ZOOGEOGRAPHY OF INSECTS[1]

BY J. LINSLEY GRESSITT
Bernice P. Bishop Museum, Honolulu, Territory of Hawaii

The study of the geographical distribution of insects is a subject which has received attention from many entomologists, yet one which is still in an infant stage of development. Knowledge of the distribution of higher vertebrates has progressed to the point where it is fairly well understood, but this is by no means true for insects. Not only are very many insects yet to be discovered or named, but the complete distribution is known for very few. Also, rather little is known of the evolutionary history of insects and there is much contradiction among conclusions relating to the history of insect distribution.

It is important enough to know the ranges of the species that occur in an area, in searching for biological control agents, in evaluating pest potentials, crop selection and danger from diseases of plants, animals and man; but zoogeography is much more, however, than the mere determination of the ranges of species or groups. It is, furthermore, a field of interrelation of ecology, physiology, systematics, phylogeny, paleontology, geography and geology. It is not a static subject but dynamically relates the tolerances of individuals and populations to their origin, evolution, and dispersal in terms of changing climates, vegetation and topography.

The study of insect distribution has progressed to very different degrees in different parts of the world, and for different groups of insects, more or less in proportion to the extent of entomological research. In Europe, where the species and their respective ranges are well known in most groups, very thorough studies have been possible. In some cases it has apparently been possible to work out in detail not only present but past distribution. In other continents where species are still being described and their ranges determined, much pioneering work remains to be done. In few groups of insects has it been possible to determine the course of development and spread of the world fauna, but in recent years a few excellent attempts have been made (168, 121).

Though the extremes of geographical range of a species may be easily outlined on a map, it must be remembered that the actual occurrence of a species in most cases involves not only discontinuous macrogeographic distribution, but also limitation to a specialized niche within the areal range. Distribution maps should show occurrence by dots, and be supplemented by indication of niche and general habitat or zone, in addition to recording of place-names. More emphasis is now being given to the importance of ecology in zoogeography.

The application of insect zoogeography to phylogeny and systematics is

---

[1] The survey of the literature pertaining to this review was completed in June, 1957. The author has not seen proofs.

treated in great detail by Hennig (80), who stresses ecology and chorology, cites former glacial refuges as centers of multiplication, and states that the named synonyms of widespread species are often described from the margins of their ranges.

METHODS

Ross (168) has presented a plan of procedure for interpreting the evolution and distribution of a group, based on his work with caddisflies. First, one must study the characters of living and fossil species and work out phylogeny and distribution patterns. These patterns should then be correlated with the geological time scale using the dated fossils. The geological data then show dispersal possibilities, and comparisons may be made with known history of other groups. The more definite and complete the data, of course, the more reliable are the conclusions. Naturally larger groups including fossil material offer greater possibilities of solution. In determining routes of dispersal, qualitative approach is essential, rather than statistical, as shown by Kinsey (99) for an annectant series with the most primitive in southern Mexico, which was determined as the original home. In integrating phylogeny and distribution, changes in environment, extinction of lines, and variation in both rate of evolution and rate of dispersal must be borne in mind. And with isolated species, or sister groups on separate continents, the point of origin may be indeterminable without other evidence.

DISPERSAL

That the living species of insects have not evolved continuously in the same areas they now inhabit is generally accepted. It is also well established that there have been climatic changes or cyles. In the Pleistocene Period there were four ice ages associated with some shifting of the poles of the earth, extension of ice caps southward in Europe and North America, and lowering of the sea level. Farther back, the climates are less well known, but fossils of tropical animals and plants have been found in rocks of various periods in areas of cool climate today. There is some evidence to indicate that insects do not quickly change their climatic tolerances. One line of evidence is the occurrence together in ancient deposits of fossils of various groups which have similar macroclimatic tolerances today. Other evidence includes some parallels between the evolution and dispersal of insects and host-plants to which they are attached [Gressitt (69)], or correlation with other niches [Ross (168)]. Studies of both cold-adapted and warm-adapted groups [Emerson (48)] indicate somewhat similar dispersals at different times. In New Guinea there has been some radiating of tropical forms into high young mountains which lacked a temperate fauna (73, 189).

This field has been treated recently by Williams (204). The power of dispersal,[2] or vagility, seems to be characteristic of living things, but various

---

[2] The term "migration" should be reserved for movement of insects in a direction or for a distance over which they have control.

groups spread in differing ways, and at varying rates. So many factors are involved in rate of dispersal, that it can probably never be determined to the satisfaction of all, particularly for past ancestors. Normal population pressure and the consequent tendency to spread is tempered by competition within the species and with other forms and numerous climatic and other factors. Andrewartha & Birch (2) stress the innate tendency toward dispersal among insects, and state that accentuation of dispersal tendencies as a result of overcrowding of populations may or may not result in extension of range.

In addition to normal vagility, passive (accidental) dispersal must often enter in. This may consist of transport in air currents, on the bodies of birds or other animals, on streams, floating logs, or by other accidents (10, 34, 46, 65, 66, 70, 72, 74, 209). Air currents seem to play a most important role, and various evidence seems to point particularly to this factor in the dispersal of insects to oceanic islands. Wellington (202) has discussed the physical factors involved in air dispersal of insects, indicating that long-distance dispersal is negligible, and short-distance dispersal is common, from the standpoint of dispersal of pests in continental areas. Gislen (65) considers that minute insects are so easily carried by air that they are not subject to the same distributional limitations as other insects and are therefore of no significance in zoogeography. Salmon (171) and Mockford & Gurney (137) would appear to dispute this to some degree, from the data they present on faunal differences for some small insects. Gislen states that the greatest limiting factor in air transport is desiccation, which is serious only in clear weather; but he may minimize the adverse factors. Palmên (147) describes great numbers of insects washed up on beaches in Finland, many of them alive, and mostly winged insects. Heberdey (79), in discussing range extension, stresses the importance of means of dispersal in determining phylogenetic age on a distributional basis. Savile (173) treats dispersal rates.

In estimating the degree of relationship of different zoogeographical regions, attention must be paid to the movements of man as well as other natural factors, particularly for the noneconomic species. The spread of pests is often clearly traceable, but not so with noneconomic species which may have been transported to new areas where thorough collecting has rarely been done in advance. Lindroth (117) demonstrates in detail that many species of ground-inhabiting beetles, and other insects, were transported from southwestern England to Newfoundland and to the Maritime Provinces of Canada in rock and soil ballast on ships going for lumber in early colonial days. Since the climates of the two areas are similar, many colonizations succeeded, and there are about ten times as many insects introduced from Europe to North America as the reverse. Palmên (148) shows that of 42 species of myriapods and terrestrial isopods in Newfoundland, 36 are European, two cosmopolitan, and only five American. Gurney (74) treats this question for some of the lower orders of insects.

Lindroth (115) believes that attempts to correlate the ranges of insects with isotherms or other climatic averages is an incorrect practice, for microclimatological differences are very great, and control actual distribution in the main. Though many workers have placed temperature as the most important factor controlling insect occurrence, other factors, particularly humidity, may be most the important. Lindroth (115) has shown that some apparent association of ground beetles with limestone actually proved to be controlled by thermal and hygric, rather than chemical, factors. In response to this, Janssens (91) insists that there are definite associations of insects with limestone. The most thorough treatment of the operation of factors affecting insect distribution is that of Andrewartha & Birch (2). Some important aspects of the relation of climatic factors to distribution were introduced by Matthew (128). The effects that changes in the environment have on distribution is treated by Franz (59), who shows that the more frequent the changes, the poorer the fauna. Cold relicts are frequently found among insects, but not so with warm-blooded animals, and warm relicts are rarely found among insects [Lindroth (115)]. Races may be produced more rapidly on small islands, isolated peaks or valleys, and during periods of changing climate.

The work of Schilder (174) emphasizes the importance of isolation in the development of races, but neglects aspects of historical geology and uses some examples based on outdated taxonomy. Iablokoff (88) discusses biotic factors and an ecological plasticity in relation to distribution.

Ross & King (170) develop the hypothesis that a species becomes adapted to a particular ecological niche and stays there as long as it survives. If the species, or part of it, is able to move into a different ecological niche, selection pressures of the new environment will favor beneficial genetic changes in the population. If then, through geographic isolation, many species arise from a single one, the least changed or primitive species should represent the one still remaining in the ancestral habitat, and the most changed or specialized species should be the one in the habitat differing most from the ancestral habitat.

Although the knowledge of insect zoogeography is imperfect and uneven, some firm bases have been laid for zoogeography in general, especially for the higher vertebrate animals (82, 131, 132, 133, 143, 181). Only minor changes have been made in the outlines of Wallace's zoogeographical regions (200), and there still remain disagreements on some of these changes. The recent, excellent general treatment of zoogeography by Darlington (38) largely concerns the better known vertebrates.

The importance of ecology to distribution is stressed by Janssens (91, 92), who indicates that phytogeography has progressed beyond zoogeography, and makes some vigorous criticism of much of the work concerning insect distribution. Kiriakoff (100, 101) praises Janssens' papers but states that to accept them fully endangers phylogeny, but agrees on the importance of ecology. Kiriakoff thinks that in many of the cases where genera are reported as found in different southern continents, actually different genera are involved, indicating older separation. Hennig (80) & Brehm (16) relate distribution and taxonomic characters.

ZOOGEOGRAPHICAL REGIONS

Wallace (200) established six zoogeographical regions: Palearctic, Ethiopian, Oriental, Australian, Nearctic and Neotropical. These are not of equal distinction, and may be arranged in groups. Palearctic and Nearctic, the north temperate regions, are very closely related, and are often treated as subgroups of the Holarctic Region. Though there is invasion of the Nearctic from the Neotropical, and Palearctic from Oriental, the Palearctic and Nearctic have more in common, showing that climate and history are more important than present geographical continguity. The Ethiopian is most clearly related to the Oriental Region, though the former has some exchange with the Mediterranean Subregion of the Palearctic. Ethiopian and Oriental are sometimes combined as Paleotropical, which to some also includes the Australian Region. Nearctic, Palearctic, Ethiopian and Oriental are sometimes grouped together as Arctogaea, while Neotropical is segregated as Neogaea and Australian as Notogaea. Two large islands with associated smaller islands having distinctive faunae, Madagascar and New Guinea, do not fit perfectly into the above systems. Another classification of regions is by type of barriers [Darlington (36, 38)]; the climate-limited regions being the Palearctic and Nearctic, the barrier-limited regions being the Neotropical, Australian and Malagasy, and the main regions (which are in part barrier- and climate-limited) being Ethiopian and Oriental.

To some workers, the zoogeographical regions are purely arbitrary divisions, and some feel that the drawing of outlines of common or average ranges of groups of species has no real significance because factors controlling distribution of different groups may be quite unrelated.

The desert areas of North Africa and Southwest Asia form a unit as important as a zoogeographical region according to Uvarov (192), although they cannot be outlined satisfactorily on a map. Uvarov uses the term ecofauna to designate the lowest zoogeographical units. For the Sahara (193) he designates four ecofaunae: deserticolous, saxicolous (on rocky country), arbusticolous (among trees) and graminicolous (among grasses). Most species would be involved in only one of these ecofaunae, but each ecofauna may include forms of various origins, such as Paneremian (widespread desert forms), Ethiopian, Lemurian, and Angaran.

In spite of the fact that South America, Africa and Australia are each separated in one of the three major divisions of the world, the southern portions of each have numerous elements in common in many groups of insects [Edmunds (44); Hardy (77)], vertebrates and plants. The fossil evidence for insects is imperfect, but in plants a conspicuous ancient southern group, typified by *Glossopteris*, is characteristic of these areas and of Antarctica (Seymour Island, 64°S., south of the northern tip of the continent). This and other evidence has been the basis for the Wegenerian Hypothesis, or theory of continental drift, which explains the origin of continents as starting with a single southern continent. This continent cracked into the forms of the present continents and drifted apart and northwards to their present positions. This theory is firmly adhered to by many European workers

[Demoulin (41); Fraser (60); Maran (125)], and one of its stoutest champions is Jeannel (93, 94). Fraser cites yearly westward flights of butterflies and dragonflies from the Western Ghats in India to the Indian Ocean as evidence of continental drift. Mammalogists, who have abundant fossil evidence [Simpson (181)], can show that changing climates, and a Bering Straits connection between Asia and North America (also abundantly shown by fossil florae) and old connections between Asia and Australia, can account for present distribution in the main. Rehn (157) and others point out that continental drift creates many new problems. Rehn also severely criticizes Jeannel's attributing similarity of Nearctic and Palearctic faunae to a Greenland-Iceland-Europe connection (93), because there is little actual evidence for that, but much for the Siberia-Alaska connection. Detailed treatment of the Pleistocene ice ages is given by Flint (56).

Another argument against the Wegenerian Hypothesis is the weight of evidence for the permanence of the present oceans. Wallace (200) dwelt on this, as have many since then. Although there is evidence of more extensive former islands in the mid-Pacific [Hamilton (76)], these were still surrounded by deep ocean. They could have served as stepping stones in the dispersal of insects to the more isolated island groups, like Hawaii. Likewise, there is little likelihood that the mid-Atlantic ridge once formed a continent "Atlantis," as described by Malaise (122) and others.

Many workers, in order to explain apparent close relationships of insects on distant continents or islands, have hypothecated land bridges permitting dispersal from one area to another. In most cases these enthusiasts have failed to explain the lack of other dispersals which such bridges might have permitted. The evidence for air transport of insects can in most cases reasonably explain the populating of oceanic islands, and the evidence for changing climates and the Bering land bridge can explain most continental relationships, through long-distance dispersal.

Munroe (141) demonstrates methods of comparing related faunae, showing that comparison of vicarious elements of shared superspecies provided a good measure of differences between faunae in which autochthonous radiative evolution is not an important factor, but the historical interpretation is difficult.

Ross (168) demonstrates for certain Trichoptera that during the Cretaceous there was wide dispersal of primitive forms; in the Paleocene the greatest dispersal of cold-adapted types, in the Eocene the greatest dispersal of subtropical forms, during the mid-Cenozoic the greatest dispersal of temperate forms, and in the Pliocene and Pleistocene chiefly intrasystem dispersal of montane elements. Ross states that these groups show that dispersal to the southern continents had their origins in the northern hemisphere, and that Africa, particularly, had infrequent cool climate connections with the north. Seevers (177) admirably delineates spread and evolution of termitophilous Staphylinidae in relation to the same for termites, correlating his findings with those of Emerson (48).

Holarctic.—Most of the recent workers (38, 48, 116, 168, 181) ascribe all interchange between Eurasia and North America requiring continuous land connection to have taken place across the Bering bridge at various periods. Ross (168) cites seven possible Cenozoic connections: Paleocene, early Eocene, late Eocene to early Oligocene, early to mid-Miocene, late Miocene, late Pliocene, and Pleistocene, with the most extensive exchange in the early Eocene and Pleistocene connections. Though Emerson (48) felt that late Cretaceous was the last time tropical forms could cross the bridge, Ross thinks it may have been later. Lindroth (116, 117) treats in detail the relationships of the Palearctic and Nearctic. Obenberger (144) discusses the relationship in the Buprestidae. The north-south nature of the North American mountains, and the more east-west alignment of the Eurasian ranges provided different situations, particularly as regards southward migration during glaciation. Gurney (74) has also discussed species in common between the Nearctic and Palearctic.

Palearctic.—The Palearctic insect fauna is rich and varied, but lacks many Ethiopian and Oriental types barred by climatic factors. The fauna is probably more varied at the east and west extremes—in Japan, Northeast Asia, and Europe—than in the intermediate area between which is more strictly bounded on the south by both deserts and very high mountains. In the east and west extremes, the environments are more varied, and mixtures from the neighboring regions have occurred. Many species in Europe and Japan are closely related or identical. The Mediterranean Subregion is fairly arid and poorer in representation of many groups than both Central Europe and the Ethiopian Region. The Manchurian, or Japanese Subregion is extremely rich and varied, having some elements otherwise known only from Western, or Eastern, North America, and many others which have extended northward from the Oriental Region, with the lack of effective barrier between, and the coastal areas washed by the warm sea current. Warnecke (201) discusses the northern Palearctic fauna, stressing Angara origin. In Europe there is considerable north-south discontinuous distribution, frequently involving Fennoscandia in the north and the Alps, Pyrenees, Caucasus and other mountains in the south. Much of this is result of the advance and retreat of the glacial period ice sheet, pushing populations southward and leaving many in isolated pockets in the southern mountains as glacial relicts. Studies of relicts in particular groups are treated by Daniel (33), Reiss (159), and others. There exist in Europe many remarkable specialized and localized cave-inhabiting insects of many groups. The distribution of these has been treated by Holdhaus (84) and Jeannel (93). The European fresh water fauna is treated in detail by Theinemann (188), particularly from the standpoint of glacial influence. For the European boreo-alpine Orthoptera, Anders (1) points out that many of the north-south isolations are independent, and developed at different times, and that many of them represented Angara elements which came in from Siberia because they were already cold-resistant at start of the fourth ice age. Jordan (96) treats ice relicts on cold moors, and states that *Notonecta lutea* is frozen 260 days of the year. The taiga (coniferous forest) fauna is treated by Florov (57). and flora by Faunov.

The fauna of the British Isles is one of the very best known. According to Beirne (7), it includes over 20,000 species of insects, one-half the fauna of Europe. There are three centers of distribution: south and southeast, highlands of Scotland, and the southwest. About one-half the species occur in Ireland, but there are few endemics there. Of the total, 2 per cent or less are endemic, although there are many endemic subspecies. There has been much exhange back and forth with the continent. Berine states that 35 per cent could have been carried by air, but probably 95 per cent spread over land connections as the fauna is quite harmonic. There have been several connections during the past 600,000 years. Even skeletons of large land animals have been found on Doggersland, a sunken connection lying west of Netherlands. If it is true that the temperate (less cold-adapted) insects in England are post-glacial invaders, then evolution (with small populations) has been rapid and many new species have evolved in the past 6,000 years. But other evidence indicates that it took over 100,000 years to produce many of the endemic subspecies. Kruseman (103) discusses a *Bombus* which may be a relict of Doggersland, pointing out that some species have one subspecies on both sides of the English Channel and another subspecies in eastern Holland and Germany. Very detailed studies have been made for various parts of Europe (31, 115 and others).

Baltic aquatic glacial relicts are discussed by Lindberg (113) showing that the weakly saline nature of the Baltic Sea renders rather slight the distinction between fresh-water and sea habitat, with many insects in the shore water. In general, the fresh-water rock pools contain insects of the far north, and the brackish pools harbor more southern insects at the north ends of their ranges. Szent-Ivany (186) shows western Hungary to be a faunal meeting place, with alpine and Mediterranean elements more numerous than the Ponto-pannonic and Carpathian elements. For the Middle East, Theodor (187) shows that the Diptera fauna is mainly Palearctic with northern species spreading southward to varying degrees and Mediterranean species spreading eastward, in many cases into northwest India.

The Atlantic islands are volcanic and populated by air and sea currents, according to Balachowsky (3) and others. According to Lindberg (114) the Canaries and Cape Verde Islands were never connected, but both have been joined to Africa. The younger steppe fauna consists of small winged insects which came through wind dispersal; the older fauna is limited, and in the mountains. Chopard (30) shows that the Azores and Madeira have an impoverished Mediterranean fauna, the Canaries a richer, more distinctive Mediterranean fauna with some African elements, and the Cape Verdes an Ethiopian fauna with feeble endemism.

Nearctic.—In discussing the origin of the Nearctic insect fauna, Ross (167) indicates general dispersal in Cretaceous and later with many colonizations from Asia and South America. There was relatively little extermination during glacial periods, and much multiplication of species and southward spread. There is also no evidence of connections between the mountains of eastern and western North America. In treating the origin of the northern Nearctic fauna, Munroe (142) shows that most of Canada was glaciated in the Wisconsin Period, but that there were Amphiberingian refuges, as well as other refuges on the coasts, and perhaps in Greenland. There are ten types of existing distributions: circumpolar, widely distributed American, Amphiberingian, Alaskan, Pacific-coastal, Cordilleran, Amphi-Atlantic, high Arctic American, northwest Canadian and northeast Canadian.

For Greenland, Strenzke *et al.* (185) show that of the soil fauna, 23 species are of wide Arctic to subtropical distribution, 13 are Arctic or upper Palearctic, and four are endemic but may be found later elsewhere. Vibe (97) stresses the circumpolar elements. Within Greenland, de Lesse (111) shows that distribution zones are determined largely by amount of sunshine. The life zones in Alaska, according to Mason (127), are Canadian, Hudsonian and Arctic, with five main distribution patterns. Klots (102) shows that many species have their southernmost extensions in Appalachian acid bogs, as well as Alpine areas. Darlington (34) shows how the insect fauna of the Antilles could largely have come by air dispersal. Dillon (43) has discussed in detail the climate of the Wisconsin Period (last glacial) in North America, in relation to insect distribution. Van Dyke (194) discussed the North American beetle fauna, showing eight distinct faunae, of which five are derived from Eurasia across the Bering bridge, and three derived from South America, none being of North American origin. He stresses the diversity and distinctiveness of the Vancouveran fauna, which nevertheless is derived from northeastern Asia. The aquatic insects of California are well treated by Usinger *et al.* (191). For lower California, Ross (166) reports that of 14 species of Trichoptera, four are widespread through much of North America, four are known from widely separated localities in the Southwest, two are known from western California, and four are endemic. Of the latter, one is of Rocky Mountain relationship and three belong to the southwestern fauna and might be found in Mexico.

Neotropical.—Connections between North and South America, according to Ross and King (169, 170), were one in mid-Cretaceous and several between the Eocene and present, with two successive partial bridges in late Oligocene and lower Miocene, but also long periods of separation of the two continents. This permitted much specialization in South America. Speciation of some butterflies and moths on islands of the Antilles is discussed by Munroe (139, 141). For one group of pyralids, three waves of immigration are cited. Large size, great north-south extension, and very slight submersion of South America gave much opportunity for movement in times of changing climate, permitting preservation of ancient types, as well as diversification [Malaise (122)]. Many living groups appear to have originated there. Zonation in Bolivia is treated by Forster (58), who shows the distinct separation of environments, largely by altitude. Ringuelet (163) discusses the faunal relations of the southern Cordillera in Argentina. Neotropical and Ethiopian relationships are discussed by Mayr *et al.* (133).

Schweiger (176) discusses beetle distribution in southern South America, in relation to the subantarctic islands, showing that much of the area was not covered during ice ages. He states that Andean forms are found in Tierra del Fuego and that the Falkland Islands fauna differs from that of Tierra del Fuego in lacking xylophagous species. Brinck (17, 18, 19) shows that with the beetle faunae of South Atlantic islands, aside from cosmopolites brought by man, the species largely belong to endemic genera and many are flightless. In the absence of land connections, ancestors of all of these must have been brought by winds, but the land and fauna may have been more extensive earlier. He points out that most of the sub-antarctic beetles are phytophagous, whereas most subarctic beetles are carnivores.

Galapagos beetles are treated by Van Dyke (195), showing ancient derivation from barren grounds of Ecuador and Peru. He believes they are continental islands isolated by subsidence, but most workers consider them oceanic. Wirth (207) treats some Juan Fernandez Diptera, making comparisons and demonstrating flightless species.

Ethiopian.—Most people draw the northern border along the south edge of the Sahara, and eastward to include southern Arabia. Oldroyd (146) in treating Ethiopian Tabanidae states that the group arrived in Africa both from north and south, the primitive ones from the latter. He favors the Gondwanaland theory, but states that he has no new evidence for it, and that continental drift need not be invoked if there was a larger Antarctic continent. Uvarov (192, 193) shows that species on high African mountains are not related to European species, and are old elements, possibly from central Asia. He says that southward migration from Europe is not applicable in African acridiids, and that the Sahara was encroached upon by Ethiopian savannas, which left relicts in oases, rather than having been cool enough in the Quaternary Pluvial to permit north-south migration of Mediterranean or northern forms, as suggested by Jeannel.

Madagascar is generally considered a strong subregion of the Ethiopian Region, but sometimes separated as a Malagasy Region [Emerson (49)] or "Lemuria." Paulian (152) discusses the insects of Madagascar, stressing the highly endemic, initially disharmonic, yet diversified fauna. He states that the Mascarenes were never connected with Madagascar, and obtained their insects by over-sea dispersal. Madagascar was connected to Africa in mid-Jurrassic but, according to Delamare Deboutteville and Paulian (39), it has been impossible to prove a connection between Madagascar and India. The Mascarene fauna is oceanic, disharmonic, and influenced by Madagascar, according to Viette (198), and the Reunion fauna is similar to that of Mauritius, but the two islands were never connected. Vinson (199) shows that in the Carabidae, Mauritius has 41 per cent endemism, Reunion 39 per cent endemism, and Rodriguez no endemism. Indications of discontinuous distribution between Pacific and Indian Ocean islands is presented by Delkeskamp (40), Gressitt (72), and Fennah (54). Some of these cases undoubtedly involve the preservation of primitive forms as a result of lack of competition on oceanic islands, with the forms having become extinct in continental portions of their former ranges.

Oriental.—The mountains of West China and Himalaya are among the oldest and best preserved Tertiary relict areas. The higher mountains, including those in Burma, South China and Taiwan, fall within the Palearctic Region, as there is no barrier in the east. Caradja (28) discusses some of these problems. India was an island until towards the Pleistocene [Malaise (122)].

In considering mosquitoes, Lee & Woodhill (110) place the boundary between the Oriental and Australian regions between the Lesser Sunda Islands and Celebes on the one hand and the Moluccas and Timor on the other. They point out that most of the Australian species are in the north and east, which seems to suggest recent Oriental intrusion, and that the Papuan area might form a very strong subregion of the Oriental Region, and include the species in Australia. There are a number of groups which show very conspicuous Philippine-Papuan distribution, extending into Micropolynesia, but with practically no representation in the Sunda Islands or Australia (72, 126). Some of these continue on in part to New Zealand through New Caledonia. The question of this Oriental-Australian boundary is discussed by Mayr (132) who cites percentages of representation of Oriental and Austral-Papuan faunae, based only in small part on insects. Southeast Asia and the Malay Archipelago were land at the end of the Mesozoic, alternately connected with the New Guinea area, while southern New Guinea was connected with Australia. At that time perhaps, and even up to the Pliocene, central New Guinea was beneath the sea and the rest consisted of strings of islands, with more extensive land to the north where the Bismarcks and Solomons are, and farther west (73, 168, 189). An outer Melanesian arc extended eastward to the New Hebrides, and perhaps closer to Fiji than at present, but only as islands. The inner Melanesian arc extended to New Zealand, and may have existed in the Cretaceous and been of short duration.

Although the mammals of New Guinea are Australian, many groups of insects show more distinct Asian origins, derived largely before the development of higher mammals. Then occurred a long isolation from Australia during the Tertiary, until the Pleistocene interchange. New Guinea has a highly autonomous fauna, with almost no true temperate Australian or northern alpine elements in many groups (189). Oriental groups extending through New Guinea to the Solomons or Fiji, or groups concentrated in the Philippine-New Guinea area, are lacking in Australia or found there only in North Queensland (126, 189, 196 and others). Wilson (205, 206) demonstrates that in the case of the ants, New Guinea has mixed Indomalayan, Australian and endemic elements, with none predominating, and that the New Caledonia fauna is close to that of Australia. This more nearly approaches the situation in birds than in the above cited examples.

New Guinea has been placed in the Australian Region by many (e.g., 38, 200), in the Oriental Region (72, 73, 189), as a separate Papuan Region more closely related to Oriental than Australian (49), and as a zone of equal mixture of the Oriental and Australian regions (42). Hennig (80) refers to the Oriental-Papuan Region.

Samoa's insect fauna is reviewed by Buxton (27), who shows its oceanic, disharmonic fauna, related to continental areas to the west through Fiji. Kaszab (97) calls Fiji continental, but I (72) feel that its disharmonic fauna is oceanic. Esaki (50) considered Palau, Yap and Fiji to be continental islands and part of the Melanesian Subregion. I (72) have treated all the islands north and east of the Solomons, to Hawaii and Easter Island, as Polynesian and oceanic, placing Hawaii and New Caledonia in special subcategories of their own. Many workers have also considered these islands primarily Oriental in their relationships, while apparently leaving New Guinea, the source of much of the fauna, in the Australian Region. Zimmerman (208, 209) treats the faunae of southeastern Polynesia and Hawaii, and Gressitt (70, 72), Micronesia and Pacific islands in general. Lord Howe Island is oceanic and has mixed elements, many of them probably derived from the ancient Inner Melanesian island arc. Lord Howe's fauna is discussed by Paramonov (149).

Australian.—Riek (162) presents some information on Australian fossil insects supplementary to Tillyard's extensive work, and sheds some light on past climatic conditions and faunal changes. When the northeastern part of Queensland is excluded as part of the Oriental Region, the insect fauna of Australia stands out in most groups as extremely distinct from other regions, except for moderate recent interchange with New Guinea and some archaic groups shared with the other southern continents.

In many respects the New Zealand fauna is quite distinct from that of Australia, with little recent interchange. Salmon (171) shows how the connection between Australia and New Zealand must have been a northern one, and never direct, and Ross (168) demonstrates immigration to New Zealand via the Inner Melanesian island arc, from New Guinea through New Caledonia. In treating the insect fauna of the subantarctic islands south of New Zealand, Hudson *et al.* (87) assume that Antarctica was connected to Patagonia and New Zealand. It may have been that Antarctica and the intervening islands were once larger, as well as more temperate, but that insects were exchanged by air dispersal over narrower sea barriers, which were sufficient to prevent migration of land mammals. Lane (107) does not require an antarctic connection.

Leclercq (109) suggests a migration route, not necessarily continuous land. He discusses the temperature of the Bering bridge, and the possibility of ancestors having been more temperature-tolerant than descendants. Malaise (123) hypothecates a land bridge across the South Pacific from New Guinea to South America to explain some relationships found in the Malay area, New Guinea, and South America, but not in Australia. More likely, however, these crossed over the Bering bridge. Malloch (124), is somewhat skeptical of a southern connection, indicating that if it existed, it must have been before the evolution of calyptrate Diptera. Mackerras (120) also discusses southern relationships from the standpoint of Diptera, without reaching conclusions as to the mode of dispersal.

DISTRIBUTION OF INSECT GROUPS

Collembola.—Salmon (171) discusses dispersal factors in Collembola, showing the New Zealand fauna to demonstrate northern connections with Asia and Australia, but possibly also a source of Antarctic fauna, though he disfavors the idea of a major Antarctic continent or Gondwanaland. He suggests a northern origin for the order.

Ephemeroptera.—Edmunds (44) discusses the very close relations between Australia, New Zealand, and southern South America, with four subfamilies, each with one or more representatives in each of these three areas.

Odonata.—Frazer (60) treats relationships of part of the Ethiopian fauna. Laidlaw (105) shows that the Ceylon species are 57 per cent lowland Oriental or Paleotropical, 18 per cent related to Indian species, but differentiated through isolation. The remainder are related to forms in Burma and Malay, carried by monsoon winds, or spread in Pleistocene times when climate was different along coasts of the Bay of Bengal. Lieftinck (112) discusses the replacement of races among two sympatric species showing differing abilities to overcome various barriers, the younger species jumping over niches of the older.

Plecoptera.—Some notes on world distribution of Plecoptera are given by Ricker (161), who shows that some of the primitive groups are southern. The distribution of the European *Isoperla* are treated by Illies (89) in terms of evolution and ecology.

Orthoptera.—The distribution of the Grylloblattidae, a Holarctic, or Amphiberingian, group has been treated by Gurney (75), who shows that both species and genera are very limited in range. For the Mantodea, Beier (6) states that it is a tropical group, with one endemic subfamily in Australia, and the Neotropical fauna very distinct from that of the Old World. Ragge (156) discusses the spread of some tettigoniid genera through South Asia, into Indonesia and the Philippines. Rhen (158) cites North America as area of origin of some groups of acridiids.

Isoptera.—Termite zoogeography has been admirably worked out by Emerson (48, 49) who shows that the distribution of this old group, which has several cosmotropical genera, can be explained without reference to continental drift or land bridges except between adjacent areas such as the Bering Straits. He shows that Australia was isolated from Malaya at the end of the Mesozoic, before the subtropical Bering migration route from Malaya to South America was cut off, that the Oriental Region was a general area of exchange between most of the other regions, and that exchange between North and South America took place before early Eocene and after late Pliocene.

Psocoptera.—Gurney (74) and Mockford and Gurney (137) have discussed psocids common to Europe and North America, stressing the role of air currents in the distribution of these insects.

Thysanoptera.—In analyzing the distribution of thrips of east central Europe, Oettingen (145) shows that many are steppe species, some prairie species, fewer are forest species, a few are limited to specific hosts, and quite a number are of Palearctic or Holarctic distribution. Stannard (183) shows that the thrips fauna of the prairie peninsula in midwestern United States differs from that of the Great Plains and that this is based on poor ground drainage as a result of glacial deposit.

Hemiptera.—Zoogeography of Homoptera has been discussed by Metcalf (134). Fennah (54), in treating Micronesian Fulgoroidea, shows that the group entered the area mainly from the west through Palau, but also in the east from the Solomons, and stresses the need for host and other data to determine why some groups repeatedly colonize islands and others fail to. Evans (51) discusses the evolution and spread of the different groups of Jassoidea for the world on the basis of continental drift. The Psyllidae of the Australian Region are treated by Harrison (78), who cites several waves of immigration, including Tertiary influx from Malaya. Tuthill & Taylor (190) revise some of this work. For the scale genus *Kermes*, Balachowsky (4) shows that all 40 species are Holarctic and most of them are on oaks, often limited to one species or species-group of host.

For Heteroptera, the aquatic fauna of Syria and Iran is indicated as predominantly Palearctic, by Brown (23), with more Eurosiberian elements than Mediterranean and Sahara-Sind elements combined, and the constitution similar to that of Turkey except for a slight Ethiopian intrusion. Jordan (96) considers Heteroptera (except Corixidae and Miridae) good zoogeographical indicators because of their weak flight and their habitats.

Trichoptera.—Several very valuable discussions of caddisfly dispersal and evolution are presented by Ross (165 to 168) and Ross and King (169, 170). For *Atropsyche* (170) it is shown that the most primitive species occurs in the Mexican Plateau (and this is probably the area of origin), but that it arose from an Eurasian ancestor reaching Central America in late Cretaceous, becoming segregated into North and South American segments which were separated during the Eocene, the North American segment being *Atopsyche*. Later connections of North and South America permitted two-way crossing of species groups, some of which developed from immigrants from North to South America. In treating three families of cool-adapted caddisflies, Ross (168) shows that they are primarily Holarctic, but occur elsewhere in mountains and in temperate southern areas, only one group in each family becoming warm-adapted. He shows that there are sufficient fossils and enough survival to trace evolution and spread. He ascribes major dispersal to the

Bering bridge and finds no indication of dispersal between Australia and South America, except in one group where another explanation proves just as satisfactory.

Lepidoptera.—Considerable discussion of geographic subspeciation in Lepidoptera is presented by Remington *et al.* (160). Distribution of Greenland Lepidoptera is treated by de Lesse (111), who shows that of 36 species, 22 are Holarctic, six in North America but not in Europe, two in Europe but not in North America, and six endemic. Brachypterous jumping flightless moths of islands south of New Zealand are treated by Hudson *et al.* (87) and Salmon & Bradley (172), although fully winged endemic species are also present. The microlepidoptera of central New Guinea are treated by Diakonoff (42), who states that the faunae of neighboring regions are too little known to make satisfactory comparisons, but the fauna seems to represent the result of somewhat equal competition between Australian and Oriental elements. In the pyralids, Box (14) discusses changes in distribution relating to changes in hosts, as from grasses to cane, among others, and the effect on native parasitic wasps. For the Nymphaulinae, Lange (108) analyzes the world distribution, showing that the Australian and Oriental Regions are richest, the group having a tropical origin, with few adapted to cold conditions. For Kashmir agrotids, Boursin (13) indicates four elements: (*a*) West China-Himalayan, (*b*) suberemic Eurosiberian, (*c*) endemic (possibly relicts of Pamir fauna), and (*d*) subtropical Oriental. Spreading back and forth of lines of Saturniidae between Asia and North America is discussed by Michener (135). The larger moths of Rennell Island are shown by Fletcher (55) to have come largely from the Louisiades, secondarily from the Solomons or Bismarcks.

The ecological zoning of butterflies in Bolivia is treated by Förster (58). Distribution of the *Euploea* butterflies on Pacific islands is discussed in detail by Carpenter (29). He indicates general agreement with Mayr's conclusions for the birds of the area, but states that relations between species in the Moluccas and Solomons proves continental drift, but this can be countered by evidence of former more extensive land area to the immediate north of New Guinea. It can apparently be inferred that the Australian species are recent Pleistocene immigrants. Hoffmeyer (83) shows that the Danish macrolepidoptera entered from the east during the past 10–12,000 years. Mexican and Antillean Papilionoidea are treated by Comstock & Huntington (32). The arctic-alpine North American *Erebia* are discussed by Ehrlich (47), particularly as to barriers to dispersal. The distribution of arctic and subarctic butterflies is considered by Freeman (62). Oriental elements in eastern Palearctic butterfly distribution are discussed by Shirozu (180).

Diptera.—Mackerras (120) gives an excellent discussion of the zoogeography of Diptera, mainly working from the standpoint of the Australian fauna. Séguy (178) presents a general review of the world distribution. He recognizes a Malagasy Region and separates Oriental and Australian between the Moluccas and New Guinea. World distribution is also treated by

Hardy (77), who shows that many families are primarily tropical, but that the Apioceridae, Pelecorhynchinae, Ceratomerinae groups of Leptidae and Chiromyzidae are found primarily in Australia, Tasmania, New Zealand, southern South America and South Africa (all with larvae in swamps or damp soil), and relates this distribution to continental drift. Hennig (80) treats Diptera distribution as divided into two types, Holarctic and southern, stating that they show that existence of Gondwanaland until Triassic explains elements in common between Africa, South America and Australia, but that there were also upper Cretaceous and older Tertiary connections between Africa and South America.

The world distribution of Culicidae is tabulated by Lane (107) who shows that the Neotropical and Australian Regions are richest, the former demonstrating connection only with Nearctic and the latter only with Oriental, with Nearctic and Palearctic not very distinct. He states that haematophagia is not related to dispersal. Edwards (45) and Mattingly (129) outline African mosquito distribution. Edwards shows that the Ethiopian mosquitoes have much in common with those of the Oriental Region as far as genera are concerned, although more species are possessed in common with the Palearctic Region. There is little in common with the Neotropical Region except cosmopolitan genera. Mattingly classifies 17 districts in six provinces of two subregions, mainly following Chapin's system for birds. Mattingly and Knight (130) treat Arabian mosquitoes showing that the mosquito fauna of Arabia corresponds with that of the birds, in that the southern portion is Ethiopian and the northern is Palearctic, with a narrow strip of Oriental Region on the opposite coast of Iran, beyond which is Palearctic again. Iyengar (90) treats distribution of South Pacific Culicidae, dividing the islands into northern (Micronesia), eastern (Samoa, Tonga, Ellice, southeastern Polynesia), intermediate (Fiji, New Hebrides, New Caledonia), and western (New Guinea, Solomons) areas. The distribution of South Pacific species from the ecological standpoint is treated in detail by Laird (106), who points out that *Anopheles*, which is not found south and east of Aneityum, New Hebrides, could establish in Fiji and Samoa, but not in New Caledonia. Australasian *Anopheles* distribution is treated by Lee & Woodhill (110). For Micronesian mosquitoes, Bohart (12) indicates 62 per cent species endemism, no endemic genera, and relationships dominantly Oriental proper and secondarily Papuan. Belkin (8) treats southwest Pacific mosquitoes. Alaskan mosquito distribution is referred to by Frohne (63) who emphasizes the short season, cold tolerance, habitats, and life cycle modifications of these insects.

The Ethiopian Simuliidae, according to Freeman & de Meillon (61) comprise a distinct fauna, which is controlled by available habitats, and consists of an east and west part, with Madagascar separate but with links with East Africa, vague links with Australia, but none with the Orient. Nearctic simuliid patterns were studied by Shewell (179) and Alaska ecology and distribution by Sommerman *et al.* (182). In discussing "Australasian"

Phlebotomus, Fairchild (53) points out the relative lack of diversity as compared with the Neotropical representation, and also mentions that so far no members of the genus have been found in Chile. The occurrence of chironomids in old lakes of southern Sweden is considered in detail by Brundin (26). The history and spread of *Culicoides* is reviewed by Khalaf (98) who feels that many groups evolved in the Oriental Region, or farther north when climate was warmer.

The history of the spread of tsetse flies is treated by Evens (52) on the basis of Jeannel's Wegenerian patterns. He believes that they are of a possible Angara rather than Gondwana source, and shows that the pupal diapause indicates a cool-climate origin. In an excellent study of Tabanidae, Mackerras (121) treats history of distribution, mentioning Gondwana and Antarctic faunae, but not drift or bridges. He speaks of a southern distribution of primitive forms, and for specialized groups, of both a southern regional radiation and a northern radiation like that of Eutherian mammals. Oldroyd (146) gives a fine treatment of the Ethiopian distribution. Philip (154) discusses Mackerras' and Oldroyd's ideas in a generally favorable vein. For Tephritidae, Hering (81) shows that proportional representation of Tephritinae and Trypetinae changes somewhat between Indonesia and New Guinea. Drosophilid distribution is discussed by Patterson and Wheeler (151). Roback (164) attempted to correlate phylogeny and distribution of Sarcophaginae of the world, in connection with a Nearctic study.

Siphonaptera.—The northern Nearctic flea distribution, according to Holland (85), shows that not all species have the same range as their hosts, and that some of the Holarctic species are limited in the Nearctic to the part of the Alaska-Yukon area that was ice-free at the height of the Pleistocene.

Coleoptera.—For Carabidae, Darlington (35) has shown that selection for flightlessness is related to size of area and the reduced usefulness of wings on mountains and islands, and demonstrates similarities in these two types of environments. For the New Guinea Agonini, Darlington (37) shows that most of the genera are endemic but probably had an Oriental origin, besides those which are clearly Oriental or widespread. Britton (22) states that the tribe Broscini demonstrates a Cretaceous Palaeantarctic origin, and that the group reached South America by way of a southern land connection. From there it traveled to Africa across another bridge, but could not have reached Asia because the latter was separated from the southern areas from late Jurassic till late Tertiary. Ball (5) states that the Broscini distribution can prove nothing about former land connections, and that geological evidence is against a direct land connection between South America, Antarctica, New Zealand and Australia. The paussids, according to Darlington (36), are mainly tropical, poorly represented on islands, fairly young as a group and not pre-Jurassic. They were not distributed by continental drift as claimed by Jeannel, or by an Antarctic land bridge as claimed by Kolbe. Janssens (91) disputes some of Jeannel's conclusion on paussid distribution. Jeannel has used the Pselaphidae also in explaining distribution by continental drift

(94). Park (150) and Schuster & Marsh (175) treat ecological factors governing distribution and phylogeny of Pselaphidae. For Australian gyrinids Brinck (20) feels the distribution offers no indication of migration between South America and Australia, as suggested by others, but, rather, old and recent exchanges with Asia. For South African gyrinids Brinck (21) indicates a purely Ethiopian fauna, with no connections to South America or Australia, and with endemic centers in the southwest and southeast, probably representing refuge areas in periods of drought.

For Erotylidae, Delkeskamp (40) shows that most species are in only one region. The Neotropical region is richest and most primitive, and the Madagascar fauna is Ethiopian. The Chinese Cassidinae demonstrate a filter-bridge barrier during the later Bering connections of New and Old World and correlation between evolution of the beetles and their host plants [Gressitt (69)]. Chinese Cerambycidae (68) demonstrate the mixing of Palearctic and Oriental elements, and the striking contrast between the fauna of the Philippines on one hand and Hainan and Taiwan on the other. Micronesian cerambycids (71) show a disharmonic fauna lacking many of the dominant tribes in the Philippines and New Guinea, and possessing largely oceanic genera including some flightless endemic genera and species. Distribution of North American Cerambycidae is treated by Linsley (118). The Balearic Chrysomelidae [Jolivet (95)] shows the islands to be continental and to demonstrate Miocene connections with Corsica and Sardinia or Sicily, and Pliocene connection with Spain. Tenebrionidae of the Thar Desert of North India are shown to be related to the Baluchistan and southern Persian faunae by Kulzer (104). The weevil tribe Celeuthetini [Marshall (126)] shows a very distinct Philippine-Papuan distribution, spreading into Polynesia. The Cossoninae are described by Peyerimhoff (153) as well developed on oceanic islands, but not on Madagascar.

Hymenoptera.—Distribution and history of Tenthredinoidea is treated by Malaise (122), who invokes land bridges, but not continental drift. Orussid distribution is treated by Benson (9). The origin of *Cynips* in Mexico is shown by Kinsey (99), with two lines, one of which spread to Eurasia, probably in the Oligocene. Stohl (184) in outlining distribution of Gasteruptionidae, states that some forms of primitive appearance may actually be more advanced physiologically. Brown (25) discusses the stages of tramping of ants through human agency, pointing out that most tramp ants seem to be of African origin, and some of them have become dominant on islands, as in the Indian Ocean, through lack of competition, and were spread thence to other areas. Brown (24) feels that the distribution of the Dacetini can be accounted for by separate waves of dispersal centered in the Old World tropics, each major wave representing a genus or species-group in the present classification. Each genus or group tends to replace the preceding one from the central area outward. Some of the older waves are now represented only by specialized relicts surviving in peripheral areas or in particularly favorable, but limited, habitats. For the Scoliidae, Betrem (11) indicates waves of southward migrations, prompted by the ice ages, from both India and China into the Malay area, and Bradley (15) indicates primitive ancestors in Palearctic Africa and in Madagascar, and also a tendency for wing coloration characteristic of different parts of Africa among many species. The distribution of Zethini and Eumenini in the eastern Mediterranean area is compared with that of other groups by Giordani Soika (64) and the elements shown to be Mediterranean, Saharo-Sind, endemic Palestine, Irano-Turanian, Sahelo-Sudan and Eurosiberian, in order of decreasing representation. For the Crabronidae, Leclercq (109) indicates a definite Holarctic fauna, and clear Australian-South American relationships. Moczar (138) treats faunal elements of Carpathian pompilids. Some melittid distribution is treated by Popov (155). Malyshev (125) and Michener (136) treat distribution of bees. Maa (119) shows that the honeybees are eurythermous and that their primary distribution center is the Malaysian Subregion.

Arachnida.—Opiliones of Chiapas, Mexico, show unclear patterns but roughly fit in three zones, north bulge lowlands, high central mountains, and Pacific slope lowlands, [Goodnight & Goodnight (67)]. Hoogstraal (86) treats tick distribution in the Malagasy area. Wharton & Fuller (203) show that trombiculids are best represented in Australia, southern Asia, Africa and adjacent islands. Some genera are widespread, and some may have originated outside the above area.

Myriapoda.—Some data on Newfoundland myriapods is presented by Palmén (148).

LITERATURE CITED

1. Ander, K., *Opuscula Entomol.*, **14,** 89–104 (1949)
2. Andrewartha, H. G., and Birch, L. C., *The Distribution and Abundance of Animals* (University of Chicago Press, Chicago, Ill., 782 pp., 1954)
3. Balachowsky, A., *Mem. Soc. Biogeographie,* **8,** 209–18 (1946)
4. Balachowsky, A., *Proc. 8th Intern. Congr. Entomol.*, 342–46 (1950)
5. Ball, G. E., *Coleopterists' Bull.*, **10,** 33–52 (1956)
6. Beier, M., *Verhandl. VII Intern. Congr. Entomol.*, **1,** 5–15 (1939)
7. Beirne, B. P., *The Origin and History of the British Fauna* (Methuen & Co., Ltd., London, England, 164 pp., 1952)
8. Belkin, J. N., *Pacific Sci.*, **9,** 221–46 (1955)
9. Benson, R. B., *Proc. Roy. Entomol. Soc. London,* [B]**24,** 13–23 (1955)
10. Berland, L., *Ann. soc. entomol. France,* **104,** 73–96 (1935)
11. Betrem, J. G., *Proc. 8th Intern. Congr. Entomol.*, 347–50 (1950)
12. Bohart, R. M., *Ins. Micronesia (Bishop Museum),* **12,** 1–85 (1957)
13. Boursin, C., *Bull. soc. Fouad. I entomol.*, **38,** 81–100 (1954)
14. Box, H. E., *Proc. 8th Intern. Congr. Entomol.*, 351–57 (1950)
15. Bradley, J. C., *Proc. 8th Intern. Congr. Entomol.*, 358–60 (1950)
16. Brehm, V., *Zoogeographica,* **1,** 54–62 (1932)
17. Brinck, P., *Avhandl. Norske Videnskaps-Akad. Oslo,* 3–23 (1945)
18. Brinck, P., *Tristan da Cunha,* **17,** 1–22 (1948)
19. Brinck, P., *Proc. 8th Intern. Congr. Entomol.*, 361–64 (1950)
20. Brinck, P., *Lunds Univ. Arksskr. N. F. Avd.*, **2,** 49, 1–6 (1952)

21. Brinck, P., *A. Afr. Animal Life, Uppsala,* **1,** 329–518 (1955)
22. Britton, E. B., *Trans. Roy. Soc. New Zealand,* **77,** 533–81 (1949)
23. Brown, E. S., *Ann. Mag. Nat. Hist.,* **6,** 579–600 (1953)
24. Brown, W. L., Jr., *Trans. Am. Entomol. Soc.,* **75,** 43–51, 83–96 (1949)
25. Brown, W. L., Jr., *Bull. Museum Comp. Zool.,* **112,** 3–34 (1954)
26. Brundin, L., *Rept. Inst. Freshwater Res. Drottningholm, Lund.,* **30,** 914 pp. (1949)
27. Buxton, P. A., *Insects of Samoa . . . (British Mus. Nat. Hist.),* **9,** 33–104 (1935)
28. Caradja, A., *Acad. Romana, Mem. Sect. Stünt., Bucharest* (ser. 3), **3,** 257–383 (1925)
29. Carpenter, G. D. H., *Trans. Zool. Soc. London,* **28,** 1–84 (1953)
30. Chopard, L., *Mem. Soc. Biogeographie,* **8,** 199–208 (1946)
31. Cleu, H., *Ann. soc. entomol. France,* **122,** 1–74 (1953)
32. Comstock, W. P., and Huntington, E. I., *Ann. Inst. Biol. Mexico,* **20,** 385–91 (1950)
33. Daniel, F., *Z. Wiener Entomol. Ges.,* **39,** 51–78 (1954)
34. Darlington, P. J., Jr., *Quart. Rev. Biol.,* **13,** 274–300 (1938)
35. Darlington, P. J., Jr., *Ecol. Monographs,* **13,** 37–61 (1943)
36. Darlington, P. J., Jr., *Trans. Am. Entomol. Soc.,* **76,** 47–142 (1950)
37. Darlington, P. J., Jr., *Bull. Museum Comp. Zool.,* **107,** 89–252 (1952)
38. Darlington, P. J., Jr., *Zoogeography* (John Wiley & Sons, Inc., New York, N. Y., 672 pp., 1957)
39. Delamare Deboutteville, C., and Paulian, R., *Mem. Inst. Sci. Madagascar,* **8,** 1–10 (1953)
40. Delkeskamp, K., *Entomol. Blätter,* 45–46, 131–44 (1951)
41. Demoulin, G., *Mem. soc. roy. entomol. Belg.,* **27,** 176–83 (1955)
42. Diakonoff, A., *Verhandl. Koninkl. Ned. Akad. Wetenschap. Afdel. Natuurk.,* [2]**50**(2), 1–210 (1955)
43. Dillon, L. S., *Science,* **123,** 167–76 (1956)
44. Edmunds, G. F., Jr., *Proc. Entomol. Soc. Wash.,* **59,** 245–46 (1957)
45. Edwards, F. W., *Mosquitoes of the Ethiopian Region* (British Mus. Nat. Hist.), **3,** 1–499 (1941)
46. Edwards, J. G., *Mazama,* 13–17 (1956)
47. Ehrlich, P. R., *Proc. 10th Intern. Congr. Entomol.* (In press)
48. Emerson, A. E., *Bull. Am. Museum Nat. Hist.,* **99,** 217–25 (1952)
49. Emerson, A. E., *Fieldiana, Zool.,* **37,** 465–521 (1955)
50. Esaki, T., *Proc. 8th Intern. Congr. Entomol.,* 373–79 (1950)
51. Evans, J. W., *Trans. Roy. Entomol. Soc. London,* **99,** 497–515 (1948)
52. Evens, F. M.-C., *Mem. inst. sci. natl. Belg.,* [2]**48,** 1–70 (1953)
53. Fairchild, G. B., *Proc. Linnean Soc. N. S. Wales,* **77,** 189–208 (1952)
54. Fennah, R. G., *Ins. Micronesia (Bishop Museum),* **6,** 39–211 (1956)
55. Fletcher, D. S., *Nat. Hist. Rennell. Isl., Brit. Solomon Isls., Copenhagen,* **2,** 31–66 (1957)
56. Flint, R. F., *Glacial Geology and the Pleistocene Epoch* (John Wiley & Sons, Inc., New York, N. Y., 589 pp., 1947)
57. Florov, D. N., *Zool. Zhur.,* **34,** 789–99 (1955)
58. Forster, W., *Proc. 10th Intern. Congr. Entomol.* (In press)
59. Franz, H., *Trans. 9th Intern. Congr. Entomol.,* **1,** 547–52 (1952)
60. Fraser, F. C., *Ann. Mus. Congo, Tervuren, Zool.,* **1,** 368–70 (1954)
61. Freeman, P., and De Meillon, B., *Simuliidae of the Ethiopian Region* (British Museum Natural History, 224 pp., 1953)

62. Freeman, T. N., *Proc. 10th Intern. Congr. Entomol.* (In press)
63. Frohne, W. C., *Mosquito News*, **14**, 10–13 (1954)
64. Giordani Soika, A., *Boll. Soc. Veneziana Storia Nat. e del Museo Civ. S. N. Venezia*, **6**, 5–62 (1952)
65. Gislen, T., *Biol. Rev. Cambridge Phil. Soc.*, **23**, 109–26 (1948)
66. Glick, P. A., *U. S. Dept. Agr., Tech. Bull. 673*, 1–150 (1939)
67. Goodnight, C. J., and Goodnight, M. L., *Am. Museum Novitates, No. 1610*, 1–81 (1953)
68. Gressitt, J. L., *Longicornia (Paris)*, **2**, 1–667 (1951)
69. Gressitt, J. L., *Proc. Calif. Acad. Sci.*, **27**, 433–592 (1952)
70. Gressitt, J. L., *Ins. Micronesia (Bishop Museum)*, **1**, 1–257 (1954)
71. Gressitt, J. L., *Ins. Micronesia (Bishop Museum)*, **17**, 61–183 (1956)
72. Gressitt, J. L. *Syst. Zool.*, **5**, 11–32, 47 (1956)
73. Gressitt, J. L., *Proc. 10th Intern. Congr. Entomol.* (In press)
74. Gurney, A. B., *J. Wash. Acad. Sci.*, **39**, 56–65 (1949)
75. Gurney, A. B., *J. Wash. Acad. Sci.*, **43**, 325–32 (1953)
76. Hamilton, E. L., *Mem. Geol. Soc. Am.*, **64**, 1–97 (1956)
77. Hardy, G. H., *Entomologists' Monthly Mag.*, **87**, 99–102 (1951)
78. Harrison, G. H., *Ann. Mag. Nat. Hist.*, **XII**, 641–60 (1949)
79. Heberdey, R. F., *Verhandl. VII Intern. Congr. Entomol.*, **1**, 151–64 (1939)
80. Hennig, W., *Grundzüge einer Theorie der phylogenetischen Systematik* (Deutsche Zentralverlag, Berlin, Germany, 370 pp., 1950)
81. Hering, E. M., *Treubia*, **21**, 263–90, 507–24 (1952)
82. Hesse, R., Allee, W. C., and Schmidt, K. P., *Ecological Animal Geography*, 2nd edition (John Wiley & Sons, Inc., New York, N. Y.; Chapman and Hall, London, 715 pp., 1951)
83. Hoffmeyer, S., *Entomologist*, **83**, 193–98 (1950)
84. Holdhaus, K., *Zoogeographica*, **1**, 1–53 (1932)
85. Holland, G. P., *Proc. 10th Intern. Congr. Entomol.* (In press)
86. Hoogstraal, H., *Bull. Museum Comp. Zool., Harvard*, **111**, 37–113 (1953)
87. Hudson, G. V., Broun, T., *et al.*, *Subantarctic Islands of New Zealand*, **1**, 48–181 (1909)
88. Iablokoff, A. K., *Ann. soc. entomol. France*, **118**, 95–112 (1951)
89. Illies, J., *Beitr. Entomol.*, **2**, 369–424 (1952)
90. Iyengar, M. O. T., *S. Pacific Comm. Tech. Paper*, **86**, 1–47 (1955)
91. Janssens, E., *Inst. roy. sci. nat. Belg. Bull.*, **26**(51), 1–19 (1950)
92. Janssens, E., *Inst. roy. sci. Nat. Belg. Bull.*, **28**(51), 1–21 (1952)
93. Jeannel, R., *La Gênèse des Faunes Terrestres* (Presses Univ. de France, Paris, France, 513 pp., 1942)
94. Jeannel, R., *Trans. 9th Intern. Congr. Entomol.*, **2**, 154–56 (1953)
95. Jolivet, P., *Misc. Entomol.*, **48**, 102–5 (1953)
96. Jordan, K. H. C., *Zool. Anz.*, **147**, 79–84 (1951)
97. Kaszab, Z., *Proc. Hawaiian Entomol. Soc.*, **15**, 423–563 (1955)
98. Khalaf, K., *Ann. Entomol. Soc. Am.*, **47**, 34–51 (1954)
99. Kinsey, A. C., *Indiana Univ. Publ., Sci.* [4], 1–334 (1936)
100. Kiriakoff, S. G., *Bull. ann. soc. entomol. Belg.*, **89**, 126–34 (1953)
101. Kiriakoff, S. G., *Bull. ann. soc. entomol. Belg.*, **90**, 185–98 (1954)
102. Klots, A. B., *Proc. 10th Intern. Congr. Entomol.* (In press)
103. Kruseman, G., *Proc. 8th Intern. Congr. Entomol.*, 427–28 (1950)
104. Kulzer, H., *Entomol. Arb. Mus. Frey*, **7**, 635–53 (1956)

105. Laidlaw, F. F., *Entomol. News*, **62,** 77–83 (1951)
106. Laird, M., *Roy. Soc. New Zealand, Bull.*, **6,** 1–213 (1956)
107. Lane, J., *Arquiv. Museu Paranaense Curitiba*, **7,** 247–64 (1949)
108. Lange, W. H., Jr., *Wasmann J. Biol.*, **14,** 59–144 (1956)
109. Leclercq, J., *Trans. 9th Intern. Congr. Entomol.*, **1,** 576–82 (1952)
110. Lee, D. J., and Woodhill, A. R., *Univ. Sydney, Publ. Zool.*, **2,** 1–209 (1944)
111. Lesse, H. de, *Ann. Soc. Entomol. France*, **119,** 97–116 (1952)
112. Lieftinck, M. A., *Proc. 7th Pacific Sci. Congr., New Zealand*, 75–82 (1953)
113. Lindberg, H., *Proc. 8th Intern. Congr. Entomol.*, 429–33 (1950)
114. Lindberg, H., *Proc. 10th Intern. Congr. Entomol.* (In press)
115. Lindroth, C. H., *Göteborgs Kgl. Vetenskaps.-Vitterhets-Sämhall. Handl.*, [B]**4**(3), 1–911 (1949); see also *Ecology*, **34,** 657–66 (1953); and *Trans. 9th Intern. Congr. Entomol.*, **2,** 145–53 (1953)
116. Lindroth, C. H., *Faunal Relations between North America and Europe* (John Wiley & Sons, Inc., New York, N. Y., 344 pp., 1957)
117. Lindroth, C. H., *Proc. 10th Intern. Congr. Entomol., Montreal, 1956* (In press)
118. Linsley, E. G., *Proc. New England Zool. Club*, **21,** 17–42 (1942)
119. Maa, T. (T.C.), *Treubia*, **21,** 525–640 (1953)
120. Mackerras, I. M., *Australian J. Sci.*, **12,** 157–61 (1950)
121. Mackerras, I. M., *Australian J. Zool.*, **2,** 431–54 (1954); **3,** 439–511, 583–633 (1955)
122. Malaise, R., *Opuscula Entomol.*, Suppl. **4,** 288 pp. (1945)
123. Malaise, R., *Proc. 8th Intern. Congr. Entomol.*, 434–37 (1950)
124. Malloch, J. R., *Diptera of Patagonia and South Chile* (British Museum), **7,** 171–346 (1934)
125. Malyshev, S. I., *Eos (Madrid)*, **11,** 201–309 (1936)
126. Marshall, G. A. K., *The Otiorrhynchine Curculionidae of the tribe Celeuthetini (Col.)* (British Museum of Natural History, London, England, 134 pp., 1956)
127. Mason, W. R. M., *Proc. 10th Intern. Congr. Entomol.* (In press)
128. Matthew, W. D., *N. Y. Acad. Sci., Spec. Publ.*, **1,** 223 pp. (1939)
129. Mattingly, P. F., *Proc. Linnean Soc. London*, **165,** 49–61 (1954)
130. Mattingly, P. F., and Knight, K. L., *Bull. Brit. Museum Nat. Hist. Entomol.*, **4,** 91–141 (1956)
131. Mayr, E., *Systematics and the Origin of Species* (Columbia University Press, New York, N. Y., 513 pp., 1942)
132. Mayr, E., *Quart. Rev. Biol.*, **19,** 1–14 (1944)
133. Mayr, E., *et al.*, *Bull. Am. Museum Nat. Hist.*, **99,** 81–258 (1952)
134. Metcalf, Z. P., *Compt. rend. 13ᵉ Congr. Intern. Zool. Paris, 1948*, 538–44 (1949)
135. Michener, C. D., *Bull. Am. Museum Nat. Hist.*, **98,** 339–501 (1952)
136. Michener, C. D., *Bull. Am. Museum Nat. Hist.*, **104,** 1–176 (1954)
137. Mockford, E. L., and Gurney, A. B., *J. Wash. Acad. Sci.*, **46,** 353–68 (1956)
138. Moczar, L., *Proc. 8th Intern. Congr. Entomol.*, 438–46 (1950)
139. Munroe, E. G., *J. N. Y. Entomol. Soc.*, **58,** 211–40 (1950)
140. Munroe, E. G., *Can. Entomologist* (In press)
141. Munroe, E. G., *Science* (In press)
142. Munroe, E. G., *Proc. 10th Intern. Congr. Entomol.* (In press)
143. Newbegin, M. I., *Plant and Animal Geography*, 3rd ed. (Methuen & Co., Ltd., London; E. P. Dutton & Co., Inc., New York, 298 pp., 1950)
144. Oberberger, J., *Proc. 10th Intern. Congr. Entomol.* (In press)

145. Oettingen, H. von, *Beitr. Entomol.*, **1**, 44–59 (1951)
146. Oldroyd, H., *Horse-flies of the Ethiopian Region* (British Museum Nat. Hist., vol. 3, 489 pp., 1957)
147. Palmén, E., *Proc. 8th Intern. Congr. Entomol.*, 450–53 (1950)
148. Palmén, E., *Proc. 10th Intern. Congr. Entomol.* (In press)
149. Paramonov, S. J., *Pacific Sci.*, **12** (In press)
150. Park, O., *Bull. Chicago Acad. Sci.*, **9**, 249–72 (1953)
151. Patterson, J. T., and Wheeler, M. R., *Univ. Texas Publ., No. 4920*, 207–33 (1949)
152. Paulian, R., *Mem. Inst. Sci. Madagascar*, [E]**1**, 1–22 (1952); see also *Proc. 10th Intern. Congr. Entomol.* (In press)
153. Peyerimhoff, P. de, *Proc. 8th Intern. Congr. Entomol.*, 460–74 (1950)
154. Philip, C. B., *Ann. Entomol. Soc. Am.*, **50**, 550–55(1957)
155. Popov, V. V., *Dokl. Akad. Nauk S.S.S.R.*, **101**, 569–72 (1955)
156. Ragge, D. R., *Proc. Zool. Soc. London*, **127**, 205–83 (1956)
157. Rehn, J. A. G., *Ecology*, **31**, 307–11 (1950)
158. Rehn, J. A. G., *Entomol. News*, **65**, 57–65 (1954)
159. Reiss, H., *Z. Wiener Entomol. Ges.*, **38**, 131–41 (1953)
160. Remington, C. L., Cary, M. M., Klots, A. B., Beirne, B. P., Munroe, E., and Grey, L. P., *Lepidopterists' News*, **5**, 17–35 (1951)
161. Ricker, W. E., *Proc. Indiana Acad. Sci.*, **59**, 197–209 (1950)
162. Riek, E. F., *Australian J. Zool.*, **3**, 654–91 (1955)
163. Ringuelet, R. A., *Notas Museo Eva Peron, Zool.*, **18**, 81–121 (1955)
164. Roback, S. S., *Illinois Biol. Monographs*, **23**(3–4), 1–181 (1954)
165. Ross, H. H., *Evolution*, **5**, 102–15 (1951)
166. Ross, H. H., *Proc. Calif. Acad. Sci.*, [4]**27**(3), 65–76 (1951)
167. Ross, H. H., *Evolution*, **7**, 145–58 (1953)
168. Ross, H. H., *Evolution and classification of the mountain caddisflies* (University of Illinois Press, Urbana, Ill., 213 pp., 1956)
169. Ross, H. H., and King, E. W., *De Acta Zoologica Lilloana*, **12**, 501–8 (1951)
170. Ross, H. H., and King, E. W., *Ann. Entomol. Soc. Am.*, **45**(2), 177–204 (1952)
171. Salmon, J. T., *Brit. Sci. News*, **2**(19), 196–98 (1949)
172. Salmon, J. T., and Bradley, J. D., *Rec. Dom. Mus., New Zealand*, **3**, 61–81 (1956)
173. Savile, D. B. O., *Am. Midland Naturalist*, **56**, 434–53 (1956)
174. Schilder, F. A., *Einführung in die Biotaxonomie* (*Formenkreislehre*) (Gustav Fischer, Jena, Germany, 162 pp., 1952)
175. Schuster, R. O., and Marsh, G. A., *Univ. Calif. Publ. Entomol.*, **11**(2), 117–58 (1956)
176. Schweiger, H., *Trans. 9th Intern. Congr. Entomol.*, **1**, 559–60 (1952)
177. Seevers, C. H., *Fieldiana, Zool.*, **40**, 1–334 (1957)
178. Séguy, E., *Encycl. Entomol. Paris*, [A]**26**, 609 pp. (1950)
179. Shewell, G. E., *Proc. 10th Intern. Congr. Entomol.* (In press)
180. Shirozu, T., *Matsumushi, Sapporo*, **2**, 1–8 (1947)
181. Simpson, G. G., *Evolution and geography* (Oregon State System of Higher Education, Eugene, 64 pp., 1953)
182. Sommerman, K. M., Sailer, R. I., and Esselbaugh, C. O., *Ecol. Monographs*, **25**, 345–85 (1955)
183. Stannard, L. J., *Proc. 10th Intern. Congr. Entomol.* (In press)

184. Stohl, G., *Ann. Hist. Nat. Museum Hungary*, **40,** 275–84 (1947)
185. Strenzke, K., Lesse, H. de, and Denis, J., *Expt. Polaires France*, **7,** 1–84 (1955)
186. Szent-Ivany, J., *Verhandl. VII Intern. Entomol. Congr.*, **1,** 432–36 (1939)
187. Theodor, O., *Rev. Fac. Sci. Univ. Istanbul*, [B]17(2), 107–19 (1952)
188. Thienemann, A., *Die Binnengewässer*, **18,** 1–809 (1950)
189. Toxopeus, L. J., *Proc. 8th Intern. Congr. Entomol., 1948*, 508–22 (1950)
190. Tuthill, L. D., and Taylor, K. L., *Australian J. Zool.*, **3,** 227–57 (1955)
191. Usinger, R. L., *et al.*, *Aquatic Insects of California* (University of California Press, Berkeley, Calif., 566 pp., 1956)
192. Uvarov, B. P., *Soc. Biogeographie, Mem.*, **6,** 231–73 (1938)
193. Uvarov, B. P., *Trans. 9th Intern. Congr. Entomol.*, **2,** 157–59 (1953)
194. Van Dyke, E. C., *Proc. 6th Pac. Sci. Congr.*, **4,** 255–68 (1939)
195. Van Dyke, E. C., *Calif. Acad. Sci., Occ. Papers*, **22,** 1–181 (1953)
196. van Regteren Altena, C. O., *Trans. 9th Intern. Congr. Entomol.*, **1,** 565–68 (1952)
197. Vibe, C., *Proc. XIV Intern. Congr. Zool.*, 126–27 (1956)
198. Viette, P., *Proc. 10th Intern. Congr. Entomol.* (In press)
199. Vinson, J., *Mauritius Inst. Bull., Port Louis*, **3,** 266–78 (1954)
200. Wallace, A. R., *Island Life* (The Macmillan Co., London, 522 pp., 1880)
201. Warnecke, G., *Proc. 10th Intern. Congr. Entomol.* (In press)
202. Wellington, W. G., *Can. Entomol.*, **77,** 7–15, 21–27, 44–48 (1945); see also *Ann. Rev. Entomol.*, **2,** 143–62 (1957)
203. Wharton, G. W., and Fuller, H. S., *Mem. Entomol. Soc. Wash.*, **4,** 1–185 (1952)
204. Williams, C. B., *Ann. Rev. Entomol.*, **2,** 163–80 (1957)
205. Wilson, E. O., *Bull. Mus. Comp. Zool., Harvard*, **116,** 355–86 (1957)
206. Wilson, E. O. (Personal communication, 1957)
207. Wirth, W. W., *Rev. Chilena Entomol.*, **2,** 87–104 (1952)
208. Zimmerman, E. C., *Am. Naturalist*, **76,** 280–307 (1942)
209. Zimmerman, E. C., *Insects of Hawaii* (Univ. Hawaii Press, Honolulu, T. H., 206 pp., 1948)