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THE GEOLOGICAL RECORD OF INSECTS

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INTRODUCTION

Insects constitute the largest class of the phylum Arthropoda. Like other members of the phylum, they have an exoskeleton and are metamerically segmented. The insect head consists of six fused segments; the thorax three segments, each with a pair of segmented legs; and the abdomen eleven segments, which may be reduced or modified in some specialized species. Most insects have two pairs of wings attached to the second and third thoracic segments, but some have only one pair, and others have secondarily lost both pairs.

Wings are important in the classification of insects at both the ordinal and familial levels, and especially so for fossil specimens. The cuticular nature of the wings helps their preservation as fossils, even in situations where the rest of the insect has been decomposed or otherwise destroyed.

Insects are basically terrestrial, and they respire by a series of tracheal tubes that open laterally on the thorax and abdomen. Nevertheless, many orders of insects have become secondarily adapted to freshwater habitats, either as immature stages or as adults, or both. In these instances, the tracheae terminate in gills that allow oxygen in solution in the water to diffuse into the insect's respiratory system.

Most insects become fossils by falling into a body of water, where they may be entombed in silts or other fine sediments and eventually be preserved, if not destroyed by various scavengers and detritivores. Chitin and protein, primary constituents of the insect exoskeleton, are rapidly destroyed by a variety of microorganisms, and insects must generally undergo immediate burial under anaerobic conditions for fossilization to take place. Hence, most insects are fossilized under only very precise

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(usually catastrophic) environmental conditions; under normal conditions, preservation is an unlikely event. Thus it must be stressed that there is much bias in the fossil record of the insects, and that the absence of an order or family from a fossil-bearing deposit does not necessarily mean that the taxon was not in existence at the time.

The origin of insects is not clear. Several diverse theories have been advanced, suggesting their origin from trilobites, crustaceans, myriopods, or the hexapod class Diplura. For all of these proposals, however, the evidence is very weak and speculative. Since the insects and the members of these other groups have evolved along very different lines for at least 350 Myr, the absence of convincing evidence among existing arthropods for such a relationship is not surprising. The fossil record, as presently known, contributes nothing to our understanding of the actual origin of the insects. The earliest known insects, although belonging to the more generalized part of the insect hierarchy, show no morphological features indicative of their ancestral stock. On the other hand, there is a bewildering array of fragmentary remains of arthropods from the Cambrian to the Lower Carboniferous that do not fall within any of the known higher arthropod categories, existing or extinct. It is probable that the ancestral stock of the insects will eventually be found among such material. Until then, we can only speculate on their nature.

Although differing views on insect evolution have been presented in the literature (Martynov 1937, Rohdendorf & Rasnitsyn 1980), the concept currently accepted by most entomologists is that there were four main stages in the history of the insects. The first stage consisted of primitively wingless species comprising the subclass Apterygota, represented now by bristletails (order Archaeognatha) and silverfish (order Zygentoma). In nearly all respects, both morphological and physiological, the Apterygota are the most generalized insects known.

The second stage began with the origin of the winged insects, or Pterygota. This was probably the most important step in the history of the insects, and it is almost certainly more responsible for the success of the group than any other factor. Flight not only provided an effective means of dispersal but also offered a means of escape from predators and greater flexibility in obtaining food. It is not surprising that over 99% of all extant insects belong to the subclass Pterygota. Nevertheless, the origin of wings in insects is by no means clear; several theories have been proposed, but none of them has received general acceptance by entomologists concerned with insect evolution (Kukalová-Peck 1978, Rasnitsyn 1981, Kingsolver 1984). The most primitive of the winged insects, termed the paleopterous Pterygota, have a simple, hinged articulation of the wings to the thorax. They are represented in the present fauna by only two orders: the dragonflies (order Odonata) and the mayflies (order Ephemeroptera) (Martynov 1925). Although many of the Paleoptera are good fliers, the nature of their wing articulation prevents them from flexing their wings back over the abdomen when they are at rest [Figure 1 (*top*)]. These paleopterous Pterygota make up less than 1% of the species of insects in existence today.

The third stage was marked by the development of a more complicated wing articulation (resulting from a modification of the third axillary sclerite) that allowed the wings to be placed back over the abdomen when the insect was at rest (Snodgrass 1935). This enabled these insects, termed the neopterous Pterygota, to exploit a diversity of new habitats. No longer hindered by outstretched wings, they were able to crawl into dense foliage or seek refuge under bark or stones or in soil [Figure 1 (*bottom*)]. Many of them have modified their wings in various ways. In several orders, such as the fleas (Siphonaptera) and lice (Anoplura), the wings have been secondarily lost as an adaptation to ectoparasitism. In others, the fore wings are present but have been modified as either leathery or thickened protective covers, as in the cockroaches (order Blattodea), grasshoppers (order Orthoptera), true bugs (order Hemiptera), and several other orders. The most primitive of these neopterous Pterygota undergo direct postembryonic development: the immature stages, usually termed nymphs, pass gradually through a series of molts to the adult form. Since the wings develop externally, increasing in size each nymphal instar, these insects are termed exopterygote Neoptera. Nymphs typically resemble the adults, feed on the same food, and live in the same habitat. Fifteen existing orders, including the three orders mentioned above, are part of this group, which accounts for about 12% of the living species of insects.

The fourth, and presently final, stage of the insects' history occurred when some of the Neoptera evolved a more complicated or indirect type of postembryonic development. In these insects, known as the endopterygote Neoptera, wing buds develop in the immatures, or larvae, as invaginations of the body wall. The wings are not evaginated until the insect reaches the pupal stage—a quiescent, nonfeeding state, during which marked reorganization of larval tissues and organs take place. The larvae show little morphological resemblance to the adults, feed on different food, and live in different habitats. Nine existing orders are assigned to the endopterygote Neoptera. These are the largest and most familiar of the insect orders and include the beetles (order Coleoptera), true flies (order Diptera), ants, bees, and wasps (order Hymenoptera), etc. Approximately 85% of all living insects belong to this category.

The geological record of these four stages in the evolution of the insects shows several surprises (Figure 2). The earliest known insects are from

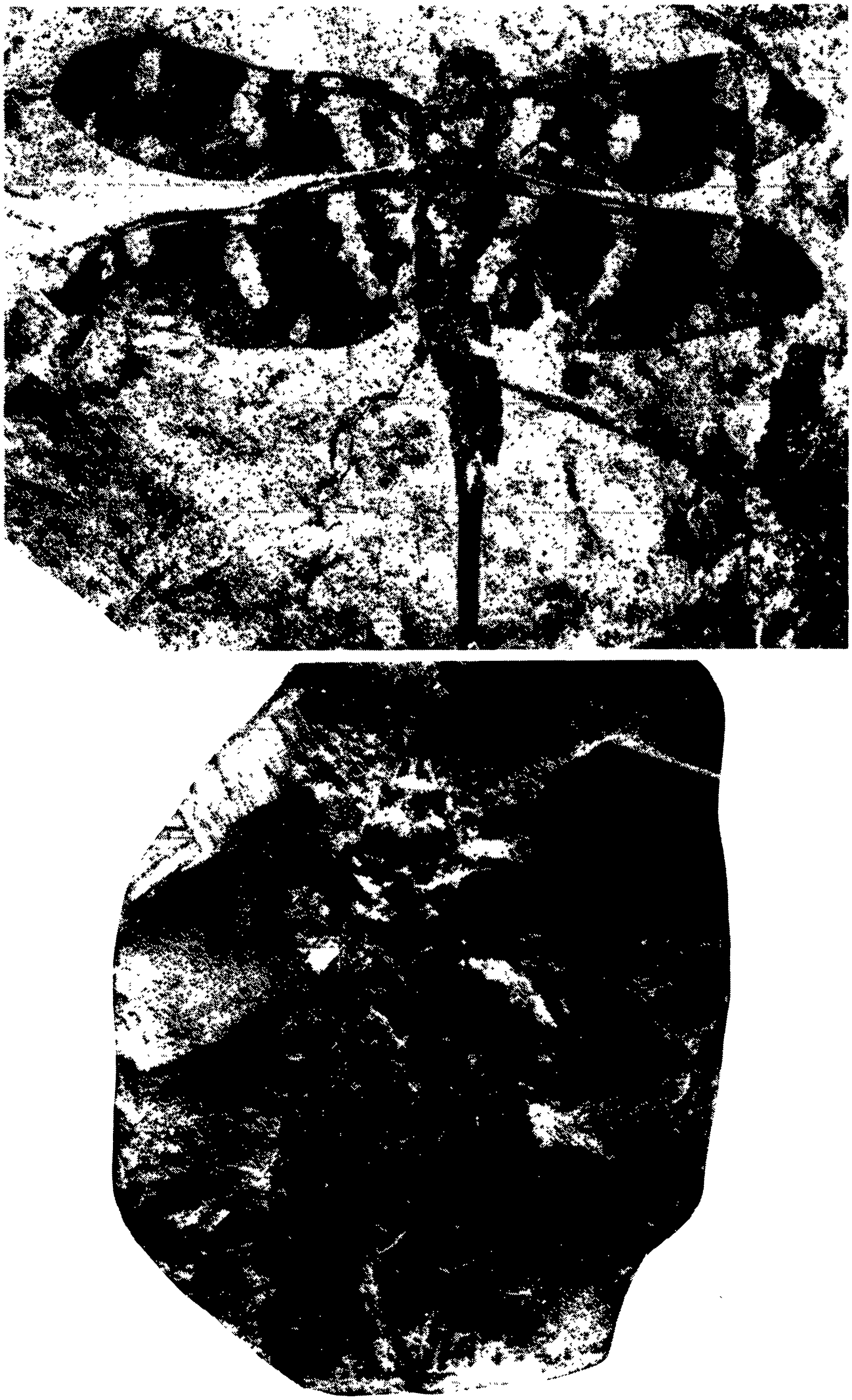

Figure 1 (*top*) *Dunbaria* (Palaeodictyoptera, Permian, Kansas, Division Paleoptera). (*bottom*) *Gerarus* (Protorthoptera, Upper Carboniferous, Illinois, Division Neoptera).

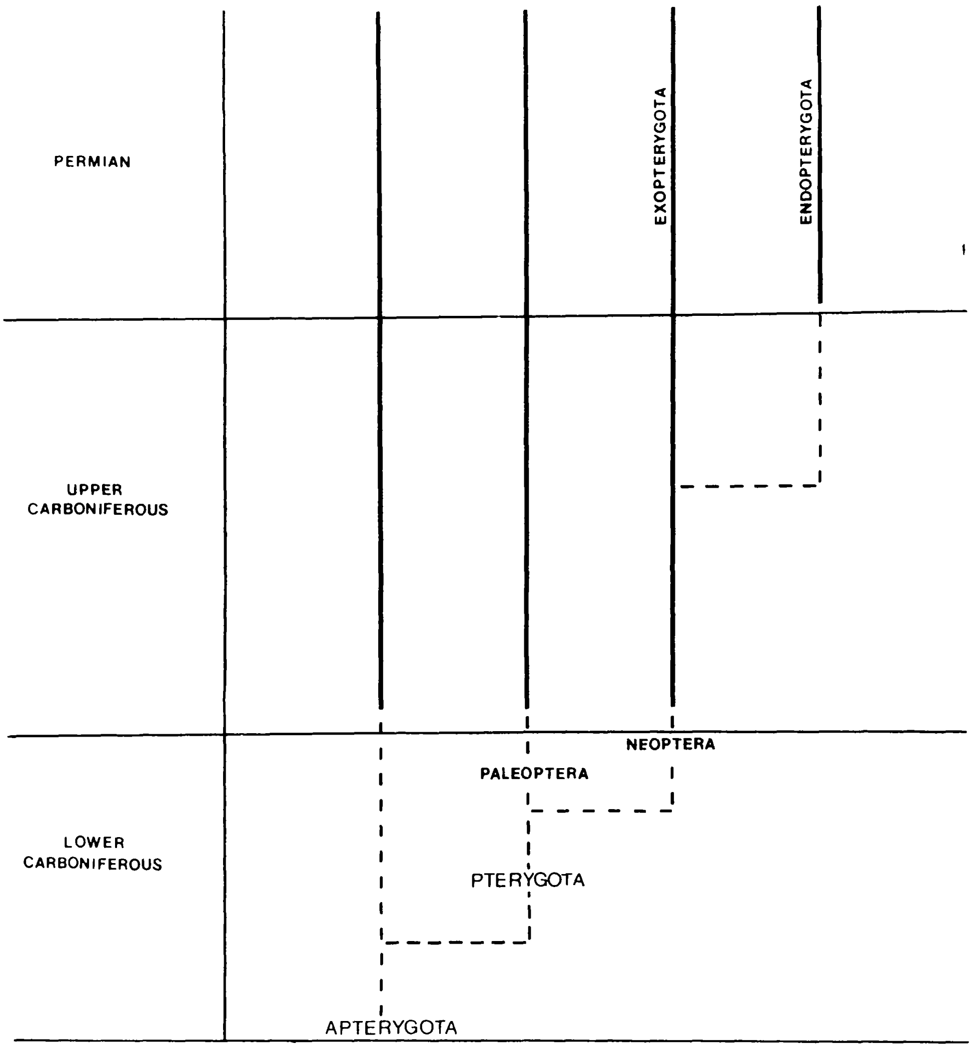

Figure 2 Geological record of main stages in insect evolution. Broken lines indicate absence of fossil record.

Upper Carboniferous deposits, and it is obvious that the insects had already reached three of the four stages in their evolution by this time. The endopterygote Neoptera first appear as early as the Lower Permian, where they are represented by two living orders, the scorpion flies (order Mecoptera) and lacewings (order Neuroptera). Since both these orders show considerable diversity, we can infer that the endopterygotes undoubtedly arose in the Upper Carboniferous. Presumably, also, wings and wing-flexing arose earlier than the Upper Carboniferous, probably in the Lower Carboniferous. This means that these four stages in insect evolution had taken place before the end of the Carboniferous, and that most probably the first three stages were attained even earlier. Unfortunately, we have no fossil evidence for this assumption at present.

Table 1 Geological ranges of the orders of insects

Classification	Geologic range
Subclass Apterygota	
Order Archaeognatha	U. Carb.–Recent
Order Zygentoma	Tert.–Recent
Subclass Pterygota	
Division Paleoptera	
Order Ephemeroptera	U. Carb.–Recent
Order Palaeodictyoptera[a]	U. Carb.–Perm.
Order Megasecoptera[a]	U. Carb.–Perm.
Order Diaphanopterodea[a]	U. Carb.–Perm.
Order Protodonata[a]	U. Carb.–Perm.
Order Odonata	Perm.–Recent
Division Neoptera	
Section Exopterygota	
Order Plecoptera	Perm.–Recent
Order Protorthoptera[a]	U. Carb.–Perm.
Order Grylloblattodea	Recent
Order Blattodea	U. Carb.–Recent
Order Dermaptera	Jur.–Recent
Order Caloneurodea[a]	U. Carb.–Perm.
Order Manteodea	Tert.–Recent
Order Isoptera	L. Cret.–Recent
Order Zoraptera	Recent
Order Protelytroptera[a]	Perm.
Order Orthoptera	U. Carb.–Recent
Order Phasmida	Tri.–Recent
Order Embioptera	Tert.–Recent
Order Miomoptera[a]	U. Carb.–Perm.
Order Psocoptera	Perm.–Recent
Order Mallophaga	Recent
Order Anoplura	Recent
Order Thysanoptera	Perm.–Recent
Order Hemiptera	Perm.–Recent
Section Endopterygota	
Order Mecoptera	Perm.–Recent
Order Neuroptera	Perm.–Recent
Order Glosselytrodea[a]	Perm.–Jur.
Order Trichoptera	Perm.–Recent
Order Lepidoptera	L. Cret.–Recent
Order Coleoptera	Perm.–Recent
Order Strepsiptera	Tert.–Recent
Order Diptera	Tri.–Recent
Order Siphonaptera	Tert.–Recent
Order Hymenoptera	Tri.–Recent

[a] Extinct orders.

The discussion that follows traces the geological history of the insects (Table 1). During the past century, over 50 extinct orders of insects have been named and described, but most of these were based on fragmentary material and have subsequently been synonymized. At present, only 9 extinct orders are sufficiently well known to justify their recognition; 4 belong to the Paleoptera, 4 to the exopterygote Neoptera, and 1 is considered to belong to the endopterygote Neoptera (Brues et al 1954, Carpenter 1976, Wootton 1981).

PALEOZOIC ERA

Upper Carboniferous

Eleven orders of insects belonging to the Apterygota, Paleoptera, and exopterygote Neoptera are recorded from the Upper Carboniferous. Seven of them are extinct. Insects occur only rarely in Upper Carboniferous deposits, and the majority of them have been found at only three well-known localities: Commentry, France; Illinois, USA; and Kuznetzk Basin, USSR. Most of the specimens are from Westphalian and Stephanian beds, although the few specimens from the Namurian belong to neopterous as well as paleopterous orders and therefore suggest a much earlier origin for the Paleoptera.

APTERYGOTA The existing order Archaeognatha is represented in Upper Carboniferous beds of France and Illinois by species belonging to an extinct suborder, Monura. In most respects, Monura are considered more generalized than the extant members of the Archaeognatha (Sharov 1957b, Carpenter 1985a,b, Carpenter & Richardson 1985). They lacked a pair of terminal processes, or cerci, characteristic of all living Apterygota, but they did have the median process well developed. The absence of cerci has generally been considered a derived condition, but their absence in the Monura suggests that this may in fact represent an ancestral condition. Although only a few species of Archaeognatha are known from the Upper Carboniferous, they show considerable diversity in structure (Carpenter & Richardson 1985).

PALEOPTEROUS PTERYGOTA The existing order Ephemeroptera (mayflies) is represented in the Upper Carboniferous of France by a single adult specimen. Since the order is generally recognized as the least specialized of the Pterygota, its presence in the Upper Carboniferous is not unexpected. Unlike existing species, in which the hind wings are much reduced in size, the fore and hind wings in this Carboniferous species are nearly identical. The abdomen bears a pair of cerci and a median process, as in existing mayflies (Carpenter 1963).

The extinct order Palaeodictyoptera was one of the largest in the Upper Carboniferous, having a total of 17 families. Most of the species were of moderate size, but a few had wingspans as great as 40 cm (Kukalová 1969a,b, 1970). Typically, fore and hind wings were similar, but in more specialized species the hind wings are distinctly broader than the front wings. The prothorax bore a pair of small, winglike lobes, and the abdomen terminated in a pair of long cerci. The most unusual feature of these insects was the nature of the mouthparts, which formed a sucking beak containing five slender stylets. Such a beak is characteristic of insects that feed on liquid food, and it is presumed that the Palaeodictyoptera used their beaks to pierce plants and thus obtain nutrients in the form of phloem. Several nymphs belonging to this order have been found, and all of them have divergent wing buds and beaks like the adults. Since these nymphs show no structural modifications for an aquatic life, they are presumed to have been terrestrial.

Members of the extinct order Megasecoptera resembled the Palaeodictyoptera and had similar mouthparts, but they lacked the small winglike lobes on the prothorax, and their wings had a more specialized venation and shape. The nymphs were like those of the Palaeodictyoptera and are also presumed to have been terrestrial. This was a much smaller order in the Carboniferous than the Palaeodictyoptera, however, with only about eight families.

The extinct order Diaphanopterodea was related to the Palaeodictyoptera and Megasecoptera and had similar mouthparts, but differed from them in having a more reduced venation. Most distinctive about the Diaphanopterodea was their ability to fold their wings back over the abdomen at rest. Examination of the wing articulation has shown that this wing position was not accomplished by modification of the third axillary sclerite, as in the Neoptera, but by a different mechanism (Kukalová-Peck 1974). Consequently, the Diaphanopterodea are considered highly specialized Paleoptera that evolved a wing-flexing mechanism independently of the true Neoptera. The order Diaphanopterodea was small in the Carboniferous, with only four families known.

The extinct order Protodonata resembled dragonflies, with some venational differences. They had strong mandibles and very spiny fore legs. All were large insects, and some species, with a wing expanse of 70 cm, were the largest insects ever to have existed. The structure of their mouthparts and legs strongly indicates that they were predators, catching prey in flight, like modern dragonflies. Although they were widely distributed in the Carboniferous, they did not have much diversity, and only two families are known from that period (Carpenter 1943).

EXOPTERYGOTE NEOPTERA Five orders in this division are known from the Upper Carboniferous. Three of them, the Protorthoptera, Caloneurodea, and Miomoptera, are extinct. The other two, the Blattodea and Orthoptera, although closely related to the others, are both living. The development of wing flexing accounts for much of the adaptive radiation present in these insects. For example the thickening of the fore wings, which occurred many times independently, results in their diminished function in flight and in an increased role as protective covers for the insect's thorax and abdomen. As part of this same process, the hind wings were correspondingly widened, and lines of folding developed over the anal region, allowing that part of the wing to fold up like a fan. The Blattodea and Protorthoptera are examples of this phase of evolution. Subsequently, however, in several exopterygote orders the coriaceous nature of the fore wing became less marked, and the anal area was reduced to nearly its original size. Two of the extinct orders, the Caloneurodea and Miomoptera, lack an expanded area of the hind wing, and the fore wing is not coriaceous. The phylogenetic position of these orders is therefore unclear.

The insects placed in the order Protorthoptera have several conspicuous features in common, including coriaceous fore wings, at least slightly expanded anal areas of the hind wings, chewing mouthparts, cursorial hind legs, and prominent but not long cerci. In other respects, however, these insects showed extraordinary diversity of body structures. In some of the Carboniferous species, the prothorax is very elongate and armed with long spines [see Figure 1 (*bottom*)]; in others, one set of mouthparts, the maxillary palpi, are extraordinarily long; and in others the fore legs are elongate and raptorial. Attempts to divide this order into suborders and even into orders have proven unsatisfactory (Burnham 1983). As the order Protorthoptera is now understood, it is the largest of all extinct orders, and over thirty protorthopteran families have been recorded from the Upper Carboniferous alone.

The existing order Blattodea (cockroaches) is well represented in the Upper Carboniferous. Unfortunately, the classification of fossil cockroaches is difficult because morphological characters employed in the systematics of living species are not preserved in the fossils. In fact, the fore wings are usually the only parts of cockroaches preserved, and they lack the characters necessary for family- or generic-level determination. Although hundreds of species of Upper Carboniferous cockroaches have been described, they are generally placed in only four or five families. However, specimens of cockroaches are usually the most numerous of all insects in the Upper Carboniferous, comprising approximately 80% of all insects collected in this period. They are commonly found in coal shale, associated with such plants as horsetails, club mosses, and seed ferns. They probably lived in swamps and other wet regions, which provided ideal conditions for their preservation as fossils.

In general, the Upper Carboniferous cockroaches were similar in appearance to those now living, the differences in wing and body structure being slight. However, one distinctive feature of Carboniferous cockroaches was that the females had long external ovipositors. These do not occur in living species, and their presence in Carboniferous cockroaches suggests that females may have inserted their eggs in specific, perhaps concealed, places (Schneider 1977, 1978a,b).

The existing order Orthoptera (grasshoppers, katydids, crickets) includes species with the characteristics of the Protorthoptera but differs from them in having the hind legs modified for jumping. Only one family is known from the Upper Carboniferous.

The extinct order Caloneurodea included insects whose fore and hind wings were similar, but with the hind pair lacking the expanded anal area. Little is known about their body structure, except that the antennae and legs were long and slender and that short cerci were present. The order has usually been placed in the exopterygote Neoptera, but Sharov believed them to have been endopterygotes. Only two families are known from the Carboniferous (Sharov 1966).

The extinct order Miomoptera consisted of small to very small insects whose fore and hind wings were similar, without an enlarged anal area on the hind pair.

Permian

The Permian insect fauna is better known than that of any other pre-Tertiary fauna. Extensive collections from the Soviet Union, Czechoslovakia, the United States, and Australia have provided the basis for much of this knowledge. Twenty-two orders, including the 9 extinct ones, are in the Permian record. These are distributed as follows: Apterygota, 1 order; Paleoptera, 6 orders; exopterygote Neoptera, 10 orders; and endopterygote Neoptera, 5 orders. With the combination of 9 extinct and 13 extant orders, Permian insects apparently comprised the most morphologically diverse insect fauna that is known.

All of the orders found in the Upper Carboniferous continued into the Permian, some with significant changes in diversity. The Permian Archaeognatha, however, were very similar to those of the previous period and belonged not only to the same suborder (Monura) but also to the same family. The Monura were apparently already on the decline, and they are not known beyond the end of the Permian. The Ephemeroptera, on the other hand, were very diverse in the Permian. They were represented by 5 families, including many genera, and they are preserved as both nymphs and adults (Carpenter 1979). The adults had well-developed mandibles, in contrast to the existing mayflies, in which the mouthparts are atrophied and nonfunctional. The nymphs were similar to those of the living species, bearing lateral, tracheal gills. The Palaeodictyoptera were much less diversified than in the Carboniferous, with only 6 families represented. In some families there was a marked reduction and even complete loss of the hind wings (Sharov & Sinitshenkova 1977, Sinitshenkova 1980). The Megasecoptera, in contrast, were much more diverse in the Permian (Carpenter 1947), with their 12 families showing striking modifications of body and wings. The Diaphanopterodea, having 6 families, were likewise more diverse in the Permian and are considered to have been the most highly specialized of the Paleoptera. The Protodonata, although well represented in the Permian, were similar in size and venation to those of the Carboniferous and belonged to the same families. The Protorthoptera apparently reached the peak of development in the Permian, represented there by a total of at least 40 families (Carpenter 1950, 1966). The Blattodea were much less abundant in the Permian than in the Carboniferous. The Orthoptera, with 5 families, also showed much greater diversity than in the Carboniferous (Sharov 1971), as did the Caloneurodea, represented by 8 families. The Miomoptera are known from the Permian only by 3 families; one was a Carboniferous family (Palaeomanteidae), the members of which were extremely abundant in the Lower Permian and which are represented by nymphs as well as adults (Sharov 1957a).

The following orders occurred for the first time in the Permian:

PALEOPTERA The existing order Odonata (dragonflies and damselflies) was represented by six families belonging to three suborders; two of the suborders are extinct, the third (Zygoptera) is extant. All of the Permian Odonata were small and delicate (Carpenter 1931, 1947). Their nymphs are unknown.

EXOPTERYGOTE NEOPTERA The existing order Plecoptera (stone flies) is known in the Permian by several families that are closely related to the more generalized extant families, and they have been shown to possess tracheal gills and other modifications for an aquatic environment.

The extinct order Protelytroptera is known only in the Permian and by species that closely resemble the beetles (Coleoptera). The fore wings were modified in most species to form wing covers, or elytra, and the hind wings were able to fold up under the elytra at rest. However, the nature of the hind wings and the presence of cerci indicate that they were probably related to the earwigs (Dermaptera) and Protorthoptera, rather than to the Coleoptera (Carpenter & Kukalová 1964, Kukalová 1965).

The existing order Psocoptera (bark lice), which are very small insects related to the thrips (Thysanoptera), were represented by several families that were remarkably similar to some of the Hemiptera (true bugs) that occurred in the Permian (Becker-Migdisova & Vishniakova 1962).

The existing order Thysanoptera (thrips) is first recorded from Permian deposits, in which it is represented by two families and many genera. The wing venation of these Permian species is very similar in many ways to that of the Psocoptera and the Hemiptera (Homoptera); several of the genera now assigned to the Thysanoptera have previously been placed in both of those orders (Vishniakova 1981).

The existing order Hemiptera (true bugs), which are characterized by having the mouthparts modified to form a sucking beak, is known in the Permian by a very large number of families belonging to the suborder Homoptera. Four extant superfamilies and one living family (Cixiidae) have been identified (Becker-Migdisova 1960).

ENDOPTERYGOTE NEOPTERA The existing order Mecoptera (scorpion flies) first appeared in the Lower Permian, and by the end of that period it was represented by 11 families, nearly twice as many as exist now. Included are several species that apparently belonged to a living family (Nannochoristidae). In some other Permian families, the venational patterns grade into those of certain Permian Trichoptera (caddis flies) (Martynova 1962b).

The existing order Neuroptera (alderflies, snake flies, and lacewings) also made its first appearance in the Lower Permian, and by the end of the period six families belonging to all three of the extant suborders (Sialoidea, Raphidioidea, and Planipennia) were represented (Ponomarenko 1977b).

The existing order Trichoptera (caddis flies) is also known in the Lower Permian, with a total of four families for the period. The immature stages are unknown (Martynova 1962c, Sukatscheva 1976).

The members of the extinct order Glosselytrodea, known only from the Permian to the Jurassic, resemble certain Neuroptera in venation and in other details of wing structure. These features suggest that the order was endopterygote, but the evidence is by no means conclusive. Only three families are known (Martynova 1952, Sharov 1966).

The existing order Coleoptera (beetles) was represented in the Permian by six families, all of them belonging to the suborder Archostemata, the most generalized of all Coleoptera. At the present time there are only two families in that suborder (Ponomarenko 1969, 1977a).

MESOZOIC ERA

Triassic

The insect fauna of the Triassic is less known than that of any other period since the first appearance of the insects in the Upper Carboniferous. This is probably a result of the scarcity of freshwater deposits. The most striking aspect of the Triassic fauna is that all but one (Glosselytrodea) of the extinct orders that were present in the Permian are absent. In other respects, the Triassic record offers few surprises. Previously existing groups continued to diversify during this period, especially the Ephemeroptera, Odonata, and most of the exopterygote Neoptera (Pritykina 1981). The Archaeognatha were becoming increasingly modern, as evinced by the presence of a species belonging to the extant family Machilidae (Paclt 1972). Three living orders, one in the Exopterygota and two in the Endopterygota, also appeared for the first time in the Triassic:

EXOPTERYGOTE NEOPTERA The order Phasmida (walking sticks), related to the Orthoptera, is known from the Triassic of Australia and is represented by a single family (Martynov 1928, Martynova 1962a).

ENDOPTERYGOTE NEOPTERA The order Diptera (true flies) is represented in the Triassic by species assigned to eight different families, all apparently belonging to the suborder Nematocera, which contains the least specialized families of the order. These Triassic fossils have a curiously specialized wing venation, however, and may eventually turn out to belong to an extinct suborder (Rohdendorf 1964).

Representatives of the order Hymenoptera (sawflies, ants, bees, wasps) first appear in the Triassic and belong to a total of 59 genera in two families, both of which are extant and belong to the relatively unspecialized suborder Symphyta (Rasnitsyn 1964, 1969, 1975).

Jurassic

The insect fauna of the Jurassic period is better known than that of either the Triassic or Cretaceous, primarily because of the extensive insect-bearing localities discovered in the Soviet Union. Many existing families appeared during this period (Popov 1971, Rasnitsyn 1976, 1982, Vishniakova 1976), although extinct families still generally predominated. The Jurassic Diptera, for example, consisted of 29 families, of which all but 4 are now extinct; and the Hymenoptera included 17 families, of which all but 5 are now extinct. In marked contrast, however, three fourths of the Jurassic families of Coleoptera are still existing.

EXOPTERYGOTE NEOPTERA The order Dermaptera (earwigs) is the only new order to occur in the Jurassic. The fossils resembled living species in general appearance but differed in having cerci that are long and multisegmented, with only a suggestion in some of the coalescence of segments that eventually formed the forceps that are characteristic of all living Dermaptera (Vishniakova 1980).

Cretaceous

Few insect-bearing sediments from the Cretaceous are known, and our knowledge of the Cretaceous insect fauna has therefore been limited. However, relatively recent discoveries of Cretaceous ambers with insect inclusions have added greatly to the known fauna. Furthermore, the excellent preservation of most of the specimens has enabled detailed comparisons with living material. It now appears that the great majority of Cretaceous insects belong to existing families and represent an essentially modern fauna. This is, in part, owing to the origin and radiation of flowering plants that took place during the Cretaceous. Many of the Diptera and Hymenoptera preserved in amber from this period belong to families that are important pollinators. The Cretaceous is also a very important period with respect to the social insects. Ants first appeared at this time and have been found in amber from New Jersey and Siberia. Both workers and reproductive forms have been described, and it is clear that at least some form of social organization had already been achieved within the Hymenoptera (Burnham 1978). Two orders that make their first appearance in the Cretaceous are the Isoptera and the Lepidoptera:

EXOPTERYGOTE NEOPTERA The Isoptera (termites) have been found in Cretaceous sediments from both Canada and England (Jarzembowski 1981) and have been assigned to the existing family Hodotermitidae. Since all living members of this family are fully social, it is virtually certain that the Cretaceous species were also social (Jarzembowski 1981).

ENDOPTERYGOTE NEOPTERA The Lepidoptera (moths and butterflies) occur for the first time in the Cretaceous (Skalski 1979), and their appearance undoubtedly correlates with the origin of the angiosperms. Several species belonging to the extant family Micropterygidae, which is considered ancestral to the rest of the Lepidoptera, have been described.

CENOZOIC ERA

Tertiary

Since insect-bearing deposits of Tertiary age are numerous and accessible, our knowledge of the insects of this period is extensive. As early as the beginning of the Tertiary, the insect fauna was like that of the present in most respects. Nearly all of the families in the early Tertiary exist today, and by the middle of the period roughly three fourths of all genera are extant. In addition, five new orders occurred in the Tertiary:

APTERYGOTA The order Zygentoma (silverfish), although probably in existence at least as far back as the Triassic, first appears in the Lower Oligocene (Silvestri 1912).

EXOPTERYGOTE NEOPTERA The order Manteodea (mantids) is represented in the fossil record by species that have been included in extant genera belonging to two different families.

The order Embioptera (web spinners) is represented in the Tertiary by species assigned to three different families, one of which is extinct (Davis 1940).

ENDOPTERYGOTE NEOPTERA The order Siphonaptera (fleas) is known by two species belonging to a single extant genus (Peus 1968).

The Strepsiptera are entomophagous parasites and are known only from Baltic and Dominican amber. They are represented by two species belonging to two extant genera (Kinzelbach 1979).

Quaternary

Insects collected from this period occur primarily in peat and tar deposits, and (with only rare exceptions) have been assigned to existing species. These have been studied mainly in connection with the effects of Pleistocene glaciation on the geographical distribution of insects.

SUMMARY

The record of insects in the Upper Carboniferous shows that by the end of that period they had passed through all four major stages of their evolutionary history. The first three of these had apparently been completed in Lower Carboniferous time or earlier, before the fossil record of the insects actually begins. The Permian was a period of very rapid expansion of the orders. All 11 previously existing orders continued from the Carboniferous, and 11 others appeared before the end of the period. Some of the paleopterous orders had begun to dwindle, but others expanded proportionally. However, it was the exopterygote Neoptera that changed the most, resulting in a confusing combination of characters suggestive of several orders (as in the Protorthoptera), and similar radiations occurred among the Permian endopterygote Neoptera. Most of these lines died out early in the Mesozoic. Five orders had haustellate

mouthparts, presumably for feeding on plant juices. It is probable that by the end of the Permian the insects had achieved as complicated a relationship with the flora of the time as our contemporary insects have with the flowering plants, which developed rapidly during the Cretaceous. The interval of time between the development of the flowering plants and the present was about the same (100 Myr) as that from the beginning of the Upper Carboniferous to the end of the Permian.

The transition from the Permian to the Mesozoic was abrupt, with only one of the nine extinct orders surviving beyond the Permian. The Diptera and the Hymenoptera, two of our largest orders at present, appeared in the Triassic and by the Jurassic included a substantial number of existing families. The appearance of the Lepidoptera in the Cretaceous, and especially of the social insects (such as the termites and ants), set the stage for the Tertiary. By mid-Tertiary, on the average, about 60% of the genera of insects are extant. A few species, apparently morphologically inseparable from some now living, have turned up in several of the Tertiary ambers.

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