AUSTRALASIAN ANTARCTIC EXPEDITION

1911-14.

UNDER THE LEADERSHIP OF SIR DOUGLAS MAWSON, D.Sc., B.E.

SCIENTIFIC REPORTS.

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OLIGOCHÆTA OF MACQUARIE ISLAND.

BY

W. B. BENHAM, M.A. (Oxon.), D.Sc. (Lond.), F.R.S., F.N.Z. Inst.

WITH FIVE TEXT-FIGURES AND A MAP

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THE OLIGOCHÆTA OF MACQUARIE ISLAND.

By W. B. Benham, M.A. (Oxon.), D.Sc. (Lond.), F.R.S., F.N.Z. Inst., Professor of Biology, University of Otago, New Zealand.

(With five text-figures and a map).

INTRODUCTION.

The present collection is a small one, but, judging from the different parts of the island and the different habitats explored, there is little reason to suppose that much has been overlooked by that assiduous and energetic collector, Mr. Harold Hamilton, Biologist of the Macquarie Island party.

It is true that no specimen of *Enchytræus albidus* was met with in examining the material, which is not to say that it is not present, for I did not study every individual of these small worms, which were collected in considerable numbers.

The material was carefully preserved and annotated. As the geographical and physical features of the island have been dealt with by other contributors to this series of Reports, there is no need for me to say anything as to the topography.

The collection contains representatives of only four species, all of which have already been described. Three belong to the family Enchytræidæ, namely, *Lumbricillus macquariensis*, *Marionina antipodum*, and *M. werthi*. The two last have not previously been recorded from this island. The fourth species belongs to the family Magascolecidæ, namely, *Microscolex* (*Notiodrilus*) *macquariensis*.

The affinities of each of the species appear to be with those inhabiting islands to the west, and after the systematic account of the worms I have added a short Essay on their Dispersal, which may be of some general interest, as the problem is by no means a simple one and has led to much discussion amongst Oligochætologists.

Fam. ENCHYTRÆIDÆ.

LUMBRICILLUS *Oersted.*

LUMBRICILLUS MACQUARIENSIS *Benham.*

L. macquariensis Benham (1905), p. 295, pl. XIV, figs. 8, 11–13.
L. intermedius Benham (1909), p. 261, pl. X, figs. 8–11.
L. macquariensis Benham (1915), p. 189.

The collection contains a considerable number of specimens from both the sea-shore and from fresh-water streams. One lot is labelled by Mr. H. Hamilton as 'Marine worms, found under stones at about high-water mark, apparently in copulation."

It is interesting to note that the original specimens, amongst which was the type of the species, were gathered by Mr. A. Hamilton, the father of the collector of the the present specimens, who found them " in brackish pools, with Siphonaria, &c."

I commenced the study of these Enthytræids from the Macquarie Island some years ago, and have already published a short article on this species in which I show that it is identical with the worm I named in 1909, *L. intermedius*, and it is convenient to quote from that article so as to bring together here the evidence for this opinion.

> While studying the present Enchytræids I was led to re-examine my preparations of the specimens received at earlier dates, and have arrived at the conclusion that the species " *L. intermedius* " is identical with *L. macquariensis*.
>
> A comparison of the two accounts shows that the points of difference affect the following organs: (*a*) The nature of the spermathecal opening into the œsophagus; (*b*) the number of chætæ in each bundle; (*c*) the segment in which the dorsal vessel becomes free from the intestinal blood sinus; (*d*) the number of the sub-neural copulatory glands; (*e*) the size and proportions of the spermiducal funnel.
>
> A. The re-examination of the type of *L. macquariensis*, and of sections made of other specimens received at that time, shows that I made an error in affirming and figuring the existence of " a narrow duct " putting the spermatheca into communication with the œsophagus. And to this error I added some confusion in a note at the end of my account of " *L. intermedius* " by stating (1909, p. 261), " It is quite distinct from *L. macquariensis*, which belongs to another group of the genus in which the spermathecal duct is strongly marked off from the ampulla." The latter statement is clearly a *lapsus calami*, for what was intended is evidently a contrast with the " narrow communicating-duct," and not with the external opening.
>
> But it is difficult now to understand how I came to make the original statement as to the existence of the " narrow communicating-duct." The series of transverse sections show quite distinctly that there is no such " duct "—the ampulla communicates with the œsophagus by a small pore due to the sudden contraction of the ampulla, as I have described and figured for " *L. intermedius* " (pl. X, fig. 8).

In order to convince myself further I opened a specimen from the original lot, and it is certain that no such "duct" exists. The mounted specimen which served as the type, when studied without the knowledge derived from the other studies, does suggest a short duct, as the spermatheca is bent at a point close to its entrance into the œsophagus; but with the other evidence before me I recognise that the statement was due to faulty observation. (It is worth noting that Michaelsen made a similar error in his first account of *L. maximus*.)

Having discovered this mistake I proceeded to examine each of the other characters more carefully.

B. As to the chætæ, I find from a study of eight individuals that there is a considerable range of variation, as may be seen by a study of the annexed table, in which I have summarised the number of chætæ in the dorsal and ventral bundles in the pre-clitellar and in the post-clitellar region of the body in specimens from Macquarie Island and from the Campbell and Auckland Islands. It will be noted that the difference between extremes such as No. 2 and No. 5 amongst specimens from Macquarie Island is greater than the difference between No. 2 and No. 8 from two distant islands, and it is impossible to include in the diagnosis of a species a character with such a wide margin of variation.

C. It will be noted, too, that the segment in which the dorsal vessel originates shows a similar variation. It is true that in the type it commences at the hinder end of the 13th or 14th segment, while in the type of "*intermedius*," as I can confirm from renewed examination, this point is in segment 17; but even amongst those from Macquarie Island the position varies, being in two cases in the 15th, in a third in the 16th, while in one that was sectionised it lies in the 17th segment.

D. The number of the sub-neural glands exhibits the same instability, for though usually there are three glands in segments 14, 15, and 16, there is one individual from Macquarie Island in which there are six glands, and in two "*intermedius*" there are four.

E. Finally, I made a point of the proportion of length to breadth of the funnel of the sperm-duct, for in the type of *L. macquariensis* I stated that the length is twice the breadth, whereas in "*L. intermedius*" I gave it as about five times the breadth. I have measured it in three funnels of "*intermedius*" whose outlines I drew with the camera, two in a series of longitudinal sections, and one in a bisected specimen mounted as a transparent object. From these measurements I find that the length is respectively five, five and a half, and six times the breadth.

I am unable to give measurements for the funnel of *macquariensis*, as it is bent in all the preparations, but the proportions given in the original statement seem to be borne out. But the state of preservation of the type is bad; the worm was soft, and it is possible that the gland-cells around the funnel are much swollen, just as those of the sub-neural glands are. In my figure of the latter (1905, pl. XIV, fig 8) they are represented as much too broad and too high. Without at that time having well-hardened specimens for study, I did not recognise the effect of this bad preservation on the gland-cells; but a comparison of the sections with well-preserved material shows at once the fact that the gland-cells are swollen, so that the whole gland appears larger than it would be in life. Hence again the difference between the figure of *macquariensis* referred to and that given for "*intermedius*" (1909, pl. X, fig. 9).

So, I think, we may take it that in the case of the funnel gland-cells the same explanation may be given—their swollen condition increases the width of the funnel, and led me to give proportions which are no doubt untrue in life. It is not improbable, however, that the size of the gland-cells in both glands may vary according to the sexual condition of the worm, and it is likely that when fully mature in the breeding season the glands would be larger. I conclude, then, as a result of this comparison, that "*L. intermedius*" is synonymous with *L. macquariensis*, so that this species has a distribution over these three Subantarctic islands. The figures of the spermatheca, sub-neural glands, and sperm-funnel as given for "*intermedius*" must replace those given in the article on *L. macquariensis*.

Moreover, it is, it seems to me, closely allied to *L. maximus* Michaelsen (1905, p. 10), from which it differs in its smaller size, for that is stated to measure 40 mm. in length, whereas our species does not exceed 25 mm., and some of the mature individuals are less and the worm may attain maturity when only 15 or 16 mm. in length; and the variety of *L. maximus* termed "*robinson*" is but 12–16 mm. in length, and the clitellum is interrupted on the ventral surface.

TABLE SHOWING THE NUMBERS OF CHÆTÆ, ETC.

	Chætæ.				Sub-neural Glands.	Origin of D. Vessel.
	Pre-clitellar.		Post-clitellar.			
	D.	V.	D.	V.		
1. *L. macquariensis* (type)	6 (5)	5 (4, 6) *a*	4 (5)	5	14, 15, 16	13 or 14
2. ,, (cotype) ...	6 (7)	6 (5)*b*	5 (4)	6 (5)	14, 15, 16	?
3. ,, (H. H.) ...	5 (6)	6 (5)*a*	4	5	14, 15, 16	16*c*
4. ,, (H. H.) ...	6 (7)	7 (6, 5)	?	?	*d*	15
5. ,, (H. H.) ...	4	5 (6)	3	4	14, 15, 16*d*	15
6. "*L. intermedius*"	5	6	4	5	14, 15, 16, 17	17
7. ,, ...	5	6 (7)	4	3 (4)	14, 15, 16	16
8. ,, ...	6 (5)	7	5 (4)	6 (5)	14, 15, 16, 17	?

NOTES TO THE TABLE.

The numbers enclosed in brackets occur less frequently along the body.

a. In one segment there are 7 chætæ.

b. There is considerable irregularity throughout the body in this individual, the number in each bundle often differing in successive segments, and on the two sides of the body; thus each of the segments ii and iii has 8 chætæ on one side and 6 on the other.

c. In one individual sectionised the dorsal vessel occurs in the 17th segment.

d. In one individual there are 6 glands in segments 13-18, the largest being in the 15th; but in two other specimens only 3 glands exist, but I did not correlate them with the chætal formula.

? The fact was not observed in these specimens.

H. H. Specimens collected by Mr. H. Hamilton during the present expedition.

Localities.—

(*a*) Under stones at about high-water mark.

(*b*) From algæ above high-water mark (with *Marionina antipodum*).

(*c*) No particulars (with *M. antipodum*).

(*d*) In fresh-water creeks.

(*e*) In fresh-water streams, top of hill, North End.

Distribution.—Macquarie, Campbell, and Auckland Islands. As this species seems nearly related to *L. maximus* Mich., which occurs on the Crozet group, it is likely that it has arrived in these islands from the west.

MARIONINA *Michaelsen.*

MARIONINA ANTIPODUM *Benham.*

Benham (1905), p. 294, pl. XIV, figs. 9, 10.
Benham (1902), p. 262.

(Fig. 1.)

As a result of the examination of the abundant material gathered during this expedition I find it necessary to make a few corrections in, and additions to, my previous account, and although this note occupies but a few lines in the Report, yet the sectionising and study of the preparations have occupied me many hours and days before I was able to satisfy myself of the identity of these small worms. Any zoologist who has had to study these microdrilous Oligochætes will know how difficult it is to make comparisons with other species, from the study of preserved material and from sections cut in different planes.

Several specimens from different localities were measured; the mature worms do not seem to exceed 15 mm. in length with about forty segments.

The chætæ are not so constantly four in each bundle as stated in my original account, for I find worms in which this number is exceeded; indeed, in some segments of one worm the number is seven in the anterior segments.

The original material consisted of four worms, two of which were mounted entire, one was cut into transverse sections, the fourth I have lost.

Of the two individuals mounted, one is a small immature worm in which it is true that there are almost universally four chætæ in each bundle, the number sometimes being less; but in the other larger and mature specimen the numbers are greater.

Other specimens from the present collection were also analysed for this purpose. In the anterior or preclitellar segments there are more usually six or five in the ventral bundle, and five or four in the lateral; in the postclitellar segments the numbers are four ventrally and four laterally, though occasionally five and three respectively. The higher figure occurs in the most anterior segments.

I am now also able to give a more complete account of the penial apparatus, more especially of the prostate glands, than I did in my original contribution. There I gave a figure (pl. XIV, fig. 9) of the apparatus as seen in transverse sections, and it shows only one group of gland cells, lying external to and above the penial bulb, into which it opens. This is correct so far as it goes, but a re-examination of the sections in the light of observations on longitudinal sections made from worms of the present collection, shows that there are in addition one or more post-penial glands.

Some of the worms were sectionised in the sagittal and another in the frontal plane, so that the extent of these glands is more evident (fig. 1). There are two or three groups of gland cells in front of, and one or two behind, the penial bulb; each group extends upwards inside the body wall for some distance, as seen in transverse sections, to about the level of the side of the intestine. These glands all open into the penial bulb or atrium.

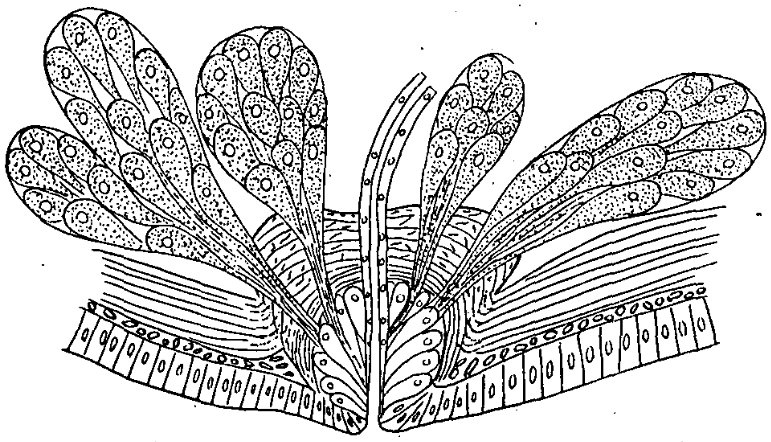


Fig. 1.

Marionina antipodum. Schematic view of the penial apparatus (x 250, approx.) compiled from a series of outline camera sketches of longitudinal sections, controlled by comparison with transverse sections. The sperm-duct passes through a subspherical group of gland-cells forming an "atrium," which is enveloped by a coat of muscle; the various prostate glands open into this "atrium," the cells of which take a stain less deeply than do the cells of the prostate.

The sperm duct, as I described it originally, enters the small bulb obliquely; this bulb consisting of a group of gland cells, whose contents do not stain as deeply with borax-carmine as do those outside the bulb, and they are surrounded by a muscular coat.

The lower part of the sperm duct loses its cilia and into this distal region the gland cells of the bulb enter. This penial bulb is, then, a typical "Lumbricillid bulb," as defined by Eisen (1905), whose paper had not reached me when I described the species.

There is a pair of extensive copulatory glands, also known as "ventral glands" and "sub-neural glands," in each of the segments 13, 14; they extend outwards from the nerve cord for a distance greater than its breadth. Here, again, I was in error in my account of the type. The type is very faintly stained, and, owing to its position as it lies on the slide, these glands are not readily seen, while the series of transverse sections unfortunately ceases just in front of the former segment. My attention was drawn to these glands by finding them in individuals in the present collection, and re-examination of the mounted type shows that they exist there.

In this species the œsophagus and intestine are covered with cells containing abundant chloragogen granules of dark yellow or even brown colour. So deeply tinted are they in some cases that the brown can be seen through the body-wall even now that the worms are in alcohol; in several instances the granules are darker on the œsophagus than further back.

In *Lumbricillus macquariensis*, on the other hand, these granules are very feebly coloured, yellowish or very pale brown; indeed, in some series of section the cells do not appear to contain any pigment, being filled with pink-stained granules. This absence of dark pigmentation was useful in enabling one to sort out one or other species from a mixture of the two; in each case the optical test was confirmed by means of sections and study of the organs.

Localities.—

(*a*) About fifty individuals "from algæ above high-water mark, West Coast."

(*b*) About thirty individuals of smaller size without definite locality.

(*c*) A number from "fresh-water creeks" (with *L. macquariensis*).

(*d*) A considerable number "from fresh-water stream, top of hill, North End." (with *L. macquariensis*).

This last lot had been preserved in osmic acid and are of a very dark grey.

As I have remarked in 1909, this species appears to be related to certain species inhabiting the Crozets and Kerguelen; and it is by no means easy to be sure that they are different from one of these species, for specific characters are in the case of these small worms difficult to express in words.

The species was originally found on Antipodes Island, and its occurrence on Macquarie Island is of particular interest, as it was not met with either on Campbell or Auckland Island, though it is of course still possible that it lives on one or both of them. If it does not, then its presence on Macquarie Island opens up a question which I discuss later. It is fairly common on Antipodes Island, and it may be that cocoons have been brought on the feet of birds to Macquarie Island, though I am not inclined to take that view.

MARIONINA WERTHI *Michaelsen.*

Michaelsen (1905), p. 13, pl. I, figs. 3–5.

(Figs. 2–5.)

Amongst the material gathered from the algæ above high-water mark mixed with the two preceding species were some half-dozen small worms of a grey colour. The presence of pigment in the body-wall is a very unusual phenomenon amongst the

Enchytræidæ, and the only species in which this pigmentation occurs in the longitudinal muscle-coat is this species, which was recorded from Kerguelen, where it also was found amongst algæ within tide marks.

The present worm may attain a length of 10 mm. by 1 mm. in diameter.

The pigment, as seen in a complete worm, covers the dorsal surface throughout its length; it extends down the sides as far as the lateral chætæ in the anterior region, while still further forwards it extends across the ventral surface. Owing to this extensive pigmentation it is impossible to make out much of the internal anatomy in an entire mount. Seen under the microscope the pigment is in the form of a dense network, which in the greater part of the worm is interrupted intersegmentally by narrow unpigmented bands, though between the anterior half-dozen segments these are absent.

Sections show that the pigment granules are dispersed throughout the longitudinal muscle layer (fig. 2), as Michaelsen has described; the granules are intensely black in the innermost portion below the cœlomic epithelium, and become paler as the circular layer of muscles is approached.

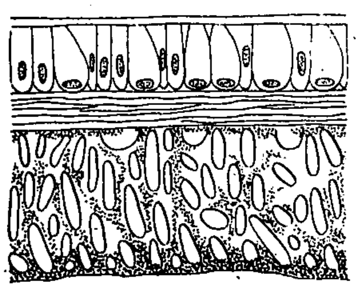


Fig. 2.

Marionina werthi. A portion of a transverse section of the body-wall (camera, × 500). The pigment granules, contained in the cells within the longitudinal muscle-coat, are almost black just within the cœlomic epithelium, but get paler as they approach the circular coat.

The chætæ are more numerous in the bundles than in the type, for Michaelsen found 7–10 in the ventral bundles of the anterior and middle region, and 5 or 6 in the lateral bundles. I find, however, as many as 10–13 ventrally, and usually the higher number in the preclitellar segments, and 8–10 in the postclitellar segments occasionally only 7.

In the lateral bundles anteriorly there are 8–11 chætæ, and further back 7 in a bundle.

The specimen from which these numbers were obtained measures 9 mm. in length and contains 40 segments.

The inequality in length of the chætæ, their sigmoid form, and the fan-shaped arrangement are as Michaelsen has described. In each bundle the chætæ form a series of increasing length, the shortest in the ventral bundle being at the ventral end of the series, and in the lateral bundle at the dorsal end of the series.

In one other point my specimens differ from Michaelsen's account, and were it not that the pigmentation is so unusual I should be inclined to make a new species

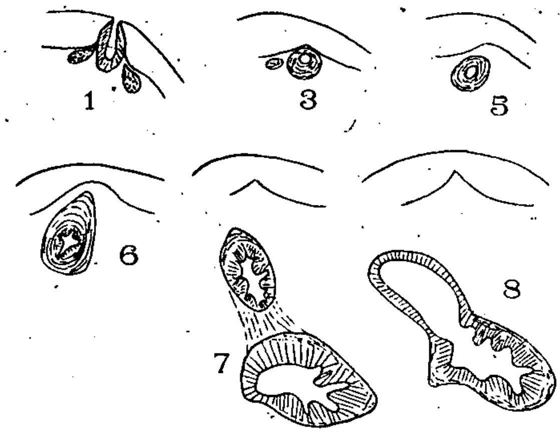


Fig. 3.

Marionina werthi. A series of camera outline of the spermatheca (x 140). The numbers below the figures indicate the number of sections in the series, the last four being consecutive sections. The first sketch shows the pore, the last the opening into the œsophagus. The organ is U-shaped, as is indicated by the relative position of the notch in the body wall. The muscular duct is distinct.

for it. He states, in regard to the spermatheca, that it exhibits no sharply marked duct, whereas I find a distinct muscular duct of some length (fig. 3). There are two groups of gland cells at the pore, one in front, the other behind; these open into the distal end of the duct (fig. 4).

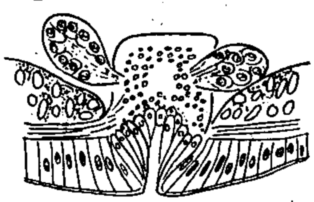


Fig. 4.

Marionina werthi. The spermathecal pore, with its two glands. The pore itself is surrounded by gland cells of a different character (x 250).

The most interesting part of the internal anatomy concerns the condition of the "penial apparatus"; that is, the penial bulb and its associated glands. Michaelsen states that the sperm duct, after coiling, opens into a minute onion-shaped bulb ("zwiebelförmig Bulbus"), entirely embedded in the body-wall, and that beside it are the prostate glands.

At the time he wrote Eisen had not drawn attention to the importance of the structure of the penial bulb in classifying the Enchytræidæ, and though Welch (1914) has recently criticised some of his conclusions as having been founded on too limited a number of species, yet he admits (1920) that the importance of the structure remains. The apparatus is very different from that met with in *M. antipodum* and other species. There is, so far as I can make out from my sections, no "bulb" in the sense in which the term is used in *Lumbricillus*, &c. The sperm duct passes nearly vertically into the body wall, between groups of gland cells constituting the prostate gland; it runs down on the mesial side of one of these groups, to perforate the body wall simply; there is neither glandular investment nor muscular covering (fig. 5).

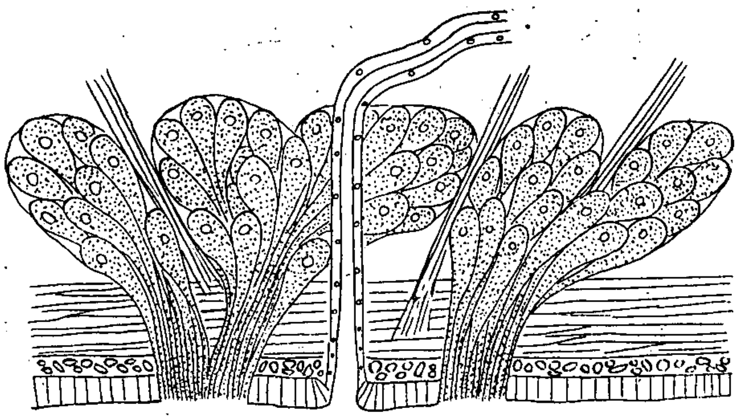


Fig. 5.

Marionina werthi. Schematic view of the penial apparatus (x 250, approx.) compiled from camera sketches of a series of longitudinal sections. The sperm-duct passes directly to the exterior, and the prostate glands open independently of the sperm pore.

The prostate glands, some in front of, and others behind the sperm pore, rise up inside the body-wall to the level of the intestine and are separated from the body-cavity by a sheet of obliquely vertical muscles fibres; a few fibres also pass between the groups of gland cells. The glands open through the body-wall independently of the duct.

In short, the penial apparatus recalls that defined by Eisen as being characteristic of the genus *Enchytræus*, though it has not this simple structure in *E. albidus*.

Stephenson (1911) has pointed out that the distinction between the genera *Enchytræus* and *Lumbricillus* is not so rigid as was formerly supposed; and Welch (1914) states that in regard to the penial apparatus the genus *Enchytræus* presents every grade between that regarded as typical of the genus and that regarded as typical of the genera *Lumbricillus* and *Marionina*.

That the latter genera are very closely alike is evident from the remarks made by Michaelsen with respect to the present species, when he states (p. 15) that he was at first in doubt as to whether the species should be placed in *Marionina* or in *Lumbricillus*, but that the structure of the male apparatus determined him. At the same time it is interesting to note the resemblances of the species to the genus *Mesenchytræus*, from which it is distinct enough in regard to this apparatus.

Locality.—

Macquarie Island, high-water mark.

Distribution.—Kerguelen.

Family MEGASCOLECIDÆ.

MICROSCOLEX *Rosa, sensu lato Michaelsen.*

MICROSCOLEX (NOTIODRILUS) MACQUARIENSIS *Beddard.*

Acanthodrilus macquariensis Beddard (1896), p. 208.

Notiodrilus macquariensis Michaelsen (1900), p. 130.

Acanthodrilus macquarensis Benham (1901), p. 132, pl. ii.

Notiodrilus macquarensis Benham (1903), p. 276, pl. xxvi, figs. 3, 11.

Microscolex macquariensis Michaelson (1907), p. 143.

Notiodrilus macquariensis Benham (1909), p. 275.

This, the only "earthworm" that has been found on Macquarie Island, was obtained by Mr. Hamilton at two localities—

(*a*) Eight individuals were found "under stones and decaying vegetation near the Victoria penguin rookery, North End (25, vi, 13)."

(*b*) Three individuals "from crevices in rocky cliff, 150 feet above sea-level, and near the sea in the neighbourhood of the Nuggets."

The worms are described as "flesh-pink" and as "red to pink" respectively; most of them are mature, and the largest measures about 65 mm. in length; as it is more or less curved, one can only give the approximate length. This specimen is larger than the average, which is about 55 mm.

The species differs from *N. aucklandicus** Benham and from *N. campbellianus* Benham in colouration during life, in dimensions, in the character of the ornamentation of the penial chætæ, in the chætal formula, as well as in various internal features, as I have noted in previous articles.

The penial chæta in the unworn condition bears triangular processes or "thorns" (figured by me in 1903), and even in the worn condition, though the thorns may have become more or less obliterated, the pattern remains; a pattern which is very different from that of the other two species in the New Zealand area, as I have already pointed out (1909, p. 274).

In addition to the pair of functional chætæ, there are three other pairs of successively smaller ones, whereas in *N. aucklandicus* I see only one pair of successional chætæ in the bundle.

* It seems unnecessary to repeat the formula "*Microscolex* (*Notiodrilus*) *macquariensis*" each time reference is made to this and allied species; so I shall for brevity speak simply of "*Notiodrilus*."

Two species, however, occurring outside this area have a somewhat similar pattern, namely, *N. crozetensis*, and *N. kerguelarum* Mich., but the shape of the penial chæta in each exhibits differences.

The spermatheca possesses the usual two diverticula, each of which is somewhat enlarged at its distal end, and has a contracted neck where it springs from the spermathecal duct; the two diverticula arise from this duct at opposite sides (1903, pl. xxvi, fig. 3).

The form of the diverticulum resembles that in *N. campbellianus*, in which, however, the two arise close together, as they do in *N. aucklandicaus.*

In the fact that the diverticula spring from opposite sides of the duct, *N. macquariensis* resembles *N. crozetensis*, but in this species the diverticula are much shorter.

On the whole, then, it seems that the present species is related, on the one hand, to *N. campbellianus*, and on the other, but more closely, to *N. crozetensis.*

THE ARRIVAL OF THE OLIGOCHÆTA ON MACQUARIE ISLAND.

A question of much interest naturally presents itself: How did *Notiodrilus macquarienisis**, *Lumbricillus macquariensis*, *Marionna antipodum*, and *M. werthi* reach this island? And a further question requires an answer: Whence did they come?

Species of *Notiodrilus* are known on the neighbouring Campbell and Auckland Islands, lying to the south of New Zealand, as well as on the South island of that country; and also on certain islands in the Subantarctic ring to the west, namely, Kerguelen, Crozet, Marion, South Georgia, and Falklands, as well as on the southern portion of South America.

An important fact about several species of *Notiodrilus* was pointed out years ago by Michaelson—not only do they live on land, but they may live within reach of the salt water. Thus *N. kerguelarum* Grube, was found at the foot of a cliff along the seashore within reach of the spray from the surf at full tide; *N. georgianus* Mich. occurs in a similar situation. Hamilton found some individuals of *N. macquariensis* in a cleft in a cliff 150 feet above high-water mark, and so no doubt within reach of the spray in these stormy regions, but also on higher ground; while I found *N. aucklandicus* not only under logs in the higher country, but also in soil at a spot about a foot above the sea on the shore of Carnley Harbour; so that its habitat was no doubt salt.

* Although strictly the worm is placed in the wider genus *Microscolex*, it is less cumbrous and less confusing to use the subgeneric title only in this portion of the Report.

To such worms that may pass down from a true terrestrial habitat to the sea shore so as to be within reach of the salt water Michaelsen has applied the term Euryhaline.*

It is evident that such worms are not, as are most earth worms, injured by a certain amount of salt water, and this seems to introduce into the problem of their means of dispersal factors which are not involved in the migration of true earthworms.

It seems to me that the answer to the first question should be applicable to other terrestrial and even some littoral animals that have a geographical distribution similar to that of these worms; and it is not necessary that the method by which Macquarie Island was peopled by these animals should be the same as that by which it was peopled by the higher plants, a subject that has been fully discussed in a masterly manner by Cheeseman (1919).

There are several possible ways in which animals may have arrived here from oversea.

1. Stephenson (1921) accounts for some of the similarities between the Indian and Australian earthworm fauna by assuming the polyphyletic origin for certain genera, for which he shows good reason. But this will not apply to the case of the sub-antarctic islands, for here we have undoubtedly one and the same genus.

2. He has noted, too, the existence of natural rafts or floating islands covered with vegetation, and gives his reasons for believing that, in that region at any rate, this means of transportation is fairly frequent. But in the Subantarctic region such floating masses of terrestrial vegetation are out of the question; the lands and islands in these southern latitudes are not of such a character as to allow such rafts to be detached, while, even if they were detached, they would soon be destroyed by the storms at sea.

3. The attachment of cocoons to the feet or other parts of birds may perhaps be one means of distribution in some parts of the world, but I cannot suppose that birds would fly from, say, Kerguelen to Macquarie Island, a distance of 3,250 miles, without settling on the water, for then, of course, the mud on their feet and any cocoons attached to or embedded in it would be washed off. Moreover, one may inquire: In what manner would the cocoons become attached to the feet of the birds? We do not know whether *Notiodrilus* deposits its cocoons near the surface of the soil, or whether at some depth below the surface, as in the case of purely terrestrial earthworms, such as those in New Zealand. If the latter be the case, then it is impossible to suppose that the cocoons would ever get attached to the birds' feet. If, however, the cocoons are laid superficially in the mud near the shore, it is possible that marine birds might

* It appears that this term was originally used by Möbius for those species of animals whichcan live in water the salinity of which varies between wide limits.

carry them away in the mud. And since Macquarie Island is only about 400 miles distant from Auckland Island, and only a little further from Campbell Island, it is quite possible for a bird to fly that distance in some twelve hours, or if the wind were favourable in less time. But, again, would the bird be able to travel that distance without alighting to feed or to rest?

Are there any facts to enable us to decide that point? I do not know of them.

Now, although one may consider the possibility of a passage from either of these islands to Macquarie, yet, since *N. macquariensis* seems, as I have pointed out, to have closer relations to *N. crozetensis* than to *N. campbellianus*, we must look rather for a means of passing from some of the islands lying to the west of it.

It does not seem useful to consider the supposition that cocoons might be conveyed in the intestine of the bird, as seeds of plants may be, for it is doubtful whether they would be able to withstand the action of the digestive juices of the birds' alimentary tract.

4. A fourth means has been suggested by Michaelsen to account for the distribution of the genus from the South American continent to the various islands round the Antarctic, viz., by floating kelp carried by the West Wind Drift.

Machelsen (1911, p. 542) states that he found on the shore of South Georgia a small mass of tangled sea-weed amongst the detritus on the beach; in and on this kelp there were at least one hundred cocoons of *Lumbricillus maximus*, a species of Enchytraeid with a distribution somewhat similar to that of *Notiodrilus*.

On this fact he builds up an enticing hypothesis—that, if the cocoons of the euryhaline *Notiodrilus* were likewise deposited in such a mass of kelp, they, too, might be carried by the West Wind Drift from Kerguelen to Macquarie. It would, he states, take about 202 days—that is rather more than half a year—to travel the distance.

It is true that Michaelsen asks himself the question: whether *Notiodrilus* would survive so long a journey and so lengthy an exposure to the sea; but he believes the answer to be in the affirmative. I confess I doubt it.

No experiments have been made with the object of ascertaining this; and, as Stephenson remarks, it is difficult to plan such an experiment to test the length of time an earthworm or its cocoon can survive in water, either fresh or salt.

And although Michaelson admits that we do not know how long is occupied by the development within the cocoon of *Notiodrilus* or any other earthworm, he makes this further assumption: that if the cocoons were deposited in cold weather on Kerguelen they would reach Macquarie in the warmer months of the year; when being landed, the young worms would hatch out and start a new colony in the new habitat.

I think that Michaelsen would agree with me that this is mere speculation, although a very interesting one, but with very few facts to support it.

He does not state definitely that the eggs or young of *Lumbricillus* that he found in the cocoons were still living when he discovered them. He gives no evidence that this mass of seaweed had come from any distance; and it may be that it had been torn off the rocks on the neighbouring part of South Georgia coast, and had not been in the sea for any length of time.

Again, no evidence is afforded that the cocoons were deposited in the kelp, before that weed had been torn off the rock, wherever that took place. According to his own account, this Enchytræid lives at South Georgia amongst the detritus on the seashore, under stones and logs, and lays its cocoons there amongst.

It seems to me quite possible that the tangle of weed may have been lying on the shore for some days before he found it—I do not find any statement that forbids that suggestion—and that the cocoons had been deposited thereon after it had arrived on the shore.

Unfortunately, he does not give a botanical name to this particular mass of seaweed; if it is anything like the kelp that grows round the shores of the New Zealand islands, *e.g.*, *Macrocystis*, or *D'Urvillaea*, &c., which grow just below low-water mark, under water, therefore, and the cocoons were laid therein before the kelp was torn away from its attachment to the submerged rocks, it would of course mean that the worms actually live in the sea or at least have entered the sea in order to lay their cocoons.

We do not know this, but it seems highly improbable. Moreover, we do not know where *Notiodrilus* lays its cocoons, whether in the soil or in mud above high-water, or amongst algæ.

After considering all these matters that are "unknown," it seems to me that Michaelsen's hypothesis—that the cocoons of this earthworm may be transported over the sea amongst floating algæ for immense distances and during a great period of time—is not supported by his discovery of the cocoons of the Enchytræid amongst the mass of kelp on shore.

As to the period of time occupied by development, an examination of the literature dealing with European earthworms—either the memoirs of the earlier naturalists, such as D'Udekem and Hoffmeister; of the embryologists, like Kleinenberg, Kowalevsky, Vejdovsky, and Wilson, or any modern text book—affords but little satisfactory information as to the period lived within the cocoon, and rather divergent statements as to the season of the year at which the cocoons are laid. No doubt temperature and climate have something to do with this. Some authors give the summer months, some the winter months; others state that cocoons are laid all the year round, though more actively in summer or spring.

The only species from the Southern hemisphere that has, so far as I know, been studied in this respect is the New Zealand *Octochœtus multiporus*, of which Beddard (1892) states that the cocoons were gathered in New Zealand in June (that is midwinter) and reached him in London in August (*i.e.*, late summer), and that during the period of seven weeks occupied by transit some worms had hatched out. It is not certain how long such cocoons had been laid before being gathered, nor how much less than seven weeks were occupied in developing.

As to the period occupied by worms in the Northern hemisphere, I can find only four definite statements, but the mean is between three and four weeks.

I append a tabular summary of the result of this search into the literature. I have used the species' names adopted by Michaelsen (1900).

TIME OF DEPOSITION OF COCOON AND PERIOD OF DEVELOPMENT THEREIN.*

Name of species (Michaelsen).	Author's name of species.	Author.	Cocoon laying.	Period of development.
Helodrilus caliginosus...	*L. communis* ...	Wilson (1889) ...	Most active in spring and summer.	...
H.c. cyaneus	*L. communis*, var. *cyaneus*.	Hoffmeister (1845) ...	Summer and autumn	Usually three weeks.
H.c. trapezoides ...	*L. trapezoides* ...	Kleinenberg (1878)...	Mid-October to mid-June.	...
H.c. trapezoides ...	*L. trapezoides* ...	Vejdovsky (1888–92)	Summer	...
H. longus	*L. terrestris*. ...	Wilson (1889) ...	Most active in spring and summer.	...
H. longus	*L. agricola* ...	Kowalevsky (1871)...	Winter (Jan.–Feb.) ...	...
Eisenia fœtida ...	*L. fœtidus* ...	Wilson (1889) ...	Throughout the year: most active in spring and summer.	2–3 weeks in lab. culture.
Criodrilus lacuum ...	*C. lacuum* ...	Collin (1888) ...	June–July	...
Criodrilus lacuum ...	*C. lacuum* ...	Oerley (1887) ...	May, June, July ...	4–5 weeks.
C. lacuum	*C. lacuum* ...	Rosa (1887)	May–June	...
Octochœtus multiporus...	*Acanthodrilus multiporus*.	Beddard (1892) ...	Winter	Less than 7 weeks.
Enchytræus albidus ...	*E. mobii* ...	Michaelsen (1886) ...	May	...

THE WIDER PROBLEM.

Whatever method of dispersal has to be assumed to account for the present distribution of these euryhaline Oligochæta should also account for the somewhat similar facts of distribution met with in various other groups of invertebrate animals.

Chilton (1909, p. 797), in the "Report on the Subantarctic Islands of New Zealand," has given a useful summary of the faunal resemblances that exist between these islands and other Subantarctic islands and lands to the west. Each of the contributors has discussed the distribution of the members of the group in which he was concerned, and from some of these I make a few extracts.

* Bahl (1922, Q.J.M.Sci., vol. lxvi, p. 56) states that the Indian worm, *Pheretima posthuma*, lays its cocoons in abundance during spring and summer (March to June), but very rarely in July and August. The period of development in *P. rodricensis* lasts not more than eight weeks.

Of the terrestrial fauna of Macquarie Island, two slugs have been met with; *Athoracophorus martensi* Suter is very common on the Auckland Islands, and *A. huttoni* Suter occurs also on the Snares Island.

Now this genus is a New Zealand one, so that the species must have been carried in some manner westward, as Cheeseman has found to be the case with some of the Macquarie Island plants.

Can the eggs of these slugs withstand immersion in salt water? Can the animal itself survive in the sea? Is there any current that would convey egg or animal from either island to the west? Could the eggs be carried by birds, either attached to feet or feathers?

Hogg, in describing the Spiders (1909, p. 156), states that the two genera represented on the Macquarie Island, *Myro* and *Rubrius*, are preponderatingly Antarctic. *Myro hamiltoni* was at that time the only spider known from the island, while *Myro kerguelenensis* Cambridge was the only spider obtained from Kerguelen. A third species of the genus occurs at the Cape of Good Hope, while two others live on the Snares, south of New Zealand.

Rainbow (1917) records that *Myro hamiltoni* was found on the hills as well as on the plant, *Cotula plumosa*, which grows on the seashore. Another spider obtained on the island during the Mawson expedition was a single specimen of a small species, *Mynoglenes marrineri* Hogg, measuring only 8 mm. in length. It was originally recorded from under stones on the seashore on Campbell Island (as well as on Enderby Island). The specimen met with on Macquarie Island was found by Mr. Hamilton "on his person" when in the neighbourhood of the sealers' huts.

Another peculiar and minute Arachnid occurring here is *Pœcilphysis kerguelenensis* Cambridge, hitherto only known from that distant island. It is a representative of a separate Order of Arachnida. It was found to be "generally distributed over Macquarie Island," though nothing is said about its living on the seashore by either author.

In regard to the Spiders, Hogg (1909, p. 155) writes: "The supposition of an ancient landlink between South America, Australia, and Southern Africa is more or less of a necessity in order to account for the present distribution of creatures, which it is difficult to believe could have reached their respective habitats by any other means."

Tillyard (1920, p. 10), in his Report on the Insects of this Island, mentions, amongst the lowly Collembola that *Entomobrya mawsoni* Tillyard, which was found under stones at the Penguin Rookery, is closely allied to a species on Tierra del Fuego. He also establishes a new species, *Arrhopalites davidi*, for an insect of which no other species occurs in the Antarctic; but species of the allied genus *Sminthurinus* live at the Crozets, and the genus *Sminthurus* occurs on Kerguelen and Tierra del Fuego.

Leaving, now, the Macquarie Island, the terrestrial fauna, of which is scanty and but little known, we may pass on to consider some examples of the fauna of the other Subantarctic islands near New Zealand.

Amongst the Coleoptera, Broun (1909, p. 78) states that the apterous genus "*Loxomerus*, with five species, is a purely Antarctic form, having *Migadops* from Tierra del Fuego and the Falkland Islands as its nearest congener." It may be noted that the species described from the Auckland and Campbell Islands were found on the seashore. If it be possible that *Notiodrilus* was carried hither by the West Wind Drift, *Loxomerus* may have been conveyed in the same manner. But I cannot imagine that these delicate beetles could withstand immersion in the sea, either as egg, grub, or imago for half a year. How could the grub or imago feed during its transportation ?

Of the Diptera, Lamb writes (1909, p. 130) ; "The new genus *Zalucodes*, formed for a wingless limnobiid from the Auckland Islands, seems to come very close to *Zalusa* from the Falkland Islands."

Carpenter (1909, p. 378), in his account of the Collembola, establishes a new species, *Triacanthella alba*, for an insect which occurs on Campbell Island at high-water mark. The genus contains two other species from Tierra del Fuego; while the genus *Triacanthurus*, from Patagonia, "is probably not distinct from it generically."

Chilton, in discussing the Crustacea (1909, p. 602), says: "These terrestrial species, like the fresh-water ones, also show a connection with South America, Falkland Islands and other Subantarctic localities. One species, *Trichoniscus magellanicus* Dana, found in both Auckland and Campbell Islands, is, I think, identical with one found in Tierra del Fuego and Falkland Islands, and is very closely related to *T. verrucosus*, which was recently described by Budde-Lund from the Crozets."

These are "true terrestrial forms, and as the young are hatched out in a pouch below the body of the female, it does not appear likely that they could readily be carried across wide stretches of sea" (p. 799).

On p. 602, he writes : "Another species, *Deto aucklandiæ* Thomson, which occurs on or near the seashore, belongs to a genus of similar distribution, for species are known from New Zealand and the neighbouring islands, from South America, Cape Colony, St. Paul (in the Indian Ocean) and Australia; and the genus is not known from any other locality."

Amongst fresh-water Crustacea we may note *Hyale hirtipalma* Dana, which is found throughout New Zealand and adjacent islands, on the Macquarie Island, and also in South America; and "there can be no doubt that the species described from Kerguelen and South Georgia also belong to this species, and it is widely distributed in the Subantarctic seas" (p. 643).

Idotea lacustris Thomson " is a species widely distributed on Subantarctic shores, and is to be found chiefly in brackish water, but has in more than one place ascended fresh-water streams (as in Campbell Island and at Dunedin), and sometimes to a considerable height." (p. 660).

Littoral Species.

In this connection we may also glance at some of the animals occurring in the Littoral Zone, which would require a coastline for their dissemination, for they are not known from deep water, and even if some of them have pelagic larvæ, it is doubtful, as I will show later, how long these can live and how far they can be carried by currents or winds.

Among littoral Echinoderms I have noted (1909, p. 295) some distributions that are similar to those just given for terrestrial species. *Asterina fimbriata* Perrier, which occurs on the Auckland Island shores, at Campbell Island and on the Snares, has been recorded from McMurdo Bay, and from the Cape of Good Hope; and, if the synonyms proposed by various authors be accepted, it is also met with on the Crozets, Marion Island, Kerguelen, Tristan d'Acunha, Falkland Islands and the Magellan Strait.

Two Holothurians, *Cucumaria leonina* Semper, and *C. brevidentis* Hutton, taken at the Aucklands also belong to the South American fauna. The former occurs at Cape Horn and at the Falkland Islands, as well as on the coast of the mainland. The latter species occurs in New Zealand and at Juan Fernandez.

It is possible, of course, that these Echinoderms, being possessed of suckers, may attach themselves to floating kelp and thus be transported by the West Wind Drift from South America to their more easterly habitats. But would the kelp float all that time and for all that distance ? Would not the animals be likely to be eaten by fishes during this long transport ?

It is more probable, it seems to me, that they have been distributed by way of a former coastline. That their larvæ are responsible for this extended distribution seems unlikely from the facts noted by me in connection with the Echinoderm fauna of the Kermadec Islands. This fauna is quite different from that of New Zealand, being Indo-Pacific in character. Now it is known that a current sets from New Zealand towards these islands, at any rate that a wind blows more or less constantly in this direction, for logs of the Kauri, which can have come from nowhere else than New Zealand, have been found cast ashore on the Kermadec Islands. Surely, if the larvæ of the New Zealand Echindoerms lived long enough they would also be carried over this comparatively short distance of sea separating New Zealand from these islands. If they do not do so, how much less is it likely that larvæ live sufficiently long to survive a transfer from one Antarctic Island to another over much greater distances ?

In my Report on the Polychæta (1909, p. 237) I wrote: "Most, if not all, of the Polychætes give origin to a pelagic larvæ, which will be affected by the West Wind Drift and so spread round the Antarctic Seas; yet certain resting places would be necessary, one would imagine, for the completion of their development. How long (I asked) can a pelagic larva live before it undergoes metamorphosis? Can it withstand for any period of time the buffeting of the tempestuous southern seas or escape for long the attacks of fishes or other enemies during its floating existence on the surface of the sea? When answers to these questions are available, we shall be better able to utilise these Annelids in any discussions on the previous existence of an Antarctic continent."

Thomson, in his report on the Brachiopoda in this series (1918, p. 38), refers to Blochmann's views as to the distribution of members of that group by means of their larvæ: "The power of distribution of Brachiopods is very limited, and the larvæ are unable to cross the ocean from one coast to another. For most species a gradual migration across the ocean bottom is impossible. Even in the case of the pelagic mouth-bearing larvæ it appears that they do not swim far from the parent, for the genera *Lingula* and *Discina* are not widely distributed."

In my report on the Polychæta of the present expedition (1921), I have enumerated those that were collected on the shores of Macquarie Island, and have given their further distribution (p. 19): "The species are typically Subantarctic in character, and have been recorded either from the southern outliers of New Zealand or from Kerguelen and Falkland Islands. They were all collected in rock pools, or under stones or rocks along the shore."

Some of them are more or less circumpolar, but they have not been found to occur at any great depths. It does not appear that they can have travelled across the sea floor from South America to Macquarie, or *vice versâ*. They, too, seem to point to migration by way of a coastline.

Land Bridges.

(5) The question, then, as to the means by which the Oligochæta arrived at Macquarie Island is part of a much larger question—their distribution on other Subantarctic islands.

If the four previously-considered possibilities of migration or dispersal, viz., polyphyly, floating rafts, carriage by birds, and by drifting seaweeds, if these cannot, so far as one can see, account for the similar distribution of all the various members of different groups of terrestrial animals, though one or other of these methods may be applicable to some of them, one is led to invoke a fifth method—that of land bridges.

The fact that species of *Notiodrilus* have been found on the widely-scattered islands above enumerated stretching round the Antarctic has naturally attracted the attention of lumbricologists; and not of these only, but also that of other naturalists who interested themselves in the geographical relations of New Zealand and her outlying islands.

It was, I believe, Beddard, who, in 1891 (p. 285), first put forward the view that these various islands and southern lands had been connected by way of an extended Antarctic continent, founding his theory mainly upon the presence of this genus on these far-flung islands. He discussed the subject later in 1893, and again in 1895 (*a* and *b*). Meanwhile Forbes (1893) had published a similar theory to account for the distribution of certain related flightless birds on the Chatham Islands and on the Mascarene Islands, in the Indian Ocean; and he brought forward many examples of other terrestrial animals in support of a tremendously extended land mass joining up the Antarctic continent with New Zealand and Eastern Australia on the one hand, and with Lemuria on the other.

In 1902, in my Address to the Biology Section of the A.A.A.S., at Hobart, and also in my Report on the Oligochæta of the Subantarctic Islands of New Zealand (1909), I accepted Beddard's views and elaborated them. I did not go so far as Forbes had done, and, indeed, argued along different lines, and arrived at a different result, so far as the direction and extent of the land bridges were concerned.

On the other hand, Michaelsen has repeatedly attacked this " Continental Hypothesis " at some length on various occasions (1902, 1905, and 1911), and has done me the honor of quoting somewhat largely from my memoirs, and has strongly criticised many of my arguments.

It is not that he is averse to the idea of previous " land bridges," by which earthworms may have travelled from one part of the world to another; for as Stephenson has recently pointed out (1921, p. 137), he has postulated several such ancient land connections: The Transatlantic bridge, joining the West Indies and Central America to Africa; another linking Africa to India; as well as shorter ones between India and Australia and between India and New Zealand, the last to account for the presence in both lands of the genus *Octochætus*. But he will not accept the necessity for such a land connection in the Antarctic; for he would explain the faunal similarity of these Subantarctic islands by assuming a carriage over-sea, as I have mentioned above.

In spite, however, of the arguments brought forward by him and also by Cheeseman (for the peopling of Macquarie Island by the vascular plants) I am still unable to imagine by what other means these islands have become peopled by these various invertebrates than by some modification of the continental theory, or rather by way of land bridges connecting these islands with the Antarctic continental mass and with the southern continents.

The details of the former views of Beddard and myself must, no doubt, be given up as too little attention was paid to the depths of the sea round and between some of these islands, of which we now have much more information than at the time we wrote. But I proceed to outline a modification of that earlier opinion.

It is admitted by Cheeseman that the land round the Antarctic pole was formerly of greater extent than at present. Whether that land is now a continent or an archipelago we are still in doubt, for we do not know whether some areas on the margin, like Enderly Land, Coat's Land, etc., are or are not portions of the mainland. This greater extension of the Antarctic mass lasted, according to him, probably till the early Cainozoic epoch.

The soundings between the South Shetlands and South Georgia and between the latter and Tierra del Fuego show that the water is less than 1,000 fathoms and much less in the immediate neighbourhood of these lands. It is suggested that at this early period the sea bottom was above the water, and Cheeseman (1919, p. 53) admits that "along this line in Oligocene, or thereabouts, Antarctica and Fuegia were either connected by a land bridge, which seems most probable, or by a chain of closely-placed islands of considerable size."

At the other end of the Antarctic land it is also admitted that there was probably an extension northwards towards the plateau upon which New Zealand and its southern islands lie, which plateau itself was then dry land, forming Greater New Zealand; and Cheeseman writes (p. 53): "If at the same time there was a northward extension of Antarctica and a similar southern prolongation of the New Zealand area, the distance which at present separates Antarctica from the New Zealand Subantarctic islands might be reduced to a space considerably smaller than what is known to have been crossed by plants and animals in other parts of the world."

But he is strongly of opinion that at no time during the Cainozoic was the deep water (1,000–2,000 fathoms) between Greater New Zealand and Antarctica completely bridged by land.

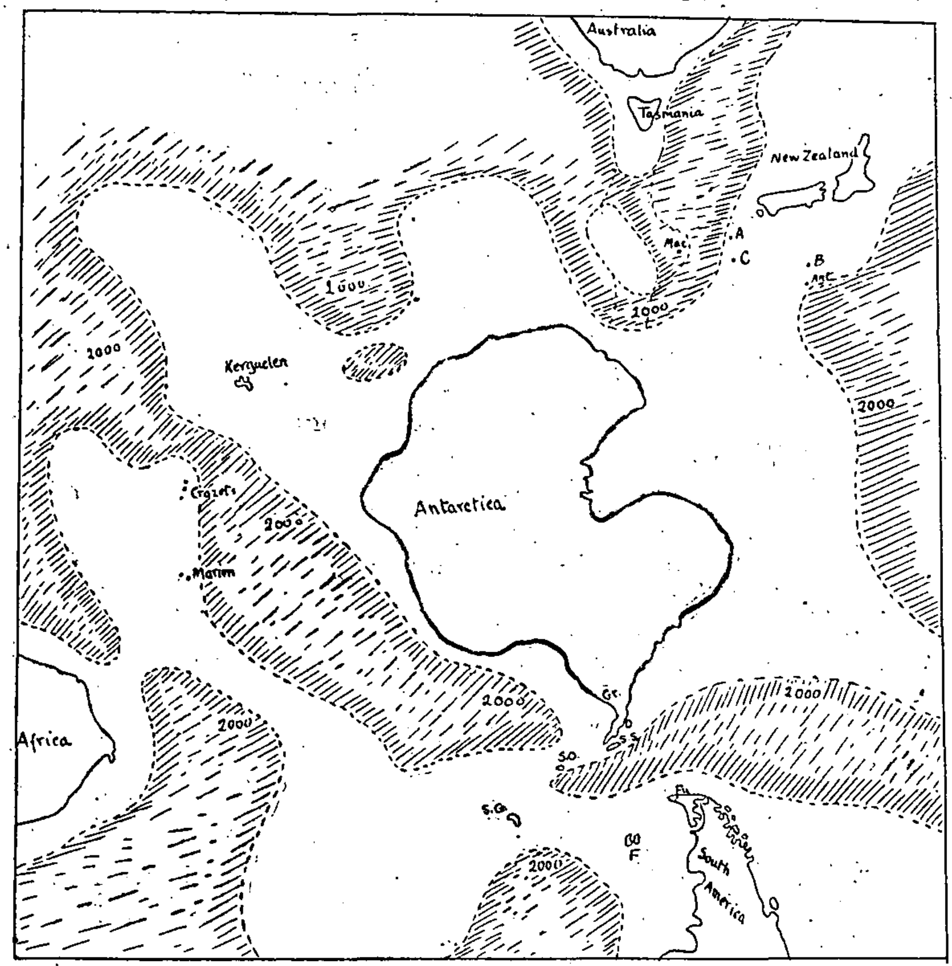
At any rate a "connection," though not necessarily a continuous land bridge, may have existed as late as the earliest Cainozoic epoch between Fuegia and New Zealand.

Turning now to the scattered islands between South Georgia and the islands south of New Zealand. Eastwards of South Georgia is a tract of ocean of a depth ranging from 1,500–2,000 fathoms extending past Bouvet Island to the plateau on which are set Marion and Prince Edward Islands, and further eastwards, the Crozet Islands; this plateau has above it a depth of water not exceeding 1,000 fathoms, and much less in some parts.

It may even be the case also—for our knowledge of all this region is not very exhaustive—that the depth of the intervening sea is not uniformly so great as 1,500 fathoms, and that there may be a submerged ridge linking Bouvet Island to this plateau on the east and to South Georgia on the west, so that an elevation at some earlier date would have placed these islands in continuity.

Are we justified by any geological facts in supposing that this could have been raised up to form a long narrow arm of land so as to link the Crozets with Fuegia?

MAP SHOWING THE GENERAL DIRECTION OF THE ASSUMED LAND BRIDGES BELOW 2,000 FATHOMS, THOUGH NOT NECESSARILY THEIR EXTENT.
(Compiled from J. A. Thomson's Map.)



NOTE.—Land in left, white; Sea is shaded.

A.—Auckland Island.
Ant.—Antipodes Island.
C.—Campbell Island.
F.—Falkland Islands.
Fu.—Tierra del Fuego.
Gr.—Graham's Land.
Mac.—Macquarie Island.
S.G.—South Georgia.
S.O.—South Orkneys.
S.S.—South Shetland Is.

Judging from the remarks by Thomson as to the Brachiopoda of Marion Island and South Africa, it appears that he does contemplate the possibility of land connection between them in Cainozoic times at a date earlier than the Miocene (p. 48).

As the depths between these two places is shown on the map to be approximately the same as that separating Crozets and Bouvet and South Georgia, what reason is there for forbidding us to assume such a land bridge here also?

There remains Kerguelen, which is likewise separated from the Antarctic by a depth of 1,500-2,000 fathoms; and if the former bridge be conceded, then an arm from the continent extending in a northerly direction may have included this island also.

Thomson (p. 57) states that Kerguelen appears to have been separated from all other lands since the Miocene. Does this not imply that it may have been linked to the Antarctic continent or other land area at an earlier date in the Cainozoic?

We come now to Macquarie Island. When we remember that it is a volcanic mountain rising from a depth of 2,000 fathoms, we meet with difficulties in supposing that it could have been connected, at any rate during the Cainozoic epoch, with any neighbouring land, such as the New Zealand plateau. One school of geologists, represented by Mathews, holds that such a depth at once negatives such an assumption. But another school, exemplified by Schuchert* (1916), does not seem to be deterred by even such a depth as this. In discussing (p. 103) the ancient Gondwana Land of the Mesozoic epoch, he states that it is a fallacy to assume that the now sunken portions of the Eastern Gondwana land were raised out of the depths of the Indian Ocean after it had become very deep. The ocean began to deepen during the sinking of the continent in early Mesozoic times.

I gather, however, that many geologists, even of this school, would limit these large movements to the Mesozoic or at least to the very earliest part of the Cainozoic. However, in referring to New Zealand (p. 96) Schuchert believes that there was continuous subsidence from later Eocene into Pliocene times, when as much as 9,000 feet (*i.e.*, 1,500 fathoms) of marine sediment had been laid down along its eastern sinking margin. Later, in Pliocene, there was a marked vertical uplift, probably as much as 4,500 feet and possibly 6,000 feet. "In the Pliocene all of eastern Australia was vertically elevated and blockfaulted between 1,500 and 7,300 feet above the level of the sea. In compensation for this elevation, the Tasman Sea sank, there being now great depths close to the continent, which in one place goes down to 18,500 feet" (that is, more than 3,000 fathoms).

I gather, therefore, that, at any rate, some geologists acknowledge that during the Cainozoic epoch a considerable amount of up and down movement has taken place; and it seems not impossible that Macquarie Island may have shared in them to the extent that it became connected, and later lost this connection, with some or other of its neighbours. Indeed, Thomson (1918) when discussing the origin and distribution of the Brachiopoda in these circumpolar seas, writes (p. 55): "The absence of (*Magellania* s.str.) in New Zealand and its presence in the Macquarie Islands seems to point to a former land bridge connecting Tasmania with Antarctica through the Macquarie Islands."

Now, since these two islands are at present separated by a depth of seas as great as that which separates Macquarie Island from Antarctica or from Auckland Island, may we not assume, from the distribution of other groups of animals, that such a land bridge also existed here? If geology allows the former bridge, will it deny the latter?

On p. 59, Thomson states—"By a consideration of the Brachiopod fauna then it seems necessary to make the following assumptions: By connection is implied not

*I have to thank my colleague, Dr. W. N. Benson, for drawing my attention to this and other papers on the subject.

necessarily land connections but at least relatively shallow submarine ridges or chains of islands at no great distance from one another." Such chains of islands would, I believe, suffice for our immediate purpose; for then birds might distribute the cocoons of these Oligochætes, while the pelagic larvæ of some of the littoral animals might be able to survive for so short a time necessary to pass across the intervening seas.

Nevertheless, if the depths of the seas would allow the uprising of the floor to form such chains of islands, it is within the limits of possibility that it would rise a little further and join those islands together, temporarily, to form a land bridge. For the Brachiopods, such a bridge is not needed; all that is demanded by that group is shallow water, but for the insects, spiders, and probably the Oligochætes, a land bridge does seem necessary.

Further on, Thomson writes—"Connection between Australia, the New Zealand region, Macquarie Island, Kerguelen Island, the Antarctic, and South America, must have occurred in the early Tertiary, but New Zealand was not connected at the same time with both Australia and the Antarctic. The connections between New Zealand, the Antarctic and South America may have existed from an earlier date."

And again,—"The circum-Pacific southern connections were all broken, much as at present, by the Miocene, and since that date there have been no renewed connections between the southern continents and island districts, except possibly between South America and the Antarctic and adjacent islands."

Thomson is a geologist, and yet is impressed by the biological problem of distribution, and fearlessly asserts that the kind of connection that Beddard and I have previously assumed must have existed to account for the distribution of the shallow-water Brachiopods.

The Date of the Origin of Oligochæta.

The date of the origin of the group of Oligochæta necessarily has a bearing on their mode of distribution; since if there has been a larger extent of land in these southern latitudes in the late Mesozoic and early Cainozoic, an opportunity for migration would be available, which would not be the case if the group had not evolved, as Stephenson suggests (1921, p. 133) till late Tertiary times.

He regards the Oligochæta as a very modern group, relying on the fact that various genera of earthworms to-day are linked together by intermediate genera, so that the phylogeny can be readily traced out in such a family as the Megascolecidæ.

But are not birds in much the same position? Are not genera and families linked together so much that the classification of the class is difficult? Yet we know they are not a modern group.

The common association of earthworms with Dicotyledonous plants suggested to me a few years back that possibly they are a recent group. But the examination of the contents of the intestine of some of our native species which live in forests showed that at the present day they do not feed exclusively on the leaves or débris of these higher vascular plants, for I found the sporangia of ferns, as well as the characteristic tracheids of their vascular bundles, quite abundantly in their intestines. I was led, therefore, to think that even before dicotyledons existed there would have been sufficient "mould" formed from rotting ferns, &c., to provide food for the worms. And I should put their origin somewhere in the early Mesozoic epoch.

It is true that *Notiodrilus* is to-day regarded as the most archaic amongst the Megascolecidæ, from which a number of other genera can apparently be derived, as both Michaelsen and Stephenson have shown. But it seems probable that this genus was preceded in time by some still more primitive form, and that until dicotyledonous plants became abundant and varied, as they did in later Mesozoic and early Cainozoic times, there was less variation amongst these worms, since there would be less variation in habitats. When the variation in the plants became greater and new plant associations became established, the evolution of the earthworms would become more rapid than in the Mesozoic; hence the evolution of new genera, which would form a series, linked on to *Notiodrilus*. No doubt in that respect the group is new, in that there is now, and has been since the commencement of the Cainozoic, far more opportunity for the evolution of new types.

Down in these southern latitudes, where conditions of life and habitat are to-day similar all round the Antarctic, we find but few different genera. Indeed, there is, as Michaelsen has shown, a merging of such unlike types as *Microscolex* with the more primitive *Notiodrilus*. As we pass northwards, along the continents, where new and varied plant associations and a variety of habitats occur, we meet with increasingly differentiated types.

Glaciation of the Subantarctic Lands.

Even if it be granted that at some period in the very early Cainozoic epoch there was a greater extension of land surface, allowing for the migration of these earthworms and of sundry other invertebrate animals, we have evidence that each of these islands concerned was covered with an ice-sheet during part of that period, which would presumably have destroyed all or almost all of the original plants, allowing only a few grasses to survive (Cheeseman). It would naturally have destroyed the animals.

An important question now arises: Did this ice-sheet exist over these lands before or after the disruption of the presumed land bridges?

We know from the discovery of fossil leaves at Graham's Land that at or immediately before the beginning of the Cainozoic Antarctica enjoyed a genial climate, and so doubtless did the assumed northern extensions. The ice-sheet appears to have gradually extended further northward, wiped out the primitive fauna and flora, but later retreated, so that the land now represented by the islands became fit for repeopling.

If the ice-sheet disappeared before the actual disruption of the land connections, before they were separated into islands, then a shore-line would have existed, along which both littoral and terrestrial animals would have been able to travel. The spiders and insects of the Macquarie Island appear to be of South American origin and to have migrated eastwards to their present habitat, as also did most of the plants. Then, after the repeopling of this land surface the various connecting land bridges slowly sank into the sea, leaving the islands much as we know them to-day. Thomson, as we have seen, would place this disruption not later than the Miocene. These islands would thus have received representative genera, which would have developed into distinct species owing to isolation.

That these events took place not so very long ago geologically is indicated by the close affinity or even identity of species occuring in these widely-separated areas.

If, therefore, the ice-sheet melted while the land bridges were still intact, we can account for the existence of these forms on Macquarie and other islands.

Perhaps it is worth noting in this relation that we know that some Oligochætes can withstand freezing and can live embedded in ice, as has been described by Moore (1899) in his account of a "Snow-inhabiting Enchytraeid," which is widely distributed over the surface of the snow-field of the glacier of Malaspina on Mount Elias, in Alaska.

He refers to the records of other species of worms, not only of those belonging to this family, but also of earthworms, being found frozen and recovering their vitality on being thawed out. Since that paper was published, Piguet (1919) has described the occurrence of *Tubifex ferox* and of *Stylodrilus heringianus* in Lake Tjaura-jauratj, on the mountain of Sarek, which lies within the Arctic circle. This lake is filled with ice during the greater part of the year, usually thawing at the end of July. It is not to be supposed that these two Oligochætes would live in the ice during these months, but at any rate their cocoons with eggs must be able to survive this extremely low temperature for many months.

It is, thus, within the bounds of possibility that the eggs of some of these Subantarctic Oligochætes may have survived on these islands during the period of their glaciation, though our knowledge of the length of time for which the worms can withstand freezing and remain dormant in the ice is necessarily insufficient to permit us to state that they are able to do so. But these observations do render it possible that in earth under the ice-sheet, or near its edge, where they would get the benefit of the short summer's sun, that the eggs in the cocoons, and even perhaps the worms themselves, might be able to live for many years. For if the eggs can remain alive in such conditions as Piguet found to obtain on Mount Sarek for the greater part of the year, there seems to be no logical reason against their remaining in a dormant condition for two years, or for two hundred years, or many more.

It is naturally impossible to conduct experiments over any comparable period of time as would be required to test the above suggestion, but the few experiments made by Schmidt (1918) on "Anabiosis of Earthworms," their loss of weight on drying, their revival after some days, especially noticeable at an ice temperature, is in this connection of much interest.

An objection has naturally been put forward in regard to the assumption of a former land connection between Australia and South America, and between the latter and New Zealand, to the effect that had this connection, which is admitted to have been in existence in the late Mesozoic, continued into the Eocene, mammals would have probably entered these eastern regions. But if such eastward extensions were still in existence at the time the earliest mammals lived on South America, and the ice-sheet caught them while on the Antarctic or other portions of the land surface, the absence of all mammals from New Zealand and of placentals from Australia would receive an explanation.

SUMMARY.

We have thus a geologist, from his study of the present and past distribution of a marine group, and a zoologist, from a study of the present distribution of spiders both asserting the "necessity" for such a land connection during early Cainozoic epoch. Although one must agree with Stephenson when he says that one ought not to assume such vast changes in level of the sea bottom until one has exhausted all other possible and probable explanations of dispersal, yet I think that the problem presented by these Oligochætes, Insects, Spiders, and terrestrial Crustacea renders it difficult, if not impossible, to imagine any other method of dispersal that will explain all the facts presented by these Subantarctic islands.

Macquarie Island, then, seems to have received the ancestors of its Oligochætes from the distant islands of Kerguelen or Crozet by way of a series of land bridges connecting them indirectly but mutually with the Antarctic continent during the early Cainozoic epoch.

It is not necessary to assume that these various land connections were contemporary with one another; they may have been successive or even alternating; nor is it necessary to assume that they, or all of them, lasted for any very great length of time; there were, no doubt, periods of uprising and depression going on over this area.

The most recent, and perhaps the one that lasted longest, was doubtless the connection between South America and Graham's Land, for here the depth is comparatively shallow. But in what order the other bridges appeared and disappeared, or how long any of them remained above sea, I do not know that we have any evidence for making a guess.

Whether Macquarie Island was ever directly connected with this Antarctic land mass or archipelago is very uncertain, unless, as Dr. Thomson has suggested, it was by way of Tasmania.*

*We do not, however, know of the occurrence of *Notiodrilus* or of any of these Subantarctic Oligochæta on the shore of Tasmania; but, as a matter of fact, we know practically nothing of the Oligochæta of the island.

ADDENDUM.

In an article in "Discovery" (1922, vol. iii, p. 114), Wegener gives a brief account of his work on "The Origin of Continents and Oceans," in which he introduces what appears to be a new and revolutionary conception as to former land connections, which involves not the changes in level of the sea floor, but the gradual movement of the continents themselves. He writes—"The continents in past ages have drifted horizontally over the surface of the earth, and are still in motion at the present time." According to this "displacement" theory, Antarctica, India, Australasia, were during Palæozoic epoch in immediate contact with South Africa and with the land then representing South America. During the successive geological epochs, after the shifting apart of these continents in the region of the equator, Antarctica, Australasia, and South America still remained in continuity at the Eocene period.

Such a conception would exactly meet the requirements of the distributional facts discussed above.

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