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ZOOGEOGRAPHY OF PACIFIC PSYCHODIDAE
(Diptera)

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Six genera of Psychodidae (moth flies and sand flies) will serve to illustrate current knowledge of the zoogeography of this family in the Pacific area. Two of these are unable to cross large water barriers and are dependent on land connections for their dispersals; the other four have colonized oceanic islands and have been able to cross expanses of open water.

PHLEBOTOMUS SAND FLIES

Sand flies are an ancient group of psychodids and their primitive characters indicate an early origin. Since fossils show that flies (the order Diptera) were well developed by the Jurassic period, it is reasonable to guess that the sand flies were present by that time, which was some 150 million years ago. It may also be assumed the group developed bloodsucking habits early in their history, since today the females of all known species feed in this manner. If this were so, reptiles, which appeared earlier than mammals and which are hosts of some of the present species, were probably the main vertebrate hosts of sand flies in that period.

In their movements over the face of the earth, sand flies apparently have been unable to cross very large water barriers. They are widely distributed throughout the tropics and rather continuously from India to Australia, but are not found on oceanic islands.

While a lack of suitable breeding sites or hosts could have prevented their colonization, I believe the physical barrier of water has been the chief obstacle to their oceanic dispersal. Such animals as bats, skinks and geckos are more widely distributed than sand flies and presumably could be suitable hosts. On high islands of the Pacific, there probably are adequate breeding sites. Furthermore, other bloodsucking insects as mosquitoes, biting midges and black flies have been quite successful in colonizing islands and finding hosts and breeding sites. While the evidence is by no means conclusive, I feel water barriers are the most likely limiting factor to sand fly dispersal and it is on this basis that the following assumptions are made. If this assumption proves wrong, then of course all other hypotheses of sand fly zoogeography proposed below will have to be recast.

The Papuan and Australian species of *Phlebotomus* probably originated in Asia and migrated eastward during the Mesozoic when there were more complete land connnections between Asia and Australia than now exist. The barriers that have prevented an exchange of mammals between Asia and Australia during the Cenozoic period probably prevented sand flies from passing through Indonesia during that time. If sand flies had to use land connections to migrate from Asia to New Guinea and Australia, they must have dispersed

during the Mesozoic when apparently there were more exposed land surfaces through Indonesia than in the Cenozoic. It is possible, therefore, that widespread distribution of *Phlebotomus* through the Oriental and Australian regions was achieved in the Mesozoic, more than 50 million years ago.

The Papuan, Australian and Asiatic species of *Phlebotomus* are not much different from each other. If the above assumptions are correct, species on either side of Wallace's Line have been separated from each other during most of the Cenozoic and their evolution has been remarkably slow and conservative. (The classic example of a slow rate of evolution is the brachiopod *Lingula*, which has undergone no perceptible change in the last 200 million years; Dobzhansky, 1941). However, there are only 6 Australian and 7 Papuan known species of *Phlebotomus* and, especially of the latter, many more must be undiscovered. These may either substantiate the Asiatic relationships or demonstrate an endemic sand fly fauna of which we now know nothing.

On the basis of the present evidence—such as it is—I hypothesize that *Phlebotomus* sand flies were well developed in Asia during the Mesozoic Era and spread from Asia to New Guinea and Australia over land connections that no longer exist. Asiatic and Papuan populations have been separated during most of the Cenozoic, but there has been little divergence above the species level and the evolution of this group has been exceedingly slow.

PERICOMA

Pericoma is another group whose dispersal is limited to land connections (as shown by their absence from oceanic islands today), but their history must have been quite unlike that of *Phlebotomus* with an entirely different distributional picture and evolutionary history. *Pericoma* is chiefly a temperate climate group. Few species are found in the tropics and none are known from the Oriental Region. The genus can be divided into three groups of related species. One in the northern hemisphere, one in Africa and the third in Australia, New Zealand and South America.

On morphological grounds, *Pericoma* appears younger than *Phlebotomus*, but also probably arose in the Mesozoic. Ancestors had to reach the continents now occupied at a time when land connections were available. There probably has been interchange between Europe and North America until recent times, so these faunas do not help in dating. Likewise, the African group could have migrated south from Europe (from which it probably originated) at almost any time, although the divergence of the African species suggests an early date. The South American and Australian species give us the best clues for dating. As mentioned above, they are related more closely to each other than to other members of *Pericoma* and seem to have come from a common source. It seems unlikely they migrated through the northern hemispheres to reach Australia and South America. To *Pericoma* apparently the tropics are a major barrier which have been penetrated infrequently and probably not at all in Asia. More likely they were able to spread directly from South America to Australia. Mammals show us that this could not have happened during the Cenozoic Era (Darlington, 1957), but there probably were land connections or an archipelago between Australia and South America via Antarctica during the Mesozoic. Mounting evidence supports such connections and I believe they were used by members of *Pericoma* living in the southern hemisphere at that time.

Pericoma may have originated somewhere in the Northern Hemisphere. One branch migrated to Africa and developed into the group now known as *Clytocerus*. Another migration led to South America. The South American *Pericoma* probably spread to Australia over Mesozoic land connections and hence the present species of South America, Australia and New Zealand appear as related groups and support the theory of earlier land connections between the southern continents.

TELMATOSCOPUS AND BRUNETTIA

The genera *Telmatoscopus* and *Brunettia* have essentially the same distributional pattern in the Pacific. They occur as far north as Japan, east to the Carolines and Samoa, south to New Zealand and Australia. (Not included is the tropicopolitan species, *T. albipunctatus*, which has been transported by man). There are 15 species or subspecies of these two genera on various Pacific islands. Progenitors gained access to the islands long enough ago to have evolved into distinct forms. This would date their entry into the Pacific before the advent of man and therefore they must have reached the islands through natural agencies.

Species of these genera appear to have originated in Asia or neighboring continental islands. With almost nothing known of the psychodids in the Philippines or New Guinea, it is impossible to speculate the most likely route by which Pacific species reached the islands or hypothesize more specifically on their origin.

PHILOSEPEDON

It would be difficult to determine the distribution of the genus *Philosepedon* under the existing classification. Some of the species belonging to the genus are assigned to the subgenus *Telmatoscopus* (*Minioceros*) and genera *Lepidopsychoda* and *Trichopsychoda*. When completed studies have been published, this awkward situation will be corrected.

Philosepedon occurs widely through Europe, North America, Asia and the Pacific. There are a few species each in Malaya, Borneo and Java and one widespread one in Borneo, the Marianas, Carolines, Samoa and Fiji. It is unlikely the genus extends south to Australia and New Zealand (psychodids there are quite well known), but certainly it must be in either or both the Philippines and New Guinea. Without some knowledge of those faunas, it is pointless to speculate about the dispersal and speciation of the genus in the Pacific.

PSYCHODA

Moth flies of the genus *Psychoda* are the smallest and most fragile members of the family. Yet they are the most numerous and most widely distributed psychodids. One species — *alternata* — is as cosmopolitan as any insect. I have seen it in many collections from Alaska to Africa and England to Hawaii. No other species of *Psychoda* equals this range, but many do occupy an extremely large area.

There are about 35 species of *Psychoda* in the Pacific islands. Three of these have such extensive distributions that I feel they have been spread in recent times by man. Many of the others have less extensive distributions and formerly I thought they too had been distributed by man in modern times and were of little zoogeographic significance.

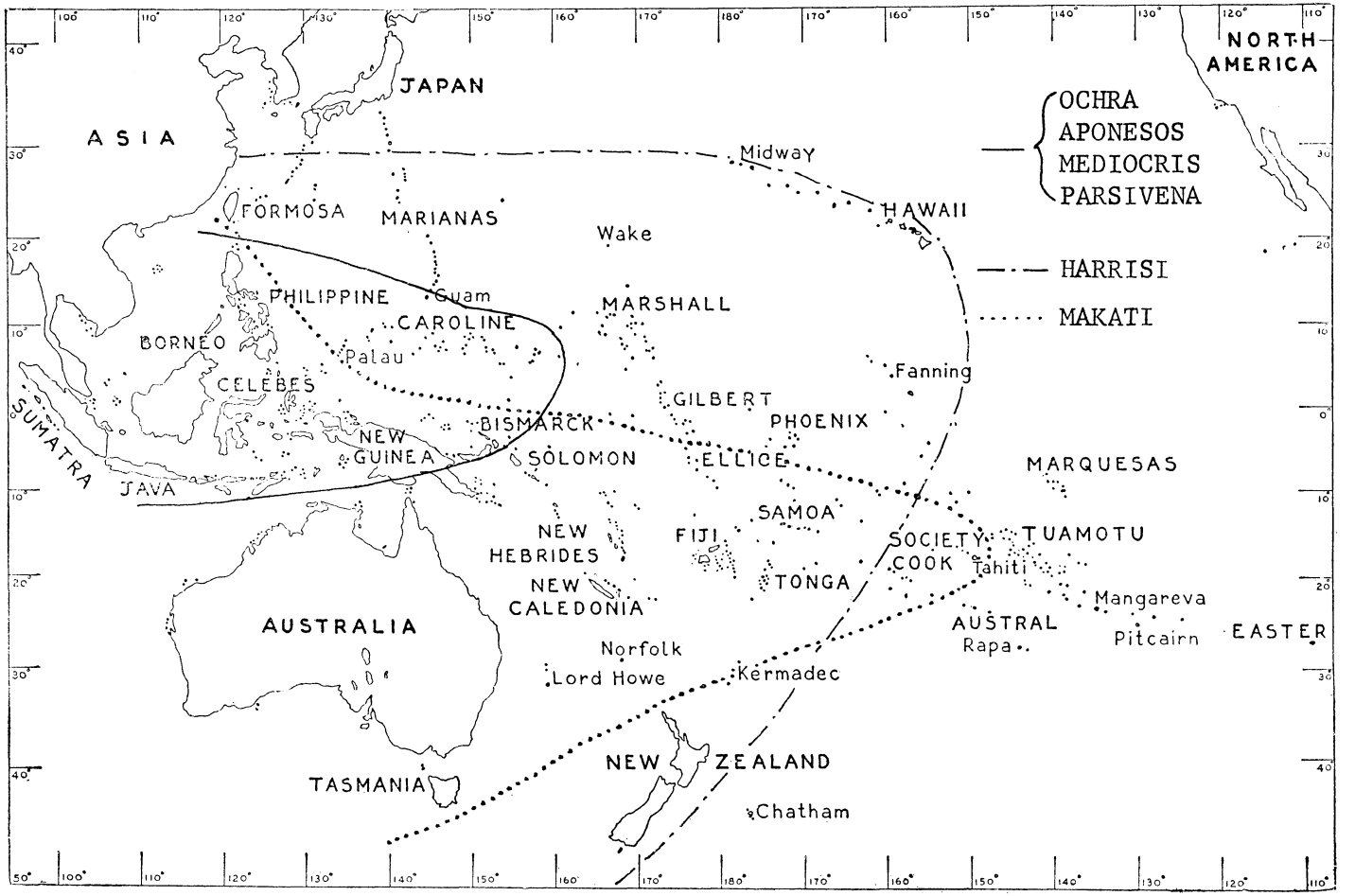

Fig. 1. Distribution of some species of *Psychoda* in the Pacific.

This may not be correct and some of these species may contribute to the zoogeography or at least human geography of the Pacific.

The most significant thing about the distribution of many of the Pacific *Psychoda* is that they extend from Asia varying distances into the Pacific and go no farther. The species of this category are found in more than one island group, are not endemic to limited areas and–of most interest–apparently do not occur on both sides of the Pacific. In this category are 17 species. The ranges of some are shown in figure 1. Fourteen of the species extend varying distances eastward from Asia but not as far as Hawaii. Only three reach Hawaii but do not go beyond. An additional two species are found in Hawaii and the U. S. mainland.

For the Pacific *Psychoda*, the evidence clearly shows the main dispersals were eastward from Asia across the Pacific. Whether this was largely through the Philippines or New Guinea is still unknown. Fewer migrations have proceeded westwards, but reached only as far as Hawaii from North America.

It does not seem likely that modern commercial transportation has been responsible for these dispersals. If the species concerned had been distributed by modern steamships or planes, it is unlikely they would have stopped in the mid-Pacific, for they seem adaptable enough to gain a foothold on the eastern borders of the Pacific. Enough is known of the U. S. and Central America psychodids to indicate that most of these common Oriental species do not extend that far east, although we must hold reservations about some of the species which eventually may be found there.

Trans-Pacific transportation could have been provided by pre-European surface craft. The furthest occurrence of the species concerned coincides with the islands occupied by Polynesians and Micronesians. The double-hulled and outrigger canoes which carried men on some of the world's greatest voyages also carried vegetable materials and soil, which may have been a suitable breeding medium for the psychodids. One argument of this mode of transport is that the species now present, with only one exception, are not differentiated into geographical segregates on the various islands. Specimens of the same species on close examination are the same in all parts of their range, which indicates they have not been isolated on the islands for a long period of time and have not had time to evolve special features. Only one species in Micronesia has segregated into different groups on different islands and this species must have had a pre-human establishment in Oceania.

Natural dispersal independent of man cannot be ruled out on the basis of what we now know. It seems unlikely psychodids would be dispersed on floating rafts or by birds, but their small size with low specific gravity would enhance their being carried long distances by wind or occasional storms running counter to the main east-west trade winds.

Whatever the method by which the widespread Pacific species of *Psychoda* reached their present areas, they most probably did so in rather recent times, but before or without the aid of modern transportation.

Aside from more details on distribution within the Pacific basin, our widest gap in knowledge of Pacific *Psychoda* is in the faunas of New Guinea and the Philippines. About a dozen species are known in the Philippines, but none from New Guinea and, judging from recent studies of Borneo Psychodidae, there are undoubtedly more than 50 species in each area.