THE GEOLOGICAL HISTORY OF MYRIOPODS AND ARACHNIDS.

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[Eighth annual address of the retiring president of the Cambridge Entomological Club.]

As the only subject of a general nature to which I have given recent attention I venture to invite you to review with me the geological history, first of myriopods and then of arachnids. Unusual attention has recently been paid to these animals, on account of the discovery of their remains in formations much earlier than those from which they had for a long time been known, and the relation of these discoveries to our previous knowledge will be best brought out by such a review, and it will, to a certain extent, be timely.

Our knowledge of the morphology, systematic position and extent of the myriopoda has been greatly increased within a recent period. The discovery of the minute Pauropus by Lubbock, and the study of this and allied forms by Ryder and others, have led to the establishment of the pauropoda as a type of living myriopods of equal taxonomic value to the two groups of chilopoda and diplopoda which had long been looked upon as the only divisions of the group. Modern investigations into the structure of the anomalous Peripatus have extended our ideas concerning the types allied to the myriopoda; while the strange forms revealed by recent researches in the carboniferous and devonian faunas have compelled us to recognize a wider range in its structure and a multiplication of its primary groups. The relations of ancient to modern forms of life prove far more important and interesting in the myriopoda than in either the arachnida or the hexapoda. That these relations are equally puzzling will appear from a brief review of the structure and development of the different groups.

In the early life of the pauropoda and of the diplopoda we have what may be fairly considered a true larval form, in which, for a brief period after leaving the egg, the body, much shorter than in after life, is provided with three pairs of legs borne upon the anterior segments of the body. These segments are never more fully provided with legs, though most of the segments posterior to them, both those which exist during this larval period and those which originate subsequently, bear two pairs. In the chilopoda, on the other hand, although the appendages of the anterior segments develop earlier than those behind them, there is no true larval condition, or perhaps one may say a larval condition is permanent, in that the same anterior legs become early and permanently developed as organs subsidiary to manducation, while the segments of the hinder part of the body develop only a single pair of legs.

The larval condition and resultant more or less highly developed metamorphosis of the higher hexapoda have been looked upon by many as a secondary after-development, and one which therefore in no sense gives any clue to the historical development of the group,
such as we frequently find mirrored in the embryonic growth of other animals. This view seems to be supported by a comparison of the modern and ancient types of myriopoda. The larval characteristics of the young of living types of myriopoda, marvelously analogous in their main features to those of the larvae of even the higher hexapoda, are confined to the apodal nature of the abbreviated abdomen, and more particularly to the specialized development of appendages on the segments directly following the head. This specialized condition of the anterior segments is, in a sense, analogous to the structure of the thorax of the hexapoda and is persistent throughout life,—in the chilopoda in a marked manner, in the other groups by the isolation of these segments as bearing but a single pair of legs. Now nothing of this specialization appears in the paleozoic types, of which of course we know only the mature forms; but the segments following the head differ in no point whatever from those of the remainder of the body in the character and number of their appendages. In one type, the archipolypoda, corresponding in a measure to the living type of diplopoda, two pairs of legs are borne on every segment; while in the other, the protosyngnatha, corresponding in a similar way to the chilopoda, a single pair of legs is found. If then we look upon the specialization of the segments (or the appendages of the segments) immediately following the head in living myriopodan types as a secondary development, or, we may say, as the initiatory stage in an acquiring metamorphosis; then we may perhaps consider the archipolypoda as the true prototypes of the diplopoda and possibly also of the pauropoda, and the protosyngnatha as the prototypes of the chilopoda.

In this view, one principal distinction between the modern diplopoda and chilopoda is shown to have existed from paleozoic times, viz: that in one group there are, over most of the body, to each dorsal scute two ventral scutes, each bearing a pair of legs; in the other group a single ventral scute with a single pair of legs; and it becomes interesting to inquire whether we can discover any indication of the condition of things from which this diversity of structures arose, and what was the line of development through which it passed. It will also help to determine the question, whether the dorsal or the ventral scutes of the diplopoda are to be looked upon as the homologs of those of the chilopoda; or, in other words, whether the dorsal scutes of the diplopoda are compound, or the ventral scutes of the same are to be looked upon as subsegments.

It should be remarked at the outset that what we know of the embryology of recent types shows that in the diplopoda two pairs of legs, in the chilopoda one pair, arise from each original body somite beyond the front portion of the body. This would indicate that the dorsal scutes of the two groups were homologous and the ventral scutes of the diplopoda should be looked upon as representing subsegments. This, however, is not the answer indicated by the paleontological evidence, nor is it what we should expect from, among
other things, the presence of stigmata on each of the ventral scutes in diplopoda.* All the carboniferous archipoly-
poda show a clear indication of the compound nature of the segments. Not
only were the ventral scutes far more
important and extensive than in the
modern diplopoda, but some at least
of the genera bore in addition to large
stigmata outside the legs, a pair of seg-
mental organs next the medioventral
line on each ventral scute; the dorsal
scute was also distinctly divided into two
areas, an anterior and a posterior. In
some types this latter distinction was
more marked than in others, in some
being carried so far that under certain
conditions of preservation one would
readily take them to be entirely sepa-
rate; and this indeed appears to be
absolutely the case in the older devo-
nian forms, from the lower old red sand-
stone of Scotland. These show an
apparently complete demarcation of the
dorsal scutes of each segment as well as
of the ventral, and present therefore a
series of alternating larger and smaller
segments, the larger bearing all the
dorsal cuticular outgrowths, but each
bearing a single pair of legs. Of this
primal condition of the body segments
the embryology of modern types gives
no hint, its earliest indications showing
nothing anterior to what must have
been the condition of things wholly
posterior to the paleozoic epoch, at least
so far as the diplopoidan series is con-
cerned; nothing anterior, indeed, to the
fixed condition of the present type.

This indicates that the present dorsal
scutes of diplopoda are compound and
formed of two originally distinct scutes;
and that, as a later development of a
similar sort, the ventral scutes of the
anterior segments have likewise con-
solidated and lost each one pair of
appendages.

Under this view the line which we
follow back from the chilopoda through
the protosynghnatha is the more nearly
allied to the simple stock type. Yet it
is the other line which has been found
earliest in the rocks, clearly showing
that the actual origin of the myriopodan
phylum must be looked for at the very
first appearance of land animals; in-
 deed the evidence that some of the
carboniferous types were amphibious
may warrant our belief that the type
may have fairly originated among aqua-
tic animals.

Fossil myriopoda were first made
known from the carboniferous rocks,
when Westwood figured, in Brodie’s
work on the older fossil insects of
England, the remains of what he sup-
posed to be a lepidopterous larva.
There had been indeed earlier refer-
ences by name merely to tertiary myri-
opoda from amber and from Aix (Ser-
res), but it was not until the publications,
 thirty years ago, of Koch, Berendt and
Menge, that the amber species were
known, and to them hardly any ad-
tions have since been made. In
1859 Sir William Dawson published the
first account of a paleozoic myriopod re-
cognized as such, and since 1868 our
horizon, as regards the older forms, has
been widened materially by the publica-
tions of Messrs. Dohrn, Meek and

*They are only borne in general on alternate seg-
ments in chilopoda.
Worthen, Peach, Scudder, and Woodward, until to-day the number of forms known from pretertiary deposits is nearly as great as those from the tertiary.

The oldest known are those described by Page and Peach from the lower old red sandstone of Scotland—two species belonging to the archipolypoda. In the carboniferous formation the archipolypoda culminate, showing a considerable variety of generic types distinct from those of the devonian, and embracing nearly thirty species, of which by far the greater number come from America, and the few remaining ones from Great Britain, with possibly a single species from Germany. Four species, imperfectly known, which have been referred to Iulus, and which come from the permian of central Europe may belong to the archipolypoda. The only mesozoic forms known are the Fulopsis cretacea of Heer, from Greenland, which is either an archipolypod or a diplopod (it is impossible to tell which), and the uncertain Geophilus proavus of Münster from Solenhofen, which is probably to be looked upon as a nereid worm.

The tertiary species are still known almost entirely from the work of Koch and Berendt, and belong entirely to the diplopoda and chilopoda, the larger proportion to the former. A few species, however, have been indicated from Aix, a single one described from the brown coal of Rott and one from the Green River deposits of North America.

The following table presents a view of the distribution of the myriopoda in time.

### Geological distribution of myriopoda.

<table>
<thead>
<tr>
<th></th>
<th>Paleozoic</th>
<th>Mesozoic</th>
<th>Cenozoic</th>
<th>Modern Period</th>
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<tbody>
<tr>
<td>Protosyngnatha</td>
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<tr>
<td>Chilopoda</td>
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<td>(4?)</td>
<td>(1?)</td>
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<tr>
<td>Archipolypoda</td>
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<td>31</td>
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<tr>
<td>Diplopoda</td>
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<td>Pauropoda</td>
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The geological history of arachnida, as known at the present time, presents some points of interest. Only a portion of the great groups into which the order is divisible are represented in the older rocks, and these, which are not confined to the lower types, attain a degree of perfection and
a diversity of structure inconsistent with a belief in our having reached the primordial forms of this phylum in our retrograde search.

When, in 1858, Bronn published his prize essay on the distribution of fossils, only two species of pretertiary arachnida were known as such, one from the carboniferous and one from the jurassic formation, and the knowledge of tertiary forms was confined entirely to the then recently published work of Koch and Berendt on the species from amber. Since then Menge has increased somewhat our knowledge of the amber fauna, and it includes to-day nine-tenths or more of the known tertiary species. But it is only within the last fifteen years that our knowledge of pretertiary arachnida has been extended beyond the description of two or three species. The number is still exceedingly few—between 20 and 30 species—but it is being constantly extended, and the abundance of arthropoda brought to light in recent years in the carboniferous deposits of Allier, Bohemia, Scotland and Illinois leads us to expect an early and considerable extension of the list. This expectation is strengthened by Lindström’s and Hunter’s discoveries of scorpions in the upper Silurian rocks of Gotland and Scotland.

The forms that have been found fossil in the earlier formations have proved, as might be expected, to belong mostly to those having a dense integument, and in the two species believed to be true araneae, the abdomen was probably provided with more or less densely chitinous dorsal plates. With these two exceptions, and a single genus of pedipalpi, all the paleozoic arachnida (only a single mesozoic form is known) belong either to the scorpiones or to a peculiar group, the anthracomartis. This group is not found later, and the single known species of mesozoic arachnida* is a true Aranea. The paucity of remains of arachnida in mesozoic strata is somewhat remarkable. Besides the species mentioned above, only one other has been indicated, a species supposed to belong to the araneae, from the English lias.

Thanks to the amber deposits of Prussia, we know far more about the tertiary history of arachnida than would be possible if our sole reliance were on the rocks, the latter furnishing us with only about double the number of those occurring in pretertiary deposits. In the amber alone occur all the suborders of arachnida, excepting the pedipalpi and the already extinct anthracomartis, as well as all the families of araneae excepting one peculiar to the jurassic; but in the tertiary rocks neither chelone-thi, scorpiones nor opiliones have been recognized; of the pedipalpi, a single species is referred to by Serres from the marnez of Aix, but too obscurely to take account of it.

Examining the araneae alone, which are far better represented in the tertiaries than are the other suborders, we find a very large number of extinct genera. In all, seventy-one are now known,

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* Pulpipes or Phalangites, believed even by Thorell to be an arachnid, has been shown by Seebach to be a stomatopodous crustacean.
sixty-six from Europe and thirteen from America, eight being common to both. Of these 37 are accounted extinct, 35 from Europe and 2 from America, and none of these have been found on both continents.

In the stratified tertiary deposits the same families of araneae are in every instance found in Europe and America, excepting the dysderides, which family has a single representative in America and none in Europe. It also appears that just those families which are represented abundantly in amber are also found to some extent in the American tertiary fauna, and (excepting, as before, the dysderides) in the European rocks.

It is only in the rocks of the temperate regions of Europe and North America that any arachnida have been found in a fossil state, and these, so far as the indications have any meaning, invariably point, whether in carboniferous or tertiary deposits, to a warmer climate than now obtains in the localities where they occur. This becomes more marked when we reach the tertiary rocks and can compare the types more closely with existing forms, a number of the genera, to which, for instance, the amber spiders belong, being now exclusively tropical.

The following table gives a general systematic view of the distribution of arachnida in the different geological formations since their first appearance in the upper silurian.

**Geological distribution of arachnida.**

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