5. Contributions to the Morphology, Classification, and Zoogeography of Indian Oligochæta. By J. STEPHEN-SON, D.Sc., F.Z.S., Lecturer in Zoology in the University of Edinburgh.

(Text-figure 1.)

CONTENTS.

I.—THE AFFINITIES AND SYSTEMATIC POSITION OF THE GENUS *EUDICHOGASTER* MCHLSN., AND SOME RELATED QUESTIONS.

The genus *Eudichogaster* was established in 1902 by Michaelsen (2) for *E. ashworthi*, then first made known, and for several other worms which had been originally described as species of *Dichogaster* (or *Benhamia*), but which were placed by Michaelsen in the Tierreich volume of 1900 in the genus *Trigaster*. The separation of these three genera is based on the presence or absence and on the position of the calciferous glands ; *Trigaster* has none, *Eudichogaster* has them in xi. and xii. (with, it may be, x. or xiii. in addition), *Dichogaster* has them in xiv., xv. and xvi., or in xv., xvi. and xvii. The diagnosis of the genus *Eudichogaster* is as follows :—

Setæ four pairs per segment. Prostatic pores two pairs on xvii. and xix., or one pair on xvii. (? or xviii.). Spermathecal pores two pairs on viii. and ix., or one pair on viii., or in groove 7/8. Two gizzards in front of the testis segments. Calciferous glands two or three pairs, in xi. and xii., or x., xi. and xii., or xi., xii. and xiii. (in one species no proper calciferous glands recognizable). Micronephridial. One or, more usually, two pairs of testes. Prostates tubular.

In the paper in which the genus was established, Michaelsen placed it in the Trigastrinæ. In 1903, however (3), he leans to the view that it is to be derived from *Octochætus*, and therefore to be included in the Octochætinæ, though he does not carry out this implication in the tables. In 1909 (4) he definitely adopts this view. In 1910 (5) he abandons it, and, deriving *Eudichogaster* from *Trigaster*, again places it in the Trigastrinæ. The object of the present communication is, by bringing forward additional evidence, to decide the question in favour of its inclusion in the Octochætinæ, by showing that it is descended from *Octochætus*, not from *Trigaster*.

The classification of the Megascolecidæ, to which both sub-families, the Octochætinæ and Trigastrinæ, belong, proceeds on phylogenetic lines; and a very considerable degree of success has been reached in the filiation, and consequently in the definition and arrangement of genera. The origin of the family, as is now generally recognized, is to be sought in the " original Acantho-driline," a form which is represented at the present day by the genus *Notiodrilus* as defined by Michaelsen in the Tierreich volume (**1**). Its essential characters (for our present purpose) are as follows : A pair of male pores on xviii., two pairs of prostates opening separately on xvii. and xix., a single œsophageal gizzard, four pairs of setæ per segment, one pair of meganephridia per segment, no calciferous glands.

The important characters of the genera which enter into the following discussion may be stated thus :—

Diplocardia, one remove from the original Acanthodriline, and the ancestor of the Trigastrinæ, differs from the original Acan-thodriline only in having two gizzards. It is found in North and Central America.

Trigaster, descended from *Diplocardia*, differs from the latter genus in being micronephridial; the posterior male organs are either of the acanthodriline type or they may have undergone the " microscolecine reduction " (disappearance of the posterior pair of prostates, and union of the male pores with the anterior prostatic openings on xvii.); there are two or three gizzards, but no calciferous glands. *Trigaster* is found in Mexico and the West Indies.

Dichogaster is similar to *Trigaster*, except that there are calciferous glands in two or three of the segments xiv.–xvii. A point to which attention has been called is that while in *Trigaster* the setal interval *cd* is greater than *ab*, in *Dichogaster* these intervals are approximately equal. *Eudichogaster* was supposed to resemble *Trigaster* in this respect, but in a few species *ab* is equal to *cd*. *Dichogaster* is endemic in tropical Africa, and probably in Central America and the West Indies, but has spread widely in the tropics and warmer temperate zones.
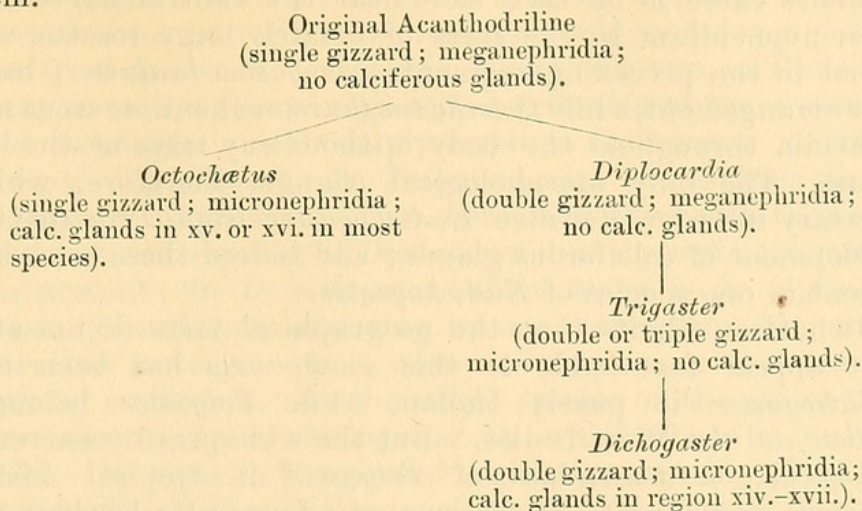
The first development, therefore, in the above line of descent (Diplocardia-Trigaster-Dichogaster), and the primary charac-teristic of the Trigastrinæ (I include *Diplocardia* in the Trigastrinæ, v. post.), is the reduplication of the gizzard.

The genus *Octochætus* belongs to a different line. It differs from the original Acanthodriline in being micronephridial, and in having a pair of calciferous glands in segment xv. or xvi. (a few species, to which more particular reference is made subse-quently, are without calciferous glands); it has the single gizzard and other characters of the ancestral form. It occurs in India and New Zealand.

The other genera of the subfamily need not be mentioned here. The first development in the Octochætinæ, and therefore their

primary characteristic, is the splitting up of the nephridial system.

Original Acanthodriline
(single gizzard ; meganephridia ;
no calciferous glands).

Octochætus
(single gizzard ; micronephridia ;
calc. glands in xv. or xvi. in most
species).

Diplocardia
(double gizzard ; meganephridia ;
no calc. glands).

Trigaster
(double or triple gizzard ;
micronephridia ; no calc. glands).

Dichogaster
(double gizzard ; micronephridia ;
calc. glands in region xiv.–xvii.).

Eudichogaster, whose position is now under discussion, has a double gizzard, is micronephridial, and has calciferous glands (except in one species) in two or more of segments x.–xiii. ; in some species the posterior male organs have undergone the microscolecine reduction. It is purely Indian in distribution.

The view, now held by Michaelsen, that *Eudichogaster* is derived from *Trigaster*, and therefore to be included in the Trigastrinæ, is based primarily on the close anatomical similarity between the two genera; the only essential difference is that calciferous glands are absent in *Trigaster* and present in *Eudichogaster*. Moreover, there is one species of *Eudichogaster* in which calciferous glands can scarcely be said to be present at all. Michaelsen, in describing *E. bengalensis* (5) says :—" a pair of lateral calciferous glands in each of segments x.–xiii., not externally demarcated." In giving additional notes on the same species (9) I have stated that " the bulgings of the œsophagus in segments x.–xiii. are thin-walled and are not at all set off from the lateral walls of the œsophagus; they are not calcareous glands any more than the similar part of the tube in, for example, *Pheretima posthuma* is a series of calcareous glands"; and in support there follows a description of the appearances seen on opening the tube. Here, then, is a form which according to strict definition is a *Trigaster*; though I imagine no one will quarrel with either Michaelsen or me for including it, on geographical grounds, in *Eudichogaster*.

Michaelsen also regards the similarity of the nephridial condition as being decisively in favour of the derivation of *Eudichogaster* from *Trigaster* rather than from *Octochætus*. The species investigated for the purpose of this comparison were *Eudichogaster ashworthi*, *Trigaster lankesteri* subsp. *calwoodi*, and *Octochætus thurstoni*. In *Eudichogaster ashworthi* there occurs in each segment a number of small loose micronephridial

tufts, each apparently with a funnel; in addition, in the hinder segments there is on each side, near the ventral nerve cord, a larger nephridium in the form of a fairly large rosette, with a funnel in the preceding segment. *Trigaster lankesteri* has the same arrangement, while *Octochætus thurstoni* has numerous micro-nephridia throughout the body, without any trace of the larger organs. The only morphological change, therefore, which is necessary in order to evolve *Eudichogaster* from *Trigaster* is the development of calciferous glands; and indeed these are scarcely present in one species of *Eudichogaster*.

Michaelsen admits that the geographical facts do not at first sight appear favourable to this view. As has been noted, *Eudichogaster* is purely Indian, while *Trigaster* belongs to Mexico and the West Indies. But the widespread occurrence of *Dichogaster*, a descendant of *Trigaster*, in tropical Africa is evidence, according to Michaelsen, of a former land-bridge across the Atlantic; and Michaelsen supposes that either (1) *Eudicho-gaster* originated from *Trigaster* in America, spread eastwards across the land-bridge to Africa, colonized Africa or parts of it, and then spread eastwards again across another land-bridge to India (it is not found in Africa at the present day because it has been extirpated there by the dominant Eudrilines and the later evolved *Dichogaster*); or (2) that *Trigaster* itself spread eastwards by the same bridges, and gave rise to *Eudichogaster* at the eastern extremity of its range, *i. e.* in India, itself later being extirpated in the middle portion of its range, *i. e.* in Africa, by the Eudrilines and its own descendant *Dichogaster*, as before.

In putting forward the view that the ancestor of *Eudichogaster* is *Octochætus* and not *Trigaster*, it may be admitted that, as Michaelsen says, *Eudichogaster* and *Trigaster* are very much alike morphologically. At the same time, I think we now possess evidence of a much closer similarity between *Eudichogaster* and *Octochætus* (or at least some species hitherto reckoned as *Octo-chætus*) than Michaelsen was aware of. The gap between the two genera is bridged almost, if not quite, as completely as that between *Eudichogaster* and *Trigaster*. The points to be discussed are the gizzards, the calciferous glands, and the nephridia.

I have described (11) in *Octochætus pallidus* a commencing doubling of the gizzard:—"The gizzard is barrel-shaped, in segment vi.; the œsophagus is distinctly strengthened in seg-ment v. also, where shining longitudinal muscular bands are seen. This seems to be the beginning of a double gizzard, such as seen in *Eudichogaster, Dichogaster* and *Trigaster*; I do not, however, suggest at present that any of these genera are derived from this species, or indeed from the genus *Octochætus* at all."

I may here call attention to the relation of the septa to the condition of duplicate gizzard. *Octochætus pallidus* is one of the rather few species of the genus which retain all the septa in the anterior part of the body (behind the level where they first

definitely begin). The presence of septa between the successive gizzards seems to be a necessity for their development as separate structures. and two gizzards probably could not develop in the majority of species of *Octochætus*, where one, two, or three septa are absent in the gizzard region; an extension of the muscularity of the œsophagus would simply result in an increase in the size of the existing gizzard. In *Trigaster*, with two or three gizzards, the septa are all present. I am not acquainted with the facts in all the numerous species of *Dichogaster*, but the septa are certainly often present; in *D. malayana*, where there is no septum 5/6, separate gizzards are, according to my observation (9), scarcely discernible in segments v. and vi.—they seem to have "run together," as it were. In the single species of the genus *Mono-gaster*—essentially a *Dichogaster* in which there is only one gizzard—the septa in the gizzard region are wanting (6) and the two gizzards of the *Dichogaster* ancestor have doubtless "run together." In those species of *Dichogaster* where septa are absent in the region of the gizzards (e. g. *D. crawi*) we may perhaps predict that the gizzards will not remain long separate, and that the condition of *Monogaster* will be arrived at. We may conclude that the duplication of the gizzard, while impossible in the majority of species of *Octochætus*, would be possible in the primitive group consisting of *O. bishambari, pachpaharensis,* and *pallidus*, and seems to be in process of accomplishment in *O. pallidus*.

Next with regard to the calciferous glands : in *Eudichogaster* these organs are in segments x.-xii. or thereabouts, in *Octochætus*, usually, in segments xv. or xvi. It would, I think, be difficult to derive *Eudichogaster* from *Octochætus* if these were constant characters of the two genera (though Michaelsen, deriving *Dicho-gaster* from *Eudichogaster* (4), sees no difficulty, apparently, in assuming a dislocation of the glands backwards; in deriving *Eudichogaster* from *Octochætus*—from the usual type of *Octochætus* that is—the dislocation would have to be forwards). But the more primitive species of the genus *Octochætus* (*O. bishambari, pachpaharensis,* and *pallidus*) have no calciferous glands ; in *Eudichogaster bengalensis*, as has been seen, they are at a very low level of development ; the morphological similarity, in this respect, between these species of *Octochætus* and *Eudichogaster* is just as close as that between *Trigaster* and *Eudichogaster*, and the derivation of the one from the other just as easy.

It will be remembered that one reason for deriving *Eudicho-gaster* from *Trigaster* rather than from *Octochætus* was the similarity of the nephridial condition in *E. ashworthi* and *T. lankesteri*, and the dissimilarity between *E. ashworthi* and *O. thurstoni*. But a wider survey of the nephridia of the latter two genera shows that not all Eudichogasters are in the same condition as *E. ashworthi*, and that not all species of *Octochætus* are like *O. thurstoni*. Of the six species of *Eudichogaster* where the descriptions are sufficiently detailed to be of use, in only one other (*E. prashadi*) is the nephridial system capable of being

described in the same way as in *E. ashworthi*; it follows there-
fore that if *E. ashworthi* is similar to *Trigaster*, the majority of
species of *Eudichogaster*, so far as known, are not. Speaking
very broadly, there is indeed some similarity between all these
six species of *Eudichogaster* and *Trigaster lankesteri*; in all, a
certain number of the micronephridia are of large size, much
larger than in *Pheretima*, for example, or *Eutyphœus*, to take two
well-known micronephridial genera. But this feature occurs also
in some species of *Octochœtus*—in exactly those three species
previously referred to; in these there are seven, three, or even
apparently only one nephridium on each side in each segment,
which make up in size what they lack in number. The majority
of species of *Eudichogaster*, in fact, approach in their nephridial
condition somewhat more closely to such forms as *Octochœtus
pallidus* and *O. pachpaharensis* than to *Trigaster lankesteri* *.

I am, however, not inclined to attach very great weight to
any argument from the nephridia. The possession of a certain
number of micronephridia of fairly large size does not necessarily
show genetic relationship : it occurs, for example, in species of
Megascolides and *Megascolex*, which belong to a different sub-
family, the Megascolecinæ. Indeed there are very diverse
conditions within these two genera themselves.

I think the above considerations show that the passage from
Octochœtus to *Eudichogaster* is just as easy morphologically as
that from *Trigaster*, and that there is no difficulty in deriving
Eudichogaster from an *Octochœtus* ancestor which had the
characters of the group *pallidus*, *pachpaharensis*, and *bishambari*.

But if the morphological evidence is equally balanced, the
geographical evidence is strongly on the side of the descent of
Eudichogaster from *Octochœtus*. *Octochœtus* is a characteristic
Indian genus, found throughout the land; *Eudichogaster* is
exclusively Indian, and is found in a broad belt across the middle

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* In *Eudichogaster ashworthi*, towards the hinder end of the body the innermost
of the transverse series of micronephridia enlarges so as to resemble a mega-
nephridium; the number of micronephridia in each segment appears to be small,—
in var. *kinneari* it is about six on each side. In *E. prashadi* much the same
occurs,—there are about five on each side, regularly arranged behind each other in
succeeding segments till towards the hinder end, where the innermost becomes
larger and the others smaller, less regular, and more numerous. In *E. barodensis*
the three most dorsally situated micronephridia on each side of each segment are
larger than the rest, while at the hinder end the innermost (most ventral) also
enlarges. In *E. bengalensis* there are two pairs of large nephridia per segment in
addition to a number of small micronephridia; towards the hinder end the inner of
the two larger nephridia becomes more conspicuous than the other. In *E. chitta-
gongensis* there are three or four nephridia on each side in each segment, arranged
behind each other in succeeding segments, the outermost in each transverse row
being the longest; near the hinder end the innermost increases in size and becomes
more conspicuous. In *E. trichochœtus* there are four longitudinal rows on each
side of the body, but here the innermost series is the smallest. In *E. parvus*,
though the nephridia are "diffuse," they are of considerable size.

In *Octochœtus pallidus* the micronephridia in the post-clitellar segments are
about seven on each side in each segment, and they increase in size from the
ventralmost to the fifth, the two most dorsal being smaller again; this difference in
size disappears towards the hinder end. In *O. pachpaharensis* there are three on
each side per segment behind the genital region, and in front even fewer.

of the country. *Trigaster* is not known outside Mexico and the West Indies. Deriving *Eudichogaster* from *Octochætus*, we need no such hypothesis as that advanced by Michaelsen—the origin of *Eudichogaster* from *Trigaster* in America, and its spread by means of land-bridges across the Atlantic and Indian Oceans (or alternatively the spread of *Trigaster* itself by the same means) as far as India. *Eudichogaster* would have arisen where we find it—in India, where its ancestor also lives.

I conclude, therefore, that *Eudichogaster* arose from *Octochætus* in India. It must therefore go into the Octochætinæ, not the Trigastrinæ.

RAMIELLA, gen. nov.

I propose now to consider the more primitive species of the genus *Octochætus* to which reference has been made in the preceding paragraphs.

In 1914 (**7**) I described a worm which I placed in the genus *Octochætus* under the name *O. bishambari*, although it differed from all species of *Octochætus* then known in having no calciferous glands, and in having only one nephridium on each side in each segment. Measured by its size, indeed, this nephridium would be a meganephridium, and the worm would not be an *Octochætus* at all, but an Acanthodriline—a " *Notiodrilus*,"—and would correspond to the original Acanthodriline, the origin of the Megascolecidæ. This, however, seemed impossible; there are no representatives of the Acanthodrilinæ in India (except one introduced species of *Microscolex*) ; and the single nephridium does not, according to the evidence of sections, come into relation with the septum in the normal way, and is therefore to be looked on as a hypertrophied micronephridium, the only one left of a former larger series.

In 1920 (**11**) two more forms closely related to the preceding came to light. While both, *Octochætus pachpaharensis* and *O. pallidus*, are without calciferous glands, the first has only three (or anteriorly perhaps fewer) micronephridia on each side per segment, and the second only about seven.

This reduction in the number of micronephridia is probably —certainly in the case of *O. bishambari*—to be looked on as secondary, while the absence of calciferous glands is probably primitive. Other primitive features are the presence of all the septa in the anterior part of the body (behind the level at which they first definitely begin), and the absence of spines or teeth on the penial setæ.

It is apparently from this group that *Eudichogaster* has arisen, as I have argued above. Since the group is a well-defined one, is differentiated from the remaining species of *Octochætus* by morphological characters of importance—absence of calciferous glands, reduction in the number of micronephridia—and has different relationships from those other species, I propose to erect for them a new genus, *Ramiella*, which I associate with
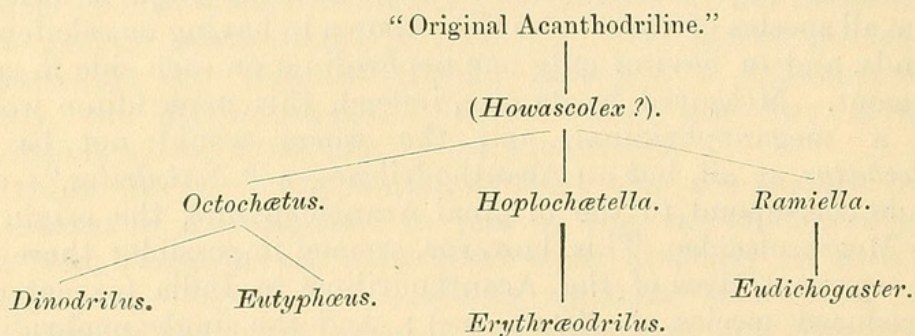
the name of my former colleague, Prof. Shiv Ram Kashyap of Lahore.

Diagnosis :—Setæ eight per segment. Male pores on xviii.; two pairs of prostatic pores, on xvii. and xix. Spermathecal pores two pairs, in 7/8 and 8/9, or on viii. and ix. Gizzard in vi. All septa present after their commencement. No calciferous glands. Micronephridia; micronephridia relatively large, few in number. Testes and funnels free in x. and xi.

Distribution :—India (Mahableshwar, S. Rajputana, Saharanpur).

It will be noted that the species extend in a line from the Western Ghats to the Western Himalayas, the most primitive (at least the one in which the reduction in the number of nephridia has made least progress) being at the southern end, the most modified at the northern.

The relationships of the genera of Octochætinæ may be set forth in the accompanying tree :—

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                "Original Acanthodriline."
                           |
                           |
                    (Howascolex ?).
                           |
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        _____
       |                   |                    |
  Octochætus.       Hoplochætella.          Ramiella.
       |                   |                    |
   ____|____               |                    |
  |         |              |                    |
Dinodrilus. Eutyphœus. Erythræodrilus.   Eudichogaster.
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(On the question of the inclusion of *Howascolex* in the ancestral line of the Octochætinæ see (8), and the references there given. On the inclusion of *Hoplochætella* and *Erythræodrilus* in the Octochætinæ see (10).)

Probably no genealogical tree expresses relationships with exactitude; every genus is strictly speaking at the end of a short side line. Thus *Ramiella* probably comes off the main stem shortly above the position of *Howascolex*; the original meganephridium seems to have broken up in a different way in these two genera—in *Howascolex* to have become one still fairly large and a number of minute nephridia, in *Ramiella* to have dissolved into a few moderate-sized organs.

The Derivation of the genus Dichogaster.

There remains the question of the origin of the genus *Dichogaster*. In 1903 and 1909 Michaelsen regarded it as derived from *Eudichogaster*; while in 1910 he states that morphologically it is best derived from *Eudichogaster*, though geographically it would appear easier to derive it from *Trigaster*; the geographical argument is, however, not by any means absolutely cogent—there is nothing in the facts essentially opposed to the derivation from *Eudichogaster*.

To this view of the origin of *Dichogaster* I cannot agree. In

Eudichogaster the calciferous glands are in segments x.–xiii., or some of them; in *Dichogaster* as a rule in xv.–xvii. It is not so easy for me as it is for Michaelsen, apparently, to imagine a " dislocation backwards " of the glands; it is easier for me to conceive *Dichogaster* arising from *Trigaster* which has no such glands, than from *Eudichogaster* which has them, but in a different place. Apart from that, the geographical argument seems to me decisive : *Trigaster* belongs to Mexico and the West Indies, and these regions are probably part of the endemic home of *Dichogaster* ; *Eudichogaster* is altogether Indian, and it is very doubtful whether there is any endemic species of *Dichogaster* in India at all—certainly there is none anywhere near the *Eudichogaster* region. The place of origin of *Dichogaster* was pretty certainly not India. I derive *Dichogaster* therefore from *Trigaster*.

Diplocardiinæ and Trigastrinæ.

There is a line of descent, the Megascolecinæ, which leads from the " original Acanthodriline," and in which the initial change is the disappearance of the anterior prostates and the union of the posterior prostatic pores with those of the vasa deferentia on segment xviii. There is another line, the Octochætinæ, in which the initial change is the breaking up of the meganephridia into micronephridia. Similarly, there is a third line, the initial change here being the reduplication of the gizzard.

This third line (there are still several others) has commonly been divided up into the two subfamilies of the Diplocardiinæ and Trigastrinæ. These subfamilies, indeed the two combined, are smaller than the Megascolecinæ or the Octochætinæ ; the Diplocardiinæ comprise only *Diplocardia* and *Zapotecia* (*Diplocardia* having two and *Zapotecia* three gizzards, a distinction which is not held to be of generic importance in the case of *Trigaster*, which contains species with both) ; while the Trigastrinæ, after the removal of *Eudichogaster*, comprise *Trigaster, Dichogaster, Monogaster*, and *Eutrigaster* (with three gizzards, and three pairs of calciferous glands in segments xv., xvi. and xvii.). I believe there would be a gain in uniformity and an increase in convenience in uniting the subfamilies under the one head of Trigastrinæ.

" Original Acanthodriline."

Diplocardia.

Zapotecia. *Trigaster.*

Dichogaster.

Monogaster. *Eutrigaster.*
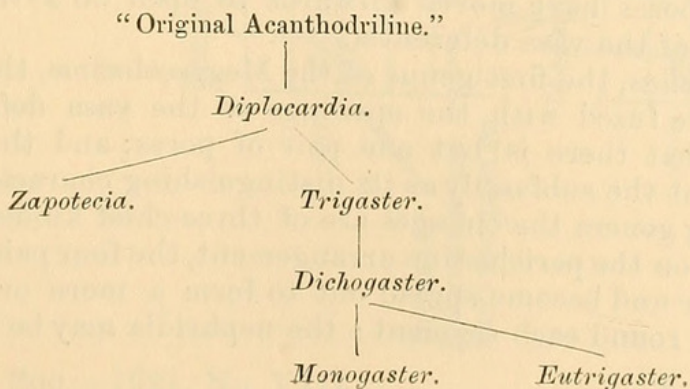
References to Literature.

1. MICHAELSEN, W.—Oligochæta, in : Das Tierreich. Berlin, 1900.

2.   „   Neue Oligochæten und neue Fundorte alt-bekannter. Mitth. Naturhist. Mus. Hamburg, vol. xix. 1902.

3.   „   Die geographische Verbreitung der Oligochäten. Berlin, 1903.

4.   „   The Oligochæta of India, Nepal, Ceylon, Burma, and the Andaman Islands. Mem. Ind. Mus., vol. i. 1909.

5.   „   Die Oligochäten-fauna der vorderindisch - ceylonischen Region. Abh. Naturw. Verein Hamburg, vol. xix. 1910.

6.   „   Oligochäten, in : Ergebnisse der zweiten deutschen Zentral-Afrika-Expedition 1910–1911. Leipzig, 1915.

7. STEPHENSON, J.—On a collection of Oligochæta mainly from Northern India. Rec. Ind. Mus., vol. x. 1914.

8.   „   On some Indian Oligochæta, mainly from Southern India and Ceylon. Mem. Ind. Mus., vol. vi. 1915.

9.   „   On a collection of Oligochæta belonging to the Indian Museum. Rec. Ind. Mus., vol. xii. 1916.

10.   „   On a collection of Oligochæta from various parts of India and Further India. Rec. Ind. Mus., vol. xiii. 1917.

11.   „   On a collection of Oligochæta from the lesser known parts of India and from Eastern Persia. Mem. Ind. Mus., vol. vii. 1920.

II.—ON POLYPHYLY IN THE OLIGOCHÆTA.

The material which I wish to use in this discussion is derived from the Megascolecidæ, and largely from the subfamily Megascolecinæ. It will be necessary first to show how the various genera of this subfamily are related (v. text-fig. 1).

The whole of the family Megascolecidæ is to be derived from an original form which has essentially the characters of the genus *Notiodrilus* as defined by Michaelsen in the Tierreich volume of 1900. These are : Testes and funnels two pairs, free in segments x. and xi. ; vasa deferentia of each side uniting in their backward course so that there is only one pair of male apertures, on xviii. ; two pairs of tubular prostates, with unbranched central canal, opening on xvii. and xix. ; setæ four pairs per segment ; one pair of meganephridia per segment ; a single gizzard far forward, in segment v. or vi.

The Megascolecinæ, however, take their origin from a form which is one remove from this—*Diplotrema*, in which the anterior pair of prostates have disappeared and the posterior pair of prostatic pores have moved forwards to open on xviii. near the apertures of the vasa deferentia.

In *Plutellus*, the first genus of the Megascolecinæ, the prostatic pores have fused with the openings of the vasa deferentia on xviii. so that there is but one pair of pores; and this remains throughout the subfamily as its distinguishing character. In the remaining genera the changes are of three chief kinds—the setæ may take on the perichætine arrangement, the four pairs multiply in number and become spread out to form a more or less complete ring round each segment ; the nephridia may be broken up,

Text-figure 1.
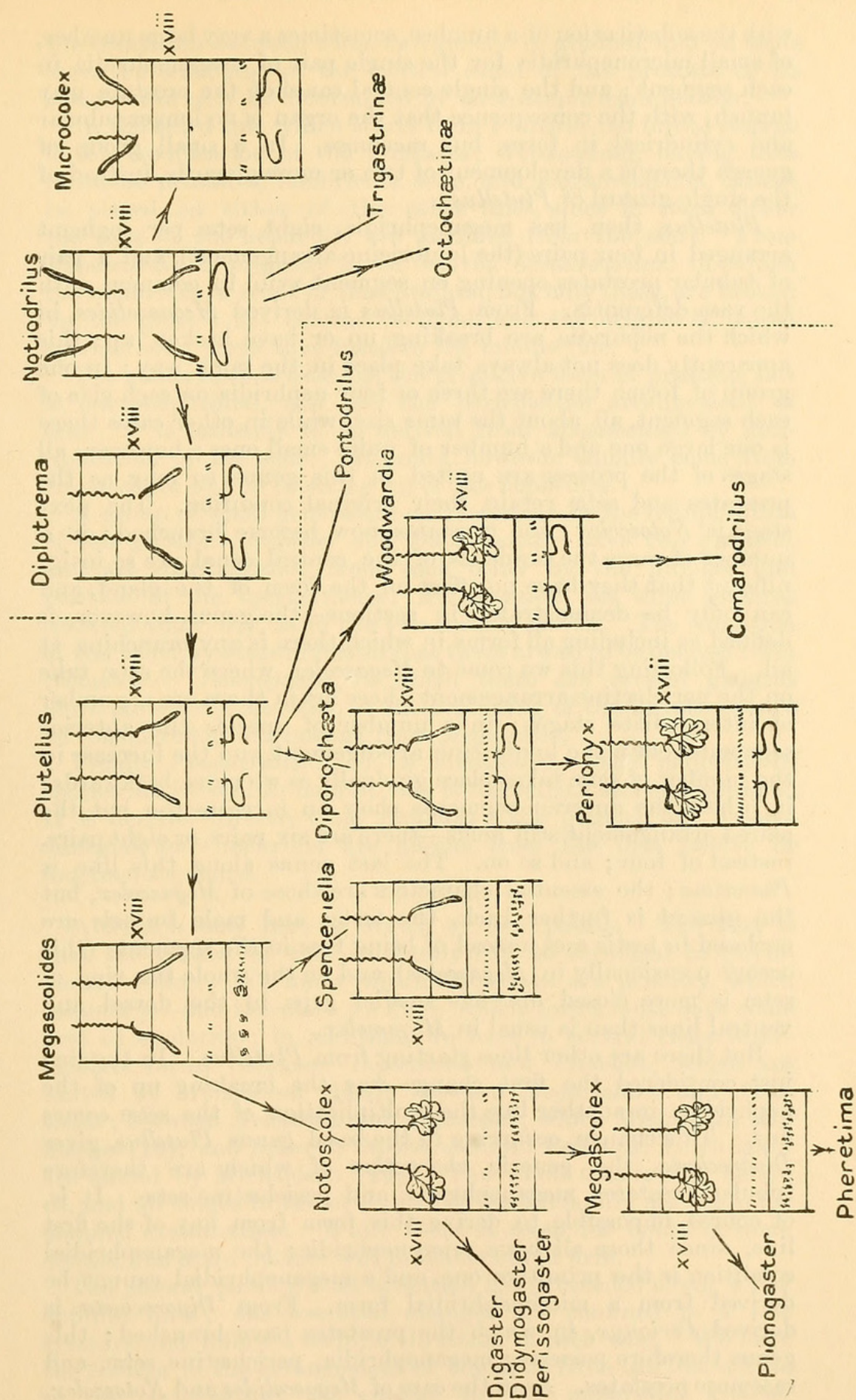
The Relationships of the Megascolecinæ (the Megascolecinæ comprise the genera to the left of the dotted line).

with the substitution of a number, sometimes a very large number, of small micronephridia for the single pair of meganephridia in each segment ; and the single central canal of the prostate may branch, with the consequence that the organ is no longer tubular and cylindrical in form, but racemose. In a small group of genera there is a development of two or more gizzards, instead of the single gizzard of *Plutellus*.

Plutellus, then, has meganephridia, eight setæ per segment arranged in four pairs (the lumbricine arrangement), and a pair of tubular prostates opening on segment xviii. in common with the vasa deferentia. From *Plutellus* is derived *Megascolides*, in which the nephridia are breaking up or have broken up ; this apparently does not always take place in the same way : in one group of forms there are three or four nephridia on each side of each segment, all about the same size, while in other cases there is one large one and a number of quite small ones ; however, all stages of the process are united in this genus, so long as the prostates and setæ retain their original condition. The next stage is *Notoscolex* : the prostates now become branched ; in a number of cases the branches of the central canal are so insignificant that they have no effect on the form of the gland, and can only be demonstrated in sections—the genus, however, is defined as including all forms in which there is any branching at all. Following this we come to *Megascolex*, where the setæ take on the perichætine arrangement ; here again there are a number of intermediate stages ; in a number of species the anterior segments retain the lumbricine arrangement, and the increase in the number of setæ takes place gradually as we move backwards ; in others the anterior segments show an increase too, but the paired arrangement still holds—there are six pairs, or eight pairs, instead of four ; and so on. The last genus along this line is *Pheretima* ; the essential characters are those of *Megascolex*, but the gizzard is further back, the testes and male funnels are enclosed in testis sacs instead of being free in the segments (this occurs occasionally in *Megascolex*), and on the whole the ring of setæ is more closed up—has smaller gaps in the dorsal and ventral lines than is usual in *Megascolex*.

But there are other lines starting from *Plutellus*. In the line just considered the first change was the breaking up of the nephridia : in another line the multiplication of the setæ comes first. This change, occurring in the basal genus *Plutellus*, gives *Diporochæta*, the generic characters of which are therefore tubular prostates, meganephridia, and perichætine setæ. It is, of course, impossible to derive this form from any of the first line, since those all have micronephridia ; the meganephridial condition is the primitive one, and a meganephridial cannot be derived from a micronephridial form. From *Diporochæta* is derived *Perionyx*, in which the prostates have branched ; this genus therefore possesses meganephridia, perichætine setæ, and racemose prostates. As in the case of *Megascolides* and *Notoscolex*,

the transition between these two genera is gradual, and in some cases the branching of the central canal of the prostate or its absence can only be determined by microscopic examination.

In the third line which starts from *Plutellus* the initial change is the modification of the prostates; *Woodwardia*, having thus racemose prostates, lumbricine setæ, and meganephridia, cannot be placed on either of the other lines, since in them either the setæ or the nephridia are modified from the start. From *Woodwardia* is probably to be derived *Comarodrilus*, in which the nephridia in front of the clitellum, but only these, are broken up, the gizzard has become vestigial, and the originally paired spermathecal pores have fused in the middle line.

The genus *Spenceriella* has the primitive form of prostate, but is micronephridial, and has the perichætine arrangement of setæ; it is probably to be derived from *Megascolides* by multiplication of the setæ. It could however equally come from *Diporochæta* by the breaking up of the nephridia.

A group of small genera are characterized by the reduplication of the gizzard. *Digaster* and *Didymogaster* have two gizzards, and are distinguished from each other by the number and position of the spermathecæ; *Perissogaster* has three gizzards situated anteriorly, as in the two former species. The condition of the other systems indicates that these are all to be derived from *Notoscolex*. *Plionogaster*, in which there are several gizzards more posteriorly situated, at the beginning of the intestine, is to be considered as originating from *Megascolex*.

Finally *Pontodrilus* is to be mentioned. The majority of species are littoral in habitat; one is terrestrial, and one is limnic. It is derived directly from *Plutellus*; the gizzard has become vestigial, and nephridia are absent from the first twelve or fourteen segments.

Attention may here be drawn to two points. The first is that the genera of this subfamily can be arranged in phylogenetic order. We know which characters are primary, which secondary—and therefore we know which forms must have come first in evolution; in addition, we have in several cases intermediate forms (between *Diplotrema* and *Plutellus*, which are united by Michaelsen (**14 a**); between *Megascolides* and *Notoscolex*; between *Notoscolex* and *Megascolex*, which Michaelsen also merges (**16**); and between *Diporochæta* and *Perionyx*, which again are united by Michaelsen (**16**)). The whole tree is still before us, and all stages in the evolution of the subfamily are there for detailed examination. While there is room for doubt in some details, the main outline will probably stand firm.

The second point is that evolution has proceeded along a few definite lines; the essential changes are confined to a few systems, and follow a definite direction in each case. We have the change in the arrangement of the setæ, from the lumbricine to the perichætine; the change in the nephridial system,

from the meganephridial to the micronephridial; and that in the prostates, from the tubular to the racemose form; in some cases we have changes in the gizzard, in the direction of reduction or reduplication. Especially, in this subfamily, the first three systems are the important ones; in the majority of genera the gizzard remains the same, and the genera are defined by the condition of the setæ, nephridia, and prostates. Since classification represents relationships, or ought to, as closely as possible, and since these three systems are those which have been affected in the course of evolution, it is these which form the basis of our generic definitions.*

Without going into detail, I may refer, in amplification of the foregoing, to two other subfamilies of the same large family.

The Octochætinæ, like all the subfamilies of the Megascolecidæ, are ultimately derived from the original *Notiodrilus* form. The first change is the breaking up of the nephridia; the whole subfamily is therefore micronephridial. In two of the branches of the subfamily the increase in the number of the setæ takes place. In one genus we have a doubling of the gizzard (*Eudichogaster*, which I place in the Octochætinæ, *cf.* No. 1 of the present series). When changes in the male organs occur they take a different line from those which characterize the Megascolecinæ; the "microscolecine reduction" which is found in certain genera, consists in the disappearance of the posterior pair of prostates and the translation forwards of the openings of the vasa deferentia to join the anterior prostatic pores on segment xvii.

The Trigastrinæ, like the Octochætinæ, are a much smaller subfamily than the Megascolecinæ. The first change in the *Notiodrilus* ancestor along this line is the doubling of the gizzard; subsequently we may have the breaking up of the nephridia and the microscolecine reduction of the male apparatus. The only other development is the appearance in certain genera of calciferous glands; the genera are therefore defined in terms of the gizzards, nephridia, male apparatus, and calciferous glands.

In these subfamilies we thus see the same thing—evolution proceeds along a few definite lines, in a definite direction in each system. Sometimes one, sometimes another system is the first to start evolving, sometimes one, sometimes another follows— and so we get a number of combinations, which characterize the different genera.

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* I do not mean to say that the diagnoses of the genera of Megascolecidæ, as we usually have them, are confined to the systems mentioned, though there is a tendency so to limit them ; compare, for example, the diagnoses of the Megascolecinæ given by Michaelsen in the Tierreich (**6**) with those by the same author in 1907 (**9**). A diagnosis usually contains an element of description, statements which hold good for all hitherto known individuals of a species, or species of a genus, but which are not necessary parts of our conception of the species or genus. Thus we often see recorded the description of species which necessitate the widening of the current diagnosis of a genus.

I now wish to argue that a number of genera of Megascolecidæ are probably polyphyletic. I take as a text a sentence of Benham's, in his paper on the Oligochætes of the Subantarctic Islands of New Zealand (4) :—" According to Michaelsen, species of *Microscolex* may arise at different times, in different parts of the world, from different species of *Notiodrilus*. This thesis involves so profound a modification in the accepted ideas of evolution that space will not permit me to discuss the problem here." I think we may take it, then, that the general view with regard to the multiple origin of species, genera, and larger groups is one of scepticism ; the orthodox view is that each group has arisen once and once only.

But we have to remember that the essential variations in the genera of this family are not innumerable, but limited. It is not the case that the modes of variation are so numerous, and the possible combinations therefore so greatly more numerous still, that there is no reasonable chance of the same combination of characters ever being repeated—this seems to be the foundation of the orthodox view. The combinations of characters that distinguish the various genera can be obtained in more than one way, and the characters and their combinations are few enough to render it possible that this has happened ; I would even say probable that this has happened, and perhaps often.

Let us remember that the perichætine arrangement of setæ is secondary to the lumbricine, the micronephridial condition secondary to the meganephridial, and the racemose prostate to the tubular, and that these changes have demonstrably taken place more than once ; and let us take such a form as *Megascolex*, with perichætine setæ, micronephridia, and racemose prostates. It may have arisen from a form with lumbricine setæ, micronephridia, and racemose prostates (i.e. *Notoscolex*) by the multiplication of the setæ ; or it may have arisen from a form with perichætine setæ, racemose prostates, and meganephridia (i. e. *Perionyx*) by breaking up of the nephridia. Both these modes of origin have, in fact, been suggested ; the point seems to be decided—for some species of *Megascolex*, at any rate—by finding a number of intermediate forms between *Notoscolex* and *Megascolex*. There is a third possibility, from a form with perichætine setæ, micronephridia, and tubular prostates, by the change of the tubular into the racemose prostate—this would mean that *Spenceriella* was the ancestor.

Or take *Perionyx*, with perichætine setæ, racemose prostates, and meganephridia. It might be derived from a form with lumbricine setæ, meganephridia, and racemose prostates (i. e. *Woodwardia*) by multiplication of setæ ; or from one with perichætine setæ, tubular prostates, and meganephridia (i. e. *Diporochæta*) by the branching of the prostatic lumen. Here the existence of intermediate forms has decided in favour of the latter.

Spenceriella is a very small genus, with one species in India

and two in Victoria in Australia. It can be derived from *Megascolides* by multiplication of setæ, or from *Diporochœta* by the breaking up of the nephridia. Both these genera, *Megascolides* and *Diporochœta*, occur both in India and Victoria. It is at least not improbable that *Spenceriella* has been evolved separately in India and Australia, from one or other of these genera, perhaps from the same, perhaps from a different one, in the two parts of its range.

It is to be noted also, that confining ourselves to that considerable group of genera of the Megascolecinæ with a single gizzard, which are distinguished by the characters of these three systems, the logical end of *any* line of evolution is *Megascolex*. The order in which the changes in the three systems have occurred varies in the different lines; the nephridia may be the first to undergo their characteristic evolution (*Megascolides* line), or the setæ (*Diporochœta* line), or the prostates (*Woodwardia* line). But as we follow out the lines other changes are added; and if, in any line, all three systems pass from the primitive to the derived condition, we arrive at *Megascolex*, with perichætine setæ, micronephridia, and racemose prostates.

There seems therefore to be an *a priori* probability that groups of worms possessing certain combinations of characters, that is certain genera, may have arisen more than once, and that the genera as we have them to-day are polyphyletic.

But we are not dependent altogether on *a priori* reasoning. The case to which Benham refers is the multiple origin of *Microdrilus* from *Notiodrilus*. The two genera are distinguished by the condition of the posterior male organs—in *Microscolex* the "microscolecine reduction" has taken place (this indeed is the origin of the term). On Possession Island (one of the Crozet group, some distance south-east of Cape Colony) Michaelsen found two species of worms, obviously very closely related, one with the original condition of the male organs (i. e. a *Notiodrilus*), the other with the microscolecine condition (i. e. a *Microscolex*); the deduction is that the latter species has been evolved on the island from the former. The two species agree in the peculiar pigmentation, in the arrangement of setæ, glandular modification of the integument in the neighbourhood of the genital pores, in the form of the penial setæ, form of the prostates, and size and shape of the spermathecal diverticula. The *Microscolex* was represented by numerous examples, and so was not an individual chance variation; and Michaelsen is doubtless right in holding (8, 9) that it has been evolved in this remote region from the *Notiodrilus* which occurs there. Of course, other species of *Microscolex* have evolved elsewhere, from other species (conceivably from one species) of *Notiodrilus*; and thus *Microscolex* has arisen at least twice, from different ancestors and at different times.

Benham, however, is wrong if, in the sentence I have quoted above, he means to imply that Michaelsen holds heretical views on evolution. Michaelsen is strictly orthodox; he will not have it that different species of a genus may arise at different places from different species of a parent genus; he merges the two genera concerned, and calls all the species *Microscolex* (8).

Again, in the Abor country, in a remote spot in the Eastern Himalayas, a worm is found named by me *Perionyx annulatus* (18); like other examples of the genus it has racemose prostates and perichætine setæ; but while the rest of the genus has only meganephridia this worm has, in addition to meganephridia, micronephridia also in all the postgenital segments. But the presence of micronephridia is just what distinguishes *Megascolex* from *Perionyx*, and by definition the worm should go in *Megascolex*. A large number of species of *Perionyx*, however, have a rather characteristic appearance—the dorsal surface is deeply pigmented, of a dark purple colour; the setæ are exceptionally numerous, and the breaks in the middorsal and midventral lines are very small; the male pores and spermathecal pores are close together near the midventral line and, internally, the gizzard is considerably reduced. These characters are not set down in the generic diagnosis; some of them are scarcely definite enough, and they are not features of all the species, though, in varying degree, they are of many; they are, however, all possessed by *Perionyx annulatus*. Lastly, *Perionyx annulatus* occurs in the heart of the *Perionyx* region, and more than a thousand miles from the Indian *Megascolex* region. There is only one possible conclusion—that this worm, by definition a *Megascolex*, has evolved where we find it from a *Perionyx*, and that it has nothing to do in its origin with any other Indian or Australian *Megascolex*. Very similar is *Megascolex dubius*, which also seems to have arisen, far away from the *Megascolex* region, from a *Perionyx*.

I have already said, however, that *Megascolex* has originated from *Notoscolex* (lumbricine setæ, micronephridia, and racemose prostates) by increase in the number of the setæ; and indeed we get so many intermediate stages in this increase that this is no doubt true for at any rate a large number of species; *Megascolex* is therefore diphyletic.

But this does not end the complexity. Michaelsen (14) has pointed out the close relation of certain Ceylon species of *Megascolex* to certain Ceylon species of *Notoscolex*—the group of *Megascolex travancorensis* to that of *Notoscolex ponmudianus*. The argument is the same as in the case of the *Notiodrilus* and *Microscolex* of Possession Island; the species of *Megascolex* have in all probability arisen from the local representatives of *Notoscolex*. There is also a similar correspondence between species of *Notoscolex* and species of *Megascolex* in another restricted area, the N. Island of New Zealand; here, too, the inference is that the second have arisen from the former.

Once more, *Spenceriella* possesses the perichætine arrangement of setæ, micronephridia, and tubular prostates, differing only in the latter respect from *Megascolex*, which has the more advanced racemose form of the glands. But Michaelsen has lately (**16**) transferred two species of *Spenceriella* to *Megascolex*; though the branching of the central canal was not to be inferred from anything in the external form of the glands, it was found to exist in a slight degree on microscopical examination of sections. It is scarcely rash to look on these apparently transitional species as descended from species of *Spenceriella*, which they so much resemble. They can hardly be descended from either *Notoscolex* or *Perionyx*; the transitional species in these cases are characterized by the incomplete setal rings, or by the incompletely broken up nephridia, and have, apparently, the fully developed racemose prostates, as is usual in *Notoscolex* and *Perionyx*.

In other words, species which anatomically belong to the same genus, *Megascolex*, have arisen from two less specialised genera, *Notoscolex* and *Perionyx*, and at least at three separate times; quite possibly *Spenceriella* is the origin of certain other species. Probably, of course, this much understates the truth; it is only a few small groups of species of *Megascolex* that we can thus trace back at present; the great bulk of species have probably originated at still other times and in still other places.

Michaelsen, having before his eyes the separate origin of *Megascolex* from *Notoscolex* in New Zealand and Ceylon, gets over the polyphyletic difficulty by merging the two genera into one (**16**). But this is too short a way with the difficulty; if, wherever we find a polyphyletic origin, we merge the genera concerned, then of course no genus will be polyphyletic, and orthodoxy will triumph. And it may be noted that even this device of fusion is not effective where a genus has a double origin from two other genera. Assuming that some species of *Megascolex* have arisen from *Notoscolex*, others from *Perionyx*, the fusion of *Notoscolex*, *Megascolex*, and *Perionyx* into a single genus leaves us where we were, since the genus now has a double origin from *Megascolides* and *Diporochæta* (*cf.* text-fig. 1).

Take now the case of *Pontodrilus*. From its ancestor *Plutellus* it differs in two primary respects—the gizzard has become vestigial, and there are no nephridia at all in the first twelve segments; it is littoral in habit, and is very widely distributed in the warmer regions of the globe. Benham in 1903 (**3**) discovered in a lake in New Zealand a worm with the above anatomical characters, which he called *Plutellus lacustris*, on the ground that the features wherein this worm agreed with *Pontodrilus* and differed from *Plutellus* appeared to be adaptive and related to an aquatic habitat; he implies, though he does not expressly state, that this worm had an origin from *Plutellus* independent of that of the bulk of the species of *Pontodrilus*, and cannot therefore be united with them in the

same genus. Michaelsen transferred the worm to *Pontodrilus* (**9**), adding later (**12**) that it might be a *Plutellus*, an example of convergence—though besides the primary features there were others also which characterized both the new worm and the previously known species of *Pontodrilus*. Benham (**4**) appears to take the same view. Lastly, Michaelsen (**11**, p. 22) appears to have definitely adopted the view that it is a *Pontodrilus*, since he speaks of the apparent absence of *Plutellus* from New Zealand.

Some time ago I found an entirely terrestrial *Pontodrilus* in material from the centre of Ceylon (**19**); this may, possibly, be the ancestor of all the littoral forms (their littoral habit is of course secondary); on the other hand, it may equally well be a descendant of some one of the species of *Plutellus* which are indigenous in Ceylon, while the bulk of the species of *Pontodrilus* originated elsewhere. In any case, we seem to have a distinct possibility—I will not say more—that worms which must, anatomically, be placed in the genus *Pontodrilus* have arisen at various times and in various places.

An extremely curious case is afforded by a genus newly described by Michaelsen as *Monogaster* (**15**). It is essentially a *Dichogaster* (subfam. Trigastrinæ) in which the two gizzards have, as it were, run together again, probably in consequence of the disappearance of the septum between them. In the evolution of *Dichogaster* the steps from the original *Notiodrilus* ancestor have been as follows :—First the doubling of the gizzard, then the development of the micronephridial condition, and then the development of calciferous glands in certain postgenital segments. In *Monogaster*, therefore, the gizzards having secondarily united, the essential characters are the micronephridial condition, the calciferous glands, and a single gizzard. But these are exactly the characters of *Octochætus*, which belongs to an altogether different subfamily, the Octochætinæ. In this line the initial change was the breaking up of the nephridia, and this has been followed in *Octochætus* by the development of calciferous glands, here too, as in *Dichogaster* and *Monogaster*, in the segments behind the ovaries; the gizzard has never been double. There is nothing in the arrangement of the male organs to distinguish *Monogaster* from *Octochætus*; the calciferous glands in *Monogaster* are three pairs, in segments xv., xvi. and xvii., while in *Octochætus* they are one or two pairs, in xv., xvi., or both : but this could not be a ground for generic distinction. There is a difference in type between the micronephridia in the two genera,—numerous and tubular in *Octochætus*, fewer and saclike in *Monogaster*; but beyond this the only distinction is in the distribution—*Monogaster* comes from Africa, from the *Dichogaster* region, while *Octochætus* has never been found farther west than the Malabar coast of India. The line of descent of each is perfectly plain; still the case illustrates my contention, that the same end may

be reached by different paths; in other words, certain groups with the same anatomical characters may have a polyphyletic origin.

Must it then be an article of faith that each genus has arisen once and once only ?   Variations may be innumerable—no doubt every organ and part may vary and does vary independently ; but the variations that mean anything, that come to anything from the point of view of evolution, are not innumerable—they are limited both in their seat and in the direction they take. And it would seem that similar steps are being taken in many parts of the range of a group; with the consequence that the end condition is similar also.   In other words, we have a polyphyletic origin of certain groups.

Objections may be raised to the above line of argument.   It may be said, for example, that what I have been discussing are cases of convergence, which nobody has ever denied.   Or it may be said that if, as I have claimed, *Megascolex* or any other genus has a multiple origin, then it is not a true genus, and that the group we know as *Megascolex* really consists of several genera with different lines of descent.

The term " convergence " is applicable to the case of *Monogaster* and *Octochætus*, just discussed ; it is applicable to that of the group of species of *Megascolex* descended from *Perionyx* and the group descended from *Notoscolex*, as well as that descended from *Spenceriella*, if this origin should be confirmed.   But it is not applicable to the different groups of species of *Megascolex* descended from different *Notoscolex* forms, nor, generally, to the multiple origin of one genus from another single genus : there is no convergence here—the developments are parallel.

Further, along with the use of the term convergence there seems to go an idea that a careful morphological examination, or a consideration of distribution, will ultimately suffice to distinguish groups of different origin, and that a different descent will always betray itself to sufficiently careful and minute investigation. My point is that it may not do so.   Naturally, in giving specific instances to support the *a priori* argument, I have had to give cases where *some* features of certain species of a genus seem to countenance a separate origin for these species ; otherwise if there had been no anatomical features at all to support the hypothesis of a double origin, the argument could have been deductive only. I have tried to show that in the genus *Megascolex* we can with some probability separate off small groups here and there which have originated at different times, from different ancestors— these ancestors, too, belonging to more than one genus.   But, even if these groups were separated off, are we prepared to say that the large number of species which remain (the great majority of the genus) own a single origin ?—that we have been able to discriminate all such independent groups ?   Such a claim would be, to my thinking, extremely rash.

As to the further point, that *Megascolex* is not a true genus but a group of genera, the matter is largely one of words. If anyone wishes to paraphrase my conclusion, and say that "different lines of descent may give rise to forms that it is impossible to separate generically by anatomical characters," I have no quarrel with him. I believe, however, that the sentence "genera may be polyphyletic" expresses this conclusion with equal correctness. For what is a genus? It is, of course, an assemblage of species having certain characters in common : are we justified in going further, and saying "A genus is an assemblage of species having certain characters in common, and owning a common descent "?

I do not think so. In the first place, the term genus was used in the first sense long before the doctrine of descent had won acceptance. Another and more important reason is that, as must be evident from what has preceded, we do not know what the lines of descent certainly are, even in so well known a group (and one so favourable for our purpose) as the Megascolecidæ. If we choose the second conception, we shall find it impossible, in the present state of knowledge, to divide up the polyphyletic group known as the genus *Megascolex* into assemblages of species having certain characters in common and owning a common descent.

Yet genera, definite assemblages, we must have ; we must have groups above species, and these groups must necessarily have limits of some kind. Since we cannot, in the present state of knowledge, define these groups by their descent, we must define them by their anatomical characters, and perhaps by their distribution. In some cases we can say that in all probability a group so defined is a genetic unity ; in many cases we do not know whether this is so or not ; in some we shall suspect or feel convinced that it is not. But till we are able definitely to mark out new groups on genetic lines, we cannot relinquish the old anatomical groups.

A classification is one thing, a phylogenetic tree another. No one believes more firmly than I do that phylogeny ought to be the basis of classification ; but candour must admit that as yet it is incapable, in many cases, of constituting such a basis. Our classification must necessarily, for practical reasons, present itself as a complete scheme ; our phylogenetic trees are and will long remain woefully incomplete. As our ideas of phylogeny become more and more settled, our classification must be revised to correspond with it. But so long as we see anatomical groups which we suspect, or can demonstrate, to be of diverse origin, without being able definitely to separate them up according to their descent, so long we shall have to put up with polyphyletic genera.

For bibliography see end of next section.

III. Some General Considerations on the Geographical Distribution of Indian Oligochæta.

The geographical distribution of Indian Oligochæta has been treated at length by Beddard and Michaelsen (Beddard 1, 2 : Michaelsen 7, 10, 11). The earlier writings of both authors are valuable for the discussions of the means by which the migrations of Oligochæta are in general effected ; but the large collections of Indian worms investigated by Michaelsen in 1909 and 1910 (10, 11) increased our knowledge of the actual facts of distribution to such an extent that the special conclusions in the later works supersede those arrived at in the earlier.

(1) *The Migrations of Oligochæta.*

Oligochæta may for the present purpose be divided into three groups—limnic, littoral, and terrestrial, each with its distinctive modes of spreading.

Limnic forms have a great diversity of means of dispersal. They may spread directly throughout a river system, through all the canals and into all the tanks and reservoirs supplied from it. Their cocoons are easily transported in the mud which adheres to the feet of wading birds ; some forms are known to encyst, and hence may be transported in this manner even in the adult state. An Enchytræid has been found frozen in a block of ice, and recovered (Beddard, 1).

As a consequence the same genera—sometimes the same species even—are found in widely distant places. The case is similar to that of the Rotifera and Protozoa, of which the same genera and species are found in ponds and streams all over the world. There appears to be but one genus. *Branchiodrilus*, of the limnic Oligochæta which is peculiar to India, while a number of species are found both in England and India, or in Europe and India (species of *Nais, Chætogaster, Dero, Aulophorus, Pristina*, etc.).

Littoral forms live on the shore, exposed at times to submersion in salt water. Like the last group, these have a wide distribution ; being, unlike earthworms in general, immune to salt water, they can be transported in masses of seaweed, or more commonly their cocoons are so transported, entangled in masses of weed or other detritus. Not only can they take possession of a whole coast, and spread along the shore-line, but they may in this way travel over sea for long distances. The most noteworthy genus is *Pontodrilus*, which occurs along the coasts of India, and has a circummundane distribution.

Terrestrial forms constitute the bulk of the Oligochæta. Here the means of spreading are more limited ; for the most part earthworms are dependent on their own activities for reaching new regions, and hence their wanderings must be very slow. According to Michaelsen, worms which are found outside their burrows apparently wandering about have for the most part been

obliged to leave their homes by illness, or by unfavourable conditions such as the flooding of the burrows; many worms, if extracted from their holes, are unable to make new ones, and must die. Some, however, certainly possess the power of active wandering, as is shown by the numbers sometimes found under heaps of manure. But it is obvious that the peopling of a territory by earthworms through their own exertions can only be very slow.

Not only so, but they are limited in their wanderings by desert tracts—some degree of moisture in the soil is essential. Snow-covered mountain ranges are another obstruction. And especially the sea limits them, the majority of earthworms being quite unable to pass even a narrow arm of salt water.

We have to recognise, however, that not all the terrestrial forms are so strictly limited in their means of dispersal as the above would imply. A tree-trunk floating down stream, or earth between the hoofs of cattle, may transport worms or their cocoons. More important is the part that man has played; Lumbricids, natives of Europe, have been introduced all over the world along trade routes; in W. Australia they are almost the only earthworms to be found near the towns; the indigenous fauna is to be sought in the remoter parts of the country. One of the commonest worms of the Punjab is *Allolobophora caliginosus*; certain species of *Pheretima* have been carried round the globe, far from the region where the genus is endemic. Small worms are more likely to be carried in this way than larger ones; and small species of *Dichogaster*, an African genus, are common throughout the Malay Archipelago, and not rare in India. Botanical Gardens are obviously likely to be centres of dispersal for such introduced species in a new country. Records at Kew and Hamburg leave no doubt of the reality and abundance of these transfers through the agency of man.

There are also, of course, differences in the powers of the worms themselves. Some species seem to be able to travel more widely than others, and more quickly, and to adapt themselves to new surroundings and establish themselves more easily; and it may thus happen that a species spreads over a large region quite apart from human interference. It is not always possible to distinguish between these cases and those of introduction by man; and Michaelsen has adopted the name peregrine for the widely wandering species, whether they owe their diffusion to man's agency or to their own unaided powers.

For the purposes of Zoogeography, the distribution of fresh water and littoral forms is of little or no importance; and the same holds for the peregrine forms among the terrestrial group. Thus, in discussions on the place of origin and past history of the genera or larger groups, as well as in coming to conclusions as to the past distribution of land and water, we are limited for our facts to earthworms in the strict sense, and to those among them that have a definite and limited range. But,

having purified our material in this way, Michaelsen holds that we have in the Oligochæta a group which is capable of yielding results for palæogeography second to those of no other group in importance and certainty; the worms cling to the soil in the most literal way, can only make use of the earth in their wanderings, and by the facts of their present distribution can thus demonstrate in the plainest manner the existence of land connections where, it may be, there is now only a wide stretch of ocean.

(2) *The Facts of Distribution and their current Explanation.*

The material which is available for use in the following discussion is derived from the following groups:—The subfamilies Megascolecinæ, Octochætinæ, and Trigastrinæ of the great family Megascolecidæ; the family Moniligastridæ; and scarcely anything else.

(a) *The Megascolecinæ.* For the phylogenetic relationships of the genera of Megascolecinæ the previous article and its text-figure may be referred to.

Diplotrema, from which the subfamily takes its origin, occurs in Queensland and New Caledonia. *Plutellus* is found in Ceylon, S. India, and the E. Himalayas; in Australia and Tasmania; several species occur in the western part of N. America. *Megascolides* occurs in S. India, in W. India, and in the E. Himalayas; in Australia and Tasmania; and it has one species in western N. America. *Notoscolex* is found in the Indian region mainly in Ceylon, but also in S. India and in the E. Himalayas; outside India it occurs in Australia and New Zealand. *Megascolex* is found especially in Ceylon, to a somewhat less extent in S. India, and hardly anywhere else in the Indian region; outside India it is found in Australia, Tasmania, the N. Island of New Zealand, and Norfolk I. (between New Zealand and New Caledonia). *Pheretima* is a genus of which many members have wandered widely; its proper home, however, is S.E. Asia and the neighbouring islands— the whole of the Malay Archipelago; from Burma on the one side it reaches to Japan on the other; a few endemic species are found in India proper, but they hardly entitle India to be considered as part of its proper home; one species is perhaps endemic in Queensland, and perhaps one in the Comoro Is. *Diporochæta* is only represented by one species in India, and the record is an old one: no locality is given, but it was probably found in S. India; the headquarters of the genus is Victoria and Tasmania; species are also found in Queensland, New Zealand, and (one species) on the Chatham Is. (east of New Zealand). *Perionyx* occurs as the dominant genus in the E. Himalayas, and is also scattered over India generally; it occurs also in Victoria, Tasmania, and the Auckland Is., and one species is found in Sumatra and Java (as usual, peregrine species are omitted from this review).

Woodwardia is found in Ceylon and S. India, and in Burma ; also in Australia and in Java. *Comarodrilus* is purely Indian—there is only one species, found in the extreme south. *Spenceriella*, a small genus, occurs in S. India and Victoria.

A few other small genera of terrestrial Megascolecinæ, characterized by an increase in the number of gizzards, do not occur in India ; two are Australian, one is common to Australia and New Zealand, and one occurs in the Philippines and Moluccas.

It will be seen that nearly the whole of the Indian genera (all except the small genus *Comarodrilus*) are represented in Australia ; a number are found also in New Zealand, a few in the islands near New Zealand, and a few in the islands of the Malay Archipelago.

The conclusion drawn from the occurrence of the parent genus *Diplotrema* in Queensland is that the subfamily took its rise from somewhere in this region, which is not very far from the centre of the area now inhabited by the subfamily. The descendants have travelled further afield—towards India, towards Tasmania, towards New Zealand and the neighbouring islands, and northward throughout the Malay Archipelago to Japan. And of course the important point is that they must have travelled by land. The reason for the absence of so many of the genera from the islands intervening between Australia and India is that here the mighty genus *Pheretima* has crushed all competitors ; it is the youngest, most highly specialized, and most vigorous genus of the subfamily ; it is still spreading, many species are among those most commonly introduced by man, and they show themselves most successful colonists.

Michaelsen does not, however, assume the prolonged existence of a broad land connection between the regions mentioned. The relations were much more complicated, and were often changing. Perhaps there was not a complete bridge at any time ; the normal condition of the region intervening between Australia and New Zealand on the one hand and India on the other was that of an archipelago, which extended to Ceylon and S. India over the present Bay of Bengal. The boundaries of the islands often changed : sometimes they joined, sometimes they separated,— and no doubt in a different place ; and in this way paths became available for the continued expansion of the various genera.

Moreover, since certain Indian genera have such a definitely limited area (certain of those already noticed being confined to S. India, *Perionyx* being chiefly an inhabitant of the Himalayan region, and *Eutyphœus*, to be mentioned subsequently, being confined to the Gangetic plain), India itself was split up into a number of large islands. Thus the Malay Archipelago is the only remaining part of a larger archipelago which existed in the early Tertiary, of which the middle part is submerged, and the Western has consolidated to form the present India. The

occurrence of two of these genera (*Plutellus* and *Megascolides*) in North America is supposed to point to their having travelled over the Angara continent.

The other groups are less extensive; they reinforce the above conclusions, and permit the formulation of a few more.

(b) *The Octochætinæ.* This subfamily, as stated in the previous article, originated from the common *Notiodrilus* ancestor by a breaking up of the nephridial system; the lines along which evolution has advanced have also been mentioned. There is a form *Howascolex* in Madagascar in which the breaking up of the nephridia has not proceeded far, meganephridia coexisting with micronephridia. In *Octochætus* the breaking up is complete. *Dinodrilus* is derived from *Octochætus* by a multiplication of the setæ to the number of six pairs instead of four; the microscolecine reduction of the posterior male organs without change in the number of setæ leads to the genus *Eutyphœus.* A continued increase of the number of setæ and the consequent formation of complete chains was supposed to lead to the evolution from *Octochætus* of *Hoplochætella*; and in a previous section I have given reasons for supposing that *Eudichogaster* is also derived from *Octochætus* by a reduplication of the gizzard.

Octochætus is widely distributed in India, and occurs also in New Zealand, but not elsewhere—not in Australia. *Dinodrilus* occurs in New Zealand only. *Hoplochætella* was first found in India, and species which were referred to it were subsequently discovered in New Zealand, but these probably belong to a different genus (**20**). *Eutyphœus* and *Eudichogaster* are purely Indian genera.

Here, then, we have relationships which differ from those of the Megascolecinæ; they exclude Australia, and concern only India and New Zealand. The conclusion is that at the time of the dispersal of the Octochætinæ there was a connection between India and New Zealand which did not extend to Australia; perhaps it passed entirely to the north, through the great islands of the Malay Archipelago. The Octochætinæ do not occur at present in the Malay Archipelago because they have been unable to survive in competition with the dominant *Pheretima.*

(c) *The Trigastrinæ.* This is a small subfamily—very small as far as India is concerned. The essential character here is a duplication or triplication of the gizzard. The parent genus *Diplocardia* differs only in this respect from the *Notiodrilus* ancestor of the whole family (*Diplocardia* and a closely similar genus *Zapotecia* have been regarded as constituting another subfamily, the Diplocardiinæ). From *Diplocardia* is derived *Trigaster*, in which the meganephridia have given place to micronephridia; it therefore has the original arrangement of the male apparatus, lumbricine setæ, micronephridia, and a

reduplication of the gizzard. From *Trigaster* is derived *Dichogaster*, in which calciferous glands are developed in segments xv.–xvii. or thereabouts.

The geographical relations of this subfamily are quite different from those of the preceding groups. *Diplocardia* is found in North and Central America, and its descendant *Trigaster* in Central America and the West Indies. *Dichogaster* is endemic in Central America and the West Indies, and also in tropical Africa; all the species that are found in India are introduced, with the possible exception of one only. *Eudichogaster*, a purely Indian genus, is derived from *Trigaster* by Michaelsen (by the development of calciferous glands in segments x.–xii. or thereabouts); but in a previous section (No. I. of the present series) I have given my reasons for believing that this genus belongs to the Octochætinæ.

The view of Michaelsen is that *Trigaster* spread from its original home in Central America and the West Indies by means of a land-bridge to Africa, and thence, by a land-bridge in the Pliocene, to India, where it gave rise to *Eudichogaster*, itself disappearing in India in the transformation. *Dichogaster* had its origin from *Trigaster* on the American side of the Atlantic, crossed the Atlantic by the same bridge as *Trigaster* and reached Africa; its indigenous range at present extends no further— indeed it does not seem to have as yet quite reached the eastern shores of Africa (though a large number of peregrine species are known from farther east, including India). *Trigaster* has been exterminated in Africa by the dominant genera *Eudrilus* and its own descendant *Dichogaster*, which between them quite dominate this region, in the same way that so many genera of Megascolecidæ have disappeared from the Malay Archipelago in consequence of the spread of *Pheretima*.

(d) *The Moniligastridæ.* This family consists of only a few genera. Without going into the relationships of these, it may briefly be stated that *Desmogaster*, the supposed ancestral genus, is found in Borneo, Sumatra, and Lower Burma, and its descendant *Eupolygaster* has a similar distribution. *Drawida*, the largest genus of the family, is predominantly S. Indian (though its range has recently been shown to be more extensive than was believed); *Moniligaster*, a small genus very close to *Drawida*, belongs to the same region.

Michaelsen supposes that S. India and Ceylon were peopled by this family by means of a land-bridge across the Bay of Bengal, and rejects the supposition that the forerunners of the present S. Indian Moniligastrids could have travelled by land round the head of the Bay; they would have left some trace of their passage in that region (a number of endemic species of *Drawida* have, in fact, been recently shown to inhabit this region). Besides, the bridge was in existence when the Megascolecinæ passed over to S. India, and so was available for the Moniligastridæ too.

(3) *The Objections to the current Explanations.*

I may preface the present section by a brief statement of the reason why I feel a difficulty in accepting the existence of land-bridges as an explanation of the above facts of distribution. It is this.

Terrestrial Oligochæta are, I believe, a recent group, and some of the genera we have been considering are among the most recent of the earthworms. They have probably arisen in the most recent geological periods. But the general aspect of the fauna of Australia and New Zealand shows that no land connections with Asia have existed during these periods. It is necessary therefore to find other explanations for the existence of so large a common element in the earthworm fauna of these regions.

(a) *Terrestrial Oliogochæta a recent Group.*

The food of earthworms is vegetable mould; and presumably there were no earthworms in existence until the vegetable mould was present in sufficient quantity to nourish them. We may thus put their rise at some time not earlier than the spread of dicotyledonous plants, which took place during the Cretaceous period. This would limit the evolution of the first earthworms, the differentiation of the several families, and the evolution of the numerous genera of these along lines of descent similar to those we have followed out in the Megascolecinæ and other groups, to little more than the Tertiary and Quaternary.

The recent origin of many of the present-day genera seems also to be indicated by the extraordinary variability of a large number of genera and species. As examples, it may be mentioned that the variability of genital papillæ and other markings is a common difficulty of systematists; that the number of gizzards in the genus *Drawida* varies fairly widely in many species; that in one and the same genus of Megascolecidæ we may meet with species with testis sacs or with free testes and funnels; in another with the original ("acanthodriline") arrangement of the male organs, with the microscolecine reduction, or with the "balantine" reduction (disappearance of anterior prostates, and union of openings of vasa deferentia with the posterior prostatic pores); in another, with paired or fused genital orifices; or with spermathecæ varying in number from two to seven pairs or even more; or with seminal vesicles which may vary in number or position or both—indeed these variations of the seminal vesicles are sometimes found within the same species. The consequence is that the generic and specific diagnoses are uncommonly wide as compared with those of other groups.

Even so, the systematist often has extraordinary difficulty in referring his specimens correctly. He seems to get so many intermediate forms; in the case of single specimens it is sometimes impossible to say whether more ample material would justify the erection of a new species, or would show a range of

variability that would link it on to an existing species. The number of described "forms" and varieties is therefore large. Sometimes, as in the case of *Pontodrilus*, critical examination and the increase of knowledge results in the union of a whole series of species under a single name.

Not only are transitions between species common, but the same is true for genera. In speaking of the Megascolecinæ in the previous article it has been noted that literally all stages in the passage from the lumbricine to the perichætine arrangement of setæ, from the meganephridial to the micronephridial condition, and from the tubular to the racemose prostates are met with. The same holds for other characters which have been used as generic distinctions, *e. g.* the well-developed or the vestigial gizzard, the degree of approximation of the genital apertures, etc. The consequent difficulty of separating genera has led Michaelsen to fuse a number of genera, with, I think, a great sacrifice of convenience.

In speaking of the S. Indian earthworm fauna, I have noted (19) that the genus *Megascolex* seems to have " recently undergone a notable blossoming forth, with the production of a large number of forms and intermediate forms, and that in consequence it is extremely difficult to separate species from varieties, and varieties from examples of individual variability. The (Indian) range of *Megascolex* is of very limited extent, yet the number of species is extraordinarily large ; and still every collector, wherever he chooses to explore, brings back numerous novelties." Of the same kind is the discovery of what I have called a "nest" of related species of *Drawida* in the Chittagong district (20), and of species of *Hoplochætella* in a limited region of Western India (20). The same blossoming forth is seen in the Lumbricidæ, where the distinction of species, and especially of genera, is notoriously difficult ; genus passes into genus—often into more than one genus—and the same kinds of changes appear to be in progress in different parts of the tree, to such an extent that the confusion is almost inextricable. There is thus an appearance of incomplete differentiation, and a lack of that fixity and extinction of intermediate forms which we are accustomed to associate with old established groups.

Add to this the mere length of the line of descent from the supposed late Secondary ancestral earthworms to such forms as *Megascolex* and *Pheretima*, the latter portion of which has been traced in the previous article. It seems highly improbable that in such a vigorous group, and one so capable of adaptation to new environments, the differentiation of genera should have ceased soon after its first rise—so long ago, say, as the Eocene.

(b) *The Question of Land-Bridges in general.*

That the outlines of land and sea have changed during geological time is of course universally admitted ; but as to how great

the changes have been opinions vary ; the tide sways backward and forward, and no agreement has been reached. Zoologists will remember that Wallace inclined at first to the opinion of numerous and great changes—such fundamental changes as the bridging of the Indian Ocean by the hypothetical continent Lemuria ; but that later he came to believe in the essential permanence of all the great ocean basins. On the whole, however, the zoologists are to be found among the bridge-builders, and they have the company of some distinguished geologists ; but it is perhaps true to say that geological opinion at present is inclining to the theory of permanence.

Needless to say, no one would deny vertical movements of the order of 100 fathoms or so ; no one could refuse to believe that England had been united to the mainland, or that a large part of the Malay Archipelago had been united to the continent of Asia. And a rise of 100 fathoms would unite all the large masses of land into one, with Australia as a doubtful exception ; seen in a N. Polar projection, we should have a mass of land round the N. Pole, with three tongues, S. America, Africa, and Malaya radiating outwards towards the S. Pole. The soundings are not sufficient to determine whether there is a continuous bridge to Australia above the 100 fathom line or not. New Zealand, Madagascar, the West Indies, and numerous small oceanic islands would remain separate. A lowering of 100 fathoms would isolate N. and S. America, Asia and Africa; and Europe would form a complex of islands and peninsulas much like the East Indies to-day. It is changes of this order that are considered allowable by the more conservative school, not such changes as would bridge the N. or S. Atlantic or Pacific Oceans.

What appears to have brought about something of a change of opinion in recent years is the increasing support accorded to the theory of isostasy. The earth's crust is in a condition of approximate equilibrium, the crust being less dense under the mountains and continental masses in general, more dense under the ocean floor—this is shown by the measurements of gravity. It may be too venturesome to say that the mountains float like icebergs in water ; but the idea is that the land-masses project because they are lighter, while the bed of the oceans has sunk because this portion of the crust is heavier ; and without the most extensive lateral motion of the matter of the crust the general arrangement of continental masses and ocean cannot change.

In addition to the measurements of gravity is the fact that there are no abyssal deposits on the continental platforms wherever these have been adequately studied; i. e., the continents have never been deeply submerged, though shallow seas from time to time there may have been. And the continental shelf is so marked, obvious, and universal a feature of the earth's surface that it affords the strongest kind of evidence of the antiquity of the ocean basins and the limits beyond which the continents have not extended. I have mentioned the effect of

raising the level of the land of the globe by 100 fathoms; an elevation of five times this amount would alter the boundaries very little more.   W. D. Matthew sums up the evidence strongly in favour of general permanency (5):—" The geologic evidence for the general permanency of the abyssal oceans is overwhelmingly strong.   The continental and oceanic areas are now maintained at their different levels chiefly through isostatic balance, and it is difficult to believe that they could formerly have been reversed to any extensive degree."

(c) *The Objection to the Indo-Australian Bridges.*

I propose later to enumerate the several land-bridges which have been invoked to explain the distribution of the genera of earthworms common to India and other parts of the world.   But there is none of them the former existence of which seems to be better attested than that between Australia and India; this has almost become axiomatic in the minds of students of the Oligochæta.   The reason is, as has been said, the large number of genera that are common to India and the Australian region.

There can be no reasonable doubt that the western part of the Malay Archipelago has been joined on to the Asiatic mainland at no distant time; according to Wallace, "all the wide expanse of sea which divides the islands of Java, Sumatra, and Borneo from each other, and from Malacca and Siam, is so shallow that ships can anchor in any part of it, since it rarely exceeds forty fathoms in depth"; while the eastern part of the Archipelago has, with equal probability, formed a part of Australia.   Michaelsen assumes not only the passage of numerous genera of Megascolecidæ from the Australian side, but (or perhaps as an alternative) suggests that some may have passed back into Australia from outside (**16**).

But how does the hypothesis of land-bridges square with the other known facts of distribution?   I have given some reason for thinking that the whole of the earthworm fauna of the world, and in particular that part of it with which we are dealing at present. is of recent origin.   *Megascolex*, for example, is one of the youngest genera; its immediate ancestor *Notoscolex* is one stage further back; both are separated by a long line of ancestors from the earliest earthworms, which alone seems sufficient to bring their origin down to late Tertiary times; *Megascolex* appears to be evolving still, and has not as yet settled down to the comparative fixity of an old-established genus.

Now it is well known that, broadly speaking, Australia has no indigenous Eutherian population.   The great groups of terrestrial Eutherians originated in the Eocene—some in the very early Eocene—and spread rapidly thereafter.   How, on the supposition of a land-bridge, are we to let the Australian earthworms out to India without letting the Asian mammals into Australia?   If the door is open for the particularly slow-moving worms, it is open

for the quick-moving Carnivora; in asking for land-bridges to explain the distribution of the Oligochæta we get much more than we want. There can never have been a land connection between Australia and the great land mass to the north-west since the Eocene.

Still stronger is the case of the supposed connection between India and New Zealand. This is a necessity, according to Michaelsen, in order to explain the occurrence of the Octo-chætinæ in both lands; and since the Octochætinæ do not occur in Australia, the bridge in this case avoided Australia. New Zealand does not even contain Marsupials; yet *Octochætus*, the genus common to India and New Zealand, is not a particularly archaic genus, and its occurrence in both India and New Zealand would, on Michaelsen's view, have to be explained by, presumably, late or middle Tertiary land connections. But New Zealand is an oceanic island, and probably has never been connected at any time* with the larger land-masses, certainly not in Tertiary times.

It is quite possible that similar objections might be brought against the other land-bridges which have been postulated to explain the existence of related or identical genera of earthworms in distant lands. I have specially mentioned the above because it is so obvious, once attention has been drawn to it. The general principle is that, earthworms being a recent group, and requiring, on the hypothesis of dispersal by land, connections of some considerable permanence, other groups will have been able to pass even more easily ; and the dispersal of earthworms by land-bridges cannot be assumed unless there is a large degree of similarity between other elements of the fauna also.

(4) *Contributions towards a more satisfactory Solution.*

I trust that, in what follows, I shall not be considered to be treating too lightly the claims of zoogeography to a hearing in the discussion of the problems of palæogeography. As Michaelsen

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* Michaelsen's time-scheme can be put together somewhat as follows :—The oldest components of the Indian earthworm fauna date from the Upper Jurassic, when India was connected broadly with both Angara and Australia; *Plutellus* and *Megascolides* wandered off into Angara, reaching western N. America in the later Cretaceous. The chief part of the evolution took place in the Tertiary, the period of the changing land-bridges. In the Pliocene the now consolidated Indian peninsula became connected on the W. or N.W. with lands which had earlier received their earthworms from Tropical Africa (*Eudichogaster*).

It will be seen that he puts the evolution of the group earlier than I do; but I do not find anything which invalidates the line of argument and general conclusions of section 3 a above, especially that of the quite recent origin of the phyletically youngest genera such as *Megascolex*. The word used by Michaelsen for the period of the origin of the Indian Oligochæte fauna is "Malm," which corresponds (Ziegler, Zool. Wörterbuch) to the Upper Jura. *Plutellus* and *Megascolides* are supposed to have then been in existence ; is there any other example of genera of a variable and evolving group persisting since that period, especially genera, such as these, which are connected by intermediate gradations not only with each other, but with the genera below and above them (*Diplotrema* and *Notoscolex*), genera, that is, which are still not sharply marked off from their ancestors and descendants ?

says, " Since the present geographical distribution of earthworms depends in the first place on the configuration of land and sea in recent geological epochs, it is to be looked on as a valuable document for the history of the earth." We are not bound, that is, to accommodate our conceptions of the wanderings of the ancestors of the present-day fauna to the views founded on geological evidence only ; we also are in possession of important documents, and their evidence may perhaps be of superior cogency to that of geology. A zoologist is not likely to underrate the value of the evidence furnished by zoology ; only we must be sure what its value is.

And firstly, in the present case, even if there were no geological evidence, even if we were not told that " the geologic evidence for the general permanency of the abyssal oceans is over-whelmingly strong," it would be our duty not to introduce land connections unnecessarily. It is an old philosophical rule that " causæ non sunt multiplicandæ præter necessitatem " ; in the present case we may substitute " bridges," and say " pontes non sunt multiplicandi præter necessitatem." We have a number of agencies which are in existence before our eyes to-day : The slow extension of distribution by the normal wanderings of earth-worms, the extirpation of indigenous worms by younger forms of later introduction, the existence of natural rafts on the sea, the known ability of certain worms and their cocoons to endure salt water, the polyphyletic origin of certain genera, and moderate changes of land and sea ; and it may fairly be demanded that we exhaust the possibilities of these before we have recourse to the construction of bridges which we cannot see and which are at any rate much more hypothetical in nature.

Again, I speak only of those bridges which have been postulated in order to explain the distribution of Oligochæta, and especially of those Oligochæta which occur in the Indian and Australian regions. My contention is that the greater part of these are unnecessary in this connection ; whether they are a necessary assumption or not for other reasons, I must leave to others.

And first with regard to natural rafts. Matthew recalls the fact that these have several times been recorded as occurring over a hundred miles off the great tropical rivers such as the Ganges, Congo, Amazon, and Orinoco ; and for one such observed, a hundred may have drifted out unnoticed. Wallace, in his ' Island Life,' speaks of " those floating islands which are *often* (italics mine) formed at the mouths of great rivers. Sir Charles Lyell describes such floating islands which were encountered among the Moluccas" (*i. e.* between Celebes and New Guinea, where there is no large river) " on which trees and shrubs were growing on a stratum of soil which even formed a white beach round the margin of each raft. Among the Philippine Islands similar rafts with trees growing on them have been seen after hurricanes, and it is easy to understand how, if the sea were

tolerably calm, such a raft might be carried along by the current, aided by the wind acting on the trees, till after a passage of several weeks it might arrive safely on the shores of some land hundreds of miles away from its starting-point."

Overseas colonization is a very remote chance, it is true, in any given length of time; but, says Matthew, if we multiply the almost infinitely small chance that such colonization takes place in any given length of time, such as a year, by the almost infinite duration of geological periods, we obtain a finite and quite probable chance. For example, the time during which natural rafts have been observed covers about three centuries, while the duration of Cænozoic time is estimated as three million years; if we allow that ten cases of natural rafts have been recorded during these three centuries (the wording of the extract from Wallace given above would, however, seem to indicate that this is an understatement), a thousand may have actually occurred in this time, and hence thirty million in the whole Cænozoic (this is a miscalculation—it should be ten million). He then makes certain assumptions regarding the occurrence of living mammals on such rafts—as to the chances of there being a couple, or a gravid female, and as to the dangers of landing; and his conclusion is that the number of cases during the Cænozoic in which mammals will have established themselves on the larger oceanic islands is of the order of 300—quite enough at any rate to cover the dozen or two known cases. With invertebrates the chances would be much greater.

And certainly, whatever the possibilities of the transfer of mammals by rafts, the transfer of earthworms must be far more probable. Such rafts as have been described above may or may not bear mammals—Matthew's calculations are based on the supposition that they do so only once in a hundred times; but every one will probably contain earthworms, in the soil, under the bark of living trees, in the axils of their leaves, or in rotting wood. Nor are worms restricted to the larger rafts; the smaller worms of euryhaline groups (those that can withstand salt water) and especially their cocoons, may probably be transported for long distances in masses of tangled seaweed; Michaelsen, himself a bridge-builder, presses this point against Benham in explaining the distribution of *Microscolex* in the Subantarctic regions (13).

It may be asked, too, whether earthworms are in general so readily killed by salt water as is assumed. It is well known that many Enchytræids and Tubificids are regularly found on the shore; and among the higher groups the genera *Pontodrilus*, *Pontoscolex*, and *Microscolex* have the same habitat often, though not always; I have received *Hoplochætella* from the shore of western India, though the genus was not previously known from such localities. It is at least possible that many worms are capable of speedy acclimatization to salt, just as a fresh-water Amœba can be acclimatized by the gradual addition of salt to its water. And it is remarkable how difficult it is to come at any definite

experiment on the subject of worms and salt water; the statement that they are destroyed by it seems to be commonly accepted, without comment and without reference.

There are, of course, other possibilities of transport for worms, or for their cocoons—the mud on birds' feet for example; Benham calculates that a strongly flying bird could pass from Australia to New Zealand (1200 miles) in 36 hours. But the possibility that I most wish to insist on, after that of the occurrence of rafts—because I do not think that it has as yet received any attention—is that of the polyphyletic origin of some, at least, of the genera common to the Indian and Australian regions. I believe that this will go some distance towards explaining the presence of these common elements in the two faunas; evolution has proceeded on parallel lines, and the younger genera have not wandered from India to Australia or from Australia to India—they have been independently evolved in each region.

In my first sketch of the present argument the whole question of polyphyly in these genera was discussed in this place; it was, in fact, in reviewing their geographical distribution that I was brought up against the subject. But the space that I was obliged to devote to it seemed too great to assign to a subordinate heading, and I decided to treat it independently. The whole of the previous article, however, may logically be placed here, as a contribution towards a more satisfactory explanation of the facts of distribution.

We may finally proceed to a separate *consideration of the several bridges* which have been postulated; and here I shall usually take the conclusions of Michaelsen (with whom Beddard is in general agreement) as the basis of my own discussion, since he is the author who has treated the matter most fully. Michaelsen requires all the bridges to be mentioned, and the splitting up of India into islands as well; however, he regards himself as conservative in this matter. In a controversy with F. Sarasin (11) he says, " I am reproached with being too wanton in my bridge-building. I do not think that such a charge can be substantiated; on the contrary, I believe that we do not reckon sufficiently with the mobility of the earth's crust in this region " (*i. e.* the Indo-Australian region).

These bridges are as follows:—A bridge between Asia and N. America, to explain the occurrence of *Plutellus* and *Megascolides* in the western part of N. America; a transatlantic bridge between the W. Indies and Central America on the west and Africa on the east, and a bridge between Africa and India, to explain the occurrence in India of the Trigastrinæ; one between Australia and Further India over the present Malay Archipelago, and one across the present Bay of Bengal, said to be requisite to account for the distribution of the Megascolecinæ and Moniligastridæ; a particular bridge, at a particular time, between India and New

Zealand, to explain the distribution of the Octochætinæ; and lastly, we may add, in the opposite sense, a number of arms of the sea, stretching across India and dividing it into a number of islands, which formed a western extension of what is now the Malay Archipelago.

The bridge to N. America may be admitted. It would pass from the eastern end of Siberia to Alaska, and demands no considerable elevation of the floor of the ocean—indeed, a rise of 1000 feet would convert the N. Pacific into dry land as far south as the 60th parallel.

The case is otherwise with the bridge between Africa and India. What is asked for is something like the Lemuria of Wallace, or the Gondwana continent postulated by many geologists. The important question here concerns *Eudichogaster*, according to Michaelsen a member of the Trigastrinæ, and descended from *Trigaster*, which is endemic in the W. Indies and Mexico. Michaelsen supposes that either *Trigaster* crossed the Atlantic (by an Americo-African bridge) and made its way across Africa, and thence by the bridge now under discussion to India, where it evolved into *Eudichogaster* (suffering extermination in the African part of its range); or *Eudichogaster* originated from *Trigaster* on the American side, passed across in the same way, and was exterminated in Africa but maintained itself in India. But I think I have shown in a previous section that it is at least equally probable that *Eudichogaster* originated from *Octochætus* (or *Ramiella*); on this supposition *Eudichogaster* arose in India, to which it has thus always been confined.

I have myself argued that the Indian genus *Hoplochætella* may be descended from *Howascolex*, found in Madagascar (**20**), and Lemuria or Gondwana would form an easy path for its transport. But *Hoplochætella* is—or at any rate a number of species are—euryhaline, and are found on the shores of western India; and we must reckon with the possibility of transport from Madagascar in seaweed or other tangle; the S.W. monsoon blows in the required direction for several months of the year.

Dichogaster has reached most of the islands of the Malay Archipelago, and some of the Polynesian islands, as well as India, and there is no doubt that small species of this genus are frequently transported by man in the way of trade. It is admitted that there is no need whatever to introduce land-bridges to explain the wide occurrence of these species all over the East.

The last reason for assuming the former existence of the Indo-African bridge would be the presence of a Moniligastrid (though one widely different from the Oriental Moniligastridæ) in tropical East Africa. This African Moniligastrid is not descended from the Oriental branch of the family, nor the Oriental from the African; this follows from the position of the gizzards—in front of the genital segments in the African, behind in the Oriental worms. The alimentary tube, without special thickening in the common ancestor, has developed into a series of gizzards

in one place in the African, in another place in the Oriental branch. There is therefore no question of African forms having travelled to India, or of Indian forms to Africa ; the question is, where did the common ancestor live ? We can only say, we do not know. Smith and Green, the discoverers of the African form, do indeed suppose this ancestor to have arisen somewhere in Gondwanaland, whence the Syngenodriline branch migrated to Africa, the Moniligastrine to the Oriental region (17) ; but so far as I know there is no special reason for the supposition.

Wallace, as is well known, gave up Lemuria, and became a believer in the permanence of the ocean basins. Matthew states that there is no necessity for Gondwana, from a palæontological point of view—not even in the Palæozoic, if the interpretation of the facts of distribution is made along the lines he lays down (origin of groups in the north, spread towards the south, the more primitive groups first and furthest); the weakness of the original evidence for the former existence of Gondwana is forgotten, and new discoveries are interpreted in the light of it, as if its existence were well established.

The Americo-African bridge, from Central America to tropical Africa, does not concern us so closely, and in showing reason to believe that *Eudichogaster* originated in India, we entirely do away with the necessity for it so far as India is concerned. Whether the large number of African Dichogasters can be explained as easily as the large number of Indian and far Eastern species of this genus—as having been carried to their new homes in the way of trade or human intercourse—seems doubtful. At the same time, in assuming a land-bridge we are probably getting more than we ask for ; what we want is a passage for the extremely slow-moving earthworms, and when it is a matter of thousands of miles this passage must be one of some permanency ; what we actually get, therefore, is an easy and abundant passage, for a long space of time, for all the elements of the fauna, and a mingling of the animals of the two regions to an extent which has certainly never happened. I can only conclude that we are probably better off, on the whole, without the Americo-African bridge.

The objections to the Indo-Australian and Indo-New Zealand bridges have already been sufficiently insisted on. And not only are the objections more striking than elsewhere, but—at least in the case of the Australian bridge—the difficulty in dispensing with the connection is also smaller. The actual distance to be accounted for, as is well known, is not great. A union of the eastern part of the Malay Archipelago with Australia, and of the western part with Further India, is not only a feasible but a necessary supposition on every ground ; a land-bridge spanning the interval between the eastern and western parts of the Archipelago is objectionable except for the specific purpose of accounting for the distribution of the Oligochæta. Wallace placed the boundary between the two dissimilar faunas of the Australian and Oriental

regions between the islands of Bali and Lombok; this is the interval where the assumption of a land-bridge raises many more difficulties than it explains. But the interval is only fifteen miles; and while birds' feet and natural rafts offer a sufficient mode of transfer for worms and their cocoons, they cannot serve to transplant the mammals—not a whole mammalian fauna at any rate. It is, too, in the genera of the Megascolecinæ, the group which is common to India and Australia, that we have seen most reason to believe in polyphyletic origins; as bearing on the probability of polyphyly it is interesting to recall what Michaelsen says (7) concerning the broad differences between the Indian and Australian groups of *Megascolex*—that the Australian species are simpler, at a lower level of evolution, and more uniform, while the Ceylonese species are often further advanced and in many cases approach *Pheretima*. We can thus manage quite well with the veræ causæ we know, but the bridge would only embarrass us.

The distance to be overcome in the case of New Zealand is greater; but the general faunistic objections to a land connection with S.W. Asia (which is supposed to have avoided Australia) are greater also. We are compelled, therefore, to invoke the same agencies as before.

Michaelsen's plea for a bridge across the Bay of Bengal, by which worms from Australia, and also from Further India, could reach the south of the peninsula and Ceylon without going round by the head of the Bay, depends for its force on the presence in S. India and Ceylon of genera which are not found elsewhere in India; the argument is that if these genera had passed through the lands about the head of the Bay, they would have left there some trace of their passage. Thus *Drawida*, a Moniligastrid, common in S. India, and descended from a form which was probably not unlike *Desmogaster* (now found in Burma, Sumatra, and Borneo), was, when Michaelsen wrote, unknown from the intervening region, except for a few records of peregrine species. But more recent discoveries have shown that, both in the E. Himalayas and near the coast at the head of the Bay, there are a number of endemic species of *Drawida*; and it can no longer be urged that the Moniligastridæ cannot have passed round that way because they have left no trace of their passage. Certain genera of the Megascolecinæ also were supposed to show the same limitation of distribution. *Notoscolex* was only known from S. India and Ceylon, and the same was true of its descendant *Megascolex*. Lately, however, the E. Himalayas have been shown to harbour three species (and a variety) of *Notoscolex* (*Megascolides oneilli* is a *Notoscolex*); so that here again it can no longer be claimed that a bridge across the Bay of Bengal is necessary because otherwise the genus would have left some trace of its passage round the head of the Bay. And the polyphyletic origin of *Megascolex* is, I think, clear enough to allow us to dispense with the supposition that it migrated into India from outside, whether round the head of the Bay or by a land-bridge across it.

Finally, I do not think that Michaelsen's view that India was, in the past, divided by stretches of sea—shallow arms of the sea—into a number of disconnected islands, is necessary. A number of Indian genera do show, as he remarks, a limitation more or less definite to certain tracts of the country. These are *Megascolex* and *Notoscolex*, to the south of the peninsula and Ceylon; *Drawida*, though this genus can now scarcely be said to be even roughly limited to the south; *Eutyphœus*, to the Gangetic plain; *Eudichogaster*, to a broad belt across the middle; and perhaps *Hoplochœtella*, to western India. *Perionyx* has not now the strict limitation to the Himalayan region that was previously thought; nor is *Octochœtus* limited to any one part of the country—it seems to occur throughout. It is, on the whole, the youngest genera that are limited in distribution, and it would seem possible to explain this by supposing that they have not as yet had time to spread very widely, rather than that their dispersal has been hindered by arms of the sea. The conclusions of geology, moreover, seem to be against Michaelsen's view. "It has been conclusively proved that the peninsula of India has never been beneath the sea since the Carboniferous period at least." (Encyc. Britt., xi. ed., art. Asia, section Geology.)

References to Literature cited in Articles II. and III.

1. BEDDARD, F. E.—A Textbook of Zoogeography. Cambridge, 1895.
2.   „   Earthworms and their Allies. Cambridge, 1912.
3. BENHAM, W. B.—On some new Species of Aquatic Oligochæta from New Zealand. Proc. Zool. Soc., ii. 1903.
4.   „   Report on the Oligochæta, in : The Subantarctic Islands of New Zealand, vol. i. Wellington, N.Z., 1909.
5. MATTHEW, W. D.—Climate and Evolution. Annals N.Y. Acad. Sci., vol. xxiv. **1915.**
6. MICHAELSEN, W.—Oligochæta, in : Das Tierreich. Berlin, 1900.
7.   „   Die geographische Verbreitung der Oligochäten. Berlin, 1903.
8.   „   Die Oligochæten der deutschen Tief-See Expedition, in : Deutsche Südpolar Expedition, Ergebnisse, vol. iii. 1905.
9.   „   Oligochæta, in : Die Fauna Süd-West Australiens, vol. i. Jena, 1907.
10.   „   The Oligochæta of India, Nepal, Ceylon, Burma, and the Andaman Islands. Mem. Ind. Mus., vol. i. 1909.
11.   ,   Die Oligochätenfauna der vorderindisch-ceylonischen Region. Abh. Naturw. Verein Hamburg, vol. xix. 1910.
12.   „   Oligochäten von verschiedenen Gebieten. Mitth. Nathist. Mus. Hamburg, vol. xxvii. (Beiheft 2), 1910.
13.   „   Zur Kenntnis der Eodrilaceen und ihrer Verbreitungsverhältnisse. Zool. Jahrb., Syst. Teil, vol. xxx. 1911.
14.   „   Oligochäten von Travancore und Borneo. Mitth. Nathist. Mus. Hamburg, vol. xxx. (Beiheft 2), 1913.
14 a.   „   Oligochæta, in : Nova Caledonia, A. Zool. vol. i. 1913.
15.   „   Oligochäten, in : Ergebnisse der zweiten deutschen Zentral-Afrika-Expedition 1910–1911. Leipzig, 1915.
16.   „   Oligochäten, in : Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910–1913, pt. xiii. Stockholm, 1916.

17. SMITH, F., and BESSIE R. GREEN.—Descriptions of new African Earthworms, including a new genus of Moniligastridæ. Proc. U.S. Nat. Mus., vol. lv. 1919.

18. STEPHENSON, J.—Oligochæta, in : Zoological Results of the Abor Expedition. Rec. Ind. Mus., vol. viii. 1914.

19.   „   On some Indian Oligochæta, mainly from Southern India and Ceylon. Mem. Ind. Mus., vol. vi. 1915.

20.   „   On a collection of Oligochæta from various parts of India and Further India. Rec. Ind. Mus., vol. xiii. 1917.