EVOLUTIONARY SIGNIFICANCE OF NORTH AMERICAN
PALEOGENE INSECT FAUNAS

M. V.H. WILSON
Department of Zoology
University of Alberta
Edmonton, Alberta
T6G 2E9

North American Oligocene insect faunas contain many more families than North American Eocene faunas which are otherwise similar in their inferred paleoenvironments. Comparison of the frequencies of families in six major insect orders in Eocene, Oligocene, and Recent faunas suggests an increase in the number of families of Coleoptera and Hymenoptera between Eocene and Oligocene times, Diptera between Oligocene and Recent times, and Lepidoptera between Eocene and Recent times in the North American fauna. The suggested insect radiation may be related to the diversification of flowering plants, as well as tectonic and climatic events. The conclusion that significant numbers of insect families probably originated during the early Tertiary has stratigraphic, paleoenvironmental, biogeographic, and phylogenetic implications.

Les faunes d'insectes de l'Oligocène de l'Amérique du nord contiennent beaucoup plus de familles que les faunes de l'Eocène de cette région. Les faunes de ces deux périodes, selon toutes indications, existaient sous des conditions climatiques semblables. La comparaison de la fréquence des familles de six ordres majeurs d'insectes de l'Eocène, de l'Oligocène et d'aujourd'hui suggère un accroissement du nombre des familles pour les Coléoptères et les Hyménoptères entre l'Eocène et l'Oligocène, pour les Diptères entre l'Oligocène et le présent, et pour les Lépidoptères entre l'Eocène et aujourd'hui. Cette radiation suggérée semblent associée avec la diversification des plantes à fleur et aussi avec des événements climatiques et tectoniques. L'accroissement significatif du nombre des familles d'insectes début des temps tertiaires a des implications stratigraphiques, paléoécologiques, biogéographiques et phylogénétiques.

INTRODUCTION

The Early Tertiary insect faunas of North America were recently summarized at the family level by Wilson (1978). The composition of these Early Tertiary faunas is used here to support the hypothesis that there has been significant faunal evolution at the family level in North America during and since the Early Tertiary.

Paleogene insects fall easily within Recent family boundaries, and it is often contended that little can be learned about the evolutionary origins of insect families from the study of Tertiary fossils (e.g. Rohdendorf, 1974). However, a number of observations suggest that significant changes have occurred in insect faunas since the Early Tertiary. Scudder (1882, 1890) comparing North American Paleogene insect localities, and Brues (1933) comparing Baltic amber faunas with a Recent North American amber fauna, commented on the apparent differences in abundance of individuals within major taxa. Cockerell (1917) noted that some Recent families of Lepidoptera and Hymenoptera appear to be rare in or absent from the older Paleogene formations. The great diversification of flowering plants (Becker, 1965), mammals, and birds (Romer, 1966) near the beginning of the Tertiary, and an increase in the proportion of New World floral elements compared with Old World elements between Eocene and Oligocene times in North America (Leopold and MacGinitie, 1972), suggest a corresponding diversification in insect faunas at that time. Finally, world-wide climatic changes including cooling since the Early Oligocene (Leopold and MacGinitie, 1972), plate tectonic movements since the beginning of the Tertiary (Smith *et al.*, 1973), and major Tertiary orogenies in North

America (Robinson, 1972) may have resulted in the opening of new insect habitats.

The Oligocene faunas of North America, with more than 190 families recorded, are much more diverse in total families and in families per order than are the Eocene faunas, with about 90 families recorded (Table 1; Wilson, 1978). These simple numbers are suggestive of faunal evolution at the family level between Eocene and Oligocene times, over a time span of about 15 million years. However, three possible sources of bias must be ruled out before this conclusion may be drawn. First, much of the apparent increase in diversity between Eocene and Oligocene times may reflect more intensive and successful collecting in the Oligocene localities. Secondly, only some of the fossils in the collections may have been studied. Finally, the differences in diversity may reflect environmental differences at the time of deposition of the insect-bearing formations.

METHODS AND RESULTS

Choice of Unbiased Faunas

Collecting biases in faunal lists may be minimized by analyzing only those faunas which are relatively diverse in number of orders, which have been collected by a large number of different workers, and which have been collected from a large number of different sites and different lithologies.

Curatorial biases are minimized by choosing faunas which have been studied by a large number of investigators in different fields, or by someone who has identified most or all of the specimens collected from a fauna.

Climate in the area of the fauna at the time of deposition, and local depositional conditions such as distance from shore, may also influence which families are present. These paleoenvironmental biases may be minimized by choosing faunas with similar inferred paleoenvironmental conditions. Once the faunas have been chosen, they should further be tested for significant differences in the paleoenvironmental requirements of the contained families. These requirements are assumed to be similar to the requirements of present members of the families. The numbers of families possessing and lacking each requirement are compiled for each fauna, and tested for significant differences among the faunas using the G-statistic (Sokal and Rohlf, 1973).

Most of the Paleogene faunas summarized by Wilson (1978) can be eliminated from consideration for the purposes of this study because of obvious biases resulting from low ordinal diversity, incomplete collecting, incomplete study, and restricted collecting sites. Three of the faunas, however, are relatively diverse (Table 1), and have been collected from numerous sites and studied by numerous workers. They are the Florissant fauna of Early Oligocene age, and the Green River and British Columbia faunas of Middle Eocene age (Wilson, 1978, Table 1).

Although these three faunas were all deposited in lakes, they differed in other aspects of their paleoenvironments. As a result the faunal lists need to be tested for bias prior to drawing evolutionary conclusions. For instance, some deposition occurred near shore and some off shore. In addition, the Green River fauna represents large, fairly shallow lowland lakes while the other two represent smaller, upland lakes. Finally, the climates of the three areas differed during the Paleogene. In the Florissant area the climate was warm temperate to subtropical during the Oligocene while in the Green River area it was subtropical to tropical during the Eocene (Leopold and MacGinitie, 1972). In British Columbia, 15° farther north, it was warm temperate during the Eocene (Rouse et al., 1971).

Table 1. Family diversity of three Paleogene faunas.

	Florissant	Green River	British Columbia
Families Known	192	83	30
Number of orders known	20	13	10
Diversity (families per order)	9.6	6.4	3.0
Families not known from other two faunas (%)	62%	23%	3%

The environmental requirements of the insect families in the three faunas were compared in the following manner. The presence or absence of eight requirements or habits of Recent members of each family that occurs in one or more of the three faunas was recorded. The requirements were as follows: 1. Tropical climate; 2. Aquatic environment for immature stages; 3. Aquatic environment for adults; 4. Adults unable to fly; 5. Larval diet carnivorous; 6. Adult diet carnivorous; 7. Host for parasitic life stage needed; 8. Specialized or restricted habitat required as indicated by rarity in the present-day North American fauna. The frequencies with which these requirements occurred were then compared among the three chosen faunas using the G-statistic. No significant differences were found; probability levels ranged from 0.43 to 0.98 for the various tests. This suggests that the three faunal lists are not biased as a result of different paleoenvironmental conditions.

Comparison of Faunas

Once relatively unbiased faunas have been chosen for analysis, the resulting family lists can be used to draw evolutionary conclusions. This must be accomplished by comparing relative numbers of families in major orders, rather than total numbers of families, because the latter are related to the intensity and success of collecting. These relative numbers are tested for significant differences among faunas of different geological ages using the G-statistic. This analysis of relative frequencies has two limitations: first, only reasonably diverse orders can be used due to limitations of the statistical method; second, the test is only able to detect a significant change in the faunas if the orders have changed in family diversity at different rates. For example, if all orders increased in family diversity by 20 percent between each time horizon, then each order will account for the same proportion of the total number of families at each time horizon, and an analysis of frequencies will show no significant differences in family diversity per order at the different time horizons.

Frequencies of families falling in six major orders of insects were tabulated for the Eocene (Green River and British Columbia faunas combined), Oligocene (Florissant fauna), and Recent (Table 2). Data for the Recent North American fauna are from Borror and DeLong (1971), while those for the Recent World fauna are from MacKerras (1970). These frequencies were then analysed to detect any evolutionary changes since the Eocene.

Results confirm a significant difference among the faunas from different geological ages in relative numbers of families per order (Overall $G = 40.2$, 15 df, $p < .001$). Also significant is the comparison between the Oligocene fauna and the Recent North American fauna ($G = 14.07$, 5 df, $p \simeq .02$). The Recent North American fauna is not significantly different from the Recent World fauna ($G = 3.69$, 5 df, $p \simeq 0.6$) even though the figures were compiled from classifications prepared by different taxonomists. The comparison between the Eocene and Oligocene faunas ($G = 10.58$, 5 df, $p \simeq .06$) is not significant, but the probability level is extremely suggestive of faunal evolution between Eocene and Oligocene times.

Table 2. Numbers of families belonging to six major insect orders in Paleogene and Recent faunas. Numbers in brackets are percentages of the total number of families in the six orders for each fauna.
See text for explanation.

Order	Eocene	Oligocene	Recent North American	Recent World
Hemiptera	9 (12%)	13 (8%)	38 (9%)	54 (10%)
Homoptera	8 (10%)	11 (7%)	32 (7%)	50 (9%)
Coleoptera	26 (34%)	52 (34%)	124 (28%)	151 (27%)
Diptera	24 (31%)	31 (20%)	105 (23%)	118 (21%)
Lepidoptera	3 (4%)	11 (7%)	77 (17%)	105 (19%)
Hymenoptera	7 (9%)	35 (23%)	71 (16%)	73 (13%)

DISCUSSION

Changes in the proportions of families in major orders could be a result of addition of new families to the faunas or of loss of families by world-wide or local extinction. Addition of new families to the faunas with time may have resulted from their immigration from other continents or from restricted ranges on the same continent, perhaps due to tectonic events or shifts in climatic zones. On the other hand, it may have resulted from the evolution of new families during the Tertiary.

Faunal evolution by immigration seems an unlikely cause in view of the wide geographical ranges of most Recent families and the uniformity of world climates during the Paleogene. Judging by the similarity between the Recent faunas of North America and Australia at the family level (Borror and Delong, 1971; MacKerras, 1970) most families have an almost world-wide distribution in warm climates. Furthermore, during the Early Middle Eocene to Early Oligocene time span emphasized in this paper, warm and temperate climates appear to have prevailed as far north as Alaska (Wolfe, 1972), central British Columbia (Piel, 1971), and Ellesmere Island (West et al., 1975). However, data from other faunas and other continents will be required to discriminate between evolutionary and immigrational sources of increased diversity.

Loss of families by extinction is not a major cause of faunal evolution. No extinct families (with the exception of Cockerell's [1915] Eophlebomyiidae, which was not included in the totals of Table 2) are known from any of the North American Paleogene faunas. In addition, only one family falling in these six orders and present in the Paleogene (the Glossinidae) is now locally extinct in North America.

Assuming the proportions given in Table 2 reflect accurately the real proportions in the faunas, and taking the conservative position that in each time interval one or more orders have

not increased in diversity, we can reconstruct the probable diversity changes in the North American fauna since the Eocene (Fig. 1). Because extinction can be ruled out as a significant source of faunal evolution, it follows that orders which show a proportional decrease in diversity in Table 2 are actually those which have undergone the least amount of increase in diversity. Similarly, orders which show no change in proportional diversity with time are those which have increased in diversity at the average rate for the six orders. Finally, orders which show an increase in relative diversity have actually increased in diversity more quickly than the average rate for the six orders considered. In Figure 1, the horizontal width of each polygon at the Recent time horizon is proportional to the family diversity of the order in the Recent North American fauna (Table 2). Between Oligocene and Recent times, the Hymenoptera showed the greatest decrease in proportional family diversity (from 23% to 16% in Table 2, or a decrease of about 30% between the two time horizons). Thus the Hymenoptera are likely to have increased in family diversity less than the other five orders between Oligocene and Recent times. Taking the conservative position, for the arguments advanced in this paper, that no new families of Hymenoptera evolved in or immigrated into North America between Oligocene and Recent times, it follows that orders which show relative decreases in family diversity of less than 30% in Table 2 have actually increased in absolute number of families. The approximate amount by which each order increased in number of families was estimated by the difference between the proportional change in diversity for that order and the 30% decrease of the Hymenoptera. The horizontal widths of the polygons for the Eocene time horizon were extrapolated in a similar way from the Oligocene widths, except that for this time interval the Diptera, which showed the greatest decrease in relative family diversity, were assumed not to have changed in number of families. These estimated changes in the numbers of families must be considered approximate minima only. Undoubtedly all six orders increased in diversity to some extent, and more reliable estimates of the diversity changes will result from further studies of the included faunas and from studies of additional faunas at these and other time horizons.

Thus, the Hemiptera and Homoptera appear to have evolved little at the family level since the Eocene (Fig 1). The Coleoptera increased most rapidly in number of families between Eocene and Oligocene times. The Diptera appear to have increased most rapidly in number of families between Oligocene and Recent times. The Lepidoptera appear to have increased in number of families during both time intervals. The Hymenoptera appear, like the Coleoptera, to have evolved most rapidly at the family level between Eocene and Oligocene times. Cockerell's observation that some families of Lepidoptera and Hymenoptera are absent from the Eocene and present in the Oligocene formations now seems explicable in terms of faunal evolution rather than local paleoenvironmental or curatorial biases.

With the exception of the Lepidoptera, the insect orders analysed here have geological ranges extending back well beyond the Tertiary, and probably diversified shortly after their first appearances. However, there is evidence that the more advanced groups within these orders are considerably younger. Most of the increases in diversity during the Tertiary probably occurred in these more advanced groups. For example, among the Diptera the earliest known Cyclorrhapha are Cretaceous (McAlpine and Martin, 1966; McAlpine, 1970). Similarly, among the Hymenoptera, the earliest known Apocrita are Cretaceous (Riek, 1970). Diversification within the Tertiary is most easily understood for the Lepidoptera. The earliest known Lepidoptera are Early Cretaceous (Whalley, 1977), but the Cretaceous and Early Tertiary records of Lepidoptera are usually of primitive lepidopteran groups (e.g. MacKay, 1969, 1970).

The radiation of flowering plants, coupled with tectonic and climatic changes during the Tertiary, seems the most likely explanation for the radiation of butterflies among the Lepidoptera, bees among the Hymenoptera, some Cyclorrhapha, and some Coleoptera. In addition, certain parasitic Hymenoptera may have radiated in response to the radiations among host insects.

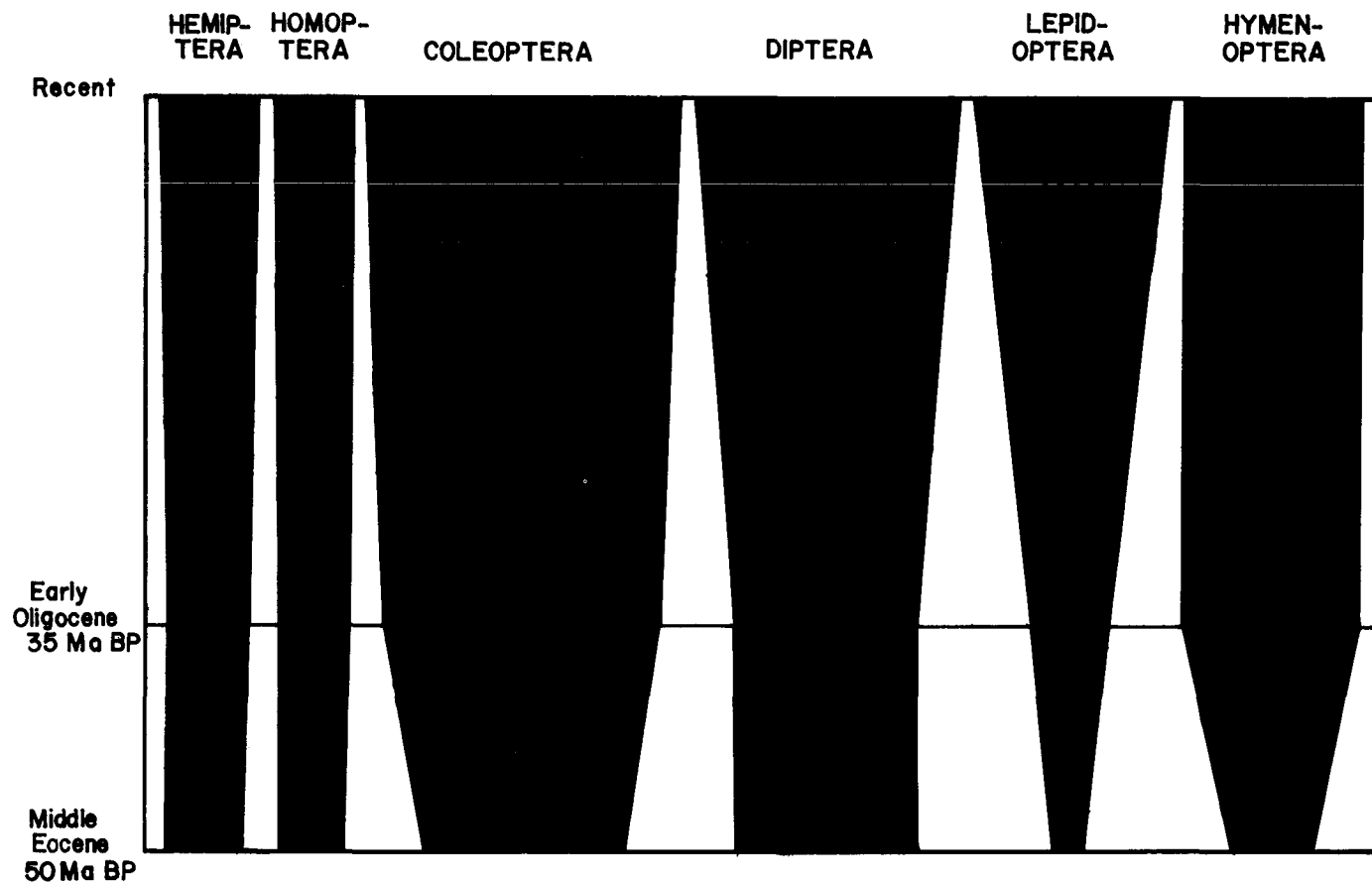It has been shown here that a significant number of insect families probably evolved in or

Fig. 1.   Changes in numbers of families in six major insect orders since the Eocene, as reconstructed from data on Early
Tertiary insect faunas of North America. Horizontal width of each polygon is approximately proportional to the
number of families extant at each time horizon. See text for explanation.

immigrated to North America during the Paleogene. Assuming, as seems likely, that similar evolutionary events occurred during the Paleogene in other faunas and other continents, some stratigraphic, paleoenvironmental, biogeographic and phylogenetic implications become evident.

First, the fossil record of these families can be used as evidence in stratigraphic dating of their formations. For example, the occurrence of butterflies and bees would suggest that the fauna concerned is younger than Middle Eocene.

Second, the fact that significant numbers of the more advanced insect families had not yet evolved in the Early Paleogene means also that their absence from an Early Paleogene formation likely has no paleoecological significance. Additional evidence will be required to determine which families have significance for stratigraphic and paleoenvironmental studies.

Third, biogeographic studies of some of the more advanced insect families must take into account the probability that distribution patterns of the families should be reconstructed on maps based on Tertiary continental arrangements, rather than on Cretaceous or earlier arrangements.

Finally, the significance for phylogenetic reconstruction of some of the more advanced insect families is that their ancestry may lie within presently defined families occurring in the Cretaceous and Paleogene. Thus Tertiary fossils do have significance for evolutionary studies of insect families.

ACKNOWLEGEMENTS

REFERENCES

Becker, H.F. 1965. Flowers, insects, and evolution. Natural History 74: 38-45.

Borrer, D.J. and D.M. DeLong. 1971. An introduction to the study of insects. 3rd edition. Holt, Rinehart and Winston, New York, N.Y., 812 pp.

Brues, C.T. 1933. Progressive changes in the insect population of forests since the Early Tertiary. The American Naturalist 67: 385-406.

Cockerell, T.D.A. 1917. Fossil insects. Annals of the Entomological Society of America 10: 1-18.

Cockerell, T.D.A. 1925. The Eocene fossil fly *Eophlebomyia*. Psyche 32: 229-230.

Leopold, E.B. and H.D. MacGinitie. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. *In* Graham, A. (Editor), Floristics and paleofloristics of Asia and Eastern North America. Elsevier, New York. 147-200.

MacKay, M.R. 1969. Microlepidopterous larvae in Baltic amber. The Canadian Entomologist 101: 1173-1180.

MacKay, M.R. 1970. Lepidoptera in Cretaceous amber. Science 167: 379-380.

MacKerras, I.M. (Editor). 1970. The insects of Australia. Melbourne University Press, Carlton, Australia, 1029 pp.

McAlpine, J.F. 1970. First record of calypterate flies in the Mesozoic era (Diptera: Calliphoridae). The Canadian Entomologist 102: 342-346.

McAlpine, J.F. and J.E.H. Martin. 1966. Systematics of Sciadoceridae and relatives with descriptions of two new genera and species from Canadian amber and erection of Family Ironomyiidae (Diptera: Phoroidea). The Canadian Entomologist 98: 527-544.

Piel, K.M. 1971. Palynology of Oligocene sediments from central British Columbia. Canadian

Journal of Botany 49: 1885-1920.

Riek, E.F. 1970. Fossil history. *In* MacKerras, I.M. (Editor), The insects of Australia. Melbourne University Press, Carlton, Australia, 168-186.

Robinson, P. 1972. Tertiary history. *In* Mallory, W.W. (Editor), Geologic atlas of the Rocky Mountain Region. Rocky Mountain Association of Geologists, Denver, Colorado, 233-242.

Rohdendorf, B. 1974. The historical development of Diptera. The University of Alberta Press, Edmonton, Alberta, Canada, 360 pp.

Romer, A.S. 1966. Vertebrate paleontology. Third edition. The University of Chicago Press, Chicago, 468 pp.

Rouse, G.E., W.S. Hopkins, and K.M. Piel. 1971. Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. Geological Society of America, Special Paper 127, 213-246.

Scudder, S.H. 1882. The Tertiary lake-basin at Florissant, Colorado, between South and Hayden Parks. United States Geological Survey, Bulletin 6: 279-300.

Scudder, S.H. 1890. The fossil insect localities in the Rocky Mountain Region. Psyche 5: 363.

Smith, A.G., J.C. Briden, and G.E. Drewry. 1973. Phanerozoic world maps. *In* Hughes, N.F. (Editor), Organisms and continents through time. Paleontological Association, London, Special Papers in Paleontology 12: 1-42.

Sokal, R.R., and F.J. Rohlf. 1973. Introduction to biostatistics. W.H. Freeman and Company, San Francisco, California, 368 pp.

Whalley, P. 1977. Lower Cretaceous Lepidoptera. Nature 266: 526.

West, R.M., M.R. Dawson, J.H. Hutchison, and P. Ramaekers. 1975. Paleontologic evidence of marine sediments in the Eureka Sound Formation of Ellesmere Island. Arctic Archipelago, N.W.T., Canada. Canadian Journal of Earth Sciences 12: 574-579.

Wilson, M.V.H. 1978. Paleogene insect faunas of Western North America. Quaestiones Entomologicae (14): 13–34.

Wolfe, J.A. 1972. An interpretation of Alaskan Tertiary floras. *In* Graham, A. (Editor), Floristics and paleofloristics of Asia and Eastern North America. Elsevier, New York, 201-233.