The Geological History and Evolution of Insects[1]

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[With 3 plates]

THE PURPOSE of this paper is to present briefly that conception of insect evolution which appears to be indicated by our present knowledge of the geological history of the group. Though some of my colleagues may not agree with my position on certain details, I believe the concept I offer will be acceptable, at least in its general aspects, to those who have given serious thought to the fossil record.

My index to the publications on fossil insects includes some 3,000 papers, contributed by 700 authors. Only two general, compilative treatises have appeared; one by Samuel Scudder in 1886 [1],[2] and the other by Anton Handlirsch in 1906–1908 [2]. Both of these authors had unique ideas on insect evolution, especially Handlirsch, whose views unfortunately are the ones usually found in textbooks of zoology, paleontology, and evolution. The material that forms the basis for the extensive literature in this field comprises the countless thousands of specimens, perhaps 500,000,[3] contained in the museums and university collections in Europe and North America. Up to the present time about 13,000 species of fossil insects have been formally described. The geological formations that have produced these specimens range from the Upper Carboniferous through to the present.

The first aspect of the evolution of insects that I shall consider is a general one. We can recognize four important stages in their history, our present insect fauna consisting of some representatives of all

[1] Based on the Sigma Xi address given at the meeting of the American Institute of Biological Sciences, Cornell University, September 1952. Reprinted by permission from American Scientist, vol. 41, No. 2, April 1953, copyrighted 1953 by the Society of the Sigma Xi.

[2] Figures in square brackets are references at end of text.

[3] This figure includes the 100,000 or more amber insects originally at the Albertus University of Königsberg, but apparently entirely destroyed by bombing during World War II.

stages. The first of these stages was a wingless insect, exemplified in our existing fauna by two orders, the Thysanura (silverfish) and the Entotrophi. The existence of such a phylogenetic group of wingless insects, termed the Apterygota, is based on the premise that wings evolved *after* the origin of insects and not *with* their origin—a conception that has been almost universally accepted by zoologists for fully 60 years. The opposite view, based on the belief that the first true insects were winged and that all wingless species are secondarily so, was advocated by Handlirsch [2, 3]; it was a corollary to his conviction that insects arose directly from trilobites, the lateral lobes of which became functional wings. So far as I am aware no one who has given serious thought to the subject, with the exception of Handlirsch, has accepted this idea. It is true that the wingless Apterygota are known only as far back as the Triassic period and that the winged insects, or Pterygota, extend to the Upper Carboniferous. However, apart from a few Baltic amber inclusions, only two specimens of Apterygota have been found in all geological strata. Their fragility and the very absence of wings, of which most fossil insects consist, make their chances of preservation as fossils very slight indeed. This is an instance in which the structure of living material furnishes more evidence than the geological record.

DEVELOPMENT OF WINGS

The second stage in the evolution of the insects began with the development of wings. The time when these appendages started to appear is not established, but three specimens of insects with fully developed wings have been found in the lowest of the Upper Carboniferous strata. Since these specimens belong to different orders, we can only conclude that wings began to evolve in the Lower Carboniferous period. However, even if the Upper Carboniferous record is accepted as the time of wing development, it is clear that the insects attained flight fully 50 million years before the reptiles and birds did—a period of time during which the insects, so far as is known, were the sole inhabitants of the air as aerial creatures. By the time flying reptiles and birds had evolved, the insects were well established in their new environment. It is intriguing, though futile, to reflect on the possibility that if the insects had not taken to the air before the vertebrates, they might never have successfully attained flight. The significance of flight for insects was undoubtedly great during the late Paleozoic. This was the age of amphibians and small reptiles. Scorpions, spiders, and spiderlike arachnids, belonging to extinct orders, were abundant. All these predators unquestionably subsisted to some extent, and probably to a great extent, on the wingless insects, which had no means of escape. It is not surprising, therefore, that the ability to fly changed the direction of insect evolution and that in our present insect world only one-tenth of 1 percent of the species are Apterygota.

The process by which wings were acquired by insects [4] has been a question of much speculation, for they are not modifications of previously existing appendages. However, significant evidence has been provided by the study of fossils. All the more generalized Pterygota of the Carboniferous period, and even some species of the Permian, possessed a pair of membranous flaps, arising from the dorsum of the first thoracic segment. These flaps contained veins and were covered with minute hairs like those of the true functional wings borne on the second and third thoracic segments. There is every indication that the true wings began, like membranous prothoracic flaps, as lateral tergal expansions. However, so far as we know, the prothoracic flaps never developed into functional wings. In most insects the flaps have completely disappeared and in others they have been absorbed into a pronotal disc.

The first winged insects, or Paleoptera, which we have been considering, had a simple wing articulation and were incapable of flexing their wings back over the body at rest; hence, they were preserved as fossils with their wings outstretched. Dragonflies and mayflies—the sole living representatives of the Paleoptera—exhibit the same limitations in wing structure. The third stage in insect evolution began with the modification of certain plates of the wing articulation so as to permit wing flexing; these insects are known as the Neoptera.[5] The survival value of wing flexing was great, for it enabled the insects, between flights, to hide among foliage or under objects on the ground. The fossil record shows that this stage was reached by early Upper Carboniferous time, when many of the paleopterous insects were predaceous and of great size, though no flying vertebrates had yet appeared. Later, when the flying reptiles, or pterosaurs, and birds appeared in the Mesozoic, the neopterous insects had all the advantage. The paleopterous insects, which had been dominant during the Carboniferous and Permian, began to wane and the Neoptera to flourish. This trend in insect evolution has continued up to the present time to such an extent that 90 percent of the existing orders, including 97 percent of the species, are now neopterous.

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[4] That the Pterygota are of monophyletic origin seems almost certain. Lemche, however, has advocated [4, 5] a polyphyletic origin, even claiming that such insects as the Grylloblattidae and the females of Zoraptera and of certain lampyrid beetles are primitively wingless (nonalate). The evidence for his conclusion seems insufficient (see, for example, Carpenter, 1948 [6]).

[5] The phylogenetic groups which are here termed the "Paleoptera" and "Neoptera" were recognized independently by Martynov [7, 8] and Crampton [9].

METAMORPHOSIS

The first of the neopterous insects were closely related to stoneflies and locusts and possessed incomplete metamorphosis, that is, they passed through a series of nymphal stages which gradually approached the adult form. These are designated as the hemimetabolous Neoptera. The fourth step in insect evolution was the development of a more complex type of metamorphosis, in which the insects pass through a series of larval stages bearing little resemblance to the adult. Eventually, they enter into one or two quiescent stages, during which extensive morphological and physiological changes take place. These, the holometabolous Neoptera, presumably had several advantages over the hemimetabolous types. The immature forms, being very different from the adults, could occupy different environments and feed on different types of foods. The tissues of other organisms, both animal and plant, were thus invaded by larval forms as internal parasites, the adult insects remaining free-living and capable of flight. The holometabolous insects make their first appearance in the Lower Permian strata. The existence of two orders, the scorpionflies or Mecoptera and the Neuroptera in the Lower Permian, shows that complete metamorphosis must have begun before the end of the Upper Carboniferous period. Starting from the beginning of the Permian, when only about 5 percent of the known species of insects had complete metamorphosis, the percentage of species has progressively increased to the present maximum of 88 percent.

A simple phylogenetic diagram, shown in figure 1, superimposed on the geological time scale, serves to summarize this general aspect of insect evolution. The three modifications—origin of wings, wing flexing, and complete metamorphosis—mark the points of separation of the phylogenetic lines. Since holometabolous insects are known to have existed from the Lower Permian strata, the upper phylogenetic division must have taken place before the end of the Upper Carboniferous; and since neopterous insects are known from the lowest of the Upper Carboniferous strata, the middle division, or wing flexing, must have taken place in the Lower Carboniferous, which is beyond the present record of the insects. The first phylogenetic division must have occurred even earlier.

FOSSIL RECORD

Turning from this phylogenetic treatment of the insects, I shall next consider their history as it is now actually known from the fossil record. This discussion will involve some mention of extinct orders and an explanation of my point of view on this controversial subject. The artificial and arbitrary nature of higher taxonomic categories is

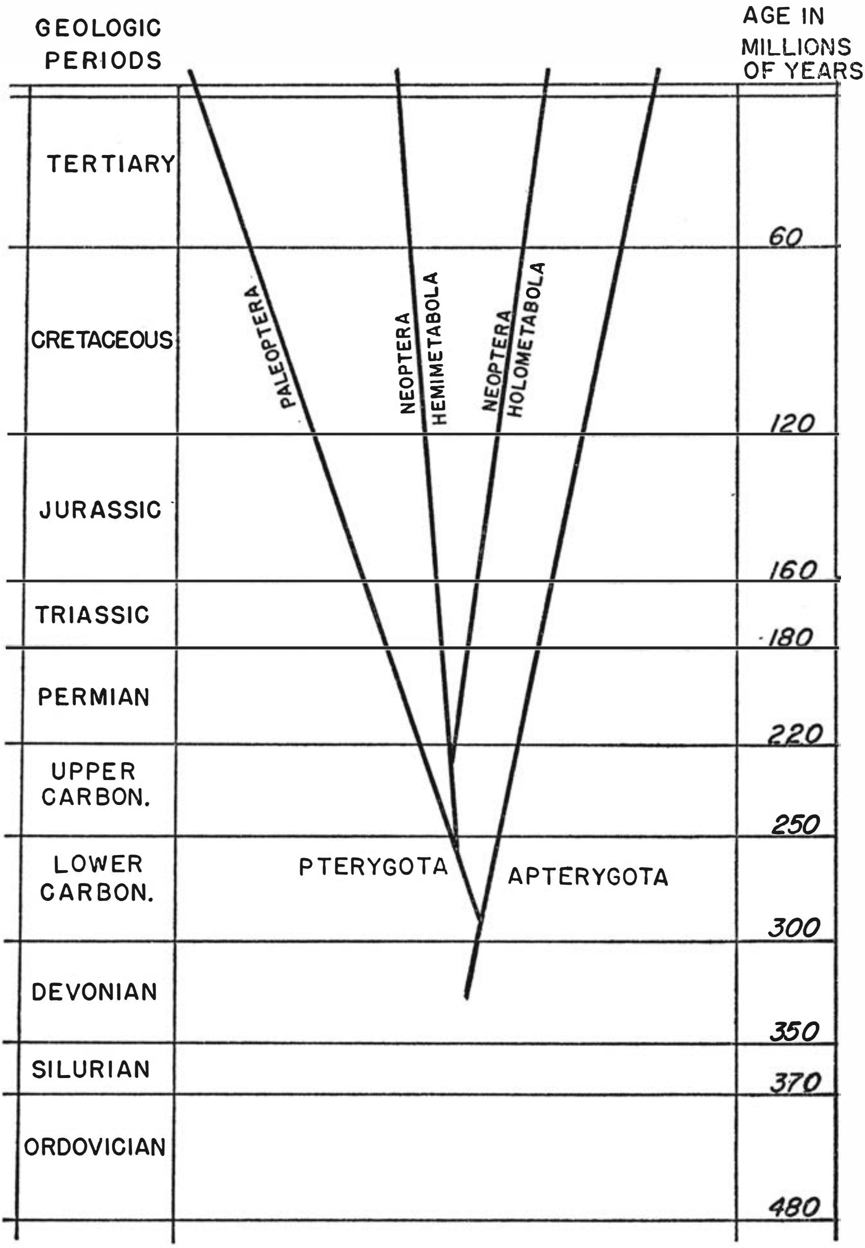

Figure 1.—Main lines of insect evolution, as described in the text.

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well known to systematists. Such categories are established for dealing with organisms in a very limited period of geological time, not with the whole geological record of a group, with annectent forms appearing at intervals. This is an elementary concept for vertebrate paleontologists, most invertebrate paleontologists, and paleobotanists. In other words, most paleontologists have come to identify these higher categories by trends or tendencies in a group, recognizing that some of its members might even lack the specific structures indicated in most of them. Unfortunately, many students of fossil insects have not followed such a concept and have erected taxonomic categories, such as families and orders, on single fragmentary specimens. Accordingly, some extinct orders of insects have been established on either very vague features or peculiar structures that might not occur in another species. Altogether, as a result of such practices, 44 extinct orders of insects have been established—almost twice as many orders as are usually recognized as now existing. From an extended study of most of the material on which these extinct orders have been based, I am convinced that only 10 of them deserve ordinal status; the other orders can be combined or merged in one way or another. In the following discussion, I shall refer only to these 10 orders.

The insect fauna of the Upper Carboniferous period was basically primitive, for although some neopterous orders were present, they were in the minority. This was the only period in the history of the insects, so far as is known, when this was the case. The paleopterous orders, of which there were five, included three main types. One of these types, comprising mayfly-like insects, was a complex of three extinct orders—the Palaeodictyoptera, Protephemerida, and Megasecoptera. Of these the Palaeodictyoptera were the most generalized; they had prothoracic wing flaps and in general the Carboniferous species showed a lack of specializations. Unfortunately, nothing at all is known of the immature stages of this order.

TABLE 1.—*Geological ranges of existing orders*

NAME OF ORDER	EARLIEST GEOLOGICAL RECORD
1. Collembola (springtails)	Devonian [?]
2. Entotrophi (bristletails)	Late Tertiary
3. Thysanura (silverfish)	Triassic
4. Odonata (dragonflies)	Early Permian
5. Ephemerida (mayflies)	Early Permian
6. Perlaria (stoneflies)	Late Permian
7. Orthoptera (grasshoppers, crickets)	Triassic
8. Blattaria (roaches)	Late Carboniferous
9. Isoptera (termites)	Early Tertiary
10. Dermaptera (earwigs)	Jurassic
11. Embiaria (embiids)	Early Tertiary
12. Corrodentia (book lice)	Early Permian

TABLE 1.—*Geological ranges of existing orders*—Continued

NAME OF ORDER	EARLIEST GEOLOGICAL RECORD
13. Mallophaga (bird lice)	[No fossils known]
14. Hemiptera (bugs)	Early Permian
15. Anoplura (sucking lice)	Pleistocene
16. Thysanoptera (thrips)	Late Permian
17. Mecoptera (scorpionflies)	Early Permian
18. Neuroptera (ant lions, dobsonflies)	Early Permian
19. Trichoptera (caddis-flies)	Jurassic
20. Diptera (flies, mosquitoes)	Jurassic
21. Siphonaptera (fleas)	Early Tertiary
22. Lepidoptera (butterflies, moths)	Early Tertiary
23. Coleoptera (beetles)	Late Permian
24. Strepsiptera (stylops)	Early Tertiary
25. Hymenoptera (bees, ants, wasps)	Jurassic

The little-known Protephemerida require no comment here, but the Megasecoptera show several unusual features. They had very long abdominal cerci, lacked prothoracic flaps, and had more highly modified wings and body structures than the Palaeodictyoptera. In some species the wings were falcate (pl. 1, fig. 1), in others petiolate; in still others the prothorax was armed with spines. Noteworthy, also, was the presence of wing markings, which are evident even in specimens preserved in black shale. What colors were originally in the wings is not known, but a definite color pattern is indicated in the fossils.

As paleopterous insects, the Megasecoptera presumably developed by incomplete metamorphosis; the presence of true nymphal forms definitely associated with adults, in the British coal measures, substantiates this conclusion. It should be noted, on the contrary, that Forbes [10], has expressed the belief that the Megasecoptera were actually holometabolous. It is true that, although most species of Megasecoptera are found preserved in paleopterous fashion with wings outspread, a few families included species that unquestionably held their resting wings over the abdomen. That these latter species represent the beginnings of the true neopterous line of evolution seems very doubtful to me in view of their several specializations; also, that they represent a distinct order, quite removed from the rest of the Megasecoptera, seems equally unlikely. I am led to believe, therefore, that the species of this order which were able to hold the wings over the abdomen developed this ability independently of the true neopterous types.

Another order of paleopterous insects, very different from the three just mentioned, was the Protodonata, which closely resembled dragonflies. Like the latter, they were predaceous, and had spiny legs and large mandibles. All the Protodonata were large and some members of one family, with a wing expanse of 2½ feet, were the largest insects known.[6] Nymphs of the Protodonata are entirely unknown, but in view of the similarity of the adults to true Odonata, we infer that the immature stages could not have been very different.

The third type of paleopterous insect in the Carboniferous fauna has no counterpart in an existing order. Although named the Protohemiptera, they were closely allied to the Palaeodictyoptera, since they possessed prothoracic wing flaps and other characteristics of the latter. But the mouth parts of the Protohemiptera were modified to form a long suctorial beak, resembling that of certain Diptera, or flies, though differently formed. The Carboniferous members of this order were so much like the Palaeodictyoptera that some of the insects whose head structure is unknown and which have been considered Palaeodictyoptera, were, I believe, Protohemiptera. The members of this order presumably fed either on plant juices from the large club mosses and tree ferns, or on the blood of amphibians and reptiles.

The neopterous insects of the Carboniferous include a vast and confusing assemblage related to the locusts and stone flies. Most of the species belong in the extinct order Protorthoptera, with a few aberrant ones in the Caloneurodea, and still others, obviously true roaches, in the Blattaria. The Protorthoptera show great diversity of structure. The more generalized species had membranous forewings and cursorial legs; others had leathery wings and either saltatorial or prehensile legs. Essentially, the Protorthoptera possessed the same amount and the kind of diversity that exists among the true Orthoptera, yet it is highly doubtful that any of these Carboniferous forms gave rise directly to the living groups they resemble.

The roaches were another interesting order in the Carboniferous. Although in numbers of individuals and described species they exceeded all other Carboniferous insect orders, I am convinced that their abundance is very misleading. The swampy areas inhabited by the roaches supplied the best of conditions for their preservation as fossils, whereas other insects might encounter such optimum conditions only rarely. This condition would account for a disproportionately large number of roaches preserved as fossils. The extensive series of described species of roaches is due to the fact that Handlirsch and others have ignored the extreme instability of wing venation in both living and extinct types. Apart from their numbers, the most notable feature of the Carboniferous roaches was their close resemblance to species now living. Recently, however, an unexpected structure has been discovered in some Carboniferous roaches from Belgium: a long, projecting ovipositor, fully as long as the abdomen [11]. In all living roaches the ovipositor is vestigial or rudimentary, and the eggs

[6] These particular insects are the only extinct insects, so far as is known, that were larger than existing species. The inference has been drawn from the Protodonata that all Paleozoic insects were very large, but this is not the case.

are either laid in large capsules or else they hatch and form nymphs in the body of the female parent. The ovipositor in some of the Carboniferous species indicates a very different method of egg laying.

From this survey of the Carboniferous fauna it is apparent that the insects had acquired surprising diversity and specializations by the Upper Carboniferous period, though some really generalized species were also included. Nevertheless, I am convinced that we have not yet begun to appreciate the extent of the Upper Carboniferous insect fauna. This conviction is based in part on the nature of the fauna in the lowest Permian strata and in part on the known diversity of the Carboniferous insects, even though represented by relatively few species. If the same number of living species were collected at a few isolated localities over the world, we could not expect to obtain from them a good idea of the complexity of the world fauna as it exists today. It is not beyond the limits of possibility, therefore, that the extinct orders of Carboniferous insects were in their time comparable in extent to the major orders now living.

The insect fauna of the early Permian period was distinctive, for it was a combination of nine extinct orders and seven living ones. None of the extinct orders, except the Protodonata, are known to have lived beyond the Permian. The Palaeodictyoptera and Protohemiptera had apparently reached their maximum development in the Upper Carboniferous, only a very few having been found in Permian strata. The Megasecoptera, on the contrary, flourished all through the period. The Protodonata, also, were more numerous than in the preceding period, and very large species, like those previously noted, have been found in Permian beds in Kansas, Oklahoma, and several parts of Europe. Since no flying vertebrates were yet in existence, these large predatory insects must have ruled the air for many millions of years, for they persisted well into the Mesozoic. They may have been an important factor in the extermination of soft-bodied and weak-flying insects, such as the Palaeodictyoptera and Megasecoptera. The Permian Protorthoptera continued to show diversity of form. Among them, for example, are some whose cerci or posterior appendages in the male were modified to form pincers, or claws, resembling those in some of the living Orthoptera.

Three additional extinct insect orders make their first appearance in the early Permian. One of these, the Protelytroptera, which were related to the earwigs, were the first insects known to develop true protective forewings, or elytra; also the hind wings were greatly expanded and contained hinges which enabled the wings to fold up beneath the overlying elytera. Another extinct order of the early Permian, the Protoperlaria, was related to the stoneflies; the adults were generalized with prothoracic wing flaps, but the nymphs were adapted for an aquatic life. The final extinct order, the Glosselytrodea, appeared in the late Permian; they were characterized by highly modified elytra with unique venation.

The living insect orders of the early Permian, in addition to the roaches, comprised the mayflies, dragonflies, bark lice, true bugs, flies, and Neuroptera. With the exception of the Neuroptera, these Permian representatives were more generalized in most respects than any existing members of their orders. The Permian mayflies, for example, had homonomous wings, whereas in all living species the posterior pair of wings are much reduced, both in size and venation. The Lower Permian was apparently close to the time of origin of most of these orders, for basic characteristics of related orders are combined in some species. A surprising feature is that these first insect representatives of existing orders are smaller in size than most present species of their orders, and some of the fossil species are as small as the smallest now living.

Before the end of the Permian, three more living orders of insects appeared. One of these, the stoneflies, included a species which can be assigned with confidence to a living family. The other two orders comprise the thrips and the beetles. The dominant insects of the late Permian were true bugs, or Homoptera, which were clearly adapted for feeding on plant juices.

As is evident from this survey, the Permian insects were a remarkable assemblage. During no other geological period has such a diverse insect fauna existed. A striking contrast is found in the Triassic, at the beginning of the Mesozoic, in which the disappearance of all extinct orders, except the Protodonata, transformed the facies of the Triassic fauna to a semblance of that at present. True orthopteran insects first appear in Triassic beds. Among them were several species having well-developed stridulatory structures on the forewings of the males. The insects had a wing expanse of about 9 inches, and stridulatory area of the wing was fully as large as that in any living insect, as shown in plate 1, figure 2.

By the beginning of the Jurassic the Protodonata became extinct, possibly because of the flying reptiles, or pterosaurs, which appeared early in the period. Earwigs, caddis-flies, true flies, and the Hymenoptera are found in middle Jurassic strata. The flies or Diptera were almost exclusively midges or cranefly-like, there being none of the higher Diptera, many of which are now conspicuously associated with flowering plants. Similarly, the Hymenoptera were either relatives of sawflies or parasitic types; the aculeates, such as bees and wasps, were absent. Many of the Jurassic insects belonged to families now living (see pl. 2, fig. 1). Looking at such specimens one finds it difficult to realize that they were contemporary with the pterosaurs, dinosaurs, and *Archaeopteryx*.

The Cretaceous insect fauna is virtually unknown, since very few specimens have been found. The gap is an unfortunate one, for a rapid development of the flowering plants and of the vertebrates took place during this long period. It is not surprising that insects of the early Tertiary period consist almost exclusively of families now living and to a large extent of living genera. The Lepidoptera and Isoptera first appear in early Tertiary rocks, but the nature of the earliest representatives shows that these groups arose in the Mesozoic. The insects of the Tertiary are better known than those of any equivalent interval of geologic time, largely because of the Baltic amber, which was formed from the resin of pine trees about 50 million years ago and which has preserved types of insects that would almost certainly not occur in rock formations. For example, two specimens of fleas, presumably from a rodent inhabiting the amber forest, have been found in the amber. The amber inclusions have also enabled more exact comparisons with living insects than ordinary preservation would permit. There are several instances of genera being recognized and established for amber species and subsequently being found in existence. More remarkable still is the occurrence in the amber of certain species of insects, mostly ants, which are apparently identical with some species now living. The Baltic amber has also furnished proof of the existence of social habits among the insects of that time, for the ants that occur there include, in addition to males and females, major and minor workers. The extent to which the complex habits of living ants had already been acquired in the early Tertiary is shown by the presence of plant lice attended by ants in search for honey dew, and by the presence of mites attached to the ants in the same manner as is characteristic today. It is worth noting, however, that by no means all of the families of insects had acquired such evolutionary stability by the early Tertiary period. The bees preserved in the amber, for example, belong to extinct genera.

A study of Tertiary insects also contributes to our understanding of the geographical distribution of living families and genera, many of which occupied very different regions from those now inhabited (see pl. 2, fig. 2; pl. 3, fig. 1). An example of this is shown in plate 3, figure 2, which depicts a peculiar scorpionfly from mid-Tertiary shales in Colorado; it belongs to a group now restricted to parts of Asia. Hundreds of examples of such changes could be given [12]. The best known of these is the occurrence in the Colorado Tertiary of tsetse flies (Glossinidae), now confined to Africa. Incidently, the suggestion has been made by several mammalogists that trypanosomiasis, a protozoan disease now transmitted by the tsetse flies in Africa, might have been a factor in the extermination of some of the Tertiary mammals in North America.

A number of inferences might be drawn from the geological history of the insects as we now know it, only a few of which have been indicated above. Certainly there is one justifiable conclusion, namely, that our existing insect fauna is but a small fragment of the total insect aggregation that has occupied the earth during the past 250 million years. Understanding of insect evolution depends to a large extent on a knowledge of the extinct insect population. The investigation of the fossil record has only begun, and progress is slow, but the significance of the record increases with each discovery.

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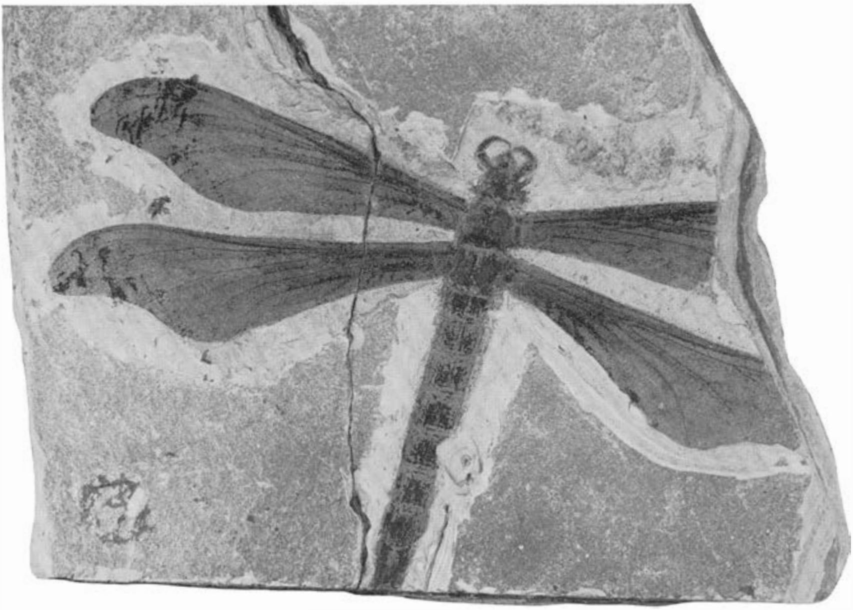
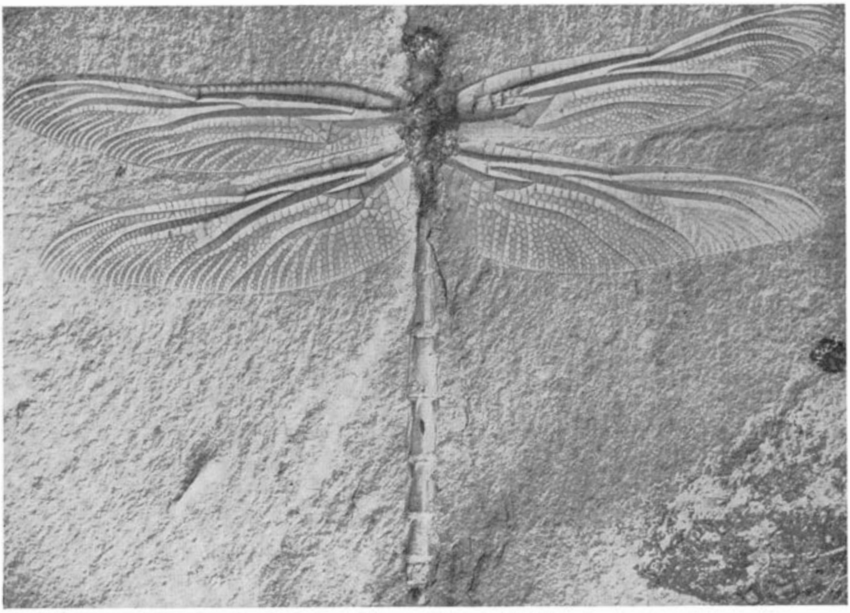
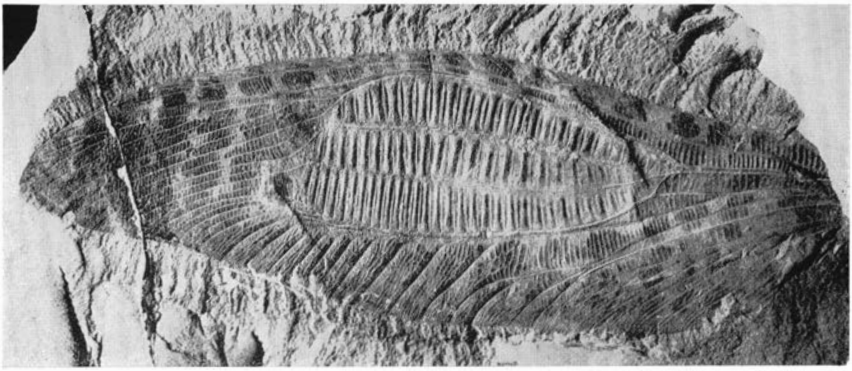


1. MISCHOPTERA NIGRA BRONGNIART.
A megasecopteron from the Carboniferous of France. $\times$ .7.

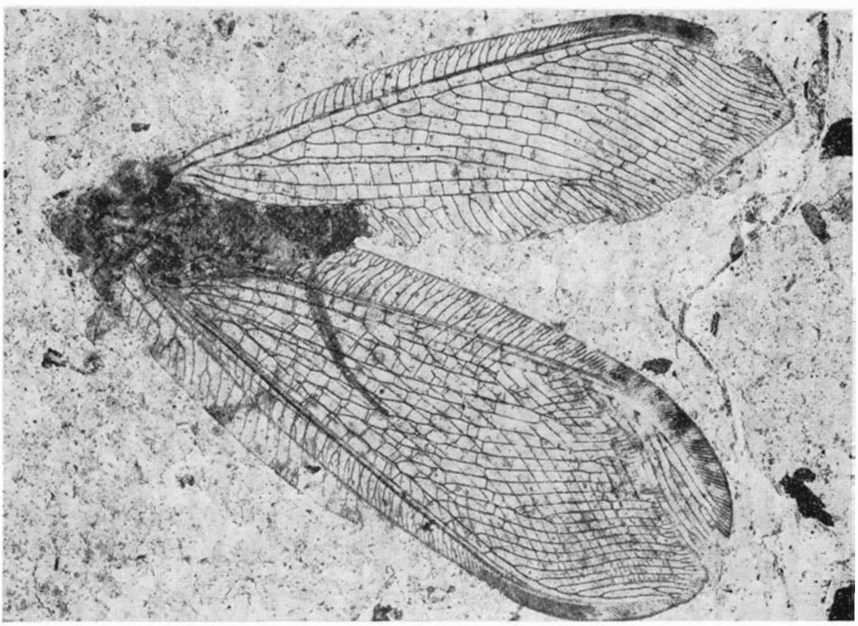


2. PROTOLINDENIA WITTEI (GIEBEL).
An odonatan from the Jurassic of Bavaria. $\times$ 1.2.



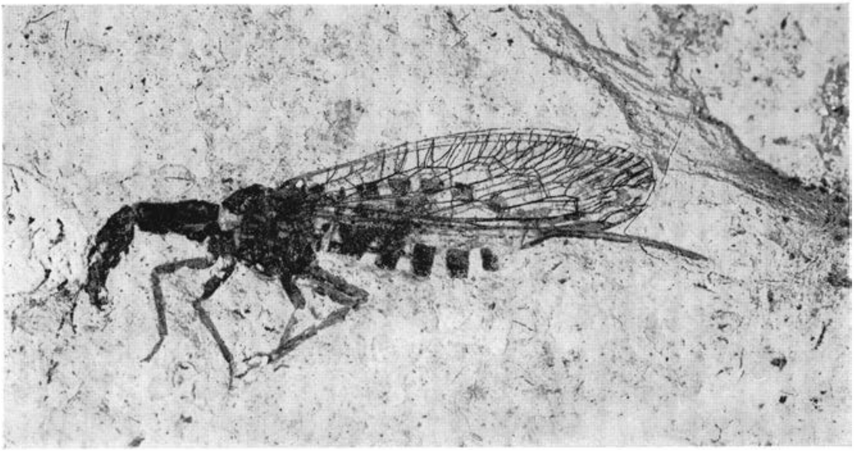
1. CLATROTITAN ANDERSONI McKEOWN.

An orthopteron with a large stridulatory organ, from the Triassic of New South Wales. × 7.



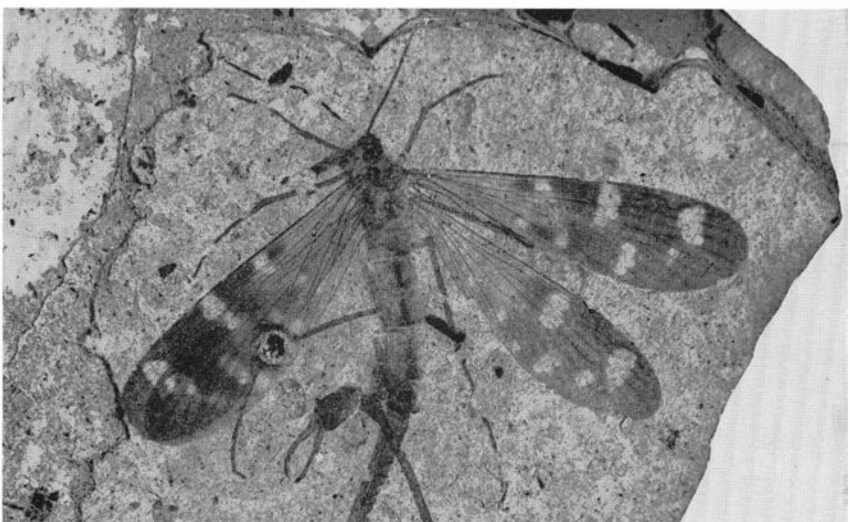
2. LITHOSMYLUS COLUMBIANUS (COCKERELL).

An osmylid fly (Neuroptera) from the Miocene shales of Colorado. The family Osmylidae does not now occur in North America. × 3.3.



1. RAPHIDIA MORTUA (ROHWER).

A snakefly from the Miocene shales of Colorado. The genus *Raphidia* does not now occur in North America $\times$ 5.



2. HOLCORPA MACULOSA SCUDDER.

A scorpionfly from the Miocene shales of Colorado. $\times$ 2.5.