

II. THE EARLY TYPES OF INSECTS; OR THE ORIGIN AND SEQUENCE OF INSECT LIFE IN PALAEOZOIC TIMES.

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Read Nov. 20, 1878.

IN THE year 1833, Audouin exhibited at a meeting of the Entomological Society of France the wing of an orthopterous insect from Coalbrook Dale in England.<sup>1</sup> This was the first discovery of insects in the coal-formation. Since then many authors, notably Germar and Goldenberg,<sup>2</sup> have added to our knowledge of the insects of the palaeozoic rocks, until now perhaps one hundred species are known. Yet insect remains in these strata may still be looked upon as the greatest rarities. By far the larger part of these hundred species are known to us by single specimens, and very fragmentary ones at that—a wing or even a mere piece of a wing being usually all that we know of a given form. It has been claimed by some writers that we should anticipate the earliest types of insects to be winged and not apterous, and the remains that have been found would seem at first glance to sustain such a hypothesis. But as the wings retain after inhumation more characteristic features than other parts of the body, it is not surprising that naturalists have made most use of them in describing the fossil forms; and we should scarcely be warranted in deducing therefrom the absence of other fragments of the body; moreover a characteristically apterous form of

<sup>1</sup> Ann. Soc. Ent. France, Vol. II, Bull., p. 7-8. It is also stated that the same specimen was exhibited by Audouin on Feb. 25, 1833, before the Académie des Sciences; but no report of the meeting was published, unless in *Le Temps* newspaper, which I have not seen. The insect was considered by Audouin as neuropterous, but has recently been shown by Swinton to be orthopterous.

<sup>2</sup> For Germar's writings on palaeozoic insects, see the following:—1. Beschreibung einiger neuen fossilen Insecten. < Münst., Beitr. z. Petref., v: 79-94, pl. 9, 13. 4°. Bayreuth, 1842.—2. Die Versteinerungen des Steinkohlengebirges von Wettin und Löbejün in Saalkreise. f. Halle, 1844-53.

For those of Goldenberg, see the following:—1. Prodröm einer Naturgeschichte der fossilen Insecten der Kohlenformation von Saarbrücken. < Sitzungsber. math.-nat. Cl. K. Akad. Wiss. Wien, ix: 38-39. 8°. Wien, 1852. (In this his name is given as Goldberger).—2. Brief an Herrn v. Carnall. < Zeitschr. Deutsch. Geol. Gesselsch., iv: 246-48. 8°. Berlin, 1852.—3. Ueber versteinerte Insectenreste in Steinkohlengebirge von Saarbrücken. < Amtl. Ber. Vers. Gesellsch. deutsch. Naturf., xxix: 123-26. 4°. Wiesbaden, 1852.—4. Die fossilen Insecten der Kohlenformation von

Saarbrücken. < Palaeontogr., iv: 17-40, pl. 3-6. 4°. Cassel, 1851.—5. Beiträge zur vorweltlichen Fauna des Steinkohlengebirges zu Saarbrücken (Uebersicht der Thierreste der Kohlenformation von Saarbrücken). < Jahresh. K. Gymn. u. Vorsch. Saarbr., 1867, 1-26. 4°. Saarbrücken, 1867.—6. Zur Kenntniss der fossilen Insecten in der Steinkohlenformation. < Neues Jahrb. f. Mineral., 1869: 158-68, pl. 3. 8°. Stuttgart, 1869.—7. Zwei neue Ostracoden und eine Blattina aus der Steinkohlenformation von Saarbrücken. < Neues Jahrb. f. Mineral., 1870: 286-89 with figures in text. 8°. Stuttgart, 1870.—8. Fauna Saraepontana fossilis. Die fossilen Thiere aus der Steinkohlenformation von Saarbrücken. Heft 1-2. 4°. Saarbrücken, 1873-77. (Heft 1 is the same as No. 5, above, with the addition of plates; a supplementary part is promised by Goldenberg.)

For other papers descriptive of the palaeozoic insects of Europe, see the writings of Andree, van Beneden and Coemans, Preudhomme de Borre, Brodie, Charles Brongniart, Buckland, Corda, Curtis, Dohrn, Fric, Geinitz, Giebel, Hagen, Heer, Jordan and Meyer, Kirkby, Mahr, Murchison, Roemer, Rost, Salter, Sternberg, Swinton, and Woodward; and for those of America, papers by Dana, Dawson, Harger, Lesquereux, Meek and Worthen, Scudder, and Smith.

cockroach<sup>1</sup> has been described from the rocks of Saarbrücken, which are as old as any of the insect-bearing beds of Europe. The insects of the middle Devonian of New Brunswick,<sup>2</sup> on the other hand, are known only by their wings and the most diligent examination of thousands of fragments of shale has failed to reveal anything else. Further discussion of this point may be dismissed with the remark that geological data are not likely to throw much light upon it.

It is of course of prime importance that we should understand the relative subordination of groups in insects, before investigating their order of succession in time. Many attempts have been made to harmonize the current views of their relative rank and geological succession; but hitherto with indifferent success, mainly from the prevalence of the opinion that Coleoptera were to be ranked highest among insects, while this suborder has been known, from the first, to occur in Carboniferous strata, and some other suborders only much later. Another obstacle which has stood in the way of a clear comprehension of the facts has been the very common division of hexapod insects into two series, upon which the English entomologists have perhaps specially insisted, called Mandibulata and Haustellata, a division based upon inadequate physiological grounds. Or if it be maintained that the function expressed in these names has a structural basis, it would be easy to point out that in either of the two divisions the diversity of structure of the mouth parts is so great as to admit of no common expression in other than physiological terms. If it were not so, the claim made by Agassiz,<sup>3</sup> on embryological grounds, of a higher rank for the haustellate insects would hold good, and we should be at a loss to account for the simultaneous appearance of Coleoptera and Hemiptera.

An apparently more rational division of the true insects into two series is that which separates those with complete from those with incomplete metamorphosis; the young in the former case unlike, in the latter resembling, the parent. This however, taken absolutely, separates closely allied groups, such as the caddice flies and dragon flies, and one form of metamorphosis shades into the other; moreover it allies the Coleoptera with the Hymenoptera rather than with the Hemiptera or Orthoptera, and disaccords to so great a degree with the general relations of structure among insects as to show that it cannot be considered as of so fundamental an importance as we should suppose it would prove. Yet it is an important factor in the life history of insects, and cannot be disregarded totally, as is done in divisions based upon the mouth parts, but must be considered in any attempted distribution of the suborders. So too must the nature of the wings, for the possession of wings is the preëminent characteristic of hexapods as a whole, and we should naturally anticipate fundamental features in the differences of their structure.

My own view of the primary relations of the suborders of hexapods was first expressed by Packard in 1863,<sup>4</sup> when he said that Coleoptera, Hemiptera, Orthoptera, and Neuroptera "seem bound together by affinities such as those that unite by themselves the bees, moths and flies." To the latter or higher series he has since applied<sup>5</sup> the term METABOLA

<sup>1</sup> (*Polyzosterites granosus*.) Goldenb., Faun. Sar. foss., 1: 18, pl. 1, fig. 17.

<sup>2</sup> These Devonian insects, which were first briefly noticed by Lee in Bailey's Observations on the Geology of Southern New Brunswick (8<sup>o</sup>. Fredericton, 1865) will form the subject of a special paper now nearly completed.

<sup>3</sup> L. Agassiz. Classif. ins. embryol. data. pp. 4-8.

<sup>4</sup> Packard. On synthetic types in insects. Bost. Journ. Nat. Hist., VII: 591-92.

<sup>5</sup> Packard. Guide to the study of Insects. Introduction. 8<sup>o</sup> Salem, 1869. In later editions these names are also introduced in the text, on p. 104, with varying spelling.

(in a more restricted sense than first used by Leach), and to the former, HETEROMETABOLA. The Metabola are unquestionably more homogeneous than the other group. One of their primary features is found in the more clearly marked regional divisions of the body; this is a consideration of great significance, since in the progress of structure, from the worms, through the crustaceans to the insects; or within the class of insects, from the myriapods, through the arachnids to the hexapods; or in the developmental history of the Metabola themselves, from the larva, through the pupa to the imago, we discover a constantly increasing concentration of the segments of which the body is composed into distinct regions, culminating in the Hymenoptera, where head, thorax and abdomen are most sharply defined. This feature was first insisted upon by Agassiz in his remarkable essay on the classification of insects (l.c., pp. 20-28), but its application to the division of the hexapods has not before been pointed out; yet a very little consideration will show how much more clearly these regions are marked in the Metabola than in the Heterometabola, especially if the separation of the thorax and abdomen is examined. This is indeed what we might, not unreasonably, look for in the highest members of a group characterized, as are the hexapods, by the possession of organs of flight: the greater development of these organs would necessitate a more compact and distinctive organization of the region devoted almost exclusively to them; and accordingly in the Metabola we have, on the one hand, a more highly organized thorax, more definitely separated from head and abdomen, than in the Heterometabola; and on the other hand, greater power of continuous flight, of poise, of rapid movement, of sudden and repeated change of direction, and a far greater grace of movement in the former than in the latter.<sup>1</sup> This specialization of the thorax led me at one time to think of proposing the term Sternoptena for the Metabola; and, in allusion to the general preponderance of the abdomen in the groups composing it, Gastroptena for the Heterometabola. For the latter series the term Gastroptena would be more distinctive, but the names suggested by Dr. Packard seem to me better adapted to general use, besides having the advantage of prior application, and I accordingly adopt them.

In addition to the primary features mentioned (which were not stated by Packard), the Metabola are characterized by a usually cylindrical body with a very small prothorax; mouth parts formed in whole or in part for sucking, the points of the mandibles seldom opposed to each other; front wings membranous and much larger than the hind wings, which latter are sometimes aborted; the larva cylindrical and very unlike the adult, and the pupa always inactive. The Heterometabola on the other hand usually have a flattened body, with a very large prothorax; mouth parts usually adapted for biting, the points of the mandibles then opposed to each other; front wings usually more or less coriaceous or with very numerous and thickened veins, and usually smaller than the hind wings, which latter are only exceptionally aborted, and never throughout large groups; the larva is usually flattened, often resembling the adult, and the pupa either active or inactive.

<sup>1</sup> This we affirm only as a general rule, taking each sub-order as a whole. There are, it is true, apterous or sub-apterous Hymenoptera, bungling and inert fliers among the Lepidoptera, and Diptera which have a heavy and direct flight; and on the other hand, groups like the Odonata among Neuroptera, whose rapidity and power of sudden

change of flight is very striking; but these do not affect the characters of suborders as wholes; and in the exceptions which might be noticed, the specialization of flight is nearly always accompanied to a certain degree by a corresponding development and distinctiveness of the thorax.

The exceptions in the former group are only in the Hymenoptera, which usually have mandibles well developed for opposing each other. In the latter, more heterogeneous group, the exceptions are more abundant. In the Coleoptera the metamorphosis is complete.<sup>1</sup> In the Hemiptera, the mandibles are developed as needles and with the other parts of the mouth form a sucking tube; in many of them also the front wings are almost wholly membranous. The Neuroptera, using the term in the Linnaean sense, are the least amenable to law; their fore wings are usually membranous, though the veins are generally thick and approximated; a few (*Ephemerina*) have small hind wings; many of them show the regional divisions of the body almost as strikingly as the *Metabola*, although the abdomen is generally developed to an excessive extent, and in such insects the prothorax is not greatly developed; while, as before stated, part of them have an incomplete metamorphosis, and so have been classed with the Orthoptera by the later German writers, and others have an incomplete metamorphosis. The structural affinities, however, of the Neuroptera proper and the so-called Pseudoneuroptera are so close that they cannot be disconnected, notwithstanding the striking differences in general features between them; and although, thus composed, the Heterometabola exhibit anomalous features in nearly every suborder contained in it, we must accord to this division of hexapods into *Metabola* and Heterometabola a closer connection with all the facts than any that has yet been proposed.

How closely this division accords with the geological succession of insects will appear from the fact that all the suborders of Heterometabola, and none of *Metabola* are represented in the palaeozoic rocks.<sup>2</sup> This is the more striking from the fact that, if we omit mention of the single discovery of insect wings in the Devonian, the three orders of insects, — hexapods, arachnids and myriapods, appear simultaneously in Carboniferous strata.<sup>3</sup>

<sup>1</sup> It would appear, at first sight, as if Dr. LeConte, in his *Classification of the Coleoptera of North America* (8°. Washington, 1861), Introduction, p. 8, held that Coleoptera were to be ranked as the highest suborder among hexapods. His table would seem to indicate this; but he speaks with hesitation, as if proposing only a provisional arrangement, remarking: "We can merely state in general terms that those [hexapods] having a perfect metamorphosis are the highest; and those having the thoracic segments agglutinated, or the prothorax separate, are to be considered above those in which the larval character of similarity among the thoracic segments is preserved." To the first proposition no one will take exception; the latter ought to be restricted in its application to those groups only to which the Coleoptera are most nearly related, viz.: to the other Heterometabola; so far as they are concerned this would seem to be an indication of special and therefore comparatively high structure; but otherwise, as a mark of inferior organization, since it is opposed to the progress of structure seen throughout the articulates, marked by a condensation, so to speak, of the thoracic segments. Many Neuroptera and Orthoptera, notably such forms as *Corydalis* and *Forficula* (the latter classed by early writers with Coleoptera), show in their prothorax a close resemblance to Coleoptera; and the very size and importance of this segment in Coleoptera, when the whole hexapod series is taken into ac-

count, should therefore be looked upon as a sign of relatively low rank. I am pleased to be able to state, from a recent conversation on this point with Dr. LeConte, that he did not intend to extend the argument drawn from the prothorax over the whole hexapod series, but only over those most nearly related to Coleoptera, and purposely expressed himself in guarded language.

<sup>2</sup> No generalization so broad as this and at the same time correct has yet been made. Many authors indeed, and notably Bronn, dividing the hexapods into two series, — Mandibulata and Suctoria (or equivalent terms) — claim that the carboniferous hexapods were all biting insects, and that the sucking insects first appeared in the Jura. The latest statement of this sort was made by Haeckel (*Gen. Morph. Organ.*, II, p. xcix, 1866), but Dohrn's *Eugereon* was published in the same year, and by the light of this strange insect many palaeozoic insects now appear, as I shall endeavor to show below, under an entirely new aspect, and render it probable that there were many, as there certainly were some, sucking insects in palaeozoic times.

<sup>3</sup> Carboniferous arachnids have been described by Corda, Frič, Harger, Meek and Worthen, Roemer, Scudder, and Woodward; while myriapods from the same formation have been described by Dawson, Meek and Worthen, Scudder, and Woodward; besides others from other palaeozoic beds by Dohrn and Geinitz.

The earliest known Diptera occur in the Liassic rocks at Cheltenham, Dumbleton and Forthampton in England; the Lepidoptera<sup>1</sup> in the middle Oolite (Solenhofen); and the Hymenoptera in the same formation.<sup>2</sup> The Metabola are then later in time and more perfect in development than the Heterometabola.

When we analyze the insect fauna of the earliest times more closely, we notice that the higher suborders of Heterometabola, the Coleoptera and Hemiptera, are represented in the palaeozoic rocks by very few types, as compared with the Orthoptera and Neuroptera; the two former groups having but three or four each,<sup>3</sup> while Goldenberg enumerates fifteen or sixteen of each of the others from Saarbrücken alone, and double that number must be known. No Coleoptera nor Hemiptera have yet been found in the palaeozoic formations of America, while I am acquainted with about forty Orthoptera and Neuroptera from these rocks. The almost entire absence of Coleoptera from palaeozoic rocks is the more remarkable, because their crust is much thicker than that of other insects, and their shards as hard as the shell of the body. This is peculiarly the case in the lowest and presumably oldest type, the weevils or Curculionidae. Their remains have been preserved with the greatest readiness in more modern strata; in fact, in all the newer rocks, Coleoptera are best represented of all insects; yet in the oldest, very few have been found in comparison with the remains of the lower suborders. This is a striking and indisputable fact, and notwithstanding the paucity of the material whereon to base a general statement, is scarcely to be explained on any other hypothesis than that of the later appearance of Coleoptera.

In the Orthoptera again, nearly all the families represented belong to the lower series; only four or five members of the saltatorial families have been found, the cockroaches of the Carboniferous period outnumbering all the other Orthoptera many times. In the last catalogue of fossil cockroaches (by Goldenberg), thirty-five species are recorded from the Carboniferous rocks and only seven from the Tertiary formation. Indeed about one-half the known species of palaeozoic insects are cockroaches.

Or, if we look at the Neuroptera, we find that the Neuroptera proper, or those with complete metamorphosis, scarcely occur at all in the palaeozoic rocks; whereas the lower Pseudoneuroptera, with incomplete metamorphosis, are comparatively abundant. Many of the reticulate-winged insects of early periods, however, combine the characters either of the Neuroptera and Orthoptera, or of the Neuroptera proper and Pseudoneuroptera. So striking, indeed, is the comprehensive nature of these early types that Dohrn, and after him

<sup>1</sup> The carboniferous *Breyeria* of de Borre (*Comptes rend. Soc. Ent. Belg.*, [2.] XIII : 7-11) is universally conceded to be a neuropterous insect. See the remarks in the same journal by Hagen, Heer, McLachlan, de Selys, Scudder, Van Volxem and others.

<sup>2</sup> A single species, doubtfully referred by Heer to the latter suborder, has, however, been found in the Lias of Schämbeben.

<sup>3</sup> The only Coleoptera known to me are *Curculioides Austicii* Buckl., from Coalbrook Dale, *Troxites Germari* Goldenb., from Altenwald, and the borings of a *Hylesinus* described by Brongniart as occurring in petrified wood from

the carboniferous limestones of Autun. Geinitz also describes borings of a larger beetle in fossil wood from the Saxon coal measures to which Frič gives the name of *Xyloryctes planus*; and Sternberg others from Bohemia of a doubtful character, which Frič calls *Xyl. septarius*. *Curc. Prestvicii* Buckl. has been shown to be an Arachnid.

The only Hemiptera from these lowest rocks are *Fulgora Ebersi* Dohrn and *Fulgorina Klieveri* Goldenb., from Saarbrücken, and *Macrophlebium Hollebeni* Goldenb., from Manebach; besides *Fulgorina lebachensis* Goldenb., from the Permian. *Eugereon Boeckingi* Dohrn, cannot be classed here, as will appear further on.

Goldenberg, proposes to group them under a new subordinal division, to which Goldenberg has applied the name Palaeodictyoptera.<sup>1</sup>

This view I am inclined to think a correct one, but no definition of the group has yet been attempted; and while, on the one hand, Goldenberg appears to have gone too far in referring to it the Carboniferous insects from Illinois described by Dana, and the Devonian insects of New Brunswick, it would seem probable that Woodward's Archimantis<sup>2</sup> should be classed therein, as well as the genera Eugereon, Dictyoneura, Paolia and Haplophlebium; and it is by no means improbable that they all possessed mouth parts structurally comparable to the remarkable Eugereon of Dohrn, which certainly can be referred to no existing group of insects. When more of their structure is known, they will probably be found to agree in the possession of a remarkably depressed, cockroach-like body, with ample thoracic segments, the prothorax well separated from the other joints, broadly expanded or extended, reticulated wings, lancet-shaped mandibles and maxillae, long labial palpi which have no direct part in the haustellate structure of the mouth, and multiarticulate antennae. This is a combination quite at variance with that of any group of recent or of newer geological times, and indeed is known to us only in the palaeozoic rocks. It forms a synthetic type in the largest sense, and may be said to combine features of all the Heterometabola.

But it was not the only such type then existing; for, as has already been noted, there are many other palaeozoic insects which combine in their structure features now characteristic of diverse groups. Such are nearly all the Devonian insects. It is also not a little remarkable to find that recent types existed in the earliest periods side by side with these. Some of the Devonian insects, for example, are to be referred with very little question, not only to the Neuroptera, but even to a particular family of Neuroptera now existing, the May flies. Indeed, the presence, at the apparition of a given group, of modern types, side by side with those which elude our classification of existing forms, is one of the peculiar problems of palaeontology.

Perhaps no more striking instance of this can be found than the recent discovery by M. Charles Brongniart, in the upper Carboniferous rocks of Commeny, of one of the most specialized forms of insects which exist; of a type indeed so modern, that, so far as I may judge from a rough sketch sent me by Brongniart, one would not have been surprised to meet with its exact counterpart in every detail, living in the tropics of the old world. It is a species of large, spinous, thick-bodied Phasma or walking-stick, with abbreviated tegmina, long wings and body, rather long and slender legs and antennae, and in all its parts

<sup>1</sup> Cf. Dohrn, *Palaeontogr.*, XIII: 338-39; XIV: 134. Goldenberg, *Faun. Sar. foss.*, II: 8. Dohrn first proposed the term Dictyoptera, but afterwards withdrew it, as preoccupied.

<sup>2</sup> Woodward. On a remarkable orthopterous insect from the coal-measures of Scotland. < *Quart. Journ. Geol. Soc. Lond.*, 1876: 60-64, pl. 9. Woodward, it seems to me, has in all probability mistaken the affinities of this insect. If his figure is placed beside Dohrn's first illustration of Eugereon, the similarity of the two will be apparent. The form and relations of the head, prothorax and broadly expanded wings (nearly all that is preserved in Archimantis) are the same in each, as well as, in a general sense,

the neurulation of the wings. The projection in front of the head, therefore, would seem to be, not a prolongation of the head itself, comparable, as supposed by Woodward, to that of the head of some living Mantidæ; but a rostrum, like that of Eugereon, though much shorter than it, and by its state of preservation apparently amalgamated with it into a single mass; or, it may be the labrum alone with the other parts removed, for it would then probably appear as an integral part of the head. The close relationship of the wing-structure in Archimantis, Eugereon and the other genera specified above render it not improbable that they were all sucking insects. Protophasma however, similarly related, certainly was not.

perfectly reproducing the customary and yet unique features of the Phasmida of to-day.<sup>1</sup> The family had not previously been known earlier than the Tertiaries.

We may glean still another fact from the scanty data the rocks afford us concerning the early types of insects. All the Hemiptera of the palaeozoic rocks belong to the Homopterous division of the suborder; indicating, what is generally conceded, that this division is lower than the Heteroptera, which first appeared in the Jura.<sup>2</sup> Now one conspicuous difference between these two divisions is found in the structure of the base of the front wings, which is coriaceous in the Heteroptera and membranous in the Homoptera; showing that differentiation of the front and hind wings is, as we should suppose it might be, a later development, the homogeneous condition preceding it. Among Orthoptera, none of the families, unless it be the walking-sticks, have more densely coriaceous fore-wings than the earwigs and the cockroaches. The earwigs first appeared in the Oolite; and while cockroaches were abundant from the earliest times, it is not, with one exception, until we reach the Lias that we find species with close approximation and multiplication of the veins of the front wings, giving them a coriaceous appearance. This exception, *Ledrophora Girardi*,<sup>3</sup> in which the veins are nearly obsolete, occurs in the Trias; and it is the earliest indication of any differentiation of the front and hind wings in cockroaches; for all the palaeozoic species had tegmina which were as distinctly veined as the wings, and could not, in any sense, be called coriaceous.<sup>4</sup> The same distinctness of the veins is apparent in all the other palaeozoic Orthoptera; so that, excepting the two species of Carboniferous Coleoptera and *Protophasma* (which do not appear to differ in this respect from living types), we may say that the wings of palaeozoic insects were homogeneous.

Inasmuch as we know the earliest insects principally from the remains of their wings, it is interesting to note in them a further striking fact. If we should formulate the charac-

<sup>1</sup> Since the above was written, I have received from M. Brongniart his final memoir on *Protophasma* (Note sur un nouveau genre d'Orthoptère fossile de la famille des Phasmiens — Ann. Sci. Nat., [6] VII, Art. 4), by which it appears that the wings must be excepted from the statement given above; for they differ remarkably from the wings of living Phasmida, and resemble extraordinarily the wings of Palaeodictyoptera, and especially those of Dictyoneura. They could not have been folded longitudinally to the degree that the wings of Phasmida are now plaited, for the anal area embraces less than one-third of the wings, and the interspaces between the veins of that part of the wing which lies above the anal area, are not straight but curved; in the number and arrangement of the veins in this upper part of the wing we have an almost exact counterpart of the wings of Dictyoneura; the same, to a less extent, may be said of the wings of the Fulgorina described by Goldenberg. This type of wing structure was therefore a very common one among palaeozoic insects, and accounts for Brongniart's suggestion, hardly to be received, that these Fulgorina should be considered Neuropterous; indeed the neuration of the wings of the numerous carboniferous Blattariæ does not lack a somewhat close adherence to the same type, and we may yet succeed in establishing an unusual degree of homogeneity in the wing structure of all or nearly all palaeozoic insects.

<sup>2</sup> Perhaps a similar statement may be made even of the few Coleoptera known. For, if we accept LeConte's primary division of Coleoptera into normal and rhyncophorous, the former the higher, and look upon the Troxites of Goldenberg, as I strongly incline to do, as a curculionid, — the only indication of the higher normal Coleoptera in the palaeozoic rocks will be the borings brought to notice by Geinitz, which were evidently made by a longicorn, a family of normal Coleoptera ranking rather low in the series.

<sup>3</sup> Heer. Ueber die fossilen Kakerlaken. < Vierteljahrsschr. naturf. Gesellsch. Zürich, IX : 297, pl., fig. 5. 8°. Zürich, 1864.

<sup>4</sup> Exception should perhaps be made to the very remarkable cockroach described by Goldenberg (Faun. Sar. foss., I : 17, pl. 2, fig. 14, 14a), under the name of *Blattina insignis*; this insect has a slender, perhaps cylindrical, abdomen with tegmina and wings which appear to be equally leathery and in which nearly all trace of veins are lost. Here, however, all the wings appear to be alike in form, consistency and structure; and Goldenberg has given us only a meagre account of it, which is the more unfortunate, since it is second in interest only to Eugereon and *Protophasma*.

teristics of the wing structure of living insects (which show, indeed, a variety of type truly marvellous, and ranging from exceeding simplicity to a complexity which nearly baffles all attempts at homology), we should not need to modify our statement in the least particular to include the wing-structure of the insects of earliest times. The plan of neurulation upon which the wings of insects were then constructed is the plan we find in all existing types. At the same time, as stated above in a note, there was an unusual degree of homogeneity in the wings of palaeozoic insects.

This review clearly indicates that the laws of succession of the insect tribes are quite similar to those which have long been known to hold in other groups of the animal kingdom; and that the facts are, in the main, such as the theory of descent demands. The exceptions to theory, however, and indeed the general facts, are such as to indicate that profound voids exist in our knowledge of the earliest history of insects. The appearance of hexapods in the middle Devonian long previous to any traces either of myriapods or of arachnids; the apparent advent of generalized groups of a comparatively narrow range, before those which are wider in scope and embrace the former; the apparition of Coleoptera, which present no indication of any divergence from the subordinal type, in Carboniferous beds first yielding an abundance of insect remains,—that is, as early as any insects whatever, excepting the homogeneous-winged Heterometabola of the Devonian; and the occasional discovery of highly specialized types at very early periods:—all point to the far earlier existence of widely comprehensive types, from which all these comparatively specialized but still more or less synthetic forms must have originated. The additions to our knowledge of palaeozoic insects within the past twenty years, and the increasing indications of dry land at earlier and earlier epochs,<sup>1</sup> must leave little doubt in the reflecting mind, not only that insects existed in no scanty numbers in Devonian and even in Silurian times, but that persistent research over wider fields will probably enable us, at no distant day, to replace hypotheses with facts.

In conclusion, we may recapitulate, as follows:—

1. With the exception of the few wings of hexapods known from the Devonian, the three orders of insects—hexapods, arachnids and myriapods—appeared simultaneously in Carboniferous strata.
2. Hexapod insects may be divided into a higher group (Metabola), including Hymenoptera, Lepidoptera and Diptera; and a lower group (Heterometabola), including Coleoptera, Hemiptera, Orthoptera and Neuroptera.
3. All Devonian and Carboniferous insects are Heterometabola, the Metabola making their first appearance in the Jurassic period.
4. Many synthetic or comprehensive types existed in palaeozoic times, combining the characters either of all the Heterometabola; of Orthoptera and Neuroptera; or of Neuroptera proper and Pseudoneuroptera.
5. The Devonian insects either belong to comprehensive types related to the two lower suborders only, or are low Pseudoneuroptera; and were undoubtedly aquatic in early life.
6. The lower suborders of Heterometabola,—Orthoptera and Neuroptera, were much more abundant in palaeozoic times than the higher,—Coleoptera and Hemiptera.

<sup>1</sup> Cf. Lesquereux. Land plants, recently discovered in the silurian rocks of the United States. < Proc. Amer. Philos. Soc., xvii: 163-73, pl. 4. 8°. Philadelphia, 1877. On

the first page of this paper will be found a résumé of our knowledge of this subject.



7. Nearly all the palaeozoic Orthoptera belong to the lower non-saltatorial families, and are almost exclusively cockroaches.

8. The Neuroptera proper were at that time much rarer than the lower Pseudoneuroptera.

9. All the earlier types were therefore of inferior organization.

10. The general type of wing structure in insects has remained unaltered from the earliest times.

11. With the exception of two species of Coleoptera and one of Orthoptera, the front and hind wings of palaeozoic insects were similar and membranous, heterogeneity making its appearance in mesozoic times. At the same time, the neuration of the wings of palaeozoic insects in otherwise widely diverse types was much more similar than now.

12. The series of facts presented to us by the progress of geological research leads to the conviction of the probable existence and possible discovery, in the Devonian and even in the Silurian formations, of winged insects, still more generalized in structure than any yet detected in the palaeozoic rocks.

It may also be added that nearly all the earlier insects were large, many of them gigantic in size, and, further, that there is a striking similarity between the carboniferous insect-fauna of Europe and North America.

NOTE. The preceding pages were printed before I chanced upon the following passage from Lacordaire (Introd. à l'Entom. I, p. 326), which may be taken as a note to the last paragraph of third page of this paper:—

“Toutes les différences que l'on observe dans le thorax des insectes proviennent du plus ou moins de développement qu'a pris chaque anneau thoracique, du nombre de pièces que chacun d'eux présente, et de la grandeur relative de chacune de ces pièces en particulier. Et le prothorax a acquis un développement extraordinaire, et s'est en quelque sorte séparé du mésothorax et du métathorax, on aura le thorax d'un Coléoptère, d'un Dermaptère, d'un Orthoptère et d'un Hémiptère. Si au contraire le prothorax est réduit à des dimensions très-exiguës, et que le mésothorax intimement uni au métathorax ait pris un accroissement énorme, on aura celui d'un Hyménoptère, d'un Lépidoptère et d'un Diptère.”

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