates 3 and 4	Average and range (in parentheses) of length and width of nematocyst capsules in microns	Number of capsules measured	Occurrence
1. Atrich	1-2	5.4(4.3- 6.6) x 3.5(3.0- 4.3)	54	common
2. Do.	5-6	9.5(8.9-11.6) x 4.9(4.0- 5.8)	9	uncommon
3. Do.	9	21.7(18.4-26.3) x 16.5(12.5-19.7)	17	uncommon
4. Eurytele	10-12	8.1(6.6- 9.2) x 5.7(3.9- 6.6)	74	common
5. Do.	14-15	13.4(11.8-15.8) x 7.8(6.3- 9.5)	46	rather common
6. Holotrich	19	13.6(11.8-15.5) x 11.4(9.9-12.8)	57	common
7. Anisorhize	29	48.6(30.9-59.2) x 5.8(4.6- 6.9)	7	rare

Table 3 (cf. table 1 and plates 3, 4). *Dermochelys coriacea*, specimen 1 (Ameland, 4-viii-1968). Survey of nematocysts obtained form various parts of the gut. Measurements mainly based on discharged nematocysts.

in any of the other species of Scyphozoa does not even come within the range of this large category. The remaining, less diagnostic categories of cnidae found in the turtle's gut (2, 5, 6) also match the cnidom of *Cyanea capillata* rather well. *Cyanea lamarckii, Chrysaora hysoscella* and *Pelagia noctiluca* do not seem to be represented. In each of these species at least one category of cnidae occurs of which the size-range does not match that of comparable cnidae derived from the turtle. In *Cyanea lamarckii* the euryteles are considerably larger, whereas the holotrichs are smaller. In addition the largest kind of atrichs of this species does not match any of the size-classes derived from the turtle. The same holds for the large atrichs of *Chrysaora hysoscella* and *Pelagia noctiluca.* The holotrichs of the latter species furthermore are considerably larger than those found in the turtle (the ranges do not even overlap) and this species, moreover, only occasionally enters the southern North Sea (Russell, 1970: 73; Van der Baan, 1967, 1980). Whether or not a minority of cnidae derived from the turtle — small atrichs (1, 2) and small euryteles (4, 5) — originates from *Aurelia aurita* can neither be proven nor disproven.

The precence of a few anisorhizes (7) seems to indicate that the turtle on some occasion — probably before if entered the southern North Sea — had consumed a species of Siphonophora or a contaminated jelly-fish.

Specimen 2 (table 4). — A medium-sized female (RMNH 16803) found entangled in the lines of a lobsterpot and caught alive off the Lizard, Cornwall, England, on 29-vii-1971. Total length 172 cm. Weight 224 kg.

This turtle also has already been described by Brongersma (1972: 53—54), who gave the following information about the gut contents: "In the stomach and also farther posteriorly in the gut plastic bags were found. The further remains of the gut were examined by Dr. W. Vervoort, Leiden, who reports that the gut contained remains of jelly-fish, of fish, and of green algae. There is one large piece of jelly-fish (probably *Cyanea*), and in the intestine small fragments of jelly-fish with distinct nematocysts are found. Also present are fragments of tissue, of bones, and of bloodvessels with erythrocytes, which must derive from fish. Considering the fragments of the bloodvessels, it appears that the fish eaten by the turtle must have been of some size, and that it was not just a small fish accidentally ingested together with a jelly-fish. One of the samples contained relatively much sand and cristalline material."

Two jars containing remains of the gut contents of this specimen, altogether about 200 cc including preservative, still turned out to be present in the RMNH-collection and were included in the present study. One of the jars (150 cc) mainly contained crystalline matter and in addition some membranous structures with few nematocysts and small clots of erythrocytes. As cited above these erythrocytes were attributed to an unidentified species of fish. In our view, however, these erythrocytes originate from the turtle itself. Both their shape, large size, and good state of preservation support this view. In fact, contamination of a turtle's gut contents with its own blood can easily happen during dissection. In several other cases — without any fish involved — we have also found small numbers of these erythrocytes, which agree entirely with those present in the vascular system of *Dermochelys coriacea.*

The contents of the other jar (ca. 50 cc) mainly consisted of membranous matter and a flocculent precipitate with low concentrations of nematocysts. An inventory of these nematocys is presented in table 4 and suggests a considerably more varied diet than found in specimen 1. A first glance shows that both Scyphozoa and Siphonophora are involved. Most striking is the presence of birhopaloids (12), a type of nematocyst so far exclusively known from the siphonophore *Apolemia uvaria*[2] (cf. Carré & Carré, 1973; Den Hartog, 1980: 606–608, pl. 5 fig. 11). The following other nematocysts listed in table 4 may also be attributed to *Apolemia uvaria*: the single, large mastigophore (9), the two stenoteles (10) and possibly part of the small holotrichs (6). Considering their scarcity and added to this the absence of several other types that form part of the cnidom of *Apolemia*, it seems likely that these nematocysts represent contaminations, indirectly derived from Scyphozoa (many of which feed on other coelenterates). The same applies to a few isolated rhopalonemes (11) which, though not occurring in *Apolemia uvaria*, also are of siphophoran origin. The origin of the small, rounded mastigophores (8) is enigmatic. They are reminescent of the cnidae described from the palpons of *Physalia physalis* (cf. Totton, 1960: 325, fig. 11); they are, however, much smaller. Considering their

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[2] This, of course, is no proof of their absence in species of Siphonophora so far not investigated. However, considering the isolated systematic position of *Apolemia uvaria* — Huxley (1859: 70) already accomodated this species in a family of its own — it seems likely that the possession of birhopaloids is a unique character.

Nematocyst type	Corresponding figure(s) in plates 3 and 4	Average and range (in parentheses) of length and width of nematocyst capsules in microns	Number of capsules measured	Occurrence
1. Atrich1)	1-4	6.0(4.8- 8.6) x 3.6(2.6- 5.4)	77	rather common
2. Do.	7-8	13.6(9.9-17.1) x 8.3(5.9-10.5)	52	rather common
3. Eurytele	10-12	7.3(6.6- 8.6) x 5.5(4.0- 6.6)	33	rather common
4. Do.2)	13-15	12.2(9.9-15.1) x 8.0(5.9-10.5)	114	rather common
5. Do.	16-17	17.3(16.5-19.5) x 10.4(9.2-11.8)	7	rare
6. Holotrich	18-19	11.7(10.5-13.5) x 9.6(8.6-11.5)	50	common
7. Do.	20-21	22.0(15.3-27.6) x 20.1(13.5-27.1)	37	rather common
8. Mastigophore	31	7.3(6.9- 8.2) x 5.6(5.3- 6.6)	20	common
9. Do.	24	29.0 x 14.5	1	rare
10. Stenotele	25-26	13 x 14 and 22.5 x 18	2	rare
11. Rhopaloneme	--3)	14.0(13.8-14.5) x 5.5(5.3- 5.9)	4	rare
12. Birhopaloid	27-284)	22.3(19.1-25.7) x 12.8(9.2-14.5)	20	uncommon

Table 4 (cf. table 1 and plates 3, 4). *Dermochelys coriacea*, specimen 2 (Cornwall, 29-vii-1971), Survey of nematocysts obtained from the gut. Measurements principally based on discharged nematocysts.

[1] This category may arbitrarily be sub-divided into two size-classes: 5.1 (4.0—5.9) × 3.1 (2.6—3.6) and 7.1 (6.3—8.6) × 4.1 (3.6—5.4).

[2] Rather variable in shape: capsules rounded or ovate, tube rather narrow to rather broad.

[3] cf. Den Hartog, 1980: pl. 2 fig. 1, pl. 5 fig. 1.

[4] cf. Den Hartog, 1980; pl. 5 fig. 9.

common presence, they do not seem to represent contaminations.

An analysis of the scyphozoan nematocysts (cf. p. 6, table 1) shows that most probably three species of Scyphozoa are represented: *Rhizostoma octopus, Cyanea lamarckii* and *Pelagia noctiluca*. It seems rather certain that the small, typically scyphozoan euryteles (3) and part of the small atrichs (1; lower values of range) derive from *Rhizostoma octopus*. The presence of two categories of holotrichs (6, 7) which almost exactly match (both in average size and range) the cnidom of *Cyanea lamarckii* and *Pelagia noctiluca*, respectively, must imply that these two species are also involved. *Cyanea capillata* and *Chrysaora hysoscella*, which have holotrichs intermediate in size, are unlikely to be involved. As regards *Cyanea capillata*, this conclusion is confirmed by the absence in the gut samples of the large atrichs so characteristic of this species. Within the combination of nematocysts listed in table 4 any nematocysts of *Aurelia aurita* could go undetected. Thus, under reserve that the presence or absence of nematocysts of *Aurelia aurita* cannot positively be established, it can be inferred that the other (less diagnostic) categories of scyphozoan nematocysts listed in table 4 and so far not discussed, also originate from *Cyanea lamarckii* and *Pelagia noctiluca*. This assumption is in reasonable agreement with the figures (cf. table 1 and 4). The nematocysts presumably originating from *Cyanea lamarckii* are: small atrichs (1; higher values of range, in part), large atrichs (2, in part), euryteles (4; higher values of range, in part; 5) and small holotrichs (6). Those derived from *Pelagia noctiluca*: small atrichs (1;

higher values of range, in part), large atrichs (2, in part), euryteles (4, in part) and large holotrichs (7).

Specimen 3 (table 5). — A medium-sized female (RMNH 20356) found dead, washed up on the beach of the island of Ameland (km 18), Netherlands, on 8-xi-1977. Total length 175 cm. Weight 247 kg.

The intestinal tract of this specimen obviously had already been dissected and emptied on a previous occasion. Results of this investigation apparently have never been published, nor could we trace a manuscript or any written notes. Upon close examination we found that some parts were wanting and also that a part of the small intestine had not been completely cleaned out. This part contained a yellowish-grey flocculent substance, principally consisting of macerated epithelium of the intestinal wall, with small numbers of nematocysts (the majority discharged and collapsed), of which a survey is presented in table 5. This survey shows that the nematocysts concerned, without exception, are of scyphozoan origin.

Nematocyst type	Corresponding figure(s) in plate 3	Average and range (in parentheses) of length and width of nematocyst capsules in microns	Number of capsules measured	Occurrence
1. Atrich	3	6.8(5.9- 7.6) x 3.9(3.0- 4.6)	20	common
2. Do.	8	14.8(13.2-16.5) x 8.7(7.9- 9.9)	20	common
3. Eurytele	10-12	8.0(7.2- 9.2) x 5.8(5.3- 6.3)	8	uncommon
4. Do.	13	11.8(10.5-12.8) x 7.4(6.6- 7.9)	20	rather common
5. Do.	--	16.0(15.5-16.5) x 9.5(8.6-10.5)	2	rare
6. Holotrich.	19	12.2(11.8-13.2) x 10.0(9.2-10.9)	20	rather common
7. Do.	20	16.2(14.5-18.8) in diameter	12	uncommon

Table 5 (cf. table 1 and plate 3). *Dermochelys coriacea*, specimen 3 (Ameland, 6-xi-1977). Survey of the nematocysts obtained from the gut. Measurements principally based on discharged nematocysts.

On the basis of the data available a full-proof species identification cannot be presented, but it seems that at least three species can be excluded: *Cyanea capillata, Pelagia noctiluca* and *Rhizostoma octopus*. In *Cyanea capillata* all categories of nematocysts are considerably larger than corresponding types listed in the table. The holotrichs found — including the largest category (7) — are too small to be attributable to *Pelagia noctiluca*. Moreover, as mentioned earlier (cf. p. 10), this species of jelly-fish only rarely enters the southern North Sea. Lastly, in *Rhizostoma octopus* the small atrichs are considerably smaller than the smallest atrichs (1) derived from the turtle; there even is no overlap. On the other hand it must be admitted that the size — both average and range — of the small, uncommon euryteles (3) happens to fit the cnidom of *Rhizostoma octopus* rather well, better than any of the other species of jelly--fish listed in table 1 (p. 6).

From table 5 it is further apparent that the majority of nematocysts comprises four categories: two size-classes of atrichs (1, 2), euryteles (4) and holotrichs (6). Among the species so far not considered, a cnidom of exactly this composition is characteristic of *Cyanea lamarckii* and *Chrysaora hysoscella*, and it is difficult to determine whether only one or both species are involved. However, a detailed analysis of the nematocysts suggests that both species are represented. To *Cyanea lamarckii* may be attributed: part of both size-classes of atrichs (1, 2), the rare large euryteles (5), part of the medium-sized euryteles (4) and part of the smallest holotrichs (6). Categories which probably derive from *Chrysaora hysoscella* are: part of both size-classes of atrichs (1, 2), the uncommon large holotrichs (7) and part of the smaller holotrichs (6).

As in the case of turtle specimen 2, the presence of nematocysts of *Aurelia aurita* might here go undetected. However, taking into account that this jelly--fish essentially is an early summer species in the North Sea (Russell, 1970: 169; Van der Baan, 1980: 12), it may be assumed that *Aurelia aurita* was not represented in the gut contents of this turtle (which was found as late as November). Russell (1970: l.c.) states: "The adults may occur around British shores from the end of April to the end of August. They generally start to disappear, or have already disappeared, in September. They are nearly always absent in October."

Specimen 4 (table 6). — A well-developed male (RMNH 21059) caught alive in the lines of a lobsterpot at Gugh, Isles of Scilly, England, on 7-ix-1980. Total length 195 cm. Weight ca. 500 kg (estimated on the spot). The turtle was dissected by the veterinary surgeon of St. Marys and its preserved intestinal tract was air-freighted to Leiden by Mr. R. Graham, St. Marys.

Between the papillae of the oesophagus of this turtle small amounts of transparent membranous structures with dark particles of tissue were found, containing very high concentrations of nematocysts, and in addition two specimens of the amphipod *Hyperia galba*. The stomach contained a few litres of grey liquid substance containing a rather high concentration of nematocysts and a single specimen of *Hyperia galba*. The pylorus was more or less blocked by a ball of compressed plastics composed of a transparent plastic bag (15 × 17 cm), a frayed sheet of white plastic and many small shreds (varying in diameter from 0.5—4 cm) apparently derived from this sheet. The small intestine contained a grey substance presumably consisting for the major part of macerated epithelium, which did not contain any nematocysts. Caecum and colon contained a few litres of a thin liquid substance with a high concentration of nematocysts. Also were present 303 specimens of *Hyperia galba* (45 ♂, 258 ♀), 14 specimens of an unidentified parasitic flatworm (varying in length from ca. 1—2.5 cm) and some non-organic material represented by several small pieces of plastic (white as well as transparent, 2—3 cm in diameter) and three pieces of nylon cord (1—6 cm long). An overall microscopic examination of the contents from different parts of the gut did not reveal any obvious differences as regards the presence and ratio of the various types and size-classes of nematocysts, be it that stenoteles were exclusively met with in the oesophagus. A detailed survey of the nematocysts derived from the oesophagus is presented in table 6.

Nematocyst type	Corresponding figure(s) in plates 3 and 4	Average and range (in parentheses) of length and width of nematocyst capsules in microns	Number of capsules measured	Occurrence
1. Atrich	3-4	6.8(5.3- 8.6) x 3.7(2.9- 4.9)	41	very common
2. Do.	8	15.6(13.2-17.8) x 9.3(7.2-11.2)	31	rather common
3. Do.	22	22.4(20.4-25.7) x 13.1(11.2-18.4)	47	uncommon
4. Eurytele	14-17	14.5(12.5-19.7) x 8.6(6.6-12.5)	54	common
5. Holotrich	18-19	12.2(10.7-13.8) x 9.8(8.3-11.2)	43	very common
6. Basitrich	23	13.7(11.6-16.0) x 3.4(2.2- 4.3)	53	rather common
7. Stenotele	30	27.1(23.7-31.6) x 15.2(12.5-18.4)	26	uncommon
8. Anisorhize	29	23.4(15.1-36.4) x 4.5(2.9- 7.3)	49	uncommon
9. Rhopaloneme	--[1]	12.4(9.8-14.6) x 4.8(4.0- 6.7)	6	rare

Table 6 (cf. tables 1, 2 and plates 3, 4). *Dermochelys coriacea*, specimen 4 (Isles of Scilly, 7-ix-1980). Survey of the nematocysts obtained from the gut. Measurements based on discharged as well as undischarged nematocysts.

[1] cf. Den Hartog, 1980: pl. 2 fig. 1, pl. 5 fig. 1.

Of the nematocysts listed, four categories (1, 2, 4, 5) were identified to be of scyphozoan origin. Considering the size of these types and comparing table 6 with table 1 (p. 6), the following species at once may be excluded: *Rhizostoma octopus* (atrichs and euryteles too small), *Aurelia aurita* (euryteles too small), *Pelagia noctiluca* (holotrichs too large) and *Chrysaora hysoscella* (euryteles too small, holotrichs on the large side). Remain to be discussed *Cyanea lamarckii* and *C. capillata*. The size of the small atrichs (1), the euryteles (4) and the holotrichs (5) derived from the turtle matches the former much better than the latter, while the average size and range of the second size-class of atrichs (2) fits neither species very well. These atrichs are rather large for *Cyanea lamarckii*, rather small for *C. capillata*. However, the merger of the two largest size-classes of atrichs (2, 3) into a single category would create a raise of the average size as compared to the medium-sized atrichs (2) and an overall range that fits *Cyanea capillata* quite well. Nevertheless we are much inclined to assume that this species is not involved. Firstly because so far it has never been recorded with certainty from the English Channel nor from south-west of Ireland (Russell, 1970: 107) and secondly because the sizes of the other nematocysts do, as mentioned, agree much better with the figures found for *Cyanea lamarckii* (cf. p. 6, table 1). It may further be noted that the small basistrichs (6) so far not discussed almost certainly derive from a species of *Aequorea*. The number of these basitrichs suggests that they were not taken in as contaminations of jelly-fish, but that *Aequorea* was actually eaten by the turtle. Three species of *Aequorea* occur in British waters (cf. p. 8, table 2). The cnidom of two of these, *Aequorea forskalea* and *A. vitrina*, in addition to basitrichs, includes large atrichs. We therefore conclude that the large atrichs (3) listed in table 6 probably also originate from *Aequorea*. The rather sparse data available on the cnidom of *Aequorea forskalea* and *A. vitrina* (cf. table 2) indicate a considerable individual variation and overlap in the size of their nematocysts. Thus, species identification on the basis of the cnidae derived from the turtle's gut (3, 6) is not possible.

Two types of nematocysts, anisorhizes (8) and rhopalonemes (9), definitely originate from a species of Siphonophora and this possibly also holds for the stenoteles (7). Taking into account the small numbers of these cnidae, they probably represent contaminations taken in with Scyphozoa (cf. p. 11).

Specimen 5 (table 7). — A well-sized male (RMNH 21060) caught and taken aboard of the fishing-vessel "Avail" in the vicinity of Eyemouth, Scotland, on 3-x-1980. Total length 168 cm. Weight ca. 500 kg (estimated on the spot). This turtle was kept in captivity, to die four days later, on 7-x-1980. The intestinal tract was secured, preserved in formalin, transported to Leiden and donated to the RMNH by Dr. R. Th. J. Moody, Department of Geology, Kingston Technical College, Kingston upon Thames.

Just as in specimen 4, small amounts of membranous structures and dark tissue containing rather high concentrations of nematocysts were found among the papillae of the oesophagus of this turtle. The stomach contained about one litre of a thin liquid substance with several pieces of spongy tissue (up to 3 cm in diameter) of unknown identity, containing small amounts of nematocysts. The contents of the pyloric region were of a green colour, presumably bile-stained. The small intestine contained a substance (also stained green) consisting of closely packed, very thin lamellae (up to 1 cm in diameter) with small amounts of nematocysts. Ceacum and colon contained about 1 litre of liquid substance, also with amounts of these thin green-coloured lamellae and relatively high concentrations of nematocysts. In addition five small bird's feathers were found, varying in length from 4 to 50 mm. A survey of the nematocysts derived from oesophagus and ceacum is presented in table 7. The majority of these nematocysts appears to be of scyphozoan origin and it is

Nematocyst type	Corresponding figure(s) in plates 3 and 4	Average and range (in parentheses) of length and width of nematocyst capsules in microns	Number of capsules measured	Occurrence
1. Atrich	3-5	7.4(5.3-10.5) x 4.3(3.0- 5.9)	140	very common
2. Do.	--	13.7(12.5-16.1) x 7.9(6.6- 9.2)	13	uncommon
3. Do.	9	23.7(19.7-27.6) x 17.1(13.8-21.1)	20	rather common
4. Eurytele	12-13	9.2(8.2-10.8) x 6.4(5.3- 8.1)	60	common
5. Do.	14-15	13.5(11.5-17.1) x 8.6(7.2-10.8)	60	rather common
6. Holotrich	19	14.4(12.5-16.5) x 12.3(10.5-13.8)	60	rather common
7. Basitrich	23	8.5(7.9- 9.9) x 2.3(2.0- 2.6)	11	rare

Table 7 (cf. tables 1, 2 and plates 3, 4). *Dermochelys coriacea*, specimen 5 (Eyemouth, 3-x-1980). Survey of the nematocysts obtained from the gut. Measurements based on discharged as well as undischarged nematocysts.

likely that more than one species is involved. A comparison with the data presented in table 1 (p. 6) shows that three species probably are not represented: *Cyanea lamarckii, Pelagia noctiluca* and *Rhizostoma octopus.* In *Cyanea lamarckii* the holotrichs are considerably smaller than those derived from the turtle; in *Pelagia noctiluca* they are considerably larger. *Rhizostoma octopus* may be excluded on the basis of its small-sized atrichs, the range of which hardly shows an overlap with the smallest atrichs (1) found in the turtle. Definitely involved is *Cyanea capillata,* as can be deduced from the presence of large atrichs (3), which can only be attributed to this species. All the other — less diagnostic — categories of nematocysts listed in table 7 also match the cnidom of *Cyanea capillata* (cf. table 1) rather well, with the exception of the small, common euryteles (4) and perhaps part of the small atrichs (1, lower values of range). This means that at least one other species of Scyphozoa is represented. The dimensions of the small euryteles (4) are of the size-order present in *Aurelia aurita* and *Chrysaora hysoscella* — the only two species thus far not discussed — and match the former better than the latter. Yet, if the lower values of the range of the large eurtyles (5) are also taken into account, *Chrysaora hysoscella* might just as well be involved (instead of, or in addition to *Aurelia aurita*). It is striking, however, that the very types of cnidae that compose the cnidom of *Aurelia aurita* (viz., small atrichs and small euryteles; cf. table 1) happen to be the most numerous types, and it may further be argued that one would have expected the medium-sized atrichs (2) to be considerably more numerous if *Chrysaora hysoscella* would be represented, for this size-class presumably also includes cnidae derived from *Cyanea capillata.* These cnidae therefore seem to point to *Aurelia* rather than to *Chrysaora.* The date of catch of the turtle (October 3rd), however, definitely is not in favour of this conclusion (cf. p. 14).

In addition to the scyphozoan nematocysts a few basitrichs of the type characteristic of *Aequorea* were found, presumably taken in as contaminations of jelly-fish. The dimensions of these basitrichs, although a little under-sized, approach those of *Aequorea pensilis* best (cf. p. 8, table 2; Russell, 1939: 350). Although a small part of the large atrichs (3) in principle might also be attributed to a species of *Aequorea* (cf. table 2), atrichs happen to be entirely absent in *A. pensilis.* These atrichs therefore — as mentioned above — are more likely to derive from *Cyanea capillata.* Even if another species of *Aequorea* would be involved, it may be noted that the numbers of basitrichs (7; rare) and large atrichs (3; rather common) do not match at all, so that the presence of *Cyanea capillata* anyhow must be assumed to explain the relative abundance of the latter.

Specimen 6 (table 8). — A fully grown male (RMNH 21058), caught alive at the Thomas Smitgat, off the island of Terschelling, Netherlands, on 4-viii-1981. Total length 216.5 cm. Weight 510 kg. The specimen died on board. After having been transported to Leiden, it was dissected on 7-viii-1981.

Between the papillae of the oesophagus of this turtle fibrous structures were found, up to 2 cm long, with few adherent nematocysts. The stomach contained two litres of a grey fluid with high concentrations of nematocysts and in addition 75 specimens of the amphipod *Hyperia galba*, a fragment (2 cm long) of the hydroid *Obelia dichotoma* (Linnaeus) and a well-preserved plastic bag (17.5 × 13.5 cm). The small intestine contained a more substantial grey liquid with macerated intestinal epithelium and a rather high concentration of nematocysts; also were found 253 specimens of *Hyperia galba* (52 ♂ and 201 ♀), a small bird's feather (3.5 cm long) and a small ball (3.5 cm in diameter) of a well-preserved green alga, *Enteromorpha prolifera*, which included a small crab, *Carcinus meanas* (Linnaeus) (carapace 3 cm across) and another fragment of *Obelia dichotoma.* From ceacum and colon about 4 litres of fluid were derived containing a high concentration of nematocysts, 48 specimens of *Hyperia galba* (6 ♂ and 42 ♀) and 10 specimens of a parasitic turbellarian. It is noticable that in addition about 500 cc of sand and mud were obtained from this part of the gut. This material must be assumed to have been taken in accidentally when the turtle was feeding in shallow water. In this connection we are inclined to think that the turtle shortly before it was captured had been foraging in the Dutch Waddensea, which is so shallow that large parts of it emerge when the tide goes out. The turtle may have been surprised by the ebb-tide and have had some trouble to reach deeper water again. It is easy to imagine that bits of sand and mud were indeliberately taken in on such an occasion.

A survey of the nematocysts found in the stomach and the ceacum is presented in table 8. At one glance it becomes clear that all the types listed, with-

Nematocyst type	Corresponding figure(s) in plate 3	Average and range (in parentheses) of length and width of nematocyst capsules in microns	Number of capsules measured	Occurrence
1. Atrich	1-2	4.5(4.0- 4.9) x 3.2(2.6- 3.6)	20	very common
2. Do.	4-6	8.5(7.2-10.4) x 4.5(3.9- 5.9)	25	rather common
3. Do.	—	12.7(11.8-15.3) x 6.9(5.9- 7.9)	20	uncommon
4. Do.	8	18.5(16.5-21.1) x 12.8(10.5-15.1)	8	rare
5. Eurytele	10-12	7.9(6.9- 9.9) x 5.8(4.9- 7.9)	30	very common
6. Do.	13-15	12.5(10.5-15.8) x 8.0(5.9-10.8)	30	common
7. Holotrich	19	13.5(12.5-15.3) x 12.1(11.2-15.3)	20	uncommon

Table 8 (cf. table 1 and plate 3). *Dermochelys coriacea*, specimen 6 (Terschelling, 4-viii-1981). Survey of nematocysts obtained from stomach and caecum. Measurements based on discharged as well as undischarged nematocysts.

out exception, are of scyphozoan origin. A comparison of table 8 with table 1 (p. 6) shows that the small atrichs (1) and the small euryteles (5) almost certainly originate from *Rhizostoma octopus.* The dimensions of these cnidae perfectly match the cnidom of this species (corresponding cnidae of the other species listed in table 1 are distinctly larger) and their comparatively large numbers (both types very common) further indicate that *Rhizostoma octopus* must have formed the main food-item of the turtle at the time of its capture.

The origin of the other nematocysts is less easy to settle. The rather small size of the holotrichs (7) excludes the possibility that *Pelagia noctiluca* is involved; this is no surprise if we take into account that this species only occasionally occurs in the North Sea (cf. p. 10). *Chrysaora hysoscella* may also be excluded as the range of the small atrichs of this species is not represented. The distinct gap between the two smallest size-classes of atrichs (1, 2) in table 8 definitely would not have been present if *Chrysaora hysoscella* had also been involved. With some reserve *Cyanea lamarckii* may also be excluded; the euryteles (6) seem rather small for this species, the holotrichs (7) on the other hand rather large, and especially the discrepancy "too small — too large" in our opinion settles this matter. Two species remain to be discussed: *Cyanea capillata* and *Aurelia aurita.* The large atrichs (4) seem to indicate positively that the former species is involved, although the largest example found of this category (21.1 × 15.1) is relatively small, especially when compared to the maximal size given by Weill (1934: 536, 35 × 25 microns). But even so, this size-class cannot possibly be attributed to any of the other species. Besides, the low maximal size encountered here may be coincidental and related to the small number of these cnidae actually found. It further appears that all the other; less diagnostic and less abundant categories of cnidae not discussed so far, also more or less (though definitely not in a perfect way) match the cnidom of this species of jelly-fish (cf. p. 6, table 1). In this connection, however, it may be brought to notice that among these categories the small atrichs (2) and the largest euryteles (6) are considerably more numerous than the other cnidae (3, 4, 7). This also fits in with our assumption that *Cyanea capillata* is involved (cf. table 1), but on the other hand it seems rather likely that these atrichs and euryteles at least partly originate from *Aurelia aurita*. This additional assumption would explain why the average size of these two categories of cnidae is a little small for *Cyanea capillata* and a little large for *Aurelia aurita*.

SUMMARY AND DISCUSSION OF THE RESULTS

An overall survey of the food items and other materials obtained from the six turtles investigated is presented in table 9. It appears that these turtles mainly fed upon Scyphozoa. This also explains the presence in two individuals of considerable numbers of the amphipod *Hyperia galba*, a well-known scyphozoan commensal. The gut contents of four turtles included nematocysts of Siphonophora and Hydromedusae, but taking into account the small numbers generally involved and bearing in mind that such coelenterates form part of the diet of many Scyphozoa (cf. Russell, 1970: 84, 102, 120, 137, 162), it seems possible that at least part of these cnidae represents contamination resulting from the intake of Scyphozoa. In other cases, where larger numbers of

Specimen	Locality	Date	Identified food items and other ingested materials
nr. 1	Ameland, Netherlands	4-viii-1968	*Cyanea capillata*, *Rhizostoma octopus*, *Aurelia aurita?*, unidentified siphonophore (c).
nr. 2	The Lizard, Cornwall, England	29-vii-1971	*Rhizostoma octopus*, *Cyanea lamarckii*, *Pelagia noctiluca*, *Aurelia aurita?*, *Apolemia uvaria* (c), unidentified siphonophore (c), remains of an unidentified fish, fragments of unidentified green algae, plastic bags.
nr. 3	Ameland, Netherlands	6-xi-1977	*Chrysaora hysoscella*, *Cyanea lamarckii*
nr. 4	Scilly Isles, Cornwall, England	7-ix-1980	*Cyanea lamarckii*, *Aequorea* spec., unidentified siphonophore(s?)(c), *Hyperia galba* (c), plastics among which a plastic bag measuring 17 x 15 cm.
nr. 5	Eyemouth, Eastern Scotland	3-x-1980	*Cyanea capillata*, *Aurelia aurita* and/or *Chrysaora hysoscella*, *Aequora (pensilis?)* (c), few small bird feathers.
nr. 6	Terschelling, Netherlands	5-viii-1981	*Rhizostoma octopus*, *Cyanea capillata*, *Aurelia aurita*, *Hyperia galba* (c), a small specimen of *Carcinus maenas*, fragments of *Obelia dichotoma*, fragments of *Enteromorpha prolifera*, a plastic bag measuring 17.5 x 13.5 cm.

Table 9. *Dermochelys coriacea*. Overall survey of the food components and other items obtained from the guts of six individuals from southern England and the North Sea. (c) = Taken in with Scyphozoa, either as contamination or as commensal.

non-scyphozoan cnidae are involved, their presence is more likely to be the result of the actual intake of their bearers. This seems especially obvious with the cnidae attributed to the leptomedusa *Aequorea* spec. present in the turtle from the Scilly Isles (specimen 4). Other material found in some of the turtles, such as traces of green algae, a small crab and a few small bird's feathers most probably were taken in accidentally. Finally, three specimens contained plastics, a phenomenon further discussed below.

The results summarized above are in accordance with the current idea that *Dermochelys coriacea* mainly feeds upon Scyphozoa (e.g. Bleakney, 1965: 124-126; Brongersma, 1969: 95; Duron, 1978: 89). One should realize, however, that practically all our information of the diet of the species has been derived from summer visitors of the relatively cold northern range of its area of distribution, far from the breeding grounds. Hence the available data do not necessarily implicate a preference of the leathery turtle for jelly-fish. These data may just as well reflect that jelly-fish form the main available food source in this part of the area of distribution and possibly therefore it is not coincidental that several of the specimens from southern origin listed by Brongersma (1969: 86, table 2, 93-94) proved to have eaten tunicates. To avoid misunderstanding, it may here be stressed that coelenterates are certainly also eaten in warmer waters (cf. e.g. Bleakney, 1965: 126; Pritchard, 1971: 14; Brongersma, 1969: 86, table 2, 92; Den Hartog, 1980: 606-608).

In our view the diet of the leathery turtle is rather based on availability of food than on preference and we have no doubt whatsoever that this species will also take dead fish, fish spawn, regurgitation rests of whales, offal etc., when present. Moreover, we are much inclined to assume that the leathery turtle does not visually recognize — in the strict sense of the word — the food items it thrives on. Indirect support of this idea may be derived from the frequent reports of intake of indigestable materials like plastics (e.g. Brongersma, 1969: 95; Hughes, 1974: 38; Duron & Duron, 1980: 40-41; Duguy, Duron & Alzieu, 1980: 686; Mrosovsky, 1981: 5-7). It has been suggested that the leathery turtle may mistake plastic bags and sheets for jelly-fish (Duron, 1978: 89; Mrosovsky, l.c.: 5; Fritts, 1982: 72-73), which implicates that its visual perception must be very poor indeed, for the resemblance between the two items in fact is extremely superficial. Moreover, such a confusion certainly cannot account for the intake of e.g. a plastic spoon as reported by Mrosovsky (1981: 5-6, fig. 1) and of a piece of bark as reported by Sears (1887: 93). The intake of such materials rather seems to indicate that the shape of potential prey is of no relevance and that the leathery turtle is a non-selective feeder attracted by all slow-moving or floating objects of any size. As the majority of these — since time immemorial — happens to be formed by macro-planktonic organisms like jelly-fish and salpae, one can imagine that such an indiscriminate way of feeding (which somewhat paradoxally results in a rather specific diet) could provide a satisfactory mechanism for the species to thrive and to survive. However, during the last decennia this supposed mechanism, which could have acted for millions of years in the very stable conditions of the marine environment, is being interfered with by man, who litters the sea with non-organic, indigestible matter like floating plastics etc., apparently forming an increasing threat to the species. The intake of these plastics, notably of large pieces or of large amounts, undoubtedly will cause obstruction and digestive problems, which may eventually result in death (Hughes, 1974: 38; Duron & Duron, 1980: 40; Duguy, Duron & Alzieu, 1980: 686; Fritts, 1982: 72). The turtles apparently cannot get rid of these materials by regurgitation (cf. p. 27, footnote 6).

In this connection we may also mention the phenomenon that leathery turtles regularly are found entangled in the lines of lobsterpots (cf. the various cases listed by Brongersma, 1972; Lazell, 1976: 191-192). Two of the six turtles studied here actually perished in this way. It may be obvious that this phenomenon is a nuisance to lobsterman, who sometimes suspect the turtles of trying to rob the contents of their pots (pers. comm. Prof. Dr. L. D. Brongersma), but so far there has never been found any evidence to substantiate this assumption. The question therefore remains why this phenomenon occurs. It seems to happen too often to be considered purely accidental, but on the other hand leathery turtles are rather clumsy manoeuvrers and when they happen to enter more or less heavily fished lobster grounds, it seems quite imaginable that they may hit and subsequently become entangled in lobsterpot lines. Lazell (1976: 191-192) prefers an explanation in which the turtles play a more active part. According to this author the turtles would mistake the pot buoys for jelly-fish (Lazell, l.c.: ".... Covered with brownish algae, some of which hangs down in long streamers, it (i.e. the buoy) just looks like a *Cyanea*...") and as a result of their attempts to devour the buoys the turtles would considerably increase their chances to become entangled. Although we certainly do not reject the idea that leathery turtles may be attracted by floating pot buoys and possibly will try to devour these, we again do not agree with the popular and rather anthropomorphic idea that these turtles would mistake (in the strict sense of the word) such a buoy for a *Cyanea* and as a consequence we are rather sceptical about Lazell's view that it would be in the advantage of both lobsterman and leathery turtles if the former would regularly clean the algae off their pot buoys.

To conclude this chapter, the extraordinary nature of the food of *Dermochelys* may be touched upon. At first sight it seems incredible that a large animal like a leathery turtle can survive and thrive on a diet of such watery organisms as jelly-fish are, but yet this must be accepted as a fact. Moreover, *Dermochelys* certainly does not stand alone in this respect. Many are the organisms subsisting partly or entirely on a diet of coelenterates, though the majority of these are invertebrates (cf. e.g. Salvini-Plawen, 1972). Vertebrate coelenterate predators are to be found among fish, the most striking example being the giant sunfish *Mola mola* (MacGinitie & MacGinitie, 1949: 435-436), and among other sea turtles, e.g. the loggerhead turtle *Caretta caretta* (Brongersma, 1972: 157-162; Van Nierop & Den Hartog, unpublished data).

Considering this, there cannot be any doubt about the nutritional value of jelly-fish and of coelenterates in general, provided these can be taken in in sufficient quantities. Published data on the composition of jelly-fish are scanty and show considerable discrepancies, but it may roughly be stated that the water contents of jelly-fish — in normal sea water, i.e., with a salinity of about 33—35‰ — varies between about 94 and 96.5% (Hyman, 1938: 166-167; 1940: 282-284). Solid substances therefore form about 3.5—6% of the total weight. They consist of the following components: inorganic salts, proteins and fat. If it is assumed that the percentage of salts more or less agrees with that of the environment[3], the amount of organic matter roughly varies between 0.5—2.5%, a variation which may partly be correlated with the stage of development of the gonads (Teissier, 1926). As far as we could find out, Lowndes (1942: 234-235) is the only author who determined the ratio of fat and protein of the organic substance in a jelly-fish (viz., *Aurelia aurita*). He found 1.24% organic matter, made up of 0.67% protein and 0.57% fat. Much lower amounts of fat, varying between 0.034 and 0.10%, were found by Sipos & Ackman (1968: 1562) in *Cyanea capillata*. Although the data here presented clearly indicate that additional investigations on this subject are highly desirable, they do at least give some idea of the nutritional value of jelly-fish.

Duron (1978), who repeatedly observed the feeding activities of the leathery turtle on the west coast of France, estimated that a fully grown individual daily devours about 50 large specimens of *Rhizostoma pulmo*, representing a total contents of some 200 litres. From this she infers that the species takes in about 8—10 kg protein per day (Duron, l.c.: 109; Duron & Duron, 1980: 40). The

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[3] Although ionic regulation in marine coelenterates must be accepted as a fact, the body fluids of these organisms probably without exception are more or less isotonic with the external medium (Krogh, 1939: 28-31; Potts, 1968: 79-80). Data on the salt concentration of body fluids of jelly-fish presented in some of the older publications seem to point to significant osmoregulation (Hyman, 1938: 166; 1940: 283-284). These figures, however, probably are based on inaccurate investigations. The salt percentage e.g. recorded by Vernon (cf. Hyman, 1938: 166) in both *Carmarina* (= *Geryonia*) (Trachymedusae) and *Rhizostoma* (Scyphozoa), viz., 4.3%, suggests that his specimen(s) had suffered considerable desiccation before being analyzed.

first two figures are rough estimates and it is difficult to judge therefore to what extent they do meet reality. The extrapolation, however, that a volume of 200 litres of jelly-fish stands for 8—10 kg of protein is unacceptable if we take into consideration the above-mentioned data concerning the composition of jelly-fish. As no references are cited by Duron, it is not clear upon what data this computation was based.

Vernon (cf. Hyman, 1938: 166) reported a percentage of 0.53% organic matter in *Rhizostoma pulmo*, or 5.3 g per litre. Using this figure, the intake of 200 l of jelly-fish would stand for 1060 g of organic matter only. However, if it is assumed that the percentage of organic matter in jelly-fish may increase up to 2.5% during the reproductive season (cf.p. 23), we come to a maximal intake of about 5 kg of organic matter a day. The actual intake of organic matter would than possibly be intermediate between these figures, in the order of 2.5 kg per day.

Accepting the figures of Lowndes (cf. p. 23), this amount consists of about equal parts of fat and protein, representing an energy intake of about 1250 × 4 + 1250 × 9 = 16250 kcal. per day (1 g fat represents 9 kcal., 1 g protein 4 kcal.). Taking the figures of Sipos & Ackman (maximally 0.10% = 200g fat), the energy intake would maximally amount to 2300 × 4 + 200 × 9 = 11000 kcal. For the sake of comparison it may be noted that such an energy intake roughly amounts to 2.5—4 times the daily energy consumption of a man performing heavy labour. It should be borne in mind, however, that part of the food taken in by the leathery turtle in northern waters is likely to be converted and stored in the form of fat deposits to cover extra energy needs during migratory movements to the breeding grounds and for reproductive activities. Hence, in conformity with e.g. migratory birds, the daily energy consumption of a leathery turtle in these waters would be considerably lower than the actual energy intake. It may be clear that the figures here presented should be considered — for many reasons — with reserve. They represent no more than a very rough attempt to obtain — on the basis of data and estimates available in the literature — an approximate impression of the daily intake and consumption of energy by the leathery turtle.

SOME GENERAL NOTES ON THE DIGESTIVE TRACT OF *DERMOCHELYS CORIACEA*, WITH SPECULATIONS ON THE FUNCTIONAL MORPHOLOGY OF THE ANTERIOR PART

The general morphology of the digestive tract of *Dermochelys coriacea* has been described by Vaillant (1886), Burne (1905: 314-316) and Dunlap (1955:

63). It may roughly be divided into oesophagus, stomach, small intestine and a part comprising caecum, colon and rectum. Data as to the length of these parts in the turtles examined by us, supplemented with data of Dunlap, are presented in table 10. Although these rough data are insufficient to allow any far-reaching conclusions, they at least seem to indicate that the overall length of the alimentary canal (and of its various sub-divisions) is not distinctly correlated with the total weight and overall length of the turtles. The gut e.g. of Dunlap's rather small specimen (7) is just as long as that of the specimens from the Scilly Isles (4) and only little shorter than that of the specimen from Terschelling (6; taking into account that the oesophagus of this specimen was not measured), which was half a metre longer and more than twice as heavy. The table further shows that the small intestine in specimen 1 (Ameland) and specimen 5 (Eyemouth) was considerably shorter than in the other specimens. This difference possibly can be attributed to the fact that these two specimens

Specimen number	Locality	Sex	Length Oesophagus	Length Stomach	Length Small Intestine	Length Colon and Caecum	Total length of gut	Total weight	Overall body length
1.	Ameland, Netherlands	♂	142	171	656	223	1192	485	244
2.	The Lizard, Cornwall, England	♀	-	-	-	-	-	224	172
3.	Ameland, Netherlands	♀	-	-	-	-	-	247	175
4.	Scilly Isles, Cornwall, England	♂	165	197	1089	205	1656	500?[1]	195
5.	Eyemouth, Eastern Scotland	♂	90+	170	700	220	1180+	500?[2]	168
6.	Terschelling, Netherlands	♂	-	310	1050	250	1610+	510	216.5
7.	Off Louisiana (Dunlap, 1955)	♀	183	203	1234		1620	224	154

Table 10. *Dermochelys coriacea.* Survey of overall body length, weight, sex and length of various parts of the alimentary tract of six individuals from southern England and the North Sea, supplemented with data by Dunlap (1955: 59, 63). Lengths in cm, weights in kg; + = incomplete, — = no data available.

[1], [2] The weight of these individuals was roughly estimated in the field. Considering their overall lengths it seems obvious that at least the weight of the turtle from Eyemouth was grossly overestimated.

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[4] The gut of the specimen from Ameland appeared practically empty when it was dissected (cf. p. 9). The specimen from Eyemouth was kept four days in captivity before it died, presumably also without taking any food. The other specimens of which relevant data are available, died and were preserved and/or dissected shortly after they were caught (i.e., after they had performed feeding and digestive activities).

had not taken in food shortly before they died[4], but it might just as well, or in addition, reflect a genuine individual variation. This latter explanation anyhow seems plausible with regard to the variation found in the length of the stomach. In four specimens it had about the same size, varying in length from 170—203 cm, while in the specimen form Terschelling (6) a length of more than three metres was measured.

Several authors have called attention to the peculiar, densely arranged, inwardly-directed, simple or compound, thick, flexible spines which line the oesophagus over its intire length. These spines may reach a length of up to 8 cm. As to their function, there is no support whatsoever for the idea forwarded by Deraniyagala (1953: 11) and Pritchard (1969: 131-132) that they might be functional in pharyngeal respiration. In that case one would expect them to be well-permeable and well-vascularized. A simple dissection, however, shows them to consist of cartilaginous connective tissue covered by a strongly developed keratinized epithelium (cf. Burne, 1905: 63). Any trace of vascularization — not to speak of the presence of a well-developed vascular system — is absent. A recent microscopical study of Yoshie & Honma (1976) on the pharyngeal spines of the olive ridley *Lepidochelys olivacea* also does not support the theory of "pharyngeal oxygen exchange". The function of these spines is now generally believed to be the prevention of prey to slip back up from the gut (Bleakney, 1965: 125; Pritchard, 1971: 14). However, so far nobody has made plausible why under normal conditions a prey, even a slippery prey like a jelly-fish, once snapped up and swallowed, would slip upwards from the gut. Generally, normal peristalsis in vertebrates is well able to prevent this. One cannot, so to speak, empty the stomach of a given vertebrate (even with liquid contents), by keeping the animal upside down. In principle this can only be achieved by pressure of the diaphragm and/or antiperistaltic contractions of the anterior part of the gut.

As mentioned above, Duron (1978: 109) estimated that the leathery turtle may consume as much as 200 litres of jelly-fish (only 0.5—2.5% of which is organic matter) per day. In addition it seems possible that a surplus of sea-water is swallowed during the act of feeding. Altogether it must be concluded that the species daily takes in a tremendous lot of sea-water, even if it is assumed that the above-mentioned estimate is too high. It seems most unlikely that such excessive amounts can be absorbed by the intestinal wall and be excreted, via the circulatory system, by the kidneys and the lachrymal salt-glands[5]. From this we infer that there must be another mechanism to get rid of this sea-water, to prevent it from entering the intestines. Here it would interfere with the digestive process by its diluting effects and by speeding up the transport of the intestinal contents by washing it down. In our view therefore this sea-water is removed by oral expulsion, presumably realized by contraction of the diaphragm muscles and/or by antiperistalsis of the anterior part of the gut (stomach and/or oesophagus). Assuming such a mechanism it seems obvious that the oesophageal spines may indeed be regarded as devices to prevent edible, more or less solid substances to escape through the mouth, functioning as an effective sieve, in this respect comparable to the baleens of whalebone cetaceans[6]. They further might take part in the mechanical breakdown ("chewing") of ingested food items.

It may be emphasized that the water content of jelly-fish principally is chemically bound (though some free water may be adhering to the body or be contained in the gastric cavity), and that it cannot simply be squeezed out by mechanical pressure of the turtle's stomach and oesophagus. Expulsion of this water (mainly contained in the mesogloea) can only be realized after the initial phase of digestion, involving liberation of this water and break-down of mesogloeal collagen and elastic (oxytalan) fibres and the interfibrillary substance (mucopolysaccharids) (Bouillon & Coppois, 1977: 340-345, 363-365).

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[5] Apart from the problem to get rid of about 200 l of water, the turtle would have to get rid of extreme amounts of excess salt. From data in the literature (e.g. Dessauer, 1970: 4, table 1; Lockwood, 1963: 59; Zandee, 1971: 159) it can be inferred that the concentration of electrolytes in sea turtle blood roughly amounts between 1/4 and 1/3 that of seawater. As the turtle kidney cannot produce urine that is hypertonic to blood (Lockwood, 1963: 57-58, 117; Bentley, 1976: 383), excess salt cannot be removed by renal excretion. This presumably therefore happens by means of the salt-secreting lachrymal glands. These are known to excrete (in *Caretta caretta*) salt solutions up to almost twice the concentration of sea-water (Lockwood, 1963: 58-59; Dunson, 1976: 15-16). Basing ourselves on this information, 200 l of sea-water (concentr. ca 3 × that of blood) would have to be excreted partly as lachrymal "tears" (X liters — concentration ca. 2 × that of sea-water) and urine (Y liters — isotonic, or even hypotonic relative to blood). From the equations $X + Y = 200$ and $200 \times 3 = X \times 6 + Y \times 1$ follows that the amount of lachrymal fluid excreted per day would be in the order of 80 l (!) and that of (isotonic) urine about 120 l per day.

[6] In vertebrates, under natural conditions, antiperistalsis of the anterior part of the gut normally happens in relation to special, although rather universally occurring functions: retching (preventing certain objects or substances to enter the gut), vomiting (e.g., following the ingestion of unsound food or poisonous matters) and regurgitation of indigestable food remains (pellets) and, in more special cases, of pre-digested food intended to feed juveniles, as is a common phenomenon in many sea-birds. In this connection it is noticeable that such common and obviously important biological functions apparently are bound to be highly ineffective in the case of the leathery turtle (and other sea turtles). Taken by itself, this must be considered a disadvantage for the species, especially nowadays, taking into account the modern phenomenon of an ocean polluted by undigestible man-made litter. The question remains why such materials are taken in at all. The visual perception of the leathery turtle presumably is poor (cf. page 21), but is seems likely that the species has at least some olfactory sense. However, this being so, the (indifferent) taste and smell of plastics apparently do not produce stimuli to reject these matters. Whether the absence of significant quantities of marine algae in the leatherbacks so far investigated can be traced back to olfactory discrimination is something to consider. The more so as marine algae (oceanic *Sargassum* as well as detached coastal forms) are not rarely found drifting about, often in considerable quantities.

The general structure of the stomach in sea turtles is a simple, bean-shaped sac. The stomach of *Dermochelys* forms the only exception and deviates considerably from this general plan. It is of unusual length, up to more than three metres, and can be divided into two parts: an interior, more or les sac-like part and a somewhat larger, posterior, tubular part. The anterior, sac-lik part is U-shaped, provided with a thick muscular wall and with the inner surface marked by distinct longitudinal furrows and ridges. The two "legs" of the U are tightly connected by mesenterium and connective tissue. The tube-like part is thinner, sub-divided at regular intervals into a number of compartments by distinct, permanent, transverse folds, each provided with a sphincter muscle. The state of development of these folds and sphincters shows considerable variation (pl. 4 figs. A, B; pl. 5). Vaillant (1886: 2) mentioned some of these folds to have the character of true diaphragms, perforated in the centre. In the specimen dissected by Burne (1905: 315) these folds apparently were much less developed. In the four individuals dissected on behalf of the present study this character showed considerable variation too. In the specimen from the Isles of Scilly the folds were in the highest state of development, showing as very pronounced diaphragms with a relatively small central perforation (pl. 4 figs. A, B; pl. 5 fig. A). A number of 16 of these diaphragms, some of these better developed than the others, divided the anterior portion of the tubular part of the stomach into 15 compartments, each about 6 cm long, the last two slightly larger. Subsequently there followed five closely arranged diafragms about 1—2 cm distant from each other, two relatively large compartments separated by a number of densely arranged muscular ridges, and ultimately the very muscular pylorus. The same general plan of the stomach including the presence of two more or less isolated compartments anteriorly of the pylorus, was found in the other individuals examined. Not only did the development of the diaphragms show, as mentioned above, a notable variation from one specimen to another, but this also held for one and the same specimen, both as regards the thickness of the septs and the diameter of the central perforation. However, the state of contraction of the sphincters often more or less blurred the real state of affairs. It may further be remarked that the diaphragms by no means are always represented by neatly arranged, simple, transversely orientated septs; they may also run obliquely and they are not rarely more or less compound, two septs merging into one or vice versa, enclosing partly open, blind spaces.

In conclusion, the morphology of the anterior part of the gut of the leathery turtle seems to be well in agreement with the idea that this turtle, apparently as an adaptation in connection with the nature of its diet, gets rid of excessive amounts of sea-water by oral expulsion: the spines of the oesophagus functioning as a sieve to prevent food particles to slip out[7], and the posterior compartmentalized part of the stomach functioning as a "buffer zone" with valves to prevent large amounts of water to go the wrong direction and to enter the intestines. The relatively large number of septa and compartments would guarantee the effectiveness of this "buffer zone".

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REFERENCES

Baan, S. M. van der, 1967. Pelagia noctiluca (Forskål) collected off the Dutch coast. — Neth. J. Sea Res. 3 (4): 601-604.

Baan, S. M. van der, 1980. The seasonal occurrence of Scyphomedusae in surface waters near the "Texel" lightvessel. — Interne Verslagen Ned. Inst. Onderzoek der Zee, Texel 1980–8: 1-18, figs. 1-3.

Bentley, P. J., 1976. Osmoregulation: 365-412. In: Gans, C. (ed.). Biology of the Reptilia 5, Physiology A. London/New York/San Francisco.

Bleakney, J. S., 1965. Reports of marine turtles from New England and eastern Canada. — Can. Fld. Nat. 79 (2): 120-128, tabs. 1–3.

Bouillon, J. & G. Coppois, 1977, Étude comparative de la mésoglée des Cnidaires. — Cah. Biol. mar. 18: 339-368, pls. 1-2.

Brongersma, L. D., 1969. Miscellaneous notes on sea turtles. II A–B. — Proc. K. Ned. Akad. Wet. C 72, 1: 76-102, figs. 1-3, pls. 1-4.

Brongersma, L. D., 1972. European Atlantic turtles. — Zool. Verh. Leiden 121: 1-318, figs. 1-42, tabs. 1-17, charts 1-8.

Burne, R. M., 1905. Notes on the muscular and visceral anatomy of the leathery turtle (Dermochelys coriacea). — Proc. Zool. Soc. Lond. 1905, Vol. I (21); 291-324, figs. 55-73.

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.

Deraniyagala, P. E. P., 1953. A. colored atlas of some vertebrates of Ceylon, 2. Tetrapod Reptiles: i-xii, 1-101, figs. 1-44, pls. I-XI + 1-35. Colombo.

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[7] It may be noted that oesophageal spines are also present in other sea turtles, even in the herbivorous green turtle *Chelonia mydas*. We don't see, however, why this would contradict our view with regard to their function in the leathery turtle. To a lesser degree they may have the same function in other turtles.

Dessauer, H. C., 1970. Blood chemistry of reptiles: physiological and evolutionary aspects: 1-72. In: Gans, C. (ed.). Biology of the Reptilia 3, Morphology C. London/New York.

Duguy, R., M. Duron & C. Alzieu, 1980. Observations de tortues luth (Dermochelys coriacea) dans les Pertuis Charentais en 1979. — Annls. Soc. Sci. nat. Charente-Marit. 1980, 6 (7): 681-691, fig., tabs. 1–3.

Dunlap, C. E., 1955. Notes on the visceral anatomy of the giant leatherback turtle (Dermochelys coriacea L.). — Bull. Tulane med. Fac. 14: 55-69, figs. 1-10, tab. 1.

Dunson, W. A., 1976. Salt glands in reptiles: 413-446. In: Gans, C. (ed). Biology of the Reptilia, 5, Physiology A. London/New York/San Francisco.

Duron, M., 1978. Contribution à l'étude de la biologie de Dermochelys coriacea (Linné) dans les Pertuis Charentais: — Thèse Univ. Bordeaux, 3me cycle, 1465: i-xii, 1-112, I-XXXVII, figs. 1-21, tabs., pls. 1-5.

Duron, M. & P. Duron, 1980. Des tortues luths dans les Pertuis Charentais. — Courrier Nat. 69: 37-41, figs.

Fritts, T. H., 1982. Plastic bags in the intestinal tracts of leatherback marine turtles. — Herpet. Rev. 13 (3): 72-73.

Glüsing, G., 1973. Zum Mageninhalt zweier Lederschildkröten, Dermochelys coriacea. — Salamandra 9 (2): 77-80.

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.

Hughes, G. R., 1974. The sea turtles of South-East Africa. I. Status, morphology and distributions. — Invest. Rep. Oceanogr. Res. Inst. Durban 35: 1-144, figs. 1-55, tabs. 1-43, pls. 1-11.

Huxley, T. H., 1859. The oceanic Hydrozoa; a description of the Calycophoridae and Physophoridae observed during the voyage of H.M.S. "Rattle Snake" in the years 1846–1850, with a general introduction: i-ix, 1-141, pls. 1-12. London.

Hyman, L. H., 1938. The water content of medusae. — Science N.Y. 87 (2251): 166–167.

Hyman, L. H., 1940. Observations and experiments on the physiology of medusae. — Biol. Bull. mar. biol. Lab. Woods Hole 79: 282-296, figs. 1-8.

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.

Krogh, A., 1939 (1965). Osmotic regulation in aquatic animals: i-x, 1-242, figs. 1-54, tabs. 1-42. New York, 1965 (unabridged and unaltered reprint of the original publication by Cambridge Univ. Press in 1939).

Lazell, J. D., 1976. This broken archipelago; Cape Cod and the islands, amphibians and reptiles: i-xi, 1-260, many figs. Quadrangle.

Lockwood, A. P. M., 1966. Animal body fluids and their regulation: i-vii, 1-177, figs. 1-30, tabs. 1-22. London.

Lowndes, A. G., 1942. Percentage of water in jellyfish. — Nature Lond. 150: 234-235.

MacGinitie, G. E. & N. MacGinitie, 1949. Natural history of marine animals: i-ix, 1-473. New York/London/Toronto.

Mrosovsky, N., 1981. Plastic jellyfish. — Mar. Turtle Newletter 17: 5-7, fig. 1.

Papenfuss, E. J., 1936. The utility of the nematocysts in the classification of certain Scyphomedusae. — Act. Univ. Lund, N. Ser. (2) 31 (11): 1-26, figs. 1-22.

Potts, W. T. W., 1968. Osmotic and ionic regulation. — Ann. Rev. Physiol. 30: 70-104.

Pritchard, P. C. H., 1969. Sea turtles of the Guianas. — Bull. Fla. St. Mus. biol. Sci. 13 (2): 85-140, figs. 1-29.

Pritchard, P. C. H., 1971. The leatherback or leathery turtle, Dermochelys coriacea. — I.U.C.N. Monogr. 1: 1-39, pls. 1-2.

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., 1953. The Medusae of the British Isles, vol. 1, Anthomedusae, Leptomedusae, Limnomedusae, Trachymedusae and Narcomedusae: i-xiii, 1-530, figs. 1-319, pls. 1-35. Cambridge.

Russell, F. S., 1970. The Medusae of the British Isles, vol. 2, pelagic Scyphozoa, with a supplement to the first volume on Hydromedusae: i-xii, 1-284, figs. 1-102, 1s-26s, pls. 1-15, 1s. Cambridge.

Salvini-Plawen, L. von, 1972. Cnidaria as food-sources for marine invertebrates. — Cah. Biol. mar. 13: 385-400, 1 pl., 2 tabs.

Sears, J. H., 1887. Dermatochelys coriacea, trunk back or leathery turtle. — Bull. Essex Inst. 18 (1886): 87-94.

Sipos, J. C. & R. G. Ackman, 1968. Jellyfish (Cyanea capillata) lipids: fatty acid composition. — J. Fish. Res. Bd. Can. 25: 1561-1569, tabs. 1-3.

Teissier, G., 1926. Sur la teneur en eau et en substances organiques de Chrysaora hysoscella (L.) aux différents stades de son ontogénèse. — Bull. Soc. zool. Fr. 51: 266-273.

Thiel, M. E., 1960. Beobachtungen über Wachstum, Variationen und Abnormitäten bei Cyanea capillata der Ostsee. — Abh. Verh. naturw. Ver. Hamburg, N. Ser. 4 (1959): 89-108, figs. 1-16.

Thiel, M. E., 1962. Untersuchungen zur Artfrage von Cyanea lamarckii Pér. et Les. und Cyanea capillata L. — Abh. Verh. naturw. Ver. Hamburg, N. Ser. 6 (1961): 277-293, figs. 1-2.

Totton, A. K., 1960. Studies on Physalia physalis (L.), part 1, natural history, and morphology. — Discovery Rep. 30: 301-408, figs. 1-31, pls. 7-25.

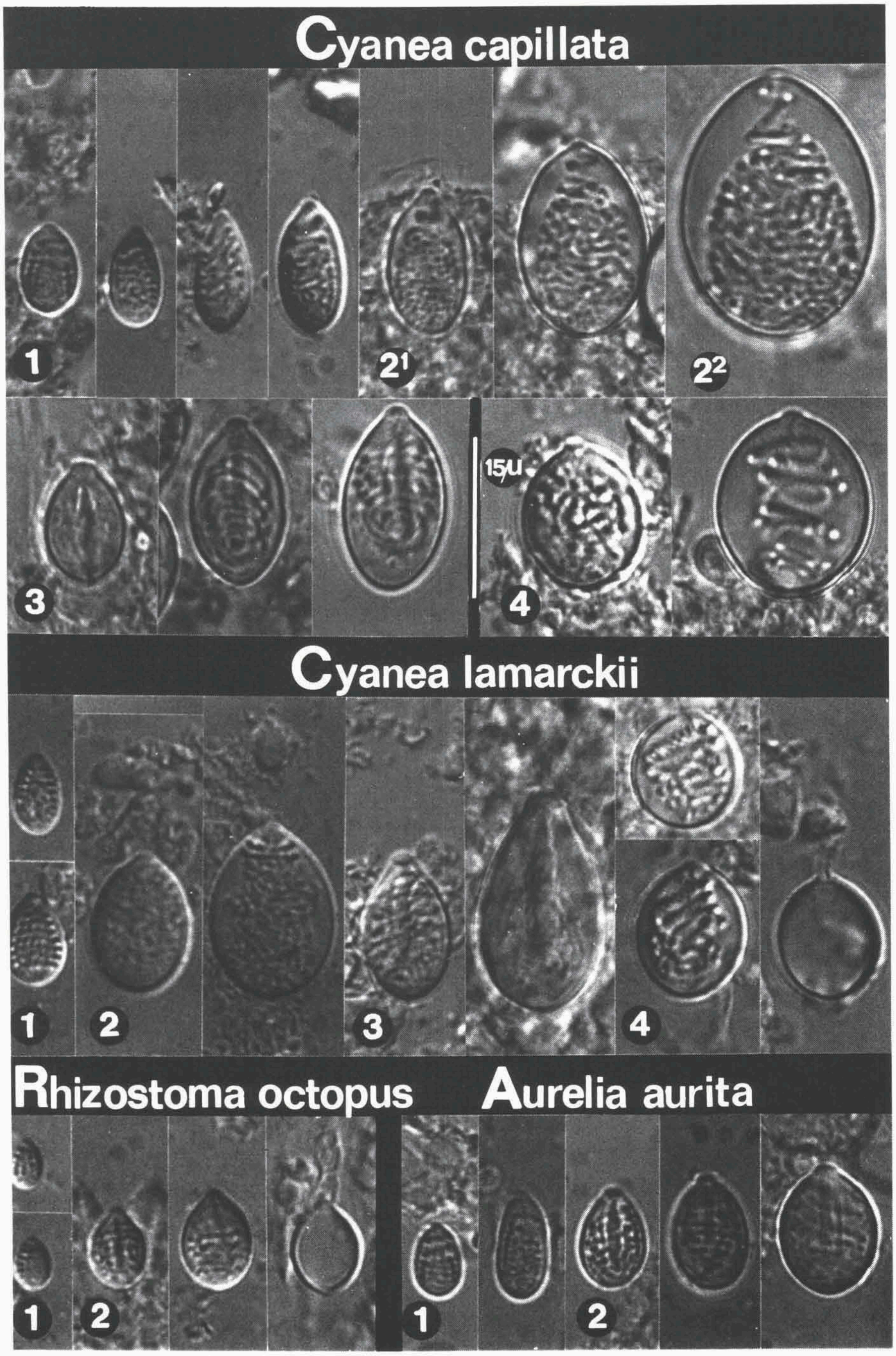
Vaillant, M. L., 1886. Remarques sur l'appareil digestif et la mode d'alimentation de la tortue luth. — C. r. hebd. Séanc. Acad. Sci. Paris 123: 654-656.

Weill, R., 1934. Contribution à l'étude des cnidaires et de leurs nématocystes — 1. Recherches sur les nématocystes (morphologie, physiologie, développement). 2. La valeur taxonomique du cnidome. — Trav. Stn. zool. Wimereux 10/11: 1-701, figs. 1-432.

Widersten, B., 1973. Den palmstruchska maneten Cyanea palmstruchii Schwartz, 1809. — Zool. Revy 35 (4): 147-152, figs. 1-8.

Yoshie, S. & Y. Honma, 1976. Light and scanning electron microscopic studies on the esophageal spines in the Pacific Ridley turtle, Lepidochelys olivacea. — Arch. histol. jap. 38 (5): 339-346, figs. 1-11.

Zandee, D. I., 1971. Osmoregulatie en excretie: 145-177. In: Dijkgraaf, S. & A. I. Vonk (ed.). Vergelijkende Dierfysiologie I. Vegetatieve functies. Utrecht.


Cyanea capillata
1
2^1
2^2
3
15µ
4
Cyanea lamarckii
1
2
3
4
Rhizostoma octopus
1
2
Aurelia aurita
1
2

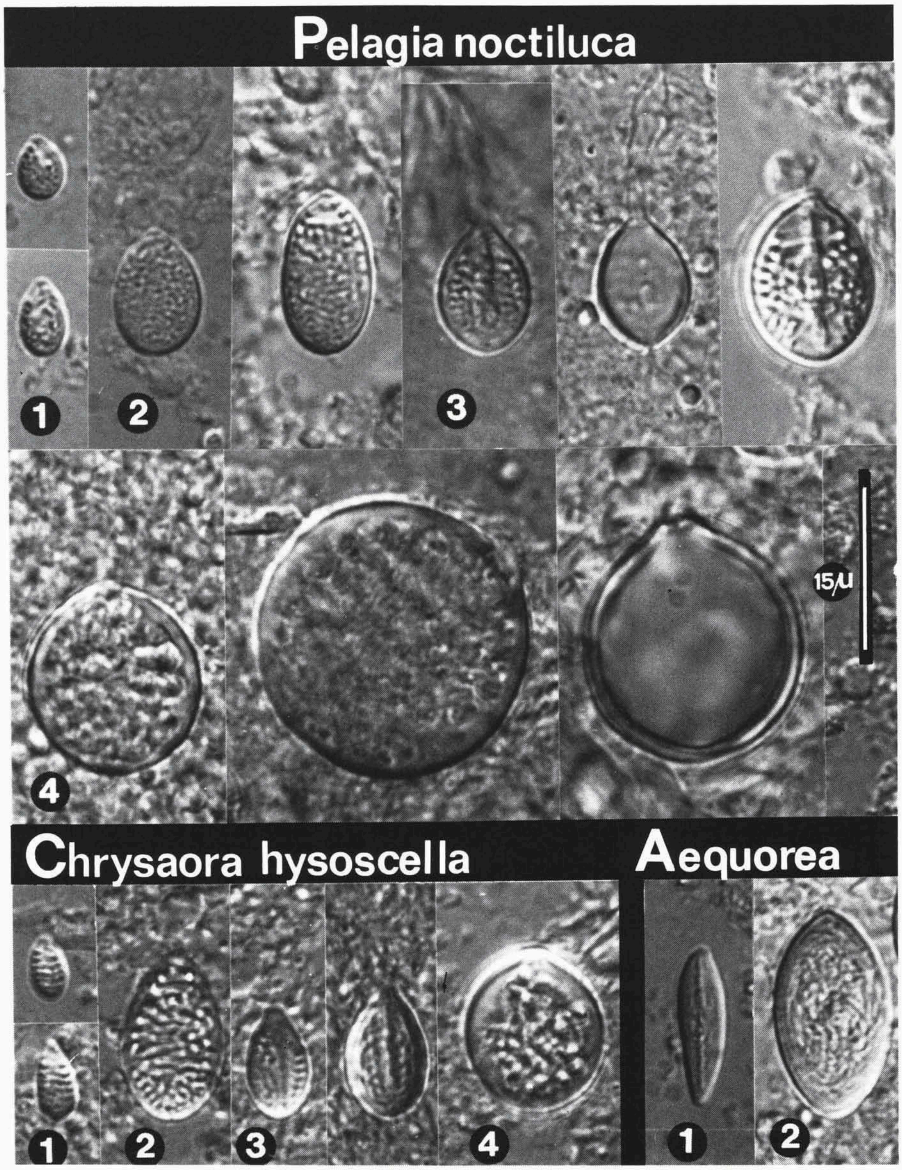


Plate 2 (cf. table 1, 2). Pictorial survey of the cnidom of the Scyphozoa *Pelagia noctiluca* and *Chrysaora hysocella*, and of the leptomedusa *Aequorea forskalea*. Numbers in the plate correspond with those in table 1 and 2, respectively.

Plate 1 (cf. table 1). Pictorial survey of the cnidom of the Scyphozoa *Cyanea capillata*, *C. lamarckii*, *Rhizostoma octopus* and *Aurelia aurita*. Numbers in the plate correspond with those in table 1.

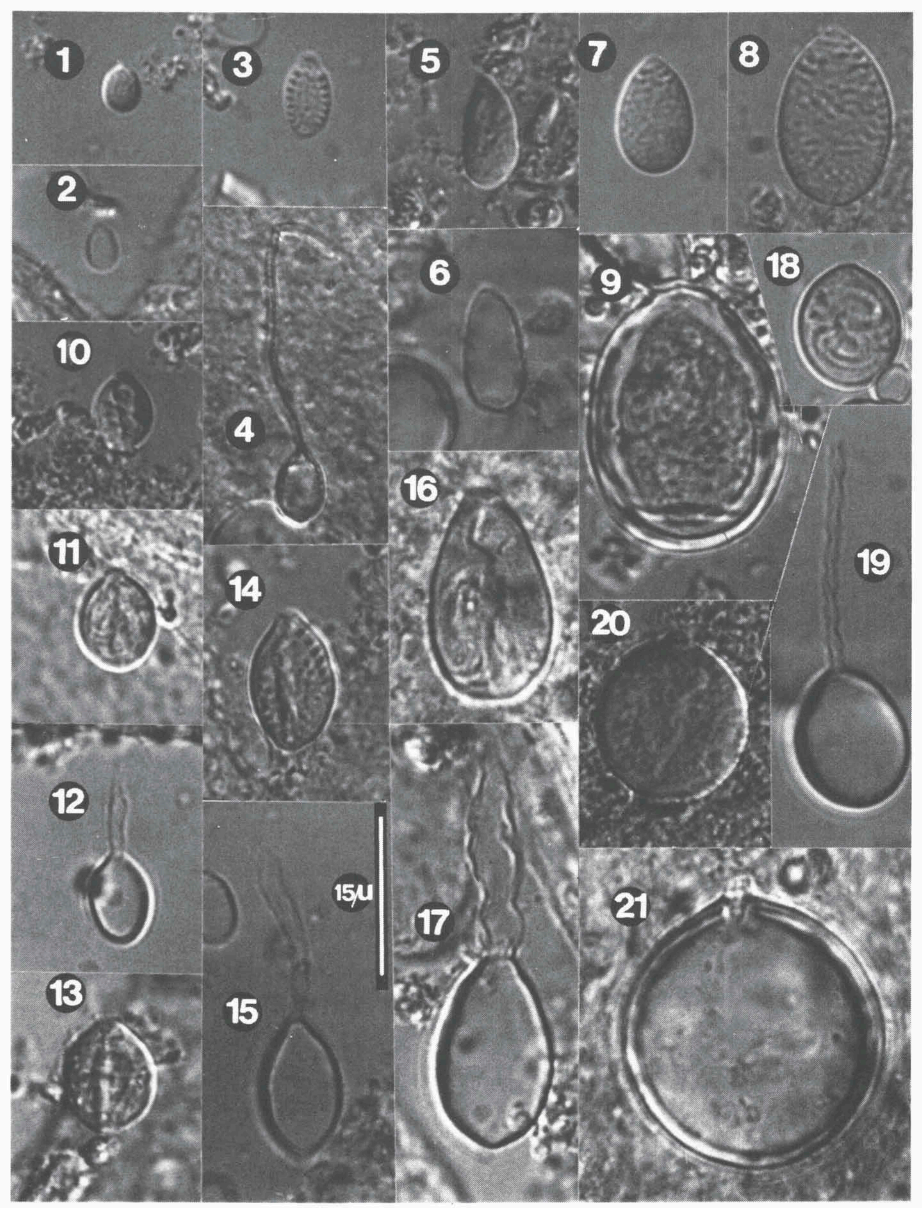


Plate 3 figs. 1—21 (cf. tables 3—8). Pictorial survey of scyphozoan nematocysts found in the alimentary canal of individuals of *Dermochelys coriacea* from southern England and the North Sea. Choice of the figured examples more or less arbitrary. Continued (figs. 22-31) on pl. 4.

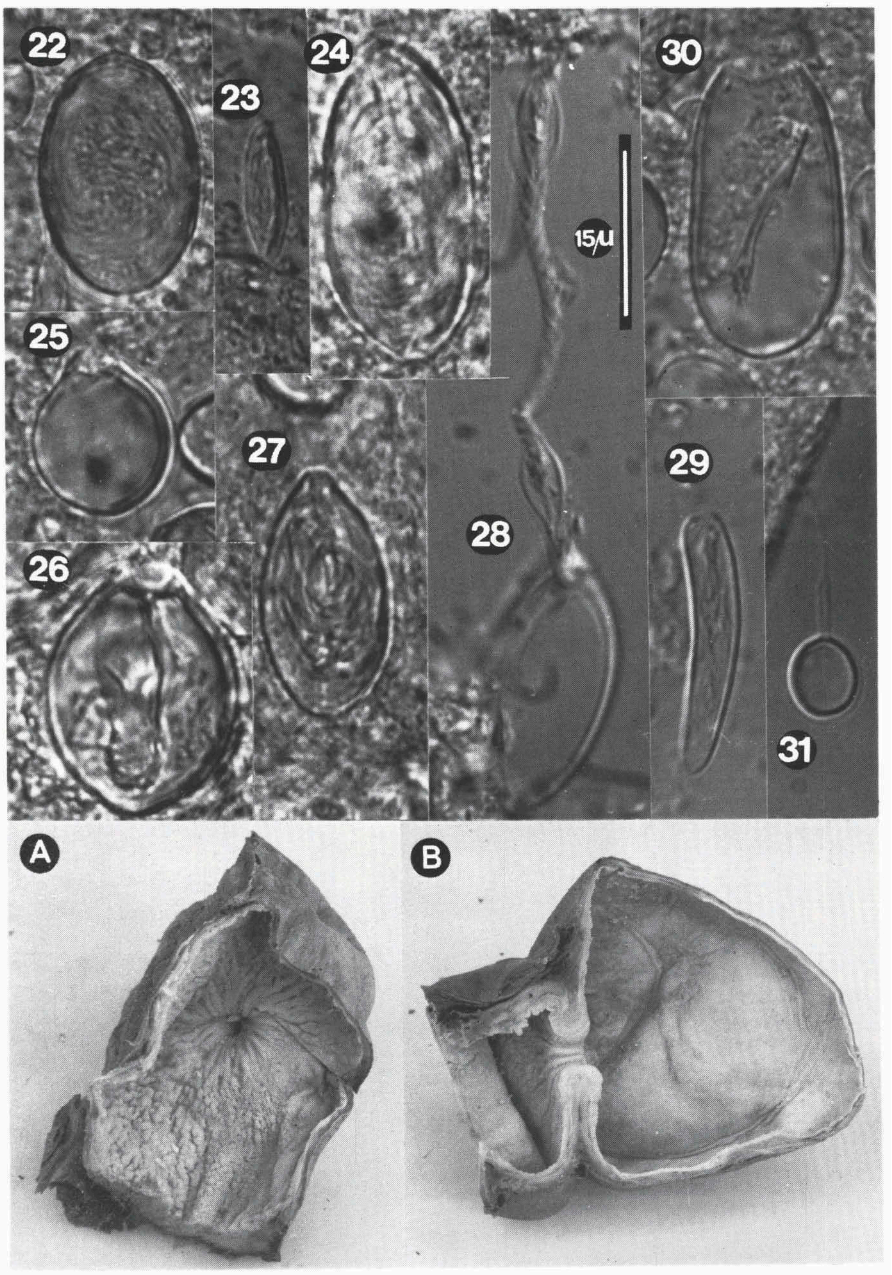


Plate 4 figs. 22-31. Continuation of plate 3 (non-scyphozoan nematocysts). Figs. A, B. *Dermochelys coriacea.* Sections through the posterior part of the stomach of specimen 4 (Scilly Isles, 7-ix-1980) showing the structure of distinct stomachal diaphragms: ca. × 0.5.

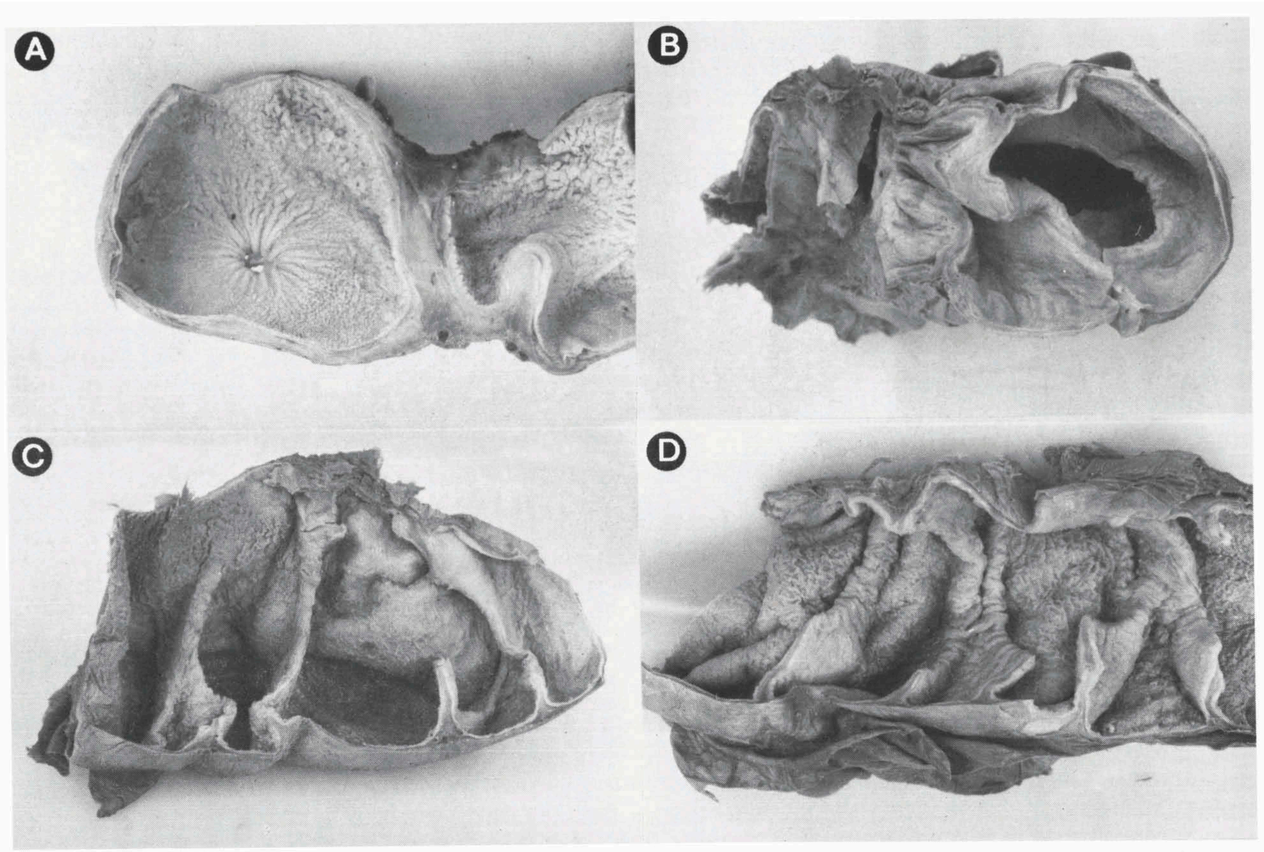


Plate 5 figs. A–D. *Dermochelys coriacea*. Sections through the posterior part of the stomach of specimen 4 (Scilly Isles, 7-ix-1980) (fig. A) and specimen 5 (Eyemouth, 3-x-1980) Figs. B–D). Note the variation in development of the transverse stomachal folds between specimen 4 (fig. A; cf. also pl. 4 figs. A–B) and specimen 5 (figs. B–D): ca. × 0.5.