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Atollidae in the Zoological Museum of Copenhagen (Coelenterata, Scyphomedusae)

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Abstract. A large material of *Atolla* has been examined and is recorded. The geographical and vertical distribution of the four species of the genus is discussed.

For quite a long time (since Mayer, 1910) we have been accustomed to regard the Atollidae as a family of coronate Scyphomedusae comprising only one genus with one species, *Atolla wyvillei* Haeckel, 1880, at some times recorded as *A. bairdi* Fewkes, 1886. Since 1957, however, three other species have been described: *A. vanhoeffeni* Russell, 1957, *parva* Russell, 1958, and *russelli* Reppin, 1962. All of these are represented in the collection of the Zoological Museum in Copenhagen. We have found it advisable, therefore, to carry out a complete revision of this collection, since the vast majority of the numerous specimens have been recorded as *wyvillei* in previous literature, also by the present senior author. The identification of this material has, for the greater part, been carried out by the junior author.

In the maps given in the present paper all records of the three recently established species are included, derived from the existing literature as well as from the collection of the Zoological Museum, but the map of distribution of *wyvillei* only includes records derived from the revision of our own collection, because records of this species in previous literature may partly be erroneous, since none of the three other species were known at the time considered.

Complete station lists for all four *Atolla* species are deposited in the Zoological Museum, University of Copenhagen. Copies of these lists can be supplied on request.

A very large part of the revision dealt with in the present paper comprises the large number of stations of the Dana expeditions, particularly of the Expedition round the World in 1928-30. The Scyphomedusae collected during these expeditions were examined by Stiasny and published in 1940. The Atollidae were all referred to *wyvillei*; as a matter of fact, many of the specimens belong to *vanhoeffeni*. Stiasny himself pointed out some features of variation

(1940:18-19), especially the presence of eight small, dark pigment spots near the distant corners of the four gastric cavities, and in the list of stations he pointed out specimens, in which such pigment-spots were observed. We know now that this is one of the most remarkable features characteristic of *vanhoef-feni* Russell. Stiasny's list of *wyvillei* also comprises a number of specimens of *parva* Russell.

Atolla russelli Repelin

Atolla russelli Repelin, 1962a:89-99, figs.1-3; 1962b:664-676, figs.3-5; Kramp 1968:76.

It was with some doubt that a specimen from 4°00'S, 41°27'E, off Kenya in East Africa, was referred to *russelli* by Kramp (1968), because it was somewhat mutilated. What was retained of the morphological features, however, pointed directly towards that species, separating it from the other members of the genus, especially by the small number of tentacles, of which there were no more than 16; the specimen was not a juvenile. *A. russelli* usually has 18, occasionally 17 or 16 tentacles. Other distinguishing characters of *russelli* are: there are only four gonadial sacs (not eight as in the other species), each of them bilobated; the marginal septa are only slightly divergent proximally, not as much as in *wyvillei*, and completely covered by the annular muscle, and this is distinctly seen in the present specimen. Dr. Repelin has kindly sent us some of his original specimens, and having seen them we feel sure that the identification of the specimen from Kenya is correct.

The original specimens of *A. russelli* were collected in a number of localities off Angola in the Gulf of Guinea, West Africa, in hauls with 600-1000 m wire out, thus at somewhat higher levels than the usual habitat of Atollidae (see fig. 1)

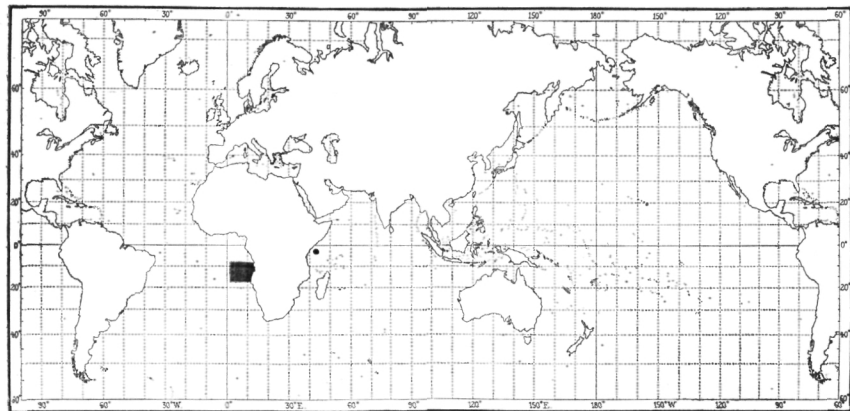


Fig. 1. Occurrence of *Atolla russelli* Repelin. Dots: material in Zoological Museum, Copenhagen; hatched areas: previous records.

Atolla parva Russell

Atolla parva Russell, 1958:1811; 1970:52-55, pl.8, fig.2, text-figs.19,24,26, 27,28.

Atolla wyvillei, in parte, Stiasny, 1940:14-18.

After a preliminary note (in 1958) Russell (1959) further described this species from a number of localities in the Bay of Biscay, with additional notes on specimens belonging to the Zoological Museum of Copenhagen, collected in the eastern and northern Atlantic. Repelin (1962b, 1964, 1966) recorded it, with a number of figures, from several localities in the Gulf of Guinea and off Angola, West Africa.

A full description and an account of the distinguishing characters of *A. parva* is given by Russell (1970).

Russell (1959:37) has hinted at the possibility that specimens with 20 and 24 tentacles represent two different species; among 59 specimens examined by us we have found 21 specimens with 20 and 32 with 24 tentacles, besides 6 specimens with other numbers, 19-26, all of which occur together in different areas.

Russell (1959:38) further observed that "in some of the specimens one of the marginal tentacles is unusually large", and he gave a figure to illustrate this (fig.3, p.37); according to Repelin (1966:25) such a tentacle, larger than the others, is always present, even in young specimens. We have noticed this in only five specimens, 13-35 mm wide, all of them in the surroundings of Iceland, and in none of these was the difference very remarkable.

Almost all the specimens in our collection are fairly small, less than 23 mm wide, and there is no indication of a correlation between size of the medusae and the depth of capture; a few specimens are up to 33-35 mm wide.

Geographical Distribution (fig. 2). In the very extensive list of "*A. wyvillei*" collected by the Dana expedition round the World in 1928-30, (Stiasny, 1940),

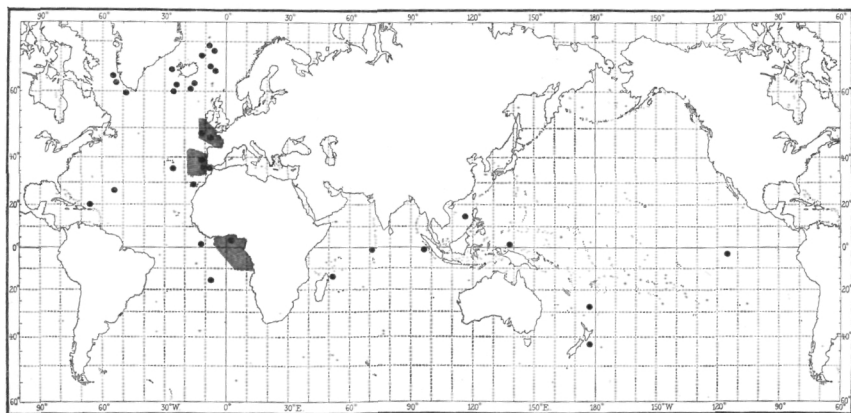


Fig. 2. Occurrence of *Atolla parva* Russell. Dots: material in Zoological Museum, Copenhagen; hatched areas: previous records.

it is worth mentioning that only a small number of specimens have proved to belong to *parva*; they were derived from warm parts of the eastern and western Atlantic and from a number of scattered localities in the Indo-West-Pacific region and the Gulf of Panama.

As a matter of fact, *parva* has a circumglobal distribution, but the records from the Indian and Pacific Oceans are remarkably few and exclusively from warm-water regions, whereas in the Atlantic area it penetrates far northwards to the surroundings of Iceland and southern Greenland.

A. parva was collected from three localities in the Indian Ocean, and from the Malayan Archipelago and the western Pacific by the Dana Expedition. It was never taken by the Galathea Expedition, even though several hauls were made at depths similar to those where it was taken by Dana. The Galathea medusae were examined by the senior author (Kramp, 1968).

As seen from fig. 2, the easternmost localities in which *parva* has been found in the Indo-West-Pacific region are near New Zealand, about 177° East. From New Zealand there is an extensive distance to the few localities in the Central-East-Pacific and the East-Pacific, where a few small specimens, 12–28 mm wide, were taken by the Dana in 1922 and 1928, at 4°S, 117°W and between the Gulf of Panama and a point west of the Galapagos Islands.

The principal area of occurrence of *parva* is evidently the East-Atlantic Basin, where it was mainly taken above the eastern slope of the deep basin, usually not very far out in the open ocean. Apparently it rarely crosses the Mid-Atlantic Ridge, since it has only twice been found in the West-Atlantic (Dana Sts. 1322, 1261). It does not penetrate through the Strait of Gibraltar into the Mediterranean.

In the East-Atlantic it has been found as far south as about 15°S, off Angola; it should be remarked that in this part of the Atlantic the deep-sea currents move slowly northwards, which may have prevented the population of *parva* from penetrating further south to the waters around the southern part of Africa.

It is comprehensible that this medusa, which occurs outside the Atlantic coasts of Europe, also occurs in the area south and west of Iceland, and also in the southern part of the Davis Strait. Its occurrence east and north-east of Iceland is peculiar, since here the deep-sea is a continuation of the deep-sea basin of the Norwegian Sea with temperatures below 0°C. It was taken at Dana St. 5143 in a horizontal haul with 2400 m wire, temp. -0.8°C, and by the Ingolf at four stations between 66°23'N and 68°27'N, in hauls with the trawl presumably not far above the bottom, depths 1802–2386 m, at temperatures of -1.9°C to -1.1°C. The specimens from the Dana station and from one of the Ingolf stations have been examined by F. S. Russell as well as by us, and there is no doubt of the identification. *A. wyvillei* was also found in some of these localities.

Vertical Distribution. *A. parva* has usually been collected in horizontal hauls with 1000–5000 m wire, i.e. about 350–2500 m below the surface, but in the area off West Africa mainly in depths of about 700 m, occasionally ascending to 370 m (Repelin, 1966).

Atolla vanhoeffeni Russell

Atolla vanhoeffeni Russell, 1957:275–279, pl.I, text-fig.1; 1970:49–52, pl.8, fig.1, text-figs.19,25,26.

Atolla wyvillei, in parte, Stiasny, 1940:14–18.

As mentioned above (p. 157) Stiasny himself pointed out the presence of eight small, dark pigment points near the corners of the stomach in some of the specimens which he identified as *Atolla wyvillei* (Stiasny, 1940:19). These and several others in his list (pp. 14–18) really belong to *vanhoeffeni*.

All records of *vanhoeffeni* before 1968 are from the Atlantic Ocean, but during the Danish Galathea Expedition in 1951–1952 this species was found in numerous localities also in the Indian Ocean and the western Pacific as far east as New Zealand (Kramp, 1968), and a revision of the Dana collections has shown that a great number of specimens referred to *wyvillei* by Stiasny (1940) belong to *vanhoeffeni*.

Geographical Distribution (fig. 3). The records of *vanhoeffeni* from the Atlantic and the Indo-Pacific up to 1970 are summarized by Russell (1970). The Galathea Expedition found this species off south-eastern Africa, north of Madagascar, in the South China Sea and around New Zealand; these localities are enumerated by Kramp (1968). All other Indo-Pacific localities are derived from the Dana Expedition. In the present place we shall give a general account, geographically arranged, of the results of the revision of this extensive collection, but for detailed information we must refer to Stiasny's list (1940) of "*A. wyvillei*".

West-Atlantic, Warm-Water Region.—In 1922 *vanhoeffeni* was taken at seven stations, partly in the Caribbean Sea, partly in the neighbouring part of the Atlantic Ocean between about 35°N and 10°N, in hauls with 1000–2000 m wire out.

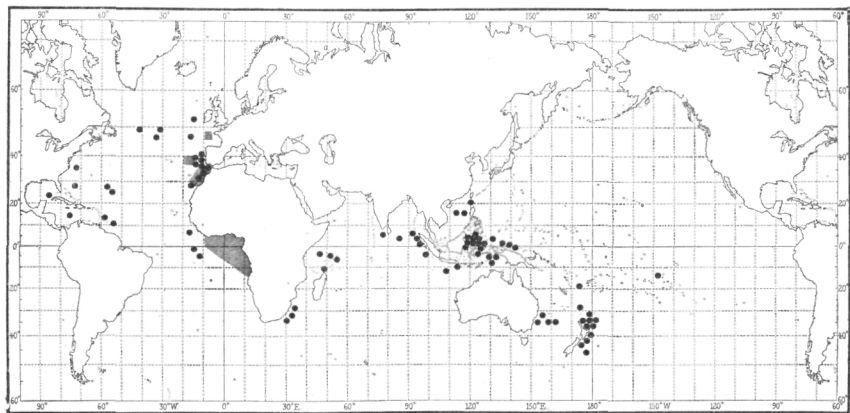


Fig. 3. Occurrence of *Atolla vanhoeffeni* Russell. Dots: material in Zoological Museum, Copenhagen; hatched areas: previous records.

East-Atlantic, Tropical.—In 1930 specimens were taken at three Dana stations outside the Gulf of Guinea, partly in considerable numbers (15 and 17 at Sts.4000,4003), not far from the area where Repelin (1964, 1966) found this species in great abundance. The Dana specimens were all taken in hauls with 1000 m wire out.

Indian Ocean.—In some localities in the western part of the Indian Ocean, north and south of Madagascar, *vanhoeffeni* was collected by the Galathea Expedition (Kramp, 1968). The Dana, however, also found the species in the eastern part of this ocean, all above the continental slopes in the neighbourhood of coastal areas, near Ceylon, west of Sumatra, and south of Java, in hauls with 1000–3000 m wire out.

Malayan Archipelago.—This area seems to be well populated by *vanhoeffeni*, as it was found at 22 stations by the Dana, usually in hauls with 1000 m wire out and never at higher levels. The localities, where the medusa was taken in very deep hauls, were in the Celebes Sea (St.3683), the Banda Sea (St.3677), and in the Ceram Sea, one of the deep, narrow passages between the Molucca Islands, thus in more or less enclosed waters with slow movements in the deep water layers. *A. wyvillei* was likewise a common species in these waters (see below).

South-West Pacific.—While within this region the Galathea found *vanhoeffeni* in only three localities, all of them near New Zealand, it was taken at twelve of the Dana stations, most of them likewise in the surroundings of New Zealand.

A special interest is attached to the six stations near the northern and eastern coasts of New Zealand, where the deep basin of the ocean approaches the coasts, and where the medusa was collected above depths of 1175 to 3040 m, usually in hauls with 1000 m wire out and usually in small numbers. At two stations (3630, 3631 near the northern coasts of the North Island) two of the hauls, however, contain a great number of specimens: St.3630, 2000 m wire: 17 specimens (a few in hauls with 1000 and 3000 m wire); St.3631: 51 specimens in a haul with 1000 m wire (and 2 with 1500 m wire). Apparently a remarkable accumulation of the medusae has taken place in these localities, for which there may be a hydrographical explanation (to be further discussed below).

Bathypelagic hauls were also made further east in the south-western Pacific, but *vanhoeffeni* was only found in an isolated locality, near Tahiti (St. 3570), and apparently it is completely absent in the eastern Pacific.

It will be observed (fig. 3) that *vanhoeffeni* was very rarely found in mid-ocean waters, but mainly at no great distances from the coasts, i.e. along the continental slopes, in the Pacific around the many groups of islands; this shall be discussed later in the present paper.

Vertical Distribution. Within the entire areas of distribution of *vanhoeffeni* the vast majority of the specimens were collected in hauls with 1000 m wire out, or somewhat more, in the northern Atlantic occasionally with only 600 m wire. In the Gulf of Guinea Repelin found it in hauls with 600–3800 m wire out, and according to this author *vanhoeffeni* is "la plus superficielle" of the Atollidae. The frequent occurrence at comparatively slight depths off the At-

lantic coast of Africa may probably be explained by the upwelling of deep water, which certainly takes place in this stretch of water; this is also stated by the occurrence of several bathypelagic Hydromedusae (Kramp, 1959:260). In Indo-Pacific waters *vanhoeffeni* was mainly taken in hauls with 1000 m wire out, and never higher up, but in several localities with as much as 5000 m wire, or even 7200–7440 m wire (Galathea, off southeast Africa). Within most of its area of distribution this species must, accordingly, be designated as an inhabitant of the deep water layers.

Atolla wyvillei Haeckel, 1880

Before 1957 and 1958, when Russell described two new species of *Atolla*, *vanhoeffeni* and *parva*, and before 1962, when *russelli* was described by Repelin, there was the possibility that some of the records of *wyvillei* in the previous literature might have belonged to some of these other species.

There can hardly be any doubt, however, that the vast majority of *Atollidae* recorded in this older literature have really belonged to *wyvillei*, and in comparison with the statements above on the geographic distribution of these other species we may safely designate *wyvillei* as a cosmopolitan species in the deep waters of the oceans.

A. wyvillei grows to a much larger size than the other species of the genus, with an umbrella diameter up to 150 mm. The senior author saw it several times while onboard the Galathea, and it was a lovely sight, when a large and undamaged specimen of this beautiful medusa was secured. Special attention was paid to it and a brief general survey of its occurrence was given (Kramp, 1968). A full description is given by Russell (1970).

Geographical Distribution (fig. 4). In contradistinction to the three other species of the genus, *wyvillei* has obtained an extensive distribution ranging from antarctic to arctic regions in all deep parts of the oceans though, as a matter of fact, with a few exceptions. The only obstruction against complete cosmopoli-

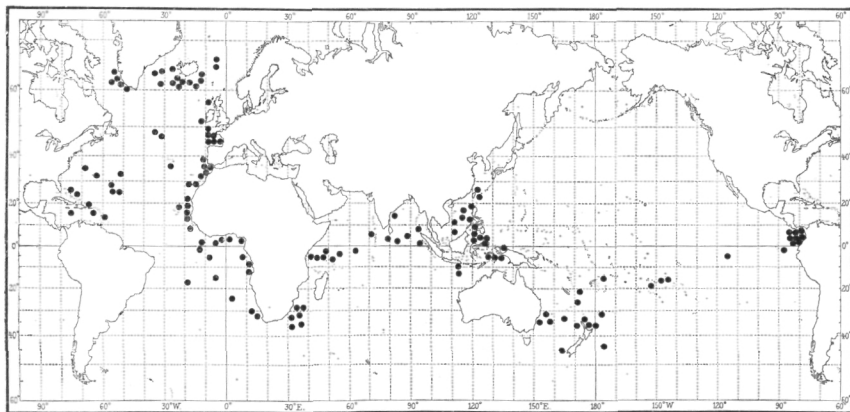


Fig. 4. Occurrence of *Atolla wyvillei* Haeckel. Material in Zoological Museum, Copenhagen.

tanism in all deep-water areas is the configuration of the sea bottom in a few places: It has never penetrated through the Strait of Gibraltar into the Mediterranean; it has frequently been taken in the deep-sea area off the southern part of the west coast of Greenland, but it has never crossed the submarine ridge across the Davis Strait between Holsteinsborg in Greenland and Cape Walsingham in Baffinland with depths of less than 700 m, thus not penetrating into Baffin Bay, and it is evidently not the low temperature in that basin, which has prevented the medusa from occurring there, since it occurs outside the east coast of Greenland, where it has been found as far north as about 80°N, between Spitzbergen and North-East Greenland, and in the Polar Sea north of Siberia. Obviously it has never crossed the Bering Strait, but its occurrence in the Polar Basin is in direct communication with the basin of the Norwegian Sea.

The Galathea Expedition provided no new information on the geographical distribution of *Atolla wyvillei*, but some valuable information was obtained, which shall be supplemented with observations from the revised Dana collection. The accompanying map (fig. 4) only comprises material deposited in the Zoological Museum of Copenhagen.

As far as the horizontal distribution is concerned, it was mentioned above that the three other species have mainly been found above the continental slopes, at no great distances from the coastal areas. *A. wyvillei*, on the other hand, has frequently been taken in mid-oceanic waters (fig. 4). The warm parts of the Atlantic Ocean were mainly examined by the Dana Expedition during the cruise in 1921–22, approximately between lat. 40°N and 10°N, partly in the Caribbean Sea, and its surroundings, but also in Mid-Atlantic areas, and *wyvillei* was found in some of these oceanic localities.

The Dana investigations in the Indian Ocean and the western Pacific were mainly carried out in coastal areas with their numerous islands, and *wyvillei* was found almost everywhere.

It was also taken at one station (3561) in the series from Panama to Tahiti in two hauls with 2000 and 3000 m wire out, above a depth of 2400 m, far from any islands. We also know from the literature (e.g. the map, pl. 48, in Bigelow, 1909) that *Atolla* was found in some mid-oceanic localities in the East Pacific Ocean. In Kramp (1957) it is recorded from two localities about mid-way between Southwest Australia and Kerguelen Island, besides from a number of localities near the Antarctic Continent.

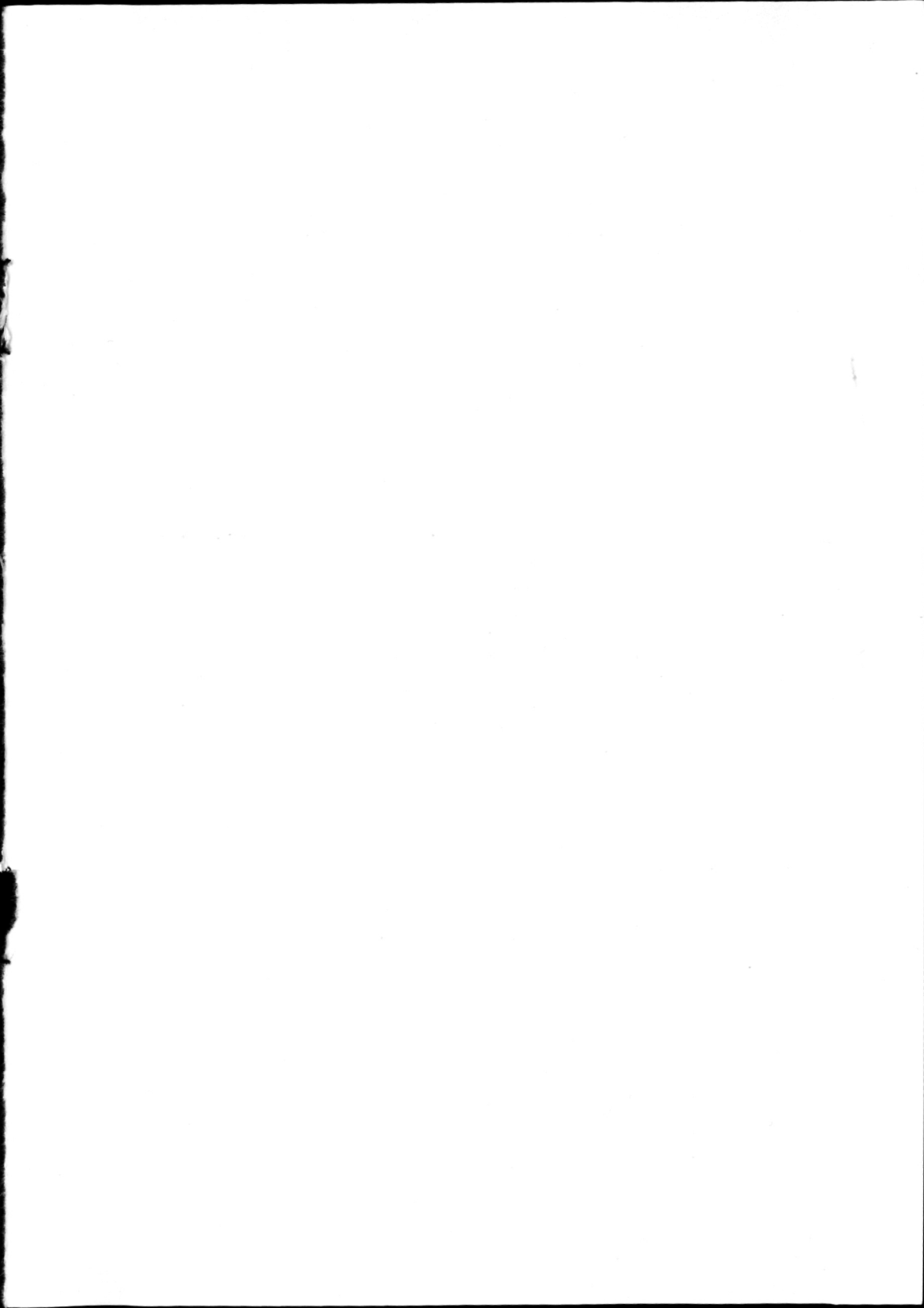
Vertical Distribution was discussed by Kramp (1968:73–74), this medusa being taken in hauls with from 1800 to 10300 m wire. During the cruise of the Dana in the warm part of the Atlantic in 1921–22 hauls containing specimens of *wyvillei* were taken with wire-lengths from 1000 to 5000 m.

During the circumnavigation in 1928–30 several hauls at different depths were taken at almost all stations with up to 6500 m wire; *Atolla* was never found in hauls with less than 1000 m wire, but from any other depth specimens might be taken, more or less occasionally and without a preference of certain depths. The reason why particularly many catches were made in hauls with 1000 m wire was presumably because especially many hauls were made at this level; apparently this medusa was rather regularly occurring at all

depths within the available range of 1000 to 6000 m wire. Moreover the vertical distribution seems to be about equal in all the geographical areas traversed by the expedition, beyond limits determined by the various depths of the sea bottom. We must, however, bear in mind that the hauls were made with open nets, so that specimens may have been caught during the hauling up through the water, but during these expeditions the gear was first drawn horizontally for a considerable time; we may, therefore, presume that at least the majority of the contents was actually caught at the estimated depth.

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