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GEOLOGICAL HISTORY OF COCKROACHES

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NO insects are more abundant as fossils, and none so widely distributed through the various formations, as are the cockroaches. Their delight in moist places, often near the banks of streams, their firmly chitinized wings and body render them of insects among the best adapted for preservation. Especially are they to be expected in association with ferns and other plants among which during life they found shelter, and together with which they were transported to their resting place in the rocks. Hardly ever will persistent search among fossil leaves of land origin, when imbedded in rocks of sufficiently fine texture, fail to bring to light at least detached wings and perhaps bodies. Even when the bodies of adults have not been preserved, not infrequently will be found the cast-off integument of the young. It is this approximately complete geological record that lends an especial interest to the cockroach family.

The cockroaches have proved themselves a remarkably conservative group having retained throughout their long existence, as compared with other insects, a relatively generalized structure. The development is direct, the young resembling the adults. The mouth parts are of the biting kind common to primitive insects. The segmentation of the abdomen and thorax is distinct. The foot is five-jointed. The venation of the wing is much less complicated than that of many of the more advanced types. Not all the organs, however, have retained this primitive simplicity. In this, as indeed in every group, some organs have outrun others in degree of specialization, so that the group early became a characteristic and well delimited one. The body is flattened, the head small and turned downwards. The covering of the first thoracic segment, the pronotum, is enlarged, rounded, more or less shield-shaped. The front wing is firmly chitinized and lies flat on the back, or slightly arched to conform to the shape of the thorax. An inner area near the base of the wing is marked off by a deep curved line, the anal furrow. The hind wing is less resistant and broader, the greater width being obtained by a greater expansion of the inner border. Hardly ever will a doubt arise as to the reference to this family of even a fragment of a specimen.

The structural characters so far mentioned made their appearance early. The rounded pronotum is as characteristic of Paleozoic as of

recent cockroaches. The thick arched front wing with strongly delimited anal area dates from the Carboniferous. The group, however, has by no means remained stationary since the Carboniferous. On the contrary, close observation reveals evidence of advance along distinct and definite lines. The Carboniferous cockroaches are provided with a long ovipositor resembling that of the katydids or crickets; modern cockroaches have a reduced and specialized ovipositor. Early cockroaches no doubt deposited their eggs in the ground or under the bark of trees or within the tissue of succulent stems; modern forms deposit their eggs in a very characteristic egg case. The front wings

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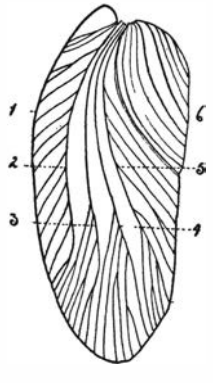

FIG. 1. Front wing of a typical Coal Measure cockroach, *Gerablattina arcuata* Sellards. 1, costa; 2, sub costa; 3, radius; 4, media; 5, cubitus; 6, anal veins. Twice natural size. Author's illustration.

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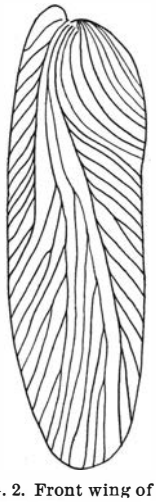

FIG. 2. Front wing of a Permian cockroach, ×5. Original drawing. Gn. sp. new. Author's Mns.

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FIG. 3. Front wing of a modern cockroach, *Ectobia germanica*, × 5. Original drawing.

From a comparison of the three types, Carboniferous (oldest), Permian (later), and (Fig. 3) modern, it is seen that: the wing has become increasingly slender and compact; the main veins have become partly fused; cross veins have developed, and the direction of the anal veins has changed.

have become in general more resistant, the venation more complicated. The hind wings have developed plications and a longitudinal fold. The value to biology of a study of the group is in direct proportion to the completeness with which these changes and the laws governing them can be traced out.

The wing of a typical cockroach of Carboniferous time is of simple structure. A border vein, the costa, traverses and strengthens the costal border. Four strong veins arising close together near the base of the wing diverge and supply the greater part of the wing membrane. The first of these, the subcosta, meets the costal border about or beyond the middle length of the wing; numerous superior branches are

given off which strengthen the upper edge of the wing. The following vein, the radius, reaches as a rule to the apex, and its branches given off from the upper side fill the apex. The medius, which is often of lesser importance, terminates on the inner border not far from the apex, and gives off a few usually superior branches. The fifth vein of the wing, the cubitus, is of more importance. It reaches along the inner border of the wing one half to two thirds the distance towards the apex, giving off strong inferior branches which strengthen the lower edge of the wing. The remaining small area on the lower inner corner of the wing is marked off by a deep furrow. The veins of this area are all simple or once forked, and pass with a uniform curve from their origin to the inner border.

The next type (Fig. 2) is from later deposits—the Permian. Here two of the main veins, the radius and media, have become fused for a little distance from their origin, so that instead of four strong veins arising from the middle of the base there are here only three. Otherwise the wing is not unlike the Coal Measure form. Many of the mesozoic wings have, in addition to a partial fusion of two or more of the main veins, a further radical change in the anal area, the veins of which, instead of ending on the inner border, run to and end on the anal furrow. The front wing of one of the living cockroaches, the common 'croton bug,' is shown in figure 3. Here cross veins are numerous, and the anal veins, as in most of the Mesozoic forms, end on the anal furrow. The wings described are those which are in a general way typical of their time. Along with each of these are found wings, some of which are more advanced, while others are of more simple structure than those illustrated. Among modern cockroaches not a few genera and species have both front and hind wings so incompletely developed as to be entirely useless, and present only as functionless wing pads. All Paleozoic cockroaches, so far as known, were provided with fully developed functional wings, the modern wingless forms having descended without doubt from winged ancestors.

The hind wings of Carboniferous cockroaches are as a rule broad with rounded inner border; the veins are evenly distributed; there are no cross veins; no indication of any fan-like plaiting such as is found in the hind wings of modern forms; apparently there was no folding, the wing lying spread out across the abdomen. Neither is there any differentiation into a thicker, brownish, outer part, and a thinner, membranous folded part. The hind wing, being less firm than the front, is naturally less often preserved. Nevertheless a considerable number have now been obtained. In the structure of the hind wing the Carboniferous cockroaches present fairly uniform characters, only occasionally, and from late Carboniferous deposits, are there indications that a folding of the wing had originated.

Some of the cockroaches of Permian time, however, had folded and plicated hind wings. A not uncommon type from the Kansas Permian is that shown in figure 5. This wing has a fold running through the anal area at (*b*), on one side of which the veins are longitudinal, while, on the other, they run down towards and end on the line of the fold. The wing in the specimen here illustrated is spread out full width. With other specimens, however, it is seen folded in the resting position, the veins of the two parts showing plainly through the thin membrane. Cross veins in the cockroach hind wing are here seen for the first time. A beginning of plication is also evident in the area between (*a*) and (*b*), while between the veins are developing accessory longitudinal veins necessary to support such plications. This wing also gives additional evidence of what had been previously demonstrated—plications, although now common to the hind wings of Orthoptera in general, nevertheless originated independently in several families of the order after they had diverged as distinct lines from the main stock. A similar need among the several families is here met by the development in each of a similar mechanism.

The hind wing of modern cockroaches presents a further development of the structures originating with these early ancestors. The hind wing is made to fit nicely under the front by a longitudinal fold. The wing is strengthened by numerous cross veins, and the anal area is very perfectly plicated. An increased expanse of the anal area is accompanied by a relative reduction in the other areas of the wing, especially the cubital. The folded area has remained flexible, while the more exposed part of the wing has become thicker, more resistant, and brownish in color.

This progressive change in the wing structure is accompanied by the reduction of the ovipositor from the long sword-shaped organ of the Carboniferous cockroach to the specialized organ of recent forms adapted to the purpose of holding and guiding the eggs into the egg case. Other organs of the body, if closely followed, would, doubtless, give evidence of similar progressive change. The organs described are those most readily preserved, hence best known in the fossil condition.

The young of any group of organisms are always of interest. A considerable number of young cockroaches have been found in the fossil condition, occurring often in deposits where the bodies of adults are rarely or never seen. In most cases the parts preserved are not the bodies of the young, but the cast off integument shed by the young cockroach with each successive molt. The body is heavy and transported with difficulty, the soft tissue hastens its decay, or more probably it is gathered up as food by the horde of hungry animals in the water or on land. It is not so with the molt, for it is useless as food, and like the detached wings with which it is always associated, is light

and easily floated by rains into streams and rivers, and thence carried by currents into larger bodies of water, where permanent deposits are accumulating. Both wings and molts are fairly resistant to decay, and thus more readily preserved than are the softer parts of the body. Such molts have been found in this country from the Coal Measures at Mazon Creek, Illinois; from the Upper Coal Measures of Eastern

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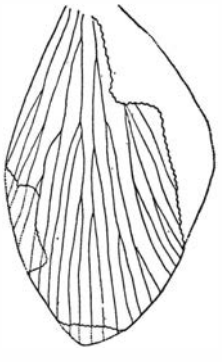

FIG. 4. Hind wing of a Carboniferous cockroach, *Promylacris rigida* Scudder. Twice natural size. Author's illustration.

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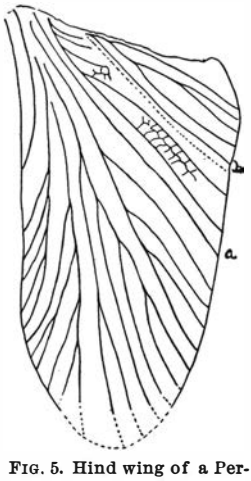

FIG. 5. Hind wing of a Permian cockroach, × 4. Original drawing.

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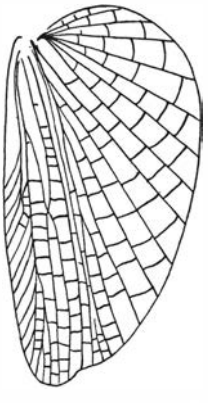

FIG. 6. Hind wing of a modern cockroach, *Ectobia germanica*. Original drawing.

The conspicuous changes in the hind wing as seen here are increased expanse of the anal area, increased proportionate breadth of the wing, origin and development of a longitudinal fold, development of plications in the folded area of the wing, development of cross veins.

Kansas; and from the Permian of Central Kansas. Recently an interesting specimen, shown in the accompanying illustration, has come to light from the Coal Measures of Clinton, Missouri.[1] A few specimens have also been obtained from the coal formation of Scotland. The young of Paleozoic cockroaches closely resemble the adults, and were evidently in form and habits very similar to young cockroaches of the present day.

The cockroaches of Carboniferous time are, on a general average, larger than those of later time. The largest described form, *Archoblattina Beecheri* Sellards, has a body, exclusive of the head, three and one half inches long, with an expanse of wings of six and one fourth inches. The Permian forms, and, also, those from mesozoic and later formations, are, so far as known, smaller than those of the Carboniferous.

There appears to be no authentic record of the occurrence of cock-

[1] Collected by Dr. J. H. Britts and transmitted by him to the National Museum. Kindly submitted to the writer for illustration by Dr. David White.

roaches in any rocks older than the Carboniferous. The single specimen reported from the Silurian of France is at best very unlike a cockroach. Its claim to affinity with the cockroach group was long ago contested by Scudder, and even Brongniart, its discoverer, has since conceded that it can not belong here. Other writers exclude the fossil entirely from the class Insecta. The oldest known species appear to be *Archimylacris parallela* Scudder and *Geroblattina fascigera* Scudder, from the Millstone Grit, or Middle Carboniferous. During Coal Measure time cockroaches became extremely abundant, more so than in any later period. They are less numerous in Middle and Upper Permian as well as in Mesozoic and later deposits. Nothing whatever is known of the insect life of the southern hemisphere during either Paleozoic or Mesozoic, and it yet remains to be seen what forms will be brought to light from this part of the world. During the Carboniferous and Permian, cockroaches were widely distributed over Europe and North America. With the uniform climatic conditions of that time it can hardly be doubted that their distribution was as wide at least as that of the tropical plants with which they are so constantly associated.

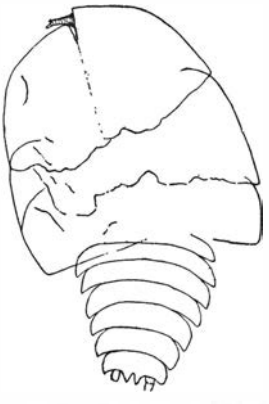

FIG. 7. Young of a Coal Measure cockroach, × 4. Original drawing.

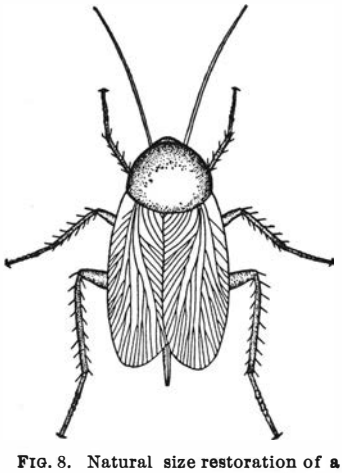

FIG. 8. Natural size restoration of a typical Coal Measure cockroach, *Etoblattina mazona*. The protruding ovipositor and simple wing venation distinguish Coal Measure from modern cockroaches. Author's illustration.

Among the laws of development operative in bringing about the changes which have occurred in the cockroach family during its long geological history, those the effects of which are most apparent may be summarized under the following headings:

Recapitulation of Ancestral Characters.—During the nymph stages of a modern cockroach the venation of the immature wing is not unlike that of the typical Coal Measure adult. The main veins of the wing, which during these early stages are free to the base, later become more or less fused and cross veins appear, thus illustrating the law common to most groups of organisms and known as a recapitulation of ancestral characters.

Parallel Evolution.—A similar need among the several related families of the order Orthoptera to which the cockroaches belong has been met by the development of identical structures. Thus both the plications and the fold of the hind wings originated independently in the cockroach and some other families of the order.

Mechanical Principle.—Both the plications and the longitudinal fold of the Orthoptera wing seem to have been developed in response to the mechanical need of some means of caring for the largely expanded inner area of these wings.

Specialization by Reduction.—The reduction of the long ovipositor of early cockroaches to the short specialized ovipositor of modern forms is apparently an illustration of the law of specialization by reduction.

Loss of Organs Through Disuse.—The reduction of the wings of several modern species to such an extent that, although presenting normal adult features of venation and articulation to the body, they are so far vestigial as to be practically functionless, is doubtless to be attributed largely to lack of use, and results from the ground habits of these insects in which they use the wings comparatively little. Not infrequently functional wings are retained by the males, even when lost by the probably less active females of the same species.

Arrestation of Development.—The wings of not a few modern forms remain as nothing more than wing-pads similar to the wing-pads of the larval stages. This further reduction is probably an instance of what has been called arrestation. Although other organs of the body have reached maturity, the wings, checked in their development, have not passed beyond the larval stages. Lack of use of the wings by the ancestors of the species, and consequent insufficient blood and food supply to this part of the body, is probably in this case an indirect cause of arrestation.