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GONIONEMUS VERTENS L. AGASSIZ (LIMNOMEDUSAE) — A ZOOGEOGRAPHICAL PUZZLE

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ABSTRACT

Gonionemus vertens was found in 1958 in two localities in western Norway. The distribution of the species is discussed, and it is concluded that most probably it has been spread by transport with ships, as part of the fouling community on the outside of the hull. From where it was originally distributed cannot now be ascertained; it may just as well have been from Europe as from North America. Nor can it safely be said when the main spreading took place, though probably this was some time ago, in the days of wooden sailing ships.

During a cruise to Hardangerfjorden (south of Bergen, western Norway), seven specimens of the medusa *Gonionemus vertens* were caught in a shore seine haul at Espevær, near the mouth of Hardangerfjorden 11 August 1958 (Station ZF. 137). The surface temperature was 15° C, the salinity 30.05 ‰. The diameter of the umbrella of the specimens varied from 11 to 21 mm, measured after preservation in formalin. Placed in a glass jar the animals swam with vigorous pulsations. They turned round in their characteristic manner when they reached the surface, and let themselves sink to the bottom with outstretched tentacles.

Two days later, an eighth specimen was found at Sandvik on Halsnöy, in the outer part of Hardangerfjorden (Station ZF. 147). It measured 14 mm across the umbrella and like the first specimens was found in a shore seine haul. The surface temperature was again 15° C, the salinity 24.47 ‰.

Both localities are rather exposed (Fig. 1). At both places the seine fished to about 6 m depth. At Espevær, the bottom substrate was sand and stones with a rather dense vegetation of laminarians. At Sandvik on Halsnöy there was more sand and less stone, with a somewhat scarce vegetation of fucaceans.

Six of the specimens are listed below; two of those from Espevær were damaged, so they could not easily be measured.

	Diam.	No. of marginal vesicles	No. of tentacles
St. ZF. 137, Espevær	21	85	90
» » » »	14	65	80
» » » »	12	61	71
» » » »	11	58	71
» » » »	11	58	68
St. ZF. 147, Sandvik, Halsnöy.....	14	60	82

All specimens had well developed gonads.

Different species of *Gonionemus* have been described from various parts of the northern hemisphere, but in later years they have been considered conspecific. (PICARD, 1952; KRAMP, 1961, p. 223 f.). THIEL (1962, p. 318, translation of NAUMOV) remarks: "nur eine Art, *G. vertens*, mit zwei Unterarten, *G. vertens vertens* L. AG. und *G. vertens murbachi* MAYERS". PICARD (1951, p. 43) gives a map, showing the world distribution.

The relation between the number of marginal vesicles (statocysts) and the number of tentacles has been used as one of the specific characters. In Fig. 2, these numbers are plotted against each other. Numbers from THOMAS (1921, p. 294); WERNER (1950, p. 489); RUSSELL (1953, p. 402), and from the present records have been used. It should be kept in mind that RUSSELL's specimens (crosses) were obtained from the Dove Marine Laboratory tanks at Cullercoats, having been transported very young to Plymouth and reared to the adult stage there. RUSSELL remarks (l.c., p. 403) that "the gonads were not as fully developed as in typical specimens". The number of statocysts may, then, have been a little low in the larger specimens. As to THOMAS' "*murbachi*" (the two open triangles) it may be remarked that they also may have been aberrant, or extreme variants (l.c., p. 295).

As is clearly seen from the diagram, there is in general a very good correlation between the number of tentacles and the number of statocysts, even if the possibly aberrant specimens mentioned above are not excluded. The differences shown can hardly justify specific differentiation.

If one accepts only one species in the genus, it seems very likely that it has been transported by man-made means from place to place. Most authors, who have commented on the distribution of the species since the early nineteen-twenties, are of the opinion that such transport has occurred. There are, however, some interesting questions which, so far, have not been satisfactorily answered. From where did the species originally spread? And by what means has it been transported?

The first representative of the genus was described by L. AGASSIZ in 1862 from the Pacific coast of North America (Puget Sound). The next record, (ac-

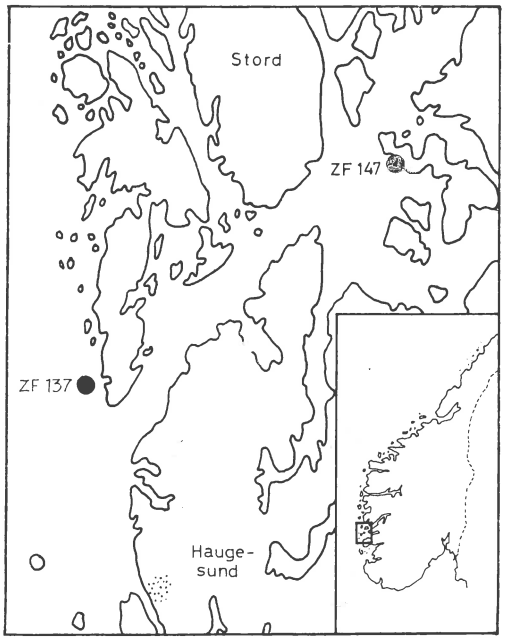

Fig. 1. Records of *Gonionemus vertens* in western Norway.

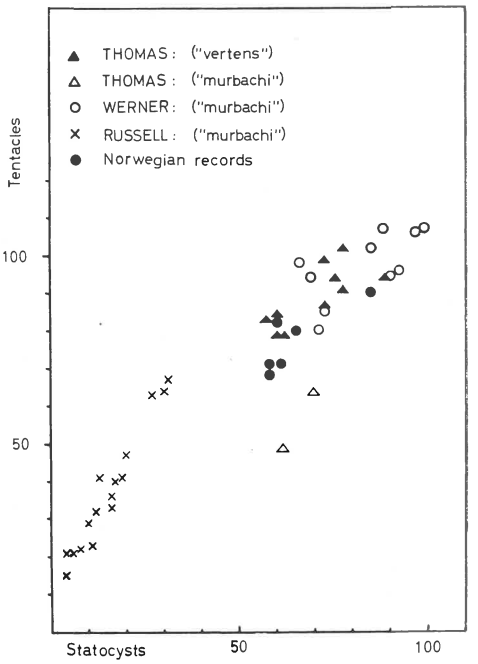

Fig. 2. The numbers of tentacles of *Gonionemus vertens* (vertical axis) plotted against numbers of statocysts of the same specimens (horizontal axis).

cording to PICARD, 1952, p. 41), is from the Mediterranean (*Cosmetira salinarum* DU PLESSIS = *G. vertens*) in 1879. The third record is SCHAUDINN's (1894) of the polyp, called *Halerimita cumulans*, from the Berlin Aquarium, which contained Mediterranean water. In 1901 the species was found in great numbers in a limited locality, called Eel Pond, at Woods Hole on the North American east coast. The year after followed records from Japan and from the Aleutean Islands.

In 1913 some small medusae were found in the aquaria in the Dove Marine Laboratory, Cullercoats, on the English east coast. They were first referred to *Cladonema* and were recognized as *Gonionemus* in 1924. In 1951 the species was rediscovered in the same laboratory.

From 1917 on *Gonionemus* specimens were collected in relatively great numbers in seawater aquaria in Praha and Wien. In both instances, the seawater came from Rovigno in the Adriatic. The small, unripe medusae were described as *G. vindobonensis* by JOSEPH in 1918. PICARD (1952, p. 40 ff.) has, however, given very good reasons for considering *G. vindobonensis* as synonymous with *G. vertens*.

In 1925 JOSEPH found the polyp in the same aquaria where his *G. vindobonensis* occurred, and identified it as *Halerimita cumulans* SCHAUDINN, 1894 (see above). He observed the formation of medusae from the polyp.

In the meantime (1921) a single specimen (identified as *G. murbachi*) had been found among algae near Dröbak in Oslofjorden (east Norway). BROCH (1929, p. 488) and KRAMP (1937, p. 128) suggested that it might have been transported from North America to Oslofjorden by a ship.

In 1923 and in 1930, again among algae, *Gonionemus* medusae were found in Gullmarfjorden on the Swedish Skagerrak coast (LÖNNBERG, 1930, p. 173). Such medusae have also been taken there later (see JÄGERSTEN and NILSSON, 1961, p. 182). In 1924 the species was collected in another aquarium, namely in Port Erin Biological Station in Great Britain, and was identified as *G. vertens*. RUSSEL (1953, p. 399) suggested import by a ship coming from the Pacific.

In 1929 and 1931 TEISSIER collected 6 specimens among algae near Roscoff in Brittany. After a second record at Gullmarfjorden as well as in Brittany it was clear that the species did now belong to the European fauna, even if it might originally have been introduced.

Later the species was found in a closed part of the harbour of Ostende in 1946 and 1947. LELOUP (1948) believed its presence there to be due to accidental transport with *Ostrea virginica* from Long Island, USA. The American oyster had been introduced into the area in 1939-40.

During several years, from 1947 on, WERNER (1950) found the species in abundance in a closed and shallow pond on the Island of Sylt in the North Sea. The occurrence was very similar to that at Eel Pond, Woods Hole, both as to ecological conditions and the great number of medusae. WERNER believed their presence in the pond — which was not open to ships — to be due to transport with aeroplanes from Oslofjorden during the war.

In June 1959 the species was found in a private aquarium in Aberdour, Fife, Scotland (HOWE, 1959, p. 1963) and in 1960 KRAMP (1961, p. 445) found one specimen among algae near Fredrikshavn in Jutland, Denmark. Some other specimens were sent to him from Ritthem in Holland.

The distribution of *Gonionemus* in Europe as outlined above has been plotted in Fig. 3.

Up to the 1930's, most authors referred *Gonionemus* to the Trachylina, in spite of the fact that JOSEPH had found a polyp stadium in 1925. In 1938, however, KRAMP established the new order Limnomedusae, to which the Olindiidae with i. a. *Gonionemus* were referred. The Limnomedusae are littoral organisms, with a preference for brackish or even fresh (as in the case of *Craspedacusta*) water. There is a polyp generation, which in some species may live for years without producing medusae, thus leading a very hidden life.

The ecology of the species may give some information as to its most likely manner of distribution. The polyp is very small, only about 2 mm high. The only place where it has been found under natural conditions is at Sylt (WERNER), but as it may live for years without producing medusae (JOSEPH, WERNER), it may be quite abundant in an area without being recorded. Even the medusa

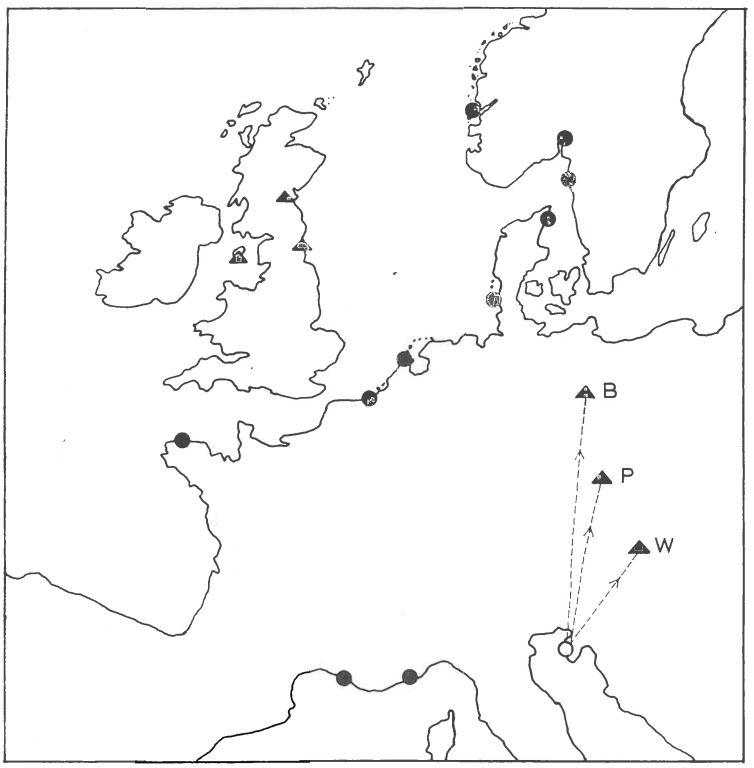

Fig. 3. The distribution of *Gonionemus vertens* in Europe. Black circles indicate places where it has been found under natural conditions, triangles indicate records from aquaria. The three Central-European finds (Berlin, Praha, Wien) all contained seawater from Rovigno at the Adriatic, but the species has, so far, not been found there.

generation is definitely littoral. For a great part of its life it moves around on algae in shallow water by help of the "suckers" on the tentacles. From time to time it ascends to the surface, turns and sinks down again. Some specimens may accidentally drift away into the open sea where they will easily get lost by sinking too deep before reaching the bottom. The chance of catching them by ordinary plankton gear, which usually seeks to avoid shallow bottoms or dense algal vegetation, is very small. Again and again it is mentioned that the species, when found, was caught "among algae" (BROCH, Oslofjorden; LÖNNBERG, Gullmarfjorden; TEISSIER, Brittany; PICARD, the Mediterranean; KRAMP, Denmark, and the present records from western Norway). Thus, the ecology of the species makes it very difficult to say for sure if it is really a new immigrant into an area where it has been discovered, or if it has lived there for years, or even "for ever".

The suggestions made shortly after the species was found in Oslofjorden (transport with ballast water in a tanker), and after the record at Ostende (transport with North American oysters) are, in the light of our present knowledge of

the systematic position, the distribution and the ecology of the species, not convincing. It is not even certain that the species was originally North-American. The facts that it was first discovered near Puget Sound and that for many years the locality near Woods Hole was the only place where it was known to exist in abundance, are not enough. WERNER's locality on Sylt is very similar to that at Woods Hole, and the mass occurrence on both places may just as well be due to similarity in ecological conditions.

Nor do the historical events give any definite evidence as to what part of the world the species did come from. It may just as well have spread from Europe —perhaps from the Mediterranean.

The world distribution of the species makes it likely, however, that it has been spread by man-made means, even if one can not with certainty point to the area from where the distribution started. The most likely means of distribution would be by transport of the polyp, presumably in the days of wooden ships. This may have been carried around, growing on the hulls. In that case, the conditions of life for the species have, through the means of civilization, been reversed. Instead of a polyp growing in a restricted area, and a medusa stage, which from time to time widened the species area within the littoral, one has got a species with a relatively "sedentary" medusa, but with a polyp which, as member of a fouling community on ships hulls, is carried around the world.

In the case of the anthomedusa *Bougainvillia macloviana* LESSON, such a form of transport has been found very likely. KÜNNE (1933, p. 249) writes: "Auf der Deutschen Südpolar-Expedition wurden auch die Polypen von *B. macloviana* gefunden, die sich am Rumpfe des längere Zeit zwischen schwärmenden geschlechtsreifen Medusen liegenden Expeditionsschiffes entwickelt hatten. Nach Jahresfrist wurden die Polypen nach der Überwinterung auf der "Gauss"-station entdeckt".

Bougainvillia macloviana, originally a subantarctic species, was introduced into the North Sea, where it was first recorded in 1895, at Heligoland. Later it has been found in the Clyde, Scotland, as well (EDWARDS, 1958, p. 1564).

Another medusa may be of some special interest in connection with the present records of *G. vertens* in western Norway. It is *Nemopsis bachei* AGASSIZ, which, according to KRAMP (1959, p. 265) may have been transported by ships from the North American east coast to a few European localities, where it has been found occasionally. If *Nemopsis heteronema* HAECKEL 1879 from Sognefjorden (western Norway) really is a synonym of *N. bachei*, the species had at that early date already been introduced in western Norway. In Scotland it may even have been found as early as 1853, if *Nemopsis crucifera* FORBES and GOODSIR, a somewhat doubtful species, can be considered a synonym of *N. bachei*. If those records really refer to *N. bachei*, there is here a parallel to *G. vertens* in the manner of transport. MAYR (1910, p. 174) mentions that the hydroid of *N. bachei* grows on submerged wood. A likely means of transport in both cases therefore

would be by means of polyps carried as part of the fouling community of wooden ships. MOORE (1962, p. 401) mentions the possible transport of hydroid colonies of *N. bachei* by ships from the Atlantic coast of USA to the northern Gulf of Mexico in recent years.

When *N. bachei* is considered, there can be no question as to its North-American origin. MILLARD (1959) gives more information on hydroids from ships hulls.

Other organisms are known to have been introduced in a similar way into North-European waters before or around 1900. In 1908 OSTENFELD traced the occurrence of the very conspicuous Asiatic planktonic diatomacean *Biddulphia sinensis* in the North Sea area, and JÖRGENSEN (1909a and 1909b) discussed its subsequent occurrence on the Bergen coast. It must have been carried to European waters in 1903 or a few years before, most probably to the harbour of Hamburg, either growing on a ships hull or living in a water tank. BÖRGESEN (1908, p. 819 ff.) discusses the possible distribution to new areas of sedentary algae growing on ships hulls and gives numerous examples, some of them from northern Europe.

Among vascular plants there is also a case from Norwegian waters. *Ranunculus cymbalaria* PURSH, a North-American littoral plant, grows in abundance on the shores of the Hvaler Islands and around the town of Fredrikstad at the mouth of Oslofjorden as well as in the neighbouring parts of Sweden. It is only 50—60 km south of the place where the first record of *Gonionemus* was made, and about 60—80 km north of Gullmarfjorden where *Gonionemus* has been repeatedly found since 1923. TAMBS-LYCHE (1937) supposed the plant to have been transported with ballast loadings, but OUREN (1959, p. 112) stated that, according to the shipping statistics, not a single ship had come with ballast from North America to the area concerned between 1835 and 1896, and probably not later either.

LUTHER (1955) pointed to the importance, for the distribution of this and other vascular plants, of dunnage ("Laderaumkehricht") which was usually thrown overboard while the ships were cleaned between harbours. It seems probable that the means pointed to by LUTHER is responsible for the transport of *Ranunculus cymbalaria*.

The other organisms mentioned here show, however, that the question of unintentional transport of marine organisms by shipping is a rather complex one. In addition to ordinary loading, ballast and dunnage, the transport of fouling organisms on the outside of the ships hull is rather important.

Many more examples can certainly be found than those mentioned here. The purpose of the present paper has not been to make a full survey of the question, but only to point to some organisms which most probably have been introduced to Norwegian and neighbouring waters through shipping.

Gonionemus vertens may be considered one of them, but it is still an open question from where as well as when it came. The transport may have taken

place quite a long time ago, in the days of smaller, wooden ships which stayed for a long time in the harbours and which came in contact, more easily than modern ships, with the algal vegetation along the shores or with the *Zostera* beds in shallow bays, localities preferred by *Gonionemus*.

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