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New Zealand Thecate Hydroids

Part V.—The Distribution of the New Zealand Thecate Hydroids

By PATRICIA M. RALPH

Abstract

DISTRIBUTION of the New Zealand thecate hydroids is discussed at the familial, generic and specific level. It is concluded that distribution is fundamentally correlated with latitude and can be explained by available dispersal mechanisms. Distribution in longitude is therefore limited by the oceanic distances involved. For forms utilizing trans-oceanic dispersion, the degree of similarity between the thecate hydroid faunas of the Southern land areas is a direct function of the distance separating them, or, in the case of forms utilizing self-dispersal, the present distribution pattern is dependent upon existing or former shorelines.

ONE of the more interesting aspects of systematic work on any group of animals is the study of the group as a whole and its distribution as indicated by its characteristic features. The New Zealand area is regarded here as including the Chatham Islands to the east, and the Subantarctic Islands (Bounty, Campbell, Auckland, Snares and Antipodes) to the south and east. Within this New Zealand area there are 139 species of known thecate hydroids in 48 genera and eight families (Fig. 1a). Since Farquhar, in 1896, named 61 thecate species in the only published check list of New Zealand hydroids, 79 more species have been described from our coastal and offshore waters. Farquhar's list shows collections from some 20 localities extending over a full coastal range from Cape Maria van Diemen in the far north to Stewart Island, approximately 1200 miles to the south. Collections were from the east and south coasts only of the main islands except for a collection from Hokianga in the north-west of the North Island, and taken in the intertidal region and storm drift, excepting a " Challenger " collection dredged in 700 fathoms off East Cape, North Island. Later descriptions of New Zealand hydroids, up to 1930 were also primarily made from material collected in the intertidal region, but in 1930, Totton's findings were published for the " Terra Nova " dredgings, in the area from North Cape to the Three Kings Islands, in depths from 11 to 300 fathoms. From this first major dredging operation on the New Zealand coast, 50 species were recorded, 20 of them new.

The material for my recent studies (1956, 1957, 1958 and in press), came from the intertidal and sublittoral regions and collections were made at 120 localities ranging from North Cape to Stewart Island and from all coasts, although the west coast of the South Island still shows inadequacies in collection. Over the last 20 years, the largest collections, both intertidal and sublittoral, were made in the

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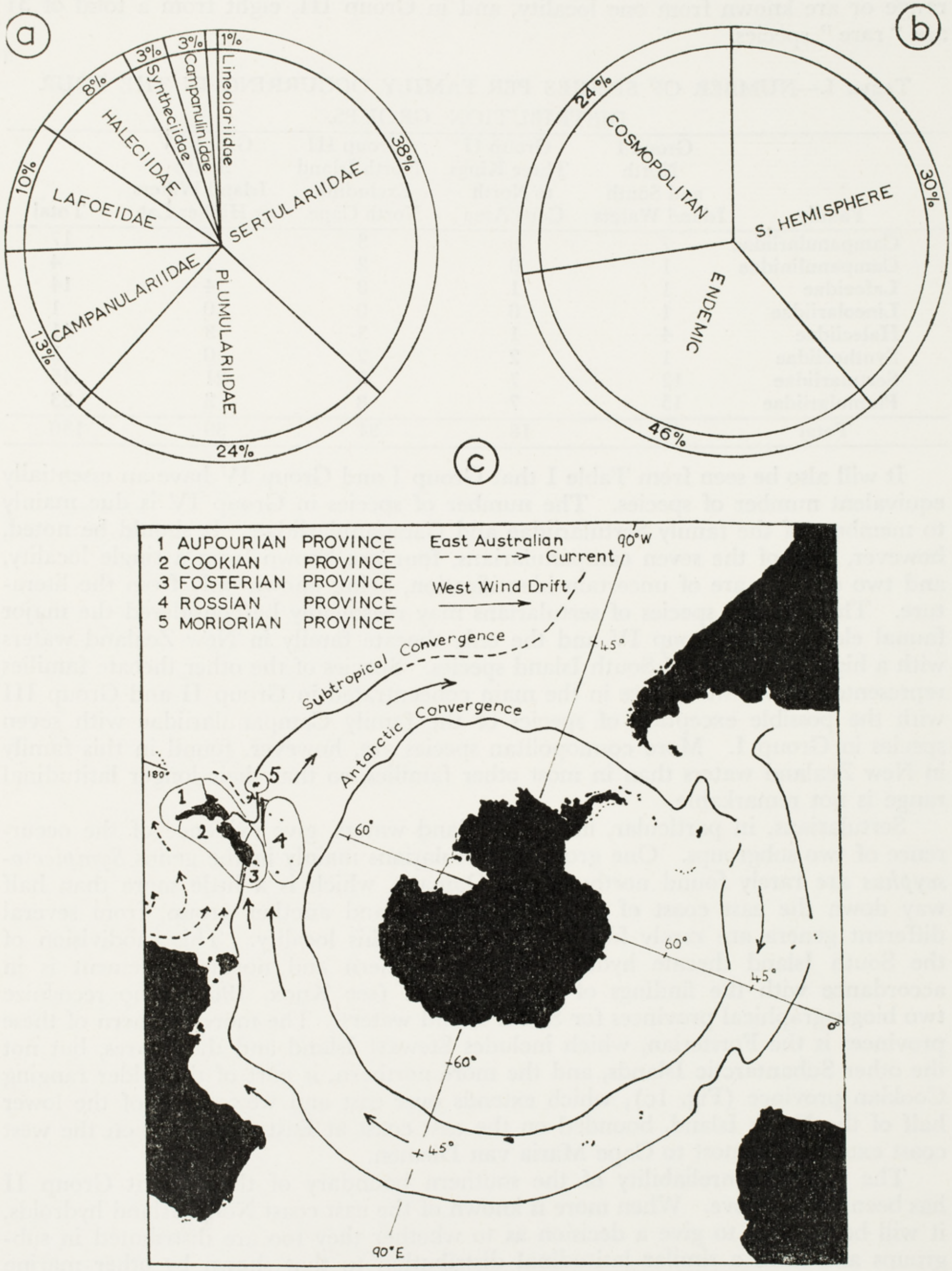
Auckland, Wellington, Bank's Peninsula and Otago Peninsula areas. Dredging in the Auckland area has been mostly in the Hauraki Gulf (by Fisheries Research vessel "Ikatere" collecting at approximately 40 fathoms); in the Wellington area, in Cook Strait, Palliser Bay region (various vessels chartered by the V.U.W. Zool. Dept., collecting from 40 to 600 fathoms); in the Bank's Peninsula area, various localities (C.U. Zool. Dept., various vessels, collecting from approximately 40 to 100 fathoms); and in the area of the Otago Peninsula, mainly off the Otago Heads, and deep-water canyons to the south and east (mostly M.V. "Alert", Captain A. Black, collecting from approximately 18 to 350 fathoms). Other localities dredged include the Bay of Plenty, a line of stations across the Bay from East Cape, then round the Coromandel Peninsula to the Hauraki Gulf (Northern Prawn Expedition, V.U.W., Zool. Dept., collecting from approximately 5 to 100 fathoms); in Hawke Bay, 20 stations (Kotuku Expedition, V.U.W., Zool., Dept., collecting from approximately 5 to 200 fathoms), and a few stations in the southern Fiord area (M.V. "Alert", and "New Golden Hind" Expedition, collecting from approximately 8 to 50 fathoms and one or two stations in Foveaux Strait and Stewart Island M.V. "Alert", collecting approximately from 3 to 40 fathoms). Chatham Island hydroids are primarily known from intertidal and sublittoral collections made by the 1954 "Chathams Expedition" under the leadership of Professor G. Knox. Sublittoral collections on the latter expedition were from approximately 3 to 400 fathoms.

In consequence, two species were recognized as new, a sertularian *Sertularella richardsoni* and a plumularian, *Thecocarpus subdichotomus*. Three new growth forms were described for *Obelia geniculata* and *Silicularia bilabiata* and one new form for *Orthopyxis crenata* and *Symplectoscyphus johnstoni*. Three invalid species were renamed; 13 species placed in synonymy; three species previously regarded as unidentifiable were determined and 15 species were new records for New Zealand.

New Zealand viewed on a world map is dwarfed by ocean expanses and by the larger southern land masses, yet our mainland islands cover some 13° of latitude, more than the distance from Sydney to Tasmania in the Australian continental area, and nearly the equivalent to that of the western seaboard of the United States of America. When, as is usual, the Subantarctic Islands are included, the New Zealand zoogeographical region ranges from 34° S. to 53° S. From north to south in this latitudinal range there is considerable change in the climate of the surface waters. The Subantarctic Islands and the east coast of the South Island lie in the cold subantarctic water zone (Fig. 1c) intermediate between the Antarctic and Subtropical Convergences. The North Island and most of the west coast of the South Island are within the zone of subtropical water.

The wide range of climate, from cold subantarctic in the south to subtropical in the north is reflected in the distribution of the thecate hydroids, which sort out naturally into four groups. Group I includes those species that occur in both North and South Island waters; Group II those that occur from the Three Kings Islands to North Cape on the North Island mainland; Group III those that occur in North Island waters from North Cape southwards to Cook Strait, and Group IV those that occur only in South Island waters and/or beyond to higher latitudes.

Table I shows the number of species per family that occur in each group, and from these numbers the calculated percentage of the whole fauna within each group is: 31½% in Group 1, 15% in Group II, 23½% in Group III, and 30% in Group IV. Several species are known as yet from a very short range, or from one locality. This is particularly so in Group II where all the species come into this category. Very little collecting has been undertaken either in the far North of New Zealand, or along the coastline between 35° S. and 37° S. Any future collection in these latitudes is likely to show that the boundary for Group II is properly further southwards. In Group IV, 20 out of a total of 39 species have a very short



TEXT-FIG. 1.—a, number of species per family expressed as a percentage of the total population of New Zealand thecate hydroids; b, percentage of species in the New Zealand area that are endemic, known from other southern hemisphere areas, or, of cosmopolitan distribution; c, diagram showing the mean positions of the Antarctic and Subtropical Convergences, the biogeographical subdivisions of New Zealand (see Knox, 1960), and the major ocean currents of the Tasman Sea.

range or are known from one locality, and in Group III, eight from a total of 31 are " rare " species.

Table I.—NUMBER OF SPECIES PER FAMILY OCCURRING IN THE FOUR DISTRIBUTION GROUPS.

Family	Group I North and South Island Waters	Group II Three Kings to North Cape Area	Group III North Island Excluding North Cape	Group IV South Island Waters or Higher Lat.	Total
Campanulariidae	7	0	3	7	17
Campanulinidae	1	0	2	1	4
Lafoeidae	1	1	8	4	14
Lineolariidae	1	0	0	0	1
Haleciidae	4	1	3	3	11
Syntheciidae	1	2	2	0	5
Sertulariidae	12	7	5	21	45
Plumulariidae	15	7	8	3	33
Total	42	18	31	39	130

It will also be seen from Table I that Group I and Group IV have an essentially equivalent number of species. The number of species in Group IV is due mainly to members of the family Sertulariidae and Campanulariidae. It should be noted, however, that of the seven campanularians, four are known from a single locality, and two of these are of uncertain identification, being known only from the literature. Thus, the 21 species of sertularians may reasonably be considered the major faunal elements of Group IV and the only thecate family in New Zealand waters with a high proportion of South Island species. Species of the other thecate families represented in our waters are in the main concentrated in Group II and Group III with the possible exception of species of the family Campanulariidae with seven species in Group I. More cosmopolitan species are, however, found in this family in New Zealand waters than in most other families, so that their longer latitudinal range is not remarkable.

Sertularians, in particular, in South Island waters, give evidence of the occurrence of two subgroups. One group of sertularians mainly in the genus *Symplectoscyphus* are rarely found northward of Oamaru, which is a little more than half way down the east coast of the South Island, and another group, from several different genera are rarely found southward of this locality. This subdivision of the South Island thecate hydroids into a southern and northern element is in accordance with the findings of other workers (see Knox, 1960) who recognize two biogeographical provinces for South Island waters. The more southern of these provinces is the Forsterian, which includes Stewart Island and the Snares, but not the other Subantarctic Islands, and the more northern, is part of the wider ranging Cookian province (Fig. 1c), which extends over east and west coasts of the lower half of the North Island, bounded on the east coast at East Cape, but on the west coast extending almost to Cape Maria van Diemen.

The possible unreliability of the southern boundary of the present Group II has been noted above. When more is known of the east coast North Island hydroids, it will be possible to give a decision as to whether they too are distributed in subgroups and have a similar latitudinal distribution to that shown by other marine animals such as the molluscs. The best that can be said at present is that the evidence suggests that the hydroids conform in distribution pattern to that already known for other groups. The molluscs indicate a north-eastern Aupourian province.

Nonetheless, the thecate hydroids show clearly a latitudinal distribution pattern with sertularians having a stronger representation in number of species in cooler South Island waters, particularly southward of Oamaru, and plumularians having a strong representation in northern North Island waters, particularly the Three

Kings Islands and North Cape regions. The species of the other six families together with some plumularians and sertularians are more or less equally distributed in the intermediate region between these two extremes. This pattern of distribution with sertularians having a stronger representation in number of species in high latitudes, gradually losing their prominent position in the intermediate regions to campanularians, halecids, lafoeids and campanulinids until in low latitudes plumularians are the major family is confirmed by the results of other workers in other southern hemisphere areas, and paralleled in northern hemisphere waters (Fraser, 1946). For example, in the Antarctic area, Stechow (1925) records 26 sertularians and six plumularians, and Totton (1930), 7 sertularians and 3 plumularians. Moving north in the range, in Tasmania (Hodgson, 1950), and in other Australian subregions and South Africa (Stechow, 1925, and Millard, 1957, 1958), the ratio of sertularians to plumularians is approximately 1:1. In the Indonesian region (Billard, 1913) records 53 sertularians and 71 plumularians.

The distribution of many genera and species, both in New Zealand waters and elsewhere, indicates that temperature tolerance varies within this pattern of familial change from south to north. In the F. Sertulariidae distribution of the genera *Sertularia, Crateritheca* and *Parascyphus* indicates that they are warm water genera and that *Sertularella* and *Symplectoscyphus* are cold water genera. In the relatively low latitude Kermadec Lslands, *Sertularia minima* is the only recorded species of F. Sertulariidae, and in New Zealand *Crateritheca* and *Parascyphus* are not known from South Island waters. It should be noted, however, that Broch (1948) refers " not without doubt " certain dried fragments from the Antarctic to *Parascyphus simplex* so that the genus may have a more extensive range in high latitudes than is at present known. The difference in ratio of the number of species of *Sertularia* to *Sertularella* in low and high latitudes is significant. In low latitude (10° S. to 28° S.) Queensland waters the ratio is 1:1, but in New Zealand high latitude waters (41° S. to 47° S.) the ratio is 1:3. (The latter genus includes here species of *Symplectoscyphus* in addition to *Sertularella* in order to give a basis comparable with that calculated from Pennycuik's (1959) Queensland check list.)

From the temperature preferences shown, it could be expected that species of *Sertularella* and *Symplectoscyphus* in New Zealand would be more frequently taken in offshore sublittoral waters in the more northern regions of their latitudinal range, and that species of *Sertularia* would occur more frequently in harbour and inshore intertidal waters in the higher latitudes of its New Zealand range. Species of these genera are found to conform to this pattern, and not only in northern waters, but throughout their latitudinal range, species of *Sertularella* and *Symplectoscyphus* are taken in offshore waters.

The F. Plumulariidae is represented by ten genera in New Zealand, and their distribution indicates that half are warm water by preference and the others of wider temperature preference. *Pycnotheca, Halicornaria, Halicornopsis* and *Thecocarpus* are not known from South Island waters, but *Plumularia, Aglaophenia, Halopteris, Antennella* and *Nemertesia* occur in coastal and offshore waters of both Islands. *Monoserius* is known in our waters by one species, with recorded locality, " New Zealand ".

The distribution of genera in the other families shows them to be mostly with wide temperature tolerances, but two genera *Obelia* and *Silicularia* in the F. Campanulariidae are cold water genera. The latter genus is not known northward of New Zealand in the Pacific Ocean, or northward of Cape San Roque, in the Atlantic Ocean. Fraser (1946) notes in northern hemisphere waters that *Obelia* " drops almost out of sight " in low latitudes. In the southern hemisphere, the readily recognizable *O. geniculata* is not known from the Queensland coast of Australia. Furthermore, the difference in growth form of the erect stem in *O. geniculata* and *Silicularia bilabiata* from south to north is striking. *O. geniculata* occurs in high latitudes with tall, freely branched stems, and in low latitudes within the Subtropical water mass with short, unbranched stems. The stems of *S. bilabiata* found in low latitudes are about half the size of those in high latitudes.

Examples from the F. Sertulariidae and F. Campanulariidae will serve to illustrate differences in distribution for species of the same genus. In the genus *Symplectoscyphus* where the majority of species are found in cold water, *S. columnarius* is recorded from Tasmania and North Island waters, and in *Diphasia* where the majority of species are found in warm water, *D. subcarinata* occurs in New Zealand in the southern Forsterian province. In the companularian genus *Obelia,* where most of the species are found in cold water, *O. nodosa* is recorded only from the warm water areas of Queensland and Auckland, New Zealand.

Endemic species are mostly found in the low latitude *F. Plumulariidae,* and high latitude F. Sertulariidae, approximately 47% in each family. This would be explained by the New Zealand area spectrum of habitat providing a range in which there is an extensive region where neither plumularians nor sertularians are excluded in terms of familial biological characteristic. Within this indifferent area, there has been the opportunity for generalized speciation.

The two dispersal mechanisms available to hydroids are both passive. First, transport by ships, and secondly by ocean currents. Carriage by ships offers an explanation for the distribution of the campanularians *Clytia elongata, Orthopyxis mollis,* the campanulinid *Phialella quadrata* and the plumularian, *Plumularia wattsi, Clytia elongata* has been taken from the hull of a ship in Auckland Harbour. It is known elsewhere from a single locality in New South Wales and Goa, South Africa. Similarly, *P. quadrata* from a ship in Auckland and Wellington Harbours and elsewhere from Belgium and England. *Orthopyxis mollis* and *Plumularia wattsi* have not been taken from the hull of a ship, but the former is known from the piles of Gladstone Pier, Lyttelton Harbour and also in other localities along the coast of the South Island and elsewhere from southern France, and the latter species from wharf-piles in Port Chalmers in the South Island, and elsewhere from Port Phillip, Australia.

The thecate hydroids most frequently carried by ships are the cosmopolitan species of the families Campanulariidae, Campanulinidae, Lafoeidae, Haleciidae and Plumulariidae. Sertularians are rarely carried by ships. The majority of species transported by ships live on seaweeds and/or the intertidal region. The question posed by Millard recently (1959) is also apt here, " is the presence of cosmopolitan species on ships' hulls a result of their world wide abundance, and ability to live under varied environmental conditions, or is their wide distribution a result of transportation by ships? " If the latter alternative is the sole dispersal mechanism for species with a cosmopolitan distribution, then it could be anticipated that the cosmopolitan species found in New Zealand waters would be present in harbours everywhere. It is therefore surprising that *Gonothyraea loveni* is known only from wharf-piles in Dunedin Harbour. Furthermore, sertularians are rarely carried on ships and sertularians are among the better known thecate hydroids with a cosmopolitan distribution. Thus, it seems the distribution of cosmopolitan species cannot wholly be explained by ship transport.

Ocean currents are effective in transporting medusae and planulae, but these reproductive phases are usually recognized as possessing a short life span, particularly the planula, and therefore, even with the aid of currents, the medusa and planula are dispersal mechanisms with a limited range allowing a slow migration along the continental shelf or deeper ocean floor.

Many thecate hydroids recorded from New Zealand and common to other southern hemisphere areas, live on seaweeds, and it seemed from the numbers of hydroids taken from storm-drifted seaweed, that ocean currents would provide an effective " long distance " transport mechanism. Nonetheless, distance between areas of land, whether continent or island, in the southern hemisphere, is great, rarely less than 1,000 miles and often more than twice this distance. If ocean currents provide an effective transport mechanism for hydroids attached to seaweeds, it could be anticipated that floating masses of the latter would have been noted in the circulation of current systems. Floating rafts of seaweed and logs have been sighted well beyond coastal waters, and there is a record of storm-drifted logs taken in Tasmania, the identity of which showed their origin to be some 5,000 miles distant from Tasmania (Barber, Dadswell and Ingle, 1959). Thus it seems that ocean currents could provide long distance transport for hydroids living on seaweeds.

New Zealand shares 41 (excluding cosmopolitan species) of its thecate hydroid fauna of 139 species, with other southern hemisphere areas. One species has a New Zealand-Antarctic distribution; two species a New Zealand-South American (southern peninsular region) distribution; three species a New Zealand-South African distribution and 21 species a New Zealand-Australian distribution. Thirteen species are more widely distributed in the Indo-West-Pacific region—namely, New Zealand, Australia, South Africa, and/or the Kermadec Islands, Indonesia and the Indian Ocean, and one, is circumpolar in high latitude islands, as well as occurring in South America, Australia and New Zealand. Of these 41 species, a little over half (28 species) are known to grow on seaweeds.

The circumpolar distribution of *Silicularia bilabiata* well known from the fronds of *Macrocystis pyrifera*; the New Zealand-South African distribution of *Symplectoscyphus macrogonus* and *Halopteris constricta*; the New Zealand-South American distribution of *Amphisbetia episcopus* and the New Zealand-Australian (S. E. Australia and Tasmania) distribution of *Lineolaria flexuosa, Diphasia subcarinata, Amphisbetia bispinosa, A. trispinosa, Symplectoscyphus rentoni, S. pygmaeus , S. pseudodivaricatus, Plumularia wilsoni, P. hyalina* and *P. setaceoides* suggests dispersal by the West Wind Drift. The Queensland-New Zealand distribution of *Obelia nodosa, Orthopyxis delicata, Opercularella hyalina* and *Aglaophenia laxa*; and the Tasmanian, northern New Zealand, Chatham Island distribution of *Crateritheca insignis* suggests dispersal on the East Australian Current. The widespread distribution in the Australian region, including Queensland, and throughout New Zealand of *Sertularella robusta* suggests dispersal on both the West Wind Drift and the East Australian Current. And finally, the distribution of the eight species occurring on seaweeds in New Zealand and other Indo-West-Pacific areas, by dispersal on the warm water East Australian Current and/or the South Equatorial current, and the Mozambique Current. These species are the plumularians *Pycnotheca mirabilis, Halicornopsis elegans, Plumularia spinulosa, P. pulchella, Aglaophenia acanthocarpa* and the sertularians *Stereotheca elongata* and *Sertularella quadridens.*

The number of species shared by New Zealand with other southern hemisphere areas gives a measure of the distance over which ocean currents operate successfully as a dispersal mechanism. Take for example, the species whose distribution suggests dispersal on the West Wind Drift. Of these, New Zealand shares one species from a total of 14 with South America, two with S. Africa, and 11 with Australia. This indicates that the distance of a thousand miles across the Tasman Sea is not too great for ocean currents to offer a satisfactory explanation of the distribution of these Australasian species. And equally, then the East Australian Current explains the distribution of the remaining species living on seaweed New Zealand shares with Australia, and very probably, the East Australian Current combined with the two other current systems noted above, explains also the distribution of the species New Zealand shares with the Indo-West-Pacific area. The one or two species New Zealand shares with South Africa and South America suggests that occasionally ocean currents are successful dispersal agents over distances greater than that of the Tasman Sea. The distance between land masses then appears to be the factor governing successful dispersal by ocean currents. The greater distance between New Zealand and South America, to the east, than between Australia and New Zealand, offers an explanation for the high percentage (46%) of endemic species in the New Zealand hydroids, in which approximately half live on seaweeds. The distance between New Zealand and South America is too great for successful dispersal.

Hydroids also grow entwined round other hydroids, on various molluscs, notably mussels, oysters and scallops, on ectoproctans, on and among sponges, on stalked ascidians, and terebellid worms, etc., and while it is possible that during storms these animals could become entangled in a kelp raft and thus dispersed by ocean currents, the latter dispersal mechanism does not offer a satisfactory explanation for the hydroid species not living on seaweed that New Zealand shares with other southern hemisphere areas.

As the dispersal mechanism of ships leaves unexplained the distribution of some cosmopolitan species and the disposal mechanism of ocean currents the distribution of those species not living on seaweeds New Zealand shares with other southern hemisphere areas, the discussion comes back to the possibility of dispersal by means of medusa and planula. For thecate hydroids to have attained their distribution by the agency of these reproductive phases implies that land masses were formerly either linked by land bridges or in juxtaposition and thus provided the necessary continuity of shoreline for hydroid dispersal. Geological evidence indicates that from time to time in the past there has been greater continuity of southern hemisphere and other shorelines than at present. Shoreline dispersal along former land masses probably explains the distribution of species not living on seaweed, New Zealand shares with other southern hemisphere areas. If dispersal along former shorelines is not recognized for these species their distribution is at present unexplained. The undoubted capacity of cosmopolitan species to survive a wide range of climates, probably means they have greater dispersal opportunity than other species and could have attained their world wide distribution by dispersal on ships, as well as by ocean currents for species living on seaweed, and along existing or former shorelines by medusa and planula.

In summary, then, the distribution of the cosmopolitan element (24%) in the New Zealand thecate hydroid fauna is explained by dispersal mechanisms—namely, ships and ocean currents, the latter acting as transport agency both for species living on seaweed, and for medusa and planula along the shoreline of land areas; and the distribution of the southern hemisphere element (30%) by ocean currents either by dispersal of kelp rafts for those species living on seaweeds, or by dispersal of medusa or planula along the shoreline of former land masses, for those species that live other than on seaweed. The high endemic element (46%) is explained by the distance between New Zealand and the nearest land mass to the east being too great for the dispersal mechanism of ocean currents to be successful.

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MISS P. M. RALPH,
Zoology Department,
Victoria University of Wellington,
P.O. Box 196,
Wellington, New Zealand.