Fig. 5. Median part of radula (magnified).
Fig. 6. Lateral part of radula.
Fig. 7. Marginal part of radula.
Fig. 8. Mandible (magnified).
Fig. 9. Reproductive organs. *hg*, hermaphrodite gland; *e*, its efferent duct; *alb*, albuminiferous gland; *od*, oviduct (prostatic portion); *od'*, oviduct (infraprostatic portion); *sp*, spermatheca; *vd*, vas deferens; *pe*, penis; *v*, vestibule.
Figs. 10, 11. Shell (magnified).

XXIII.—*Relation of Devonian Insects to Later and Existing Types.* By Samuel H. Scudder*.

It only remains to sum up the results of this reexamination of the Devonian insects, and especially to discuss their relation to later or now existing types. This may best be done by a separate consideration of the following points:—

1. There is nothing in the structure of these earliest-known insects to interfere with a former conclusion † that *the general type of wing-structure has remained unaltered from the earliest times.* Three of these six insects (*Gerephemera*, *Homothetus*, and *Xenoneura*) have been shown to possess a very peculiar neuration, dissimilar to both Carboniferous and modern types. As will also be shown under the tenth head, the dissimilarity of structure of all the Devonian insects is much greater than would be anticipated; yet all the features of neuration can be brought into perfect harmony with the system laid down by Heer.

2. *These earliest insects were Hexapods*, and, as far as the record goes, preceded in time both Arachnids and Myriopods. This is shown only by the wings, which in all known insects belong only to Hexapods, and in the nature of things prove the earlier apparition of that group. This, however, is so improbable on any hypothesis, that we must conclude the record to be defective.

3. *They were all lower Heterometabola.* As wings are the only parts preserved, we cannot tell from the remains themselves whether they belong to sucking or to biting insects; for, as was shown in the essay already referred to, this point must be considered undetermined concerning many of the older insects until more complete remains are discovered.

* From the 'American Journal of Science,' Feb. 1881.
This summary of results is the conclusion of a memoir by Mr. Scudder "On the Devonian Insects of New Brunswick," published in the 'Anniversary Memoirs of the Boston Society of Natural History,' 1880.

† "The Early Types of Insects," Mem. Bost. Soc. Nat. Hist. iii. p. 21.

They are all allied or belong to the Neuroptera, using the word in its widest sense. At least two of the genera (*Platephemera* and *Gerephemera*) must be considered as having a closer relationship to Pseudoneuroptera than to Neuroptera proper, and as having indeed no special affinity to the true Neuroptera other than is found in Palæodictyoptera. Two others (*Lithentomum* and *Xenoneura*), on the contrary, are plainly more nearly related to the true Neuroptera than to the Pseudoneuroptera, and also show no special affinity to true Neuroptera other than is found in Palæodictyoptera. A fifth (*Homothetus*), which has comparatively little in common with the Palæodictyoptera, is perhaps more nearly related to the true Neuroptera than to the Pseudoneuroptera, although its pseudoneuropterous characters are of a striking nature. Of the sixth (*Dyscritus*) the remains are far too imperfect to judge clearly; but the choice lies rather with the Pseudoneuroptera or with *Homothetus*. The Devonian insects are then about equally divided in structural features between Neuroptera proper and Pseudoneuroptera; and none exhibit any special orthopterous, hemipterous, or coleopterous characteristics.

4. *Nearly all are synthetic types of a comparatively narrow range.* This has been stated in substance in the preceding paragraph, but may receive additional illustration here. Thus *Platephemera* may be looked upon as an Ephemerid with an odonate reticulation; *Homothetus* might be designated as a Sialid with an odonate structure of the main branch of the scapular vein; and under each of the species will be found detailed accounts of any combination of the characters which it possesses.

5. *Nearly all bear marks of affinity to the Carboniferous Palæodictyoptera*, either in the reticulated surface of the wing, its longitudinal neuration, or both. But besides this there are some, such as *Gerephemera* and *Xenoneura*, in which the resemblance is marked. Most of the species, however, even including the two mentioned, show palæodictyopterous characters only on what might be called the neuropterous side; and their divergence from the Carboniferous Palæodictyoptera is so great that they can scarcely be placed directly with the mass of Palæozoic insects, where we find a very common type of wing-structure, into which the neuration of Devonian insects only partially fits. For

6. *On the other hand, they are often of more and not less complicated structure than most Palæodictyoptera.* This is true of the three genera mentioned above with peculiar neuration, but not necessarily of the others; and it is especially true when they are compared with the genus *Dictyoneura* and

its immediate allies. There are other Palæodictyoptera in the Carboniferous period with more complicated neuration than *Dictyoneura*; but these three Devonian insects apparently surpass them, as well as very nearly all other Carboniferous insects. Furthermore,

7. With the exception of the general statement under the fifth head, *they bear little special relation to Carboniferous forms, having a distinct facies of their own.* This is very striking; it would certainly not be possible to collect six wings in one locality in the Carboniferous rocks which would not prove, by their affinity with those already known, the Carboniferous age of the deposit. Yet we find in this Devonian locality not a single one of Palæoblattariæ, or any thing resembling them; and more than half the known insects of the Carboniferous period belong to that type. The next most prevailing Carboniferous type is *Dictyoneura* and its near allies, with their reticulated wings. *Gerephemera* only of all the Devonian insects shows any real and close affinity with them; and even here the details of the wing-structure, as shown above, are very different. The apical half of the wing of *Xenoneura* (as I have *supposed* it to be formed) also bears a striking resemblance to the Dictyoneuran wing; but the base (which is preserved, and where the more important features lie) is totally different. The only other wing which shows particular resemblance to any Carboniferous form (we must omit *Dyscritus* from this consideration, as being too imperfect to be of any value) is *Platephemera*, where we find a certain general resemblance to *Ephemerites Rückerti*, Gein., and *Acridites priscus*, Andr.; but this is simply in the form of the wing and the general course of the nervules; when we examine the details of the neuration more closely, we find it altogether different, and the reticulation of the wing polygonal, and not quadrate as in the Carboniferous types *. In this respect, indeed, *Platephemera* differs not only from all modern Ephemeridæ, but also from those of other geological periods †. Another prevailing Carboniferous type, the Termitina, is altogether absent from the Devonian. Half a dozen wings, therefore, from rocks known to be either Devonian or Carboniferous would probably establish their age.

* Dr. H. B. Geinitz has kindly reexamined *Ephemerites Rückerti* at my request, and states that the reticulation is in general tetragonal, but that at the extreme outer margin the cells appear in a few places to be elliptical five- or six-sided.

† The *Dictyoneuræ* and their allies, as may be inferred, are considered as belonging to the Palæodictyoptera, although their ephemeridan affinities are not disregarded.

8. *The Devonian insects were of great size, had membranous wings, and were probably aquatic in early life.* The last statement is simply inferred from the fact that all the modern types most nearly allied to them are now aquatic. As to the first, some statements have already been made; their expanse of wing probably varied from 40 to 175 millims., and averaged 107 millims. *Xenoneura* was much smaller than any of the others, its expanse not exceeding 4 centims., while the probable expanse of all the rest was generally more than a decimetre, only *Homothetus* falling below this figure. Indeed, if *Xenoneura* be omitted, the average expanse of wing was 121 millims., an expanse which might well be compared to that of the Æschnidæ, the largest, as a group, of living Odonata. There is no trace of coriaceous structure in any of the wings; nor in any are there thickened and approximate nervules—one stage of the approach to a coriaceous texture.

9. *Some of the Devonian insects are plainly precursors of existing forms, while others seem to have left no trace.* The best examples of the former are *Platephemera*, an aberrant form of an existing family, and *Homothetus*, which, while totally different in the combination of its characters from any thing known among living or fossil insects, is the only Palæozoic insect possessing that peculiar arrangement of veins found at the base of the wings of the Odonata, typified by the arculus, a structure previously known only as early as the Jurassic. Examples of the latter are *Gerephemera*, which has a multiplicity of simple parallel veins next the costal margin of the wing, such as no other insect, ancient or modern, is known to possess, and *Xenoneura*, where the relationship of the internomedian branches to each other and to the rest of the wing is altogether abnormal. If, too, the concentric ridges, formerly interpreted by me as possibly representing a stridulating organ, should eventually be proved an actual part of the wing, we should have here a structure which has never since been repeated even in any modified form.

10. *They show a remarkable variety of structure, indicating an abundance of insect life at that epoch.* This is the more noticeable from their belonging to a single type of forms, as stated under the seventh head, where we have seen that their neuration does not accord with the commoner type of wing-structure found in Palæozoic insects*. These six wings exhibit a diversity of neuration quite as great as is found among the hundred or more species of the Carboniferous epoch: in some, such as *Platephemera*, the structure is very simple; in others, like *Homothetus* and *Xenoneura*, it is some-

* *Cf.* Mem. Bost. Soc. Nat. Hist. iii. 19, note 1.

what complicated: some of the wings, as *Platephemera* and *Gerephemera*, are reticulated; the others possess only transverse cross veins, more or less distinct and direct. No two wings can be referred to the same family, unless *Dyscritus* belongs with *Homothetus*—a point which cannot be determined, from the great imperfection of the former. This compels us to admit the strong probability of an abundant insect-fauna at that epoch. Although many Palæozoic localities can boast a greater diversity of insect types if we look upon their general structure as developed in after ages, not one in the world has produced wings exhibiting in themselves a wider diversity of neuration; for the neuration of the Palæodictyoptera is not more essentially distinct from that of the Palæoblattariæ or of the ancient Termitina than that of *Platephemera* or *Gerephemera* on the one hand is from that of *Homothetus* or *Xenoneura* on the other. Unconsciously, perhaps, we allow our knowledge of existing types and their past history to modify our appreciation of distinctions between ancient forms. For while we can plainly see in the Palæoblattariæ the progenitors of living insects of one order, and in other ancient types the ancestors of living representatives of another order, were we unfamiliar with the divergence of these orders in modern times, we should not think of separating ordinarily their ancestors of the Carboniferous epoch. It may easily be seen, then, how it is possible to find in these Devonian insects (all Neuroptera or neuropterous Palæodictyoptera) a diversity of wing-structure greater than is found in the Carboniferous representatives of the modern Neuroptera, Orthoptera, and Hemiptera.

11. *The Devonian insects also differ remarkably from all other known types, ancient or modern; and some of them appear to be even more complicated than their nearest living allies.* With the exception of *Platephemera*, not one of them can be referred to any family of insects previously known, living or fossil; and even *Platephemera*, as shown above, differs strikingly from all other members of the family in which it is placed, both in general neuration and in reticulation, to a greater degree even than the most aberrant genera of that family do from the normal type. This same genus is also more complicated in wing-structure than its modern allies; the reticulation of the wing in certain structurally-defined areas is polygonal and tolerably regular, instead of being simply quadrate, while the intercalated veins are all connected at their base, instead of being free. *Xenoneura* also, as compared with modern Sialina, shows what should perhaps be deemed a higher (or at least a later) type of structure, in the amalgamation of the externo-median and scapular

veins for a long distance from the base, and in the peculiar structure and lateral attachments of the interno-median veins; in the minuter and feebler cross venation, however, it has an opposite character.

12. *We appear, therefore, to be no nearer the beginning of things in the Devonian epoch than in the Carboniferous*, so far as either greater unity or simplicity of structure is concerned; and these earlier forms cannot be used to any better advantage than the Carboniferous types in support of any special theory of the origin of insects. All such theories have required some *Zoëa*, *Leptus*, *Campodea*, or other simple wingless form as the foundation-point; and this ancestral form, according to Häckel at least, must be looked for above the Silurian rocks. Yet we have in the Devonian no traces whatever of such forms, but, on the contrary, as far down as the middle of this period, winged insects with rather highly differentiated structure, which, taken together, can be considered lower than the mass of the Upper Carboniferous insects only by the absence of the very few Hemiptera and Coleoptera which the latter can boast. Remove those few insects from consideration (or simply leave out of mind their future development to very distinct types), and the Middle Devonian insects would not suffer in the comparison with those of the Upper Carboniferous, either in complication or in diversity of structure. Furthermore, they show no sort of approach toward either of the lower wingless forms hypothetically looked upon as the ancestors of tracheate Articulata.

13. *Finally, while there are some forms which to some degree bear out expectations based on the general derivative hypothesis of structural development, there are quite as many which are altogether unexpected, and cannot be explained by that theory without involving suppositions for which no facts can at present be adduced. Palephemera* and *Gerephemera* are unquestionably insects of a very low organization related to the existing may-flies, which are well known to be of inferior structure as compared with other living insects; these may-flies are indeed among the most degraded of the suborder to which they belong, itself one of the very lowest suborders. *Dyscritus* too may be of similar degradation, although its resemblance to *Homothetus* leaves it altogether uncertain. But no one of these exhibits any inferiority of structure when compared with its nearest allies in the later Carboniferous rocks; and they are all higher than some which might be named; while of the remaining species it can be confidently asserted that they are higher in structure than most of the Carboniferous types, and exhibit syntheses of character differing from theirs.

It is quite as if we were on two distinct lines of descent when we study the Devonian and the Carboniferous insects: they have little in common; and each its peculiar comprehensive types. Judging from this point of view, it would be impossible to say that the Devonian insects showed either a broader synthesis or a ruder type than the Carboniferous. This, of course, may be, and in all probability is, because our knowledge of the Carboniferous insects is in comparison so much more extensive; but, judging simply by the facts at hand, it appears that the Carboniferous insects carry us back both to the more simple and to the more generalized forms. We have nothing in the Devonian so simple as *Euephemerites*, nothing so comprehensive as *Eugereon*, nothing at once so simple and comprehensive as *Dictyoneura*. On the derivative hypothesis we must presume, from our present knowledge of Devonian insects:—that the Palæodictyoptera of the Carboniferous are already, in that epoch, an old and persistent embryonic type (as the living Ephemeridæ may be considered today, on a narrower but more lengthened scale); that some other insects of Carboniferous times, together with most of those of the Devonian, descended from a common stock in the Lower Devonian or Silurian period; and that the union of these with the Palæodictyoptera was even further removed from us in time, carrying back the origin of winged insects to a far remoter antiquity than has ever been ascribed to them, and necessitating a faith in the derivative hypothesis which a study of the records preserved in the rocks could never alone afford; for no evidence can be adduced in its favour based only on such investigations. The profound voids in our knowledge of the earliest history of insects, to which allusion was made at the close of my paper "On the Early Types of Insects," are thus shown to be even greater and more obscure than had been presumed. But I should hesitate to close this summary without expressing the conviction that some such earlier unknown comprehensive types as are indicated above did exist and should be sought.

XXIV.—*On Siliceous Sponge-growth in the Cretaceous Ocean.*

By Surgeon-Major Wallich, M.D.

A few days after the publication of the 'Annals' for February, I obtained a sight of Mr. G. J. Hinde's very interesting little work on Fossil Sponge-spicules found in the