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PROGRESSIVE CHANGE IN THE INSECT POPULATION OF FORESTS SINCE THE EARLY TERTIARY[1]

PROFESSOR CHARLES T. BRUES

Harvard University

One afternoon some twenty years ago during a winter sojourn in northern Florida the writer was collecting insects in a pine forest given over to the production of turpentine. Following the usual practice, the bark and sapwood of each tree had been cut away for a distance on one side and a pot hung at the bottom to catch the resin. The scarred trunks of the disfigured trees were reeking with oozing resin, and here and there insects of various kinds were imbedded where they had been trapped by the sticky exudation. Mrs. Brues was with me at the time and, knowing that I was interested in amber insects, she suggested that we make a collection of these insects from the turpentine trees to compare with the fossil fauna of the amber. We could see several interesting possibilities in such an undertaking and proceeded forthwith to gather the material. The specimens were transferred to vials of alcohol and after a time we had amassed a considerable and very miscellaneous assortment which assumed a much better appearance after the alcohol had dissolved the envelope of resin.

The matter had to be held in abeyance for many years, until I had been able to devote some time to a study of one small part of the insect life of amber. It then appeared that the Florida collection was too small to be of

[1] From the Entomological Laboratory, Harvard University.

any considerable value, and another more extensive one was then made in what appears to be a much more suitable region. This I shall deal with in a few moments.

Amber is fossilized and greatly hardened resin. It occurs in lumps or nodules of various sizes, practically in the same form that it first developed as an exudation of sticky resin on the trunks of pines in the amber forests. These pieces are often of quite considerable size, frequently weighing several pounds, and represent the only known remains of magnificent forests that flourished in northern Europe in upper Eocene times. As the fresh resin exuded, its sticky surface trapped innumerable small flying and crawling insects, together with other objects that fell or were blown against it, to be engulfed and permanently preserved just as we now mount small insects in Canada balsam. Many fragments of the plants that grew in the amber forests are thus preserved also, enabling us to gain a far clearer idea of the insects and associated plants than is possible in the case of any other extinct insect-fauna.

As to the flora of the amber forests we are able to form quite a complete picture from the bits of plant remains that are preserved in amber nodules. It is believed that the most abundant tree was a true pine, *Pinus succinifera* Göppert, from which the amber was very probably derived, at least in great part. However, this tree was associated with an extensive and varied sylvan flora which included other conifers of the living genera Sequoia, Taxodium, Picea, Thuja and a somewhat dubious form known as Pinites. Among deciduous trees there were abundant oaks of numerous species, as well as chestnuts, beeches, bays (*Myrica*), magnolias, cinnamons (*Cinnamomum*) and several palms. The composition of the arborescent flora is therefore not exactly reproduced anywhere at the present time, but is quite similar to that of North America. In the eastern United States most of these trees have living relatives, several types restricted to the south, but the most abundant ones now more common farther north. Some have pointed out the great similarity of the present flora of Florida, particularly on account of the palmetto palm, magnolia and bay-tree, but the agreement here seems no greater than in New England, on account of the spruces and beeches, and certainly the terrain of the amber forests, as we know it from the caddis-fly fauna, was not that of the flat coastal plain. Undoubtedly the climate was much milder than the one which we now enjoy in the northeastern states, and the forests were clearly comparable with our own, as they existed several centuries ago before their exploitation was begun by civilized man.

The history of Baltic amber after its deposition on the tree-trunks has been quite accurately traced. The amber forests occupied an extensive area in Europe north of the Baltic sea. The amber remained after the death and disintegration of the trees which had produced it, and some is now found in a deposit of so-called ''blue earth'' which represents the amber-bearing strata of upper Eocene age. Here the amber was apparently carried by streams or rivers and thus accumulated. Much amber is found also in certain stratified sands of Miocene age, where it has been redeposited, commonly in rich pockets. Still later, smaller amounts were distributed by inland ice at the time of glaciation in the north. Most of the original deposits now lie below the surface of the Baltic Sea, where they can not be worked systematically, but from time to time through the agency of severe storms pieces are dislodged. As the amber is lighter than water it rises and drifts ashore where it may be recovered. On occasions as much as a ton or more has been collected on the shores of the Baltic after a stormy night. For a study of the inclusions the amber is commonly sawed into rectangular blocks, each containing an individual specimen and the surface polished to permit observation through the transparent matrix. Much of the amber is not transparent, and as the included insects, trash and other objects are scattered at random, the discovery and preparation of good specimens is a very slow and laborious process. Thus prepared, examination under the microscope is readily possible, even under high powers, except where flaws in the amber, clouding of the inclusions or superposition of parts interfere with clear vision. Ordinarily the more minute specimens are better preserved than the larger ones, as there is less clouding from water vapor or mould, and they are less apt to have become broken during the process of submergence in the resin.

Thus nature has preserved a very considerable fragment of the rich and varied forest fauna that flourished in Northern Europe some 40,000,000 years ago.

For a number of years I have been interested in a small part of this insect fauna of Baltic amber, comprising a series of families of parasitic species belonging to the order Hymenoptera. After some time spent in sorting, classifying and describing the new genera and species found in the amber I gradually became aware of certain apparent differences in the representation and diversity of the several groups in the fossil amber fauna and that which survives it at the present day. At first blush these seemed to indicate progressive changes in the numerical abundance of certain groups of insects that are well represented in both the amber and recent fauna.

Such changes are certainly to be expected, for we have abundant evidence in practically all groups of animals and plants that evolutionary change has entailed the appearance of numerous particular groups that have waxed abundant and later waned, often to extinction. Due to the limitations of the case, however, the paleontologist must ordinarily concern himself primarily with the morphological aspect of such changes as they relate to the appearance of types, families or genera and their diversification into lesser types and species. Aside from comparative anatomical studies, speculative deductions and the application of certain principles, our entire knowledge of the phylogeny of animals and plants rests upon this very firm foundation of observed factual evidence. One aspect of the composition of fossil faunas lends itself to observation in only a very crude and incomplete way, since we can not estimate with any degree of accuracy the proportionate numerical abundance or dominance of particular groups or of individual species. This is, of course, due to the fact that certain happy combinations of circumstances are requisite for the preservation of organisms as fossils. Moreover, we know that such combinations have by no means necessarily been similar on different occasions. Most deposits that contain insect remains have been laid down in water, but we are unable to do more than surmise what portions of the prevalent insect fauna have been preserved in any particular bed. We can piece together little evidence concerning the terrain or the flora of the immediate vicinity, nor are we able to say what part transport by wind or carriage by streams may have played in assembling the population sample that we may be fortunate enough to unearth after the lapse of long periods. If certain groups or species are well represented by specimens we know that they must have formed a considerable part of the insect population, but if others are less numerous it is quite probable that they may have for some reason escaped entombment and even if some are absent we may easily find a good reason for their failure to chance upon that spot at the appropriate time. The great preponderance of winged ants in the fauna of the Miocene shales of Florissant is very probably due to storms of volcanic dust which overwhelmed them in flight, while the contrasting abundance of wingless worker ants in the Baltic amber is no doubt due to the more peaceful method by which they were trapped. Thus neither deposit can afford data for an accurate census of the sexual and worker phases of ants during tertiary times.

To return again to the collection of amber insects mentioned previously, it will be seen that this affords an opportunity to compare with considerable accuracy the

Oligocene with the recent insect fauna. We know that the amber fossils are species that frequented the trunks of pine trees in areas of mixed forest quite similar to those now present in the northeastern United States. Furthermore, the genera of insects known from the amber show that this Eocene fauna was more similar to that of the nearctic region at the present time than to the living fauna of any other single part of the world. From his studies on the Trichoptera or caddis-flies of the amber, Ulmer (1912) has reached conclusions concerning the topography of the amber forests which supplement and confirm those drawn from a knowledge of the types of trees present there. The trees indicate a partly mountainous country, and the caddis-flies seem to demonstrate without question the existence of rushing mountain streams, slowly flowing brooks and quiet ponds. Since many genera of caddis-flies are closely restricted in habitat, Ulmer concludes from the representation of modern genera in amber that the number of genera and species requiring mountain streams greatly exceeded the other types, although the latter were present in sufficient abundance to show clearly the existence of the static or quiet water habitat.

These considerations indicate that ecological conditions in the amber forests are rather closely reproduced in the hilly forested areas of New England at the present time, and as already indicated the flora and insect fauna were quite similar to those now existing in that region.

It seemed, therefore, that this region offered a particularly good opportunity to compare in detail the numerical abundance of specific groups of insects as they are preserved in amber with the present forest fauna. This required that a census of forest insects be taken under conditions closely approximating those which led to the formation of the amber inclusions.

In order to collect a closely similar sample of the insect population we made use of the well-known tanglefoot fly paper, which is easily obtainable and proved to be eminently suited to the purpose. Tanglefoot simulates closely in its sticky surface fresh exuding resin; the sheets may be readily tacked to the trunks of trees and later removed for inspection, so that they serve to collect just that portion of the forest fauna directly comparable with the one found in the amber. It may be asked what differences may be expected when the piney odor of fresh resin is replaced by that of the tanglefoot. There is every reason to believe that odor has little influence in trapping the insects, since most of the species in amber are very evidently in no way directly associated with resin or with the trees which produced it. The trapping of most specimens is undoubtedly by pure accident, *e.g.*, the various Diptera which represent over 50 per cent. of the whole population both in the amber and tanglefoot collections. Even in the case of bark beetles of the family Scolytidae, where some of the amber species must have been associated with the resin-producing trees, the representation of this family is extremely low and quite similar to the scarcity noted in the tanglefoot collection. I believe therefore that no considerable differences in sampling have been introduced by the use of tanglefoot in place of resin.

The localities selected for the tanglefoot collections were all in the township of Petersham, which lies in northern Massachusetts, at an elevation of from 800 to 1,100 feet above sea-level. As nearly as possible areas of well-matured (including some nearly primeval) forest were chosen where there was either a predominance of conifers (white pine and hemlock) or a mixed growth including also considerable beech, oak, maple and birch. The terrain included areas of well-drained higher land, damper spots, open spaces and the borders of both swiftly and slowly flowing brooks. Thus, as nearly as could be judged, the localities which scattered for some miles through the Harvard Forest and on land adjoining our own summer home, represented the several ecological conditions known to have existed in the amber forests and in about the same proportion.

Collections were made in the several localities during the course of the entire summer of 1930 from early May till late September. Sheets of the tanglefoot fly paper were fastened by tacks at each corner to the trunks of trees at different heights that could be conveniently reached from the ground. After a few days numerous insects were caught and the surface of the tanglefoot became less sticky. The papers were than removed, each carefully curled into a cylinder with the sticky surface inside, caught thus with pins and brought into the laboratory. The immersion of each cylinder in a large jar of 95 per cent. alcohol for a few minutes dissolves the matrix and allows the specimens to float free. In spite of this treatment the insects are in very good condition and after removal to vials of clean alcohol may later be conveniently sorted in watch glasses under the microscope. During the course of our work both Mrs. Brues and myself commented frequently and vehemently on the great abundance of blackflies, mosquitoes and biting flies (Chrysops) in the forest, and gloated in prospect over the swarms of these pests that would be engulfed in the tanglefoot before the end of the season. Subsequently, when the material was sorted we were pained to learn that only 26 mosquitoes, three Chrysops and 18 Simulium appeared in the collection of 22,938 specimens, more than 21,000 of which were insects. This is an extreme case, but shows very clearly that the wielding of a net or some other method of collecting in the forest would have produced a very differently selected sample of the insect population, which could not have served for adequate comparison with the amber.

The census of the tanglefoot material has occupied some time and would have been delayed still longer had it not been for very considerable aid from Mrs. Brues and my secretary, Mrs. O'Connor, who did much of the tedious preliminary sorting. As may be seen from the accompanying tabular list, the specimens belonging to some of the more abundant orders have been sorted to families; other groups, such as the Corrodentia and Trichoptera, have not been thus divided, as my knowledge of the families was not sufficient to insure accuracy in placing broken or otherwise defective specimens.

CENSUS OF TANGLEFOOT POPULATION

Collembola	60
Orthoptera	
Stenopelmatidae	11
Acrididae	1
Thysanoptera	6
Corrodentia	209
Mallophaga	1
Homoptera	
Membracidae	2
Cercopidae	106
Jassidae	1,685
Cicadellidae	472
Aphididae	81
Chermidae	11
Hemiptera	
Tingididae	18
Nabidae	3
Miridae	51
Odonata	1
(Zygopteran nymph)	
Plectoptera	35
Plecoptera	124
(incl. 2 nymphal cases)	
Neuroptera	
Hemerobiidae	7
(incl. 2 larvae)	
Coniopterygidae	5
Mecoptera	
Meropidae	2
Panorpidae	37
Trichoptera	332
Lepidoptera	
Noctuidae	4
Geometridae	6
''Micros''	153
Nymphalidae	1
Caterpillars	12
Diptera	
Tipuloidea	260
Psychodidae	165
Chironomidae	652
Culicidae	26
Simuliidae	18
Bibionidae	3
Mycetophiloidea	2,648
Cecidomyiidae	141
Rhagionidae	906
Tabanidae	3
Therevidae	1
Asilidae	4
Empididae	559
Dolichopodidae	3,070
Phoridae	6,443
Platypezidae	1
Pipunculidae	21
Syrphidae	99
Muscoidea	
Thecostomata	287
Haplostomata	1,195
Coleoptera[2]	
Carabidae	8
Silphidae	14
Scydmaenidae	12
Staphylinidae	31
Pselaphidae	4
Scaphidiidae	2
Cucujidae	1
Lycidae	3
Lampyridae	43
Cantharidae	87
Melyridae	1
Cleridae	1
Mordellidae	101
Meloidae	1
Pyrochroidae	1
Oedemeridae	1
Elateridae	52
Eucnemidae	1

[2] I am greatly indebted to Dr. P. J. Darlington, of the Museum of Comparative Zoology, who checked the series of Coleoptera and examined all doubtful specimens in this order.

Throscidae	74
Dryopidae	1
Dascillidae	7
Helodidae	25
Dermestidae	6
Ptinidae	1
Cryptophagidae	1
Erotylidae	1
Mycetaeidae	1
Colydiidae	11
Lathridiidae	27
Endomychidae	2
Coccinellidae	2
Alleculidae	4
Melandryidae	26
Anobiidae	12
Cerambycidae	3
Chrysomelidae	5
Curculionidae	8
Scolytidae	3
Scarabaeidae	1
Hymenoptera	
Xyelidae	1
Pamphiliidae	1
Tenthredinoidea	8
Braconidae	59
Alysiidae	76
Ichneumonidae	492
Chalcidoidea	46
Mymaridae	13
Roproniidae	1
Serphidae	4
Belytidae	152
Diapriidae	23
Scelionidae	25
Calliceratidae	57
Platygastridae	114
Dryinidae	3
Cynipoidea	8
Formicidae (including one larva)	67
Vespidae	5
Other wasps	10
OTHER ARTHROPODS	
Diplopoda	9
Chilopoda	1
Araneida	1,045
Chelonethida	3
Acarina	13
Phalangida	179
Total	22,938

More than half, in fact 71.9 per cent. of the entire tanglefoot collection, are Diptera, 16,484 in all; next in abundance are Homoptera with 2,429, followed by Hymenoptera (1,165) and spiders (1,045). All other orders, together with scattering other arthropods, make up less than 8 per cent. of the collection. This must not, of course, be regarded as a sample of the entire forest population, but it is, as previously indicated, a sample on which we may rely to determine with at least some measure of accuracy what changes have taken place in the forest population during the long period that has passed since the amber was laid down.

For this purpose it will be most satisfactory to examine first two of the groups whose representation in the amber is especially well known. For one of these we have accurate and extensive data furnished by Klebs (1911). As a pioneer student of amber inclusions, Dr. Klebs amassed an enormous collection, later bequeathed to the Geologisch-paläontologisches Institut at Königsberg. The comparative representation of the more abundant families of Coleoptera in the population of Baltic amber and in the present-day New England fauna is shown in the accompanying table (Table I). Great divergence

TABLE I

COMPARATIVE REPRESENTATION OF THE MORE ABUNDANT FAMILIES OF COLEOPTERA IN THE POPULATION OF BALTIC AMBER AND THE PRESENT-DAY NEW ENGLAND FAUNA

	Amber	Per cent.	Recent*	Per cent.	Recent, Actual Numbers
Carabidae	72	3.7	27	1.4	8
Silphidae	9	0.4	47	2.4	14
Scydmaenidae	28	1.4	40	2.0	12
Staphylinidae	69	3.5	103	5.3	31
Pselaphidae	24	1.2	13	0.7	4
Cucujidae	17	0.9	3	0.2	1
Lampyridae	3	0.1	143	7.5	43
Canthariididae	51	2.6	290	14.3	87
Mordellidae	115	5.9	337	17.3	101
Hylophilidae	53	2.7	0	0.0	0
Anthicidae	49	2.5	0	0.0	0
Elateridae	286	14.1	173	8.9	52
Eucnemidae	48	2.4	3	0.2	1
Throscidae	17	0.9	247	12.2	74
Helodidae	376	19.3	83	4.2	25
Dermestidae	5	0.3	20	1.0	6
Cryptophagidae	16	0.8	3	0.2	1
Colydiidae	14	0.7	37	1.9	11
Lathridiidae	41	2.1	90	4.8	27
Alleculidae	17	0.9	13	0.7	4
Melandryidae	44	2.3	87	4.7	26
Anobiidae	236	12.1	40	2.0	12
Cerambycidae	39	2.0	10	0.5	3
Chrysomelidae	30	1.5	17	0.9	5
Curculionidae	47	2.4	27	1.4	8
Scolytidae	37	1.9	10	0.5	3
Totals	**1780**	**91.2**	**1863**	**95.5**	**585**

* These numbers have been increased, each in proportion, to compare directly the two populations on the basis of equal size, *i.e.*, the figures in this column are each increased by three and one third times.

will be noticed in the abundance of certain families in each fauna and a very marked change from one fauna to the other is shown in the case of practically every family that is especially abundant either in the amber or in the tanglefoot collection. I do not believe, however, that any definite trend is indicated, such as an increasing abundance of highly specialized types. This might appear to be true, for example, with reference to the increased abundance of Mordellidae, but this is at once offset by an increase in several unquestionably primitive families like the Carabidae, Lampyridae and Cantharididae. The last two indicate, however, a much increased abundance of the more highly modified Lampyridae. It seems, however, that several much specialized families have decreased very noticeably. We may therefore gain little information from the beetles, but as I shall show in a moment they serve to supplement evidence supplied by other groups.

On another tabular chart (Table II) I have listed the several families of parasitic Hymenoptera that I myself have studied in the Baltic amber, together with the data gathered from the tanglefoot collection. An examination of these figures shows a series of consistent changes which appear to be highly significant. Among the ichneumon flies, the two dominant families, Ichneumonidae and Braconidae, which are both well represented in each fauna, have changed places. The more primitive Braconidae, which are somewhat more abundant than the Ichneumonidae in amber, have been reduced in number to about one fourth that of the Ichneumonidae. Among the Serphoidea the families Scelionidae and Platygastridae have likewise changed places. These two families are very similar, but no one can question the more primitive nature of the Scelionidae. The latter have dropped from 15.6 per cent. to 2.4 per cent., while the population of Platygastridae has increased from 1.5 per cent. to 10.6 per cent. Another family of primitive wasps, the Bethylidae, does not appear at all in the tanglefoot col-

TABLE II

COMPARATIVE REPRESENTATION OF THE FAMILIES OF PARASITIC HYMENOPTERA IN THE POPULATION OF THE BALTIC AMBER AND THE PRESENT-DAY NEW ENGLAND FAUNA

	Amber	Per cent.	Recent*	Per cent.	Recent, Actual Numbers
Aulacidae	4	0.2	0	0.0	0
Stephanidae	5	0.3	0	0.0	0
Evaniidae	35	1.9	0	0.0	0
Megalyridae	28	1.5	0	0.0	0
Pelecinopteridae	3	0.2	0	0.0	0
Braconidae (incl. Alysiidae)	331	18.2	227	12.4	135
Ichneumonidae	292	16.1	832	45.8	492
Chalcidoidea (excl. Mymaridae)	191	10.5	78	4.3	46
Mymaridae	26	1.5	22	1.2	13
Roproniidae	0	0	2	0.1	1
Serphidae	74	4.0	7	0.4	4
Diapriidae (incl. Belytidae)	258	14.2	296	16.2	175
Scelionidae	285	15.6	43	2.4	25
Platygastridae	27	1.5	193	10.6	114
Calliceratidae	46	2.5	97	5.3	57
Bethylidae	175	9.6	0	0.0	0
Embolemidae	6	0.3	0	0.0	0
Dryinidae	12	0.7	5	0.3	3
Cynipoidea	5	0.3	13	0.7	8
Mutillidae	11	0.6	0	0.0	0
Chrysididae	3	0.2	0	0.0	0
Totals	**1817**		**1817**		**1073**

* These numbers have been increased, each in proportion, to compare directly the two populations on the basis of equal size, *i.e.*, the figures in this column are each increased by 69.5 per cent. from those in the following column as accurately as whole numbers will follow.

lection although it was represented to the extent of 9.6 per cent. by a series of highly specialized types in the amber. At the present time this family is unquestionably more abundant in warmer regions, which might account to some extent for a lesser abundance in the tanglefoot, although certainly not for its total absence, since it occurs very generally though sparingly in our region. As this family is one which appears to represent a degenerate type related to the primitive wasps, this diminution in numbers is to be expected. One family, the Megalyridae, represented by a rather common extinct genus in the amber, occurs now only in Australia and South Africa and illustrates a condition noted among other groups of insects that certain types now surviving only in Australia or Malaya existed in the amber forests. Without going into further detail it is clear that the census of these parasitic Hymenoptera shows a quite consistently increased numerical abundance of phyloneanic types with a concurrent decrease in phylogerontic ones in the tanglefoot collection. Before attempting to evaluate these findings, I should like to call attention to another difference in the composition of the two faunas. If we examine the census figures with reference to the variety of types that make up the main bulk of the population[3] in the two faunas (Table III), we find that about one half the population of the tanglefoot belongs to a single family, the Ichneumonidae; two families make up almost two thirds; three make up three quarters and four make up seven eighths. In the amber population the number of families making up these several parts are 3, 4, 5 and 7. Thus more different types are well represented in the amber sample. Also, if we count all the families of parasitic Hymenoptera represented, we find

TABLE III
PARASITIC HYMENOPTERA

	Amber	Recent
50 per cent. of population	3 families	1 family
66 per cent. of population	4 families	2 families
75 per cent. of population	5 families	3 families
87 per cent. of population	7 families	4 families
Entire population	20 families	12 families

[3] In this way we may avoid a possible cause of error due to the certain rare types which may easily be absent in one sample and present in another.

twenty families in the amber (9 of these absent in tanglefoot) and only twelve in the tanglefoot (1 of these absent in the amber). The last data are not so convincing as the first, since the tanglefoot collection was smaller and several families might have been added if it had been as extensive as the amber one.

I can see only one conclusion to be drawn from these facts relating to the parasitic Hymenoptera. This group was more diversified in the amber forests and several primitive types were represented by more numerous individuals, while several derived ones were numerically less abundant than now. From the restriction in the number of larger groups we must conclude that this series was in a more active state of evolution in the upper Eocene than it is now, that certain gerontic types are being eliminated and that the population includes fewer dominant types. In other words, this group of insects is decadent from an evolutionary standpoint. We can not attempt to say whether the behavior of these insects has become more diverse, more highly adaptive or more complex, as we have only morphological data. However, the persistence of many amber genera to the present day combined with the considerable number of previously unknown structural types (including a new family) found in the amber make it seem very probable that a knowledge of the habits of these insects in the upper Eocene would show that their behavior was certainly as varied and complex as it is at the present day.

Among the Hymenoptera the ants furnish an extreme case of divergence between the amber and tanglefoot. The amber ants have been very carefully studied by Wheeler (1914), who examined 7,819 specimens from the collections of the University of Königsberg. This same collection yielded the 1817 specimens of parasitic Hymenoptera already mentioned. On this basis we should expect to find 467 specimens of ants in the tanglefoot collection if the ants had retained the same numerical ratio to the parasitic families. Instead, there are only 52 ants, or about 11 per cent. of the expected number, indicating a great decrease in the ant population since the time of the amber, at least in this region. As ants certainly appear to be much more numerous in many tropical countries it appears that the numerical decadence of ants has not extended to the tropics. Professor Wheeler tells me that he believes a similar tanglefoot census in Australia, where ants are particularly numerous, might reveal a population as large as that of the amber forests. This in itself may be regarded as supporting the conclusion that ants are becoming less numerous since the Australian biota is on the whole the most archaic one now in existence.

If we tabulate the Coleoptera as we did the parasitic Hymenoptera, from the standpoint of population groups we find that there was a greater variety of types in the amber fauna (Table IV). Three families made up one

TABLE IV
COLEOPTERA

	Amber	Recent
50 per cent. of population	3 families	4 families
66 per cent. of population	9 families	6 families
75 per cent. of population	12 families	8 families
87 per cent. of population	22 families	12 families
Entire population	62 families	39 families

half of the population; nine made up two thirds; twelve made up three fourths and twenty-two made up seven eighths. For the tanglefoot the corresponding numbers are 4, 6, 8, 12. The amber data are for a larger collection than the tanglefoot, but it will be noticed that our table shows 62 families in the amber and only 39 in the tanglefoot. We have good reason to believe that diversification occurred much earlier among Coleoptera than among the other orders of holometabolous insects, at least with reference to the forest fauna[4] which occupies a very stable environment. If we are here concerned with an older

[4] *Cf.* Brues, '27.

group we must suppose that it is now further past its prime than the Hymenoptera, which I believe to be the case, especially as it formed only 2.5 per cent. of the whole insect population of the tanglefoot compared with about 4 per cent. in the amber.

It may now be asked how far we can extend these considerations to other groups of insects. This question may be approached first by a comparison of the numerical abundance of members of several other orders in the amber and tanglefoot. Unfortunately, I am unable to deal with the matter completely, as there is no reliable census of the amber fauna for several important groups. Those which may be considered are included in Table V.

TABLE V

	Amber	Amber	Mean	Recent	Trend
	Per cent.	Per cent.	Per cent.	Per cent.	
Thyranura	0.1	0.1	0.1	0.0	−
Collembola	6.4	10.6	8.5	0.2	−
Trichoptera	4.6	5.6	5.1	1.5	−
Lepidoptera	0.1	0.1	0.1	0.7	+
Hemiptera	3.1	7.1	5.1	10.8	+
Diptera	56.9	50.9	53.9	71.9	+
Coleoptera	3.6	4.5	4.0	2.5	−
Hymenoptera	3.4	5.1	4.2	5.0	±
Araneida	3.7	4.5	4.1	4.5	±
Acarina	6.7	8.6	7.6	0.05	−

The representation of these orders in the amber is given in percentages of the whole, based on two sources, and the average is in the third column. As these data do not distinguish between the several neuropteroid and orthopteroid orders, a number have necessarily been omitted. The data for the tanglefoot collection are in the fourth column and finally at the right has been added the general trend as to either increase or decrease in abundance. Four large groups, Thysanura, Collembola, Trichoptera and Coleoptera are clearly less numerous in individuals and three others, Lepidoptera, Hemiptera and Diptera are conspicuously more abundant. The Collembola are a very primitive type. So are the Hemiptera, but it will be noticed in the tanglefoot collections that the great abundance of this order is due to a very large number of a single type, the leaf-hoppers. Contrasting Trichoptera with Lepidoptera, the latter are the more primitive and have decreased. Diptera show an enormous increase in spite of their great abundance already in the amber fauna. Clearly the Diptera are developing rapidly and we must look forward to them as the type that is well on its way to dominate the insect world. These statements refer entirely, of course, to population or abundance of individuals and although speciation or the number of specific types in the several groups frequently shows parallel deviations, such a correlation does not necessarily exist.

As to the proportionate abundance of the families of Diptera in amber we have no numerical statistics but many years ago the most astute Dipterist of his time, Hermann Loew (1861) examined a large series of amber Diptera. He states that among the Nematocera the Mycetophilidae (*s. lat.*) are the most numerous both in species and in individuals, while the Culicidae are the most poorly represented. This agrees with the tanglefoot series so far as it extends. Among Brachycera, Loew found that the Dolichopodidae far exceed all other families both in species and individuals. Next to this come the Empididae as far as species, but the number of individuals is far less. Here the tanglefoot figures are quite different. Although numerous, Dolichopodidae (3,070 specimens) are second to the Phoridae (6,443) which exceed any other family and form nearly one third of the whole tanglefoot collection of insects.

Phoridae are well represented in the amber, but are far less numerous than they are in the tanglefoot collection. The great abundance of this family is associated with the most diverse assortment of habits and behavioristic modifications, and of secondary morphological adaptations to be found in any group of Diptera. Yet these flies form a compact group with very distinctive characters of a highly modified and constant type. This suggests that the family, although well fixed as a group, is now in a very active stage of evolution. This conclusion is borne out by their very great present abundance compared with the amber.

Still another series of Diptera are exceedingly interesting in this connection. I refer to the larger muscoid flies, Muscoidea Thecostomata or Calyptratae, acclaimed by all workers as the most recent, most difficult and unstable of all Diptera. These Diptera are surpassed numerically by the smaller Muscoid flies, Muscoidea, Haplostomata or Acalyptratae, evidently a derivative of the other type. They exhibit enormous diversity in structure and appear to represent the group of Diptera destined to become most numerous in the future. Concerning the changes in abundance of these two groups since the amber we have no exact numerical data, but Loew states that the calyptrates were present although rare and that the acalyptrates were very poorly represented by only a small part of the recognized families. Contrasting this with the tanglefoot collection we find a great difference; 287 calyptrates and 1195 acalyptrates, comprising together 9 per cent. of all the Diptera obtained.

Numerous other groups of insects might be considered. True Neuroptera seem to have become less numerous, although not abundant in either fauna. Thysanoptera have clearly decreased; nearly 70 specimens have been studied by Priesner from the Königsberg and Fritsch collections, while only six appear in the tanglefoot, which is proportionately about half as many in the total population.

From the data presented we may conclude that within the rather narrow limits we have chosen, the insect population has manifested considerable change during its long transformation from the depths of the early tertiary amber forest to a modern one which has so far escaped destruction by the axe. There are many possibilities for error to creep into our methods of collecting the materials and of evaluating the resulting evidence, but the direction of change is clearly consistent among a number of different groups. We find that in the whole population certain components have increased, others have decreased and others have remained of about equal size. Parallel to the differentiation of genera and species there has been a correlated population increase in the more modern types of insects while the reverse has been true in groups that we may regard as primitive or decadent. The demonstration of an actual numerical increase in individuals in some groups and a decrease in others is the important fact which we may surmise but can not examine statistically in the case of other fossil insect faunas.

After this comparison of an Eocene and recent forest insect fauna can we still be sure that this is the age of insects? Are insects still on the increase in numbers and variety, or have they passed the heyday of their existence during tertiary times? We can not compare their numbers as a whole as we have no reliable measure of population density. We have seen, however, that certain groups have changed greatly in their ratio to the entire population, sometimes changing places with closely similar groups. Quite generally we find more specialized types replacing ones from which they seem undoubtedly to have been derived, although both appear commonly in each fauna. Meanwhile a few species here and there appear to have persisted throughout the entire period during which numerous genera and some families have disappeared completely, indicating a great fixity that promises little adaptive change in the future. In some groups that we have been able to compare in detail we find a greater diversity in the Eocene fauna than in the present one.

All these facts lead us to believe that many abundant groups of insects have passed their prime. We may still be in the age of insects, but certainly we do not now witness them coming into bloom.

In closing our discussion we may ask whether this slow process of changing insect populations has any bearing on the present problems of applied entomology. So far as any influence on the changes which have occurred during the last century, we must undoubtedly answer in the negative. The upsetting of faunal balance through the establishment and spread of insect pests in new regions is a change of such magnitude and rapidity that it completely swamps the effect of any natural adjustments. Here without question the primary stimulus is extrinsic, involving a greatly increased food supply and a great diminution in natural checks to overpopulation. The changes we have considered appear to be wholly intrinsic, dependent upon the organisms themselves. Although they relate only to numerical abundance, they are analogous to and probably correlated with, if not dependent upon, the progressive morphological change characteristic of groups of animals whose descent can be traced accurately over long periods.

At the present time the disintegration of natural faunal areas has so far progressed that changes in insect populations can not be expected to follow any predictable path in the future.

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