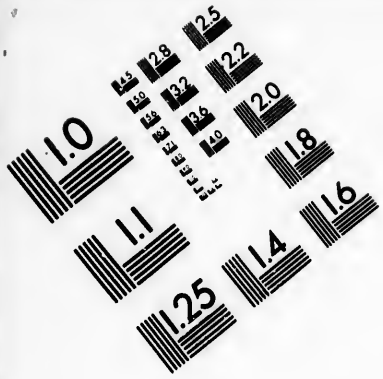

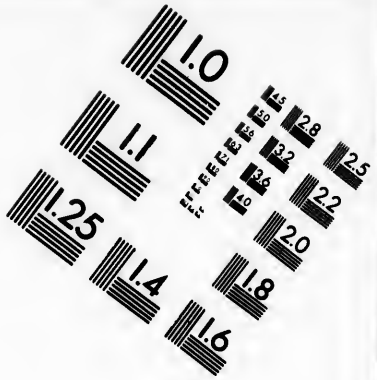

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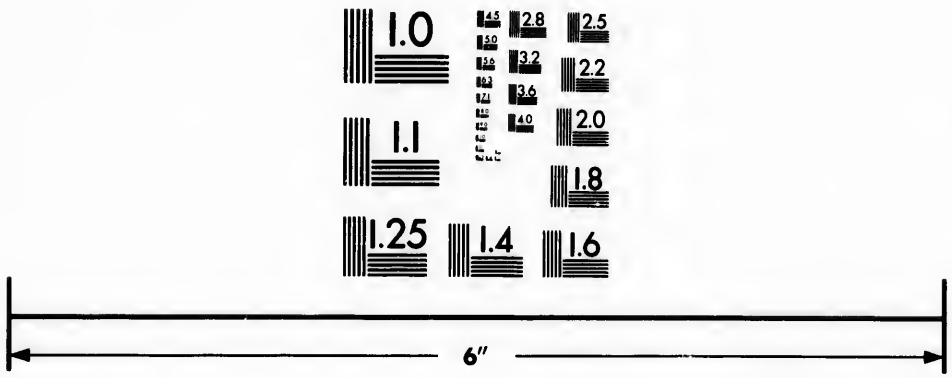

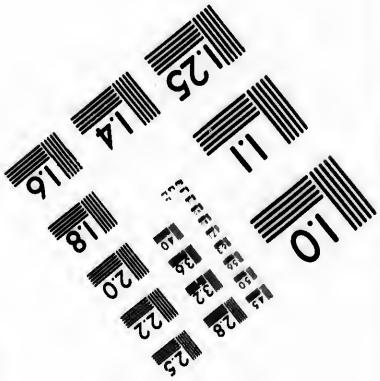

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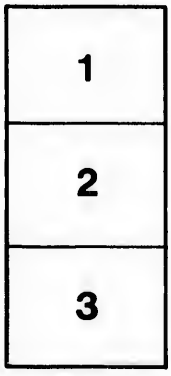

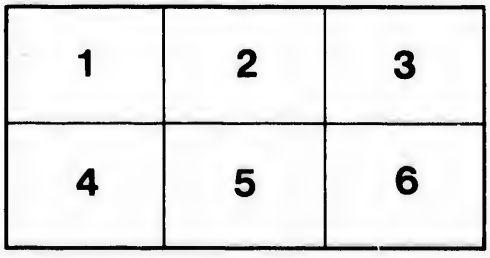

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32X

XII.—*The Fossil Cockroaches of North America.*[1]

By SAMUEL H. SCUDDER.

(Presented by Mr. James Fletcher.)

Although not in favour with the general public, the cockroach is to the palæontologist the most interesting of insects; for it alone occurs at every horizon at which insects have been found in abundance, and it is so dominant in the Carboniferous period, when insects first existed in large numbers, as to have led me to call this period, so far as its insect fauna is concerned, the "age of cockroaches." Its existence to-day is an example of the persistence of an antique but now waning type.

Fifteen years ago when I published a revision of the fossil cockroaches of the world[2] only nineteen American specimens had been seen, representing seventeen species and seven genera. To-day more than three hundred and fifty American specimens have passed under my eye, and from the Palæozoic series alone I have recognized among these no less than one hundred and thirty-two species belonging to fourteen genera. A recent study of all these forms, soon to be published by the U. S. Geological Survey, offers an occasion for some general remarks upon them which have some interest.

In 1879 I claimed that Palæozoic cockroaches, with which we are most concerned to-day, *i.e.*, those known from Carboniferous and Permian rocks, differed from modern forms of cockroaches to such an extent and by such characters as to warrant our separating them bodily as a group under the name of Palæoblattariæ. This view has been attacked, but I think unsuccessfully, and every new discovery since then (the number of fossil species having been multiplied many fold) has only strengthened my position: that Palæozoic cockroaches differ from modern forms in the far greater similarity of the fore and hind wings in texture and venation; by the presence in the fore wings of the full complement of principal veins, some of which are completely or almost completely amalgamated in modern forms; and by the course of the anal veinlets, which as a rule ran in ancient times to the hind margin of the wing parallel to each other, while now they strike the anal furrow or collect apically in a bunch near its tip. This view has received no modification whatever by later discoveries, except that we find in certain Triassic rocks of Colorado an assemblage of forms, partly Palæoblattariæ, partly Neoblattariæ, in some of the latter of which the anal veins preserve their ancient course.

In further classification of these extinct cockroaches I then separated the American forms into two groups, Mylacridæ and Blattinariæ, by the structure of the mediastinal vein of the fore wings. All the then known European forms were classed in the Blattinariæ. Now although the number of American Palæozoic genera has doubled, two genera of Mylacridæ

[1] Published by permission of the Director of the U. S. Geological Survey.

[2] Mem. Bost. Soc. Nat. Hist., vol. iii., pp. 23-134, pl. 2-6.

and five of Blattinariæ having been added, the base of separation may still be maintained. It has been stated by Brongniart that Mylacridæ occur at Commentry in France, the richest deposit of Carboniferous insects yet discovered, and that other distinctions, drawn from the form of the prothorax exist between the two groups; but the distinctions he makes cannot be maintained for the American forms, and until the publication of specific descriptions or figures we cannot consider the presence of Mylacridæ in European rocks as proven. I ought, however, to add that Mr. Brongniart has recently shown me specimens which, on cursory examination, looked like Mylacridæ of the type of Necymylaeris, *i.e.*, approximating the Blattinariæ.

With these preliminary statements let me direct attention to the following tables of geological and geographical distribution of the genera of fossil cockroaches in America, and particularly of the older forms. The first table presents in a summary form the number of species of each of the different genera found in the American Palæozoic rocks in the several coal basins and in two special localities in Ohio and West Virginia, where the greatest number of species have been found.

TABLE SHOWING THE GEOGRAPHICAL DISTRIBUTION OF AMERICAN PALÆOZOIC COCKROACHES.

	—	Western Interior Coal Basin.	Eastern Interior Coal Basin.	Acadian Coal Basin.	Rhode Island Coal Basin.	Appalachian Coal Basin.	Richmond, Ohio.	Cassville, West Virginia.	Totals.
Mylacridæ.	Mylaeris	..	5	2	1	6	..	..	14
	Promylaeris	1	3	..	..	..	..	..	4
	Paromylaeris	1	3	..	..	1	..	..	5
	Lithomylaeris	..	1	..	..	3	..	..	4
	Necymylaeris	..	..	..	..	2	..	..	2
Blattinariæ.	Microblattina	..	..	..	1	..	..	..	1
	Archimylaeris	..	1	1	..	1	..	..	3
	Etoblattina	3	2	..	8	1	17	36	67
	Gerablattina	..	..	..	2	1	3	15	21
	Anthracoblattina	1	..	..	..	..	..	1	2
	Progonoblattina	..	1	..	..	..	..	..	1
	Oryctoblattina	1	1	..	..	..	..	..	2
	Poroblattina	..	..	..	..	..	2	3	5
	Petrablattina	..	..	1	..	..	..	1	2
	Totals	7	17	4	12	15	22	56	133

This table shows at a glance how largely the two genera, Etoblattina and Gerablattina and especially the former, predominate, and that their predominance is due principally to their abundance at the two localities in Ohio and West Virginia, which have furnished more than one-half the American cockroaches. These two localities are of recent discovery and belong the one to the Barren Coal-measures, or the uppermost Carboniferous, the other, in West Virginia, to the lowest Permian, in what has been called the Dunkard Creek series. They include among them, in both these genera, cockroaches of a peculiar appearance,

characterized by a remarkable openness of the neuration in the middle of the wings, and by their frequent exceptional length and slenderness. In Ohio this type comprises nearly three-fourths of the species in these two genera, and in West Virginia about a fourth of the species. The only occurrence of a similar form in Europe is in a species from the lower Dyas of Weissig, Saxony, *Etoblattina elongata*.

Now, although these localities are not far removed either geologically or geographically, one in extreme eastern Ohio, the other in extreme northern West Virginia, not a single species has been found common to the two. Almost without exception the same may be said of any two localities in North America, even at the same geological horizon; and not a single fossil American cockroach is identical with any European form.

This leads one to believe that when the insect fauna of our rocks is better known, these insects may prove a better or rather a more delicate test of the relative age of rocks in the Carboniferous series than the plants, many of which certainly range through an enormous period of time, while insects have proved more sensitive to change.

To take a first step toward publishing evidence which may be used hereafter in such discriminations, I have made careful inquiry as to the exact locality at which each specimen was obtained and have tabulated the species by horizons, based on that information. From that tabulation I have prepared the next table, showing the geological distribution both in Europe and America, of all the genera of Palæozoic cockroaches known. In this I have roughly separated the species from the true productive Coal-measures (*i. e.*, above the "Millstone Grit" and below the "Barren Coal measures") into an upper and a lower series, endeavouring as far as possible to make the lower series correspond to the Coals A to C of the Pennsylvania series. The Palæozoic European species have been separated by the aid of tables already published by Dr. H. B. Geinitz and Herr Kliver. The later European genera are not considered. A. America; E-Europe. (See page 150.)

This table shows the genera so far known to exist on both continents at each successive horizon. It further shows that Etoblattina and Gerablattina were of the first importance in Europe as in America, Etoblattina in fact containing on either continent just about one-half of the species of cockroaches found on that continent. It also brings out conspicuously the fact that no Mylacridæ have yet been described from Europe.

The table again introduces us for the first time to our Mesozoic cockroaches and shows the vertical range and the systematic grouping of the half dozen genera occurring in a single pit in the Trias of South Park, Colorado. Later Mesozoic forms are as yet unknown in America, but in Europe they are very abundant and we already know about seventy species of ten genera. Without exception they are Neoblattariæ, *i. e.*, they differ from Palæozoic forms as do the existing types. But in the Triassic fauna of Colorado we have an assemblage of forms of an intermediate character. Here are Palæoblattariæ and Neoblattariæ side by side. The larger proportion are Palæoblattariæ, but of these all are specifically and most of them generically distinct from Palæozoic species and all rank high among Blattinariæ. We find, first, forms in which the fore wings are diaphanous, with distinct mediastinal and scapular veins, and the anal veinlets run to the border of the wing (Spiloblattina, Poroblattina); next, those having a little opacity of the fore wings, with blended mediastinal and scapular, and the anal veins as before (certain species of Neorthroblattina); then those with still greater opacity, with the same structural features (other species of Neorthroblattina); next, those having a coriaceous or leathery structure, blended mediastinal

and scapular, and anal veins falling on the inner margin (some species of Scutinoblattina); and finally, similarly thickened wings with blended mediastinal and scapular, and anal veins impinging on the anal furrow (other species of Scutinoblattina).

GEOGRAPHICAL DISTRIBUTION OF THE GENERA OF FOSSIL COCKROACHES.

		Millstone Grit.	Lower Prod'tive Coal Measures	Upper Prod'tive Coal Measures	Barren Coal Measures	Permian.	Trias.	Tertiary.	Recent.
Mylacridæ.	Mylæris	....	A	A	....	....	....	....	....
	Promylæris	....	A	....	A	....	....	....	....
	Paromylacris	....	A	A	....	....	....	....	....
	Lithomylacris	....	A	A	....	....	....	....	....
	Necymylacris	....	A	....	....	....	....	....	....
Blattinariæ.	Mieroblattina	...	A	....	....	....	....	....	....
	Archimylacris	A	A	....	....	....	....	....	....
	Spiloblattina	....	....	....	....	....	A	....	....
	Etoblattina	A?	A E	A	A E	A E	A	....	....
	Gerablattina	A	A E	....	A E	A E	....	....	....
	Anthracoblattina	....	A E	....	E	A E	....	....	....
	Hermatoblattina	....	....	....	E	E	....	....	....
	Progonoblattina	....	A E	....	E	....	....	....	....
	Oryctoblattina	....	A	E	A	E	....	....	....
	Poroblattina	....	....	....	A	A	A	....	....
	Petrablattina	....	A	....	....	A E	A	....	....
	Leptoblattina	....	E	....	....	....	....	...	....
Neoblattariæ.	Neorthroblattina	....	....	....	....	....	A	....	....
	Scutinoblattina	....	....	....	....	....	A	....	....
	Zetobora	....	....	....	....	....	....	A	A
	Homœogamia	....	....	....	....	....	....	A	A
	Paralatindia	....	....	.. .	....	....	....	A	A

No one can handle many Palæozoic cockroaches without being struck by the fact that they are of large size. I drew attention to this in 1879, remarking that "while the average was considerably above that of existing cockroaches, none were much larger than some South American species of Blabera," whose fore wings sometimes attain a length of sixty to seventy millimetres. But I have now seen a fragment of a fore wing, which when perfect must have measured eighty millimetres in length. In an estimate from the then known species of Palæozoic cockroaches I stated that "the average length of the front wing appears to have been about twenty-six millimetres."

Since then the increase in the number of species in this country has been largely from the younger Palæozoic rocks, and if we were to add the Triassic Palæoblattariæ, of still smaller size, we should find that the average length of the fore wing in ancient American cockroaches, one hundred and thirty-three species in all, was 23·2 mm. The Mylacridæ

were larger, on the average, than the Blattinariæ, a fact due in great part to the younger cockroaches being all Blattinariæ, for the fore wings of the twenty-nine Mylacridæ average 27·5 mm., while those of the one hundred and four Blattinariæ average 22 mm. only. That even this last is greater than the average size of living cockroaches, one familiar with the latter would readily venture to assert; but to put it to a fair test, I have estimated the average size of recent species from the measurements given in Brunner von Wattenwyl's Système des Blattaires (1865), the last general work on the subject. About 380 species are included in this work, but of only 239 are measurements of the length of the wings given, and from these I estimate the average length of the fore wings of living cockroaches to be 18·8 mm., which is distinctly less than the size of the Paleozoic forms.

This however is by no means the whole of the story. I have further tabulated separately the length of the fore wings for the different American species from the Millstone Grit to the Trias inclusive and find that there is a marked and regular diminution in average size from one period to another, as will appear from the following measurements of the fore wings, given in millimetres.

Millstone Grit (3 species), 26-38; average 31.

Lower Productive Coal-measures (39 species), 10-61; average 29·7.

Upper Productive Coal-measures (12 species), 163·5-33; average 26·4.

Barren Coal-measures (23 species), 9.75-31.5; average 23.4.

Permian (56 species), 8·25-28·75; average 16·9.

Trias (17 species), 6·3-24; average 13.

The only doubt about the exact accuracy of this statement is that the fauna of the Rhode Island coal basin, consisting of twelve species, is included in the Lower, when it may perhaps belong in the Upper, Productive Coal Measures. The average size of the Rhode Island species is 27·3 mm., and that of the Lower Productive Coal-measures without them is 30·7 mm.; while if the Rhode Island species were added to the Upper series, it would increase the average of that to 26·8 mm.; but this would still not disturb the regular succession of averages. The average size of the fifty species of the Productive Coal-measures as a whole is 27·4 mm., or almost precisely that of the Rhode Island species alone.

Let me not be understood as maintaining that the size of cockroaches has been steadily and continuously diminishing from the earliest times to the present, but only for that period of time which is here considered, and also, I may add, for the later Mesozoic rocks; for I have elsewhere shown that the average length of the fore wings of European Mesozoic (mostly Liassic) cockroaches was 12·5 mm., which is slightly less than that of the species of the American Trias. It is well known that the great mass of Mesozoic and especially Liassic insects of all orders were of small size; but the insects of the Tertiaries did not differ in this respect in any noticeable degree from those now living.

I have further tabulated the relative length of the fore wings in the different genera of ancient American cockroaches separately, both as a whole and in each of the periods in which they occur. The table gives these measurements in millimetres. (See page 152.)

This table shows that in general, especially where the species are numerous, the same rule holds remarkably under each genus, the average size decreasing with the lapse of time. The only noticeable exception is in the two divisions of the Productive Coal-measures, where, in the genera Paromylacris, Lithomylacris and Etoblattina, the averages are reversed from what they should be under the rule. The other exception (as in Oryctoblattina and in part

in Petrablattina, and in Archimylacris) are where only a couple of species or so are concerned. The relative average size of the species of the different genera is also shown, and proves that the average size of every genus of Mylacridæ is larger than that of any of the other genera excepting only Archimylacris, which I have elsewhere pointed out was the most antique type of all cockroaches. The table further lends support to the view that the Dunkard Creek series of rocks, in Monongalia Co., W. Va., are older than the Barren Coal-measures and should be referred to the Permian; since, in each of the three genera represented in both beds, the average size of the species from the Dunkard Creek series is the smaller.

AVERAGE LENGTH OF FORE WINGS IN THE GENERA OF AMERICAN PRE-TERTIARY COCKROACHES.

——	Millstone Grit.	Lower Prod. Coal Measures.	Upper Prod. Coal Measures.	Barren Coal Measures.	Permian.	Trias.	In all.
Mylacris		26·5-42; av. 31·1	16·35-33; av. 25·6				16·5-42; av. 28·5
Promylacris		19-20; av. 25·3		17·5			17·5-29; av. 21·7
Paromylacris		21-42; av. 28·5	30				21-42; av. 26·6
Lithomylacris		24	20-20·25; av. 27·2				24-20·25; av. 26·4
Necymylacris		25-48; av. 30·5					25-48; av. 36·5
Microblattina		8					8
Archimylacris	26	26-30·5; av. 28·25	23				23-30·5; av. 26·5
Spiloblattina						15-18; av. 16·4	15-18; av. 16·1
Etoblattina	20	14·25-61; av. 26·4	25-32; av. 28·5	14-31·5; av. 25·5	11·75-28·75; av. 17·6	12-20; av. 16	11·75-61; av. 21·3
Gerablattina	38	18-41; av. 20·5		9·75-25; av. 18·3	10-25·5; av. 16·6		10-41; av. 19·1
Anthracoblattina		30			12		12-30; av. 21
Progonoblattina		20·75					20·75
Oryctoblattina		19		21			19-21; av. 20
Poroblattina				11-22; av. 16·5	13·5-16·75; av. 15·6	10-19; av. 13·7	10-22; av. 15·1
Petrablattina		13			8·25	21	8·25-24; av. 15·1
Neorthroblattina						8·5-12; av. 9·6	8·5-12; av. 9·6
Scutinoblattina						6·3-7; av. 6·8	6·3-7; av. 6·8

In closing I wish to draw attention to a topic unusual in such a connection. In studying protective resemblance and mimicry among living animals, the exceedingly common occurrence of these phenomena has often forced upon me the conclusion that they have not been limited in their scope to recent times, but must have existed in past epochs and even, to some extent at least, in very remote epochs. This is a natural conclusion from the universality of their present occurrence. Hardly an animal exists that does not actually owe its existence to some feature or features in its form or colouring. This statement will doubtless appear strong to those who are unacquainted with or have not considered the facts. Let me re-enforce it in the words of one of its latest exponents, M. Félix Plateau, the well known professor in the University of Gand. "The thesis I wish to sustain in agreement with naturalists of high merit," he says, "would demonstrate that the phenomena [of mimicry] are general; that is to say, that there are hardly any animals which, in at least some one of the stages of their existence, do not have recourse to imitation; that in our own countries,

in temperate Europe, here in Belgium itself, the zoologist who is really an observer meets at every step cases of dissimulation which are every whit as striking as those which tropical nature offers us."[1]

The arguments I have used elsewhere in discussing this subject[2] attempt to show that in the very nature of things protective resemblance must prevail in a world where creatures are the food of others, and escape destruction when observed by their predaceous foes less easily or less frequently than their fellows. From this standpoint it would be difficult to refrain from the logical conclusion that protective resemblance was nearly or quite as much a feature of past life as of present.

Naturally, since colouring forms the next important or the most common part of protection, proof of such protection cannot be derived from the fossils. But pattern of markings is also a conspicuous element of protection in existing types, and in a few fossils among insects we can detect markings of a precisely similar nature to some which in existing insects can be proved protective; but here habit and association are often necessary factors and these can usually only be inferred in the extinct types, but inferred in some instances with considerable reasonableness.

The examples which I have in mind are all drawn from Tertiary faunas; but the reason I refer to the matter here is that it seems to me fairly reasonable to look upon some forms of Carboniferous cockroaches, if not indeed most of them, as probably imitative, and thereby protected. The first cockroach wing ever described from the coal was at first regarded as a fern leaf, and in all or nearly all the localities where their remains have been found they are associated with fern leaves in immense abundance. While searching for them in the Permian deposits at Cassville, W. Va., I was much struck by their resemblance to each other and was repeatedly obliged to use the glass to determine whether it was the wing of a cockroach or the pinna of a fern like Neuropteris I had uncovered, and the instances are not rare where they agree completely in size. The general distribution of the nervures is to cursory view the same in each and the contour is often nearly identical. Only the differentiation of the anal area in the cockroach wing at once distinguishes them, but this is really a feeble point and would often be noticed only by an expert. Is it not then plausible to suppose that the intimacy of the resemblance is due, as such an instance of associated organisms would now be regarded as due if the colour agreed, to the action of natural selection in producing protective resemblance? The ordinary colour of the fore wings of existing cockroaches is brown or testaceous, yet there are not wanting numerous examples, at least in the tropics, where they are as green as the leaves of ordinary vegetation.

[1] Bull. Acad. Roy. Belg., (3) xxiii., 92.

[2] Atl. Monthly, Feb., 1889; Butt. East. U. S. and Canada 710-720.