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THE INFLUENCE OF "WALLACEA" ON THE FAUNA OF TABANIDAE (DIPTERA) OF THE PHILIPPINE ARCHIPELAGO[1]

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A review of available collections and published records of tabanid flies in the Philippine Islands (Philip, 1959) has emphasized that the fauna is still far from completely known. Before World War II, only twenty species were recorded of which six are questioned and six others are apparent emigrants from the mainland or Indonesia. An upsurge of interest in blood-sucking arthropods of the Archipelago, stimulated by military operations, has raised the total to 54 unquestioned species, of which only 19 were previously described. Most of the remainder are probably precinctive.[2] The total number of species could predictably be doubled with eventual adequate collecting, when one considers the modest number of samples studied and the representation recorded in better-known groups of indigenous insects such as the Lepidoptera.

It is, therefore, too early to generalize on evidence which the Tabanidae may provide for the over-all biogeographic history of the Philippine Islands (P. I.), but a pattern has emerged which is useful to record with relation to the known faunas of surrounding territories.

The Archipelago is obviously rich in species but poor in genera. The high proportion of precinctive species supports the conclusion of other writers discussed below that the separation of the Archipelago from the Asiatic continent, and from neighboring islands, has been of long duration.

THE HISTORICAL RECORD

Many recent and early zoogeographic references have alluded to the fauna of the P.I. incidental to broader discussion, but the scholarly review of geologic, hydrographic, and biologic evidence by Dickerson and collaborators (1928) still remains the best presentation of biotic origins in the Archipelago. They emphasized the relationship to a southward transitional zone which they aptly named "Wallacea" dedicated to the great naturalist and zoogeographer, A.R. Wallace, who was making his astute faunal observations in the

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2 The term "endemic," more familiar to biogeographers, has unfortunate ambiguity both with customary usage in epidemiology and etymologically (the properly derived "enzootic" also conflicts with other usage). However, Darlington (1957) points out that this term is the basis for the very useful and common zoogeographic term "endemism."

area almost a century ago. They considered this transition between the Oriental and Australasian Regions to be bounded by Weber's Line on the east and Wallace's Line on the west. The last, based on later information, was revised northward (following Huxley) to pass between the Archipelago proper and the Palawan-Borneo ridge to the southwest and Taiwan on the north.

Darlington (1957) writes that "The Islands and water gaps of Wallacea form a subtraction-transition area and partial barrier between the Oriental and Australian faunas," and his caution that uncritical reliance on the familiar "numbers clues" can lead to fallacious conclusions, would appear particularly applicable to this area. Mayr (1944) used this type of faunal analysis in arguing for Weber's Line as a single boundary rather than the borderline of a formally recognized transition zone, whereas Gressitt (1956) considers this line as "in part of less value than the border of a subregion." In a rational revision of world concepts in which the inclusive area from tropical West Africa to Greater Sunda Islands is labelled the "Paleotropical Region", Schmidt (1954) proposed a "Celebesian Transition Province" bounded by Weber's and the original Wallace's Lines but does not state if the Philippines, thus excluded, would be aligned with his Malayan or Indo-Chinese provinces of his Oriental Subregion. Historically, Wallacea still seems an appropriate designation, whether this transition area be considered a zone, a subregion, or a province.

Wallace (1876) had recognized the insularity of P. I. biota compared to islands of the Indo-Malayan subregion which "are really continental" in faunal relationships. Darlington includes the Archipelago as an example of what he suggests are continental "fringe" environments which have greater differentiation than more recent continentally-associated island faunas. Gressitt considered that the peculiarities of the P. I. fauna warranted subregional delineation within a radical eastward extension of the Oriental Region as far as Polynesia; under his scheme, the Archipelago is enclosed between the arms of a northward fork of Wallace's Line. Since this Oriental expansion includes Papua and New Caledonia, the boundary line between the Oriental and Australian Regions is extended much eastward over older conceptions, as would be also the limits of Schmidt's Paleotropical Region.

The evidence adduced by Dickerson, Gressitt, and others indicates that separation of the P. I. from Taiwan and the mainland occured in ancient, pre-Miocene times. As evidence of a previous connection, however, there has persisted "a residual flora, chiefly Himalayan in origin, and a residual insect fauna of Asiatic temperate regions" on the uplands of northern Luzon which "excessive temperatures of the lowlands" have limited in southern migration. Dickerson further states, "There seem definitely to have been two routes of migration of Asiatic types into Malaysia; one through Malay Peninsula and Sumatra to Java and Borneo, and one through Formosa and the Philippines into eastern Malaya."

Though the land connections to the south were more recent, i. e., in the Early Tertiary, the evidence supports Dickerson's comment "... that if the Philippines are to be regarded as a part of the Indo-Malayan Region, their separation from adjacent land is of very great antiquity." The data indicate that southward connections from Mindanao, perhaps through the Sulu Archipelago to Celebes, were still present about the time of a prominent P. I. horizon called the Vigo-Miocene, after the tectonic separation of Palawan to the west. The evidence is conclusive of the closer relationship of the biota on Palawan to that on Borneo than to that on the rest of the P. I.

The best analysis of the composition of known insect faunas on Pacific islands, which includes the P.I., has been by Gressitt (op. cit.) who admits that only preliminary deductions are possible because the faunas are "too insufficiently known for one to draw comprehensive conclusions on the basis of distribution." His assessment by genera provides the most practical present approach to historical understanding.

THE RELATIONSHIP OF THE TABANIDAE

Mackerras (1954), has revised the higher phylogenetic relationships of this family. He postulates establishment of several well-defined tabanid elements as early as the mid-Mesozoic. Representative tribes of the more primitive subfamily Pangoniinae are known from both the Oriental and Australian regions, including the islands of New Guinea and New Caledonia, but only one undescribed "*Erephopsis*" has been credited (Kröber, 1924) to the P. I. and it would appear that the higher Tabanidae are relatively "late comers" as compared to their radiation elsewhere.

Only four genera are known in the Archipelago, namely, *Chrysops* in the subfamily Chrysopinae, and *Cydistomyia*, *Tabanus*, and *Chrysozona* in the Tabaninae ["*Erephopsis*" (probably equals *Scaptia*) would constitute a fifth if confirmed]. All but the second have displayed modern, vigorous radiation from a Holarctic (in the sense of Schmidt) distribution. It is chronologically significant that neither of the highly successful northern genera, *Atylotus* and *Hybomitra*, reached the P. I., though both are widespread in western Asia, The former entered Taiwan and so possibly did the latter, since a specimen of *H. tarandina* was reported from the mountain village of Arisan (Shiraki, 1918). Parallel to this is occurrence of a primitive element of *Silvius* on Taiwan and the mainland (Philip and Mackerras, in press) which also is lacking in P. I. collections. These all probably reached Taiwan after the ancient pre-Miocene connection to P.I., postulated by Dickerson, was submerged.

On the other hand, it appears not unlikely that a few such species as *Tabanus alticolus* and *T. baguiensis* represent a residuum on Luzon highlands with other Asiatic types discussed by Dickerson. Since no *Chrysozona* have been taken in the southern P. I., it is possible that they used this pathway also; but it seems more likely that the last came into the central P. I. *via* the early Borneo-Palawan route along with the widespread Oriental *T. ceylonicus*, *T. striatus*, and *Chrysops dispar*. The last two of these undoubtedly got to Taiwan independently in more recent times.

For purposes of the present discussion, P. I. species of *Cydistomyia* are of most interest. This is a primitive, tabanine group belonging in the generalized tribe Diachlorini (Mackerras, 1954), the ancestors of which could have taken two southern pathways from their Neotropical place of origin, postulated by Oldroyd (1957), in reaching Indonesia and/or Australia, i. e., the Lemurian Arc through Schmidt's Paleotropical Region, or a hypothetical Gondwanaland or Antarctic pathway. All species so far discovered in the P. I. are on southern islands. A recently described group of delicate, yellow-bodied, forest-inhabiting species related to *Cyd. sol* of New Guinea and others in Indonesia, appears likely to have derived from a stock which arrived in Mindanao *via* Wallacean (or even Papuan) connections about Miocene times, and subsequently moved northward as far as Negros Orientale and Panay.

The more grayish-bodied, slender *Cyd. longirostris* taken on captive crocodiles on Busanga Island on the northern tip of Palawan probably represents a derivative of another line *via* Borneo from the vicinity of Sumatra where the species was originally discovered. *Cyd. frontalis* on Mindoro could have derived from this same Oriental stock. The precursors of five recently described species of *Tabanus* from Palawan and Busanga (Philip, 1959) also must have used this pathway.

Representatives of the successful, ubiquitous genus *Tabanus* have been the most vigorous in occupation of the Archipelago. Their precursors, except for possible Luzon highland residuum, in the main undoubtedly arrived *via* Wallacea and the Borneo Palawan bridge. *T. factiosus*, recorded from Negros, was originally described from Celebes, as was *T. flexilis* with very close resemblance to two other P. I. species. *T. jucundus*, *T. dissimilis*, *T. indianus*, and possibly *T. rubidus* are other Oriental species found in the P. I. Twenty-five of the recently described species from various islands have evident Malaysian affinities. Speciation since arrival of the parent stocks has obviously been vigorous, for a majority of the species taken so far have each come from only one island, a fact which substantiates the antiquity of isolation of the P. I. observed for other biota. For example, 97 of 104 species of tetrigine grasshoppers listed for P. I. in 1928 were precinctive and even Wallace noted that 100 of 159 land birds were peculiar to P. I.

Many of the P. I. *Tabanus* are obvious derivates of stock in common with the extensive Indonesian-Oriental *fumifer-immanis* complex, but that group is characterized by a sharply divided eye pattern, blue above and green below. Only one, *T. immanis* in P. I., has been seen with that pattern, whereas most species have green eyes with purple bands or are unicolorous; this substantiates long divergence in the two areas. When more is known of the Papuan tabanid fauna, a Philippine-Papuan relationship may also emerge as has been revealed by Gressitt for several groups of beetles.

While ancient land bridges have probably provided the chief avenues of spread, overseas dispersals of such strong fliers as the tabanids have been recognized by many zoogeographers, including Darlington and Gressitt, as feasible explanations for occasional colonizers of islands. Hocking (1957) used a flight mill to show that horseflies, *Chrysops* and *Hybomitra*, are capable of continuous flight for 43 to 63 miles, and distance which could be tremendously augmented with the aid of wind, especially violent typhoons in the region. The remarkable distribution of such specialized modern species as *Chrysops dispar*, *T. ceylonicus*, *T. striatus*, and *T. rubidus* could have been accounted for in part by accidental overseas dispersal. Dr. Mackerras writes of the last two coming to light on shipboard between Java and Timor probably ten to fifteen miles from land. If this happened often, however, one would expect to find, even in the present modest P. I. collections, a wider dispersal within the Islands and more of the common Oriental species.

Of the 54 total unquestioned species of Tabanidae now known from the Archipelago, one, the common local carrier of surra, *T. striatus*, has been taken on six islands, *T. reducens* and *T. unifasciens* on five each, eight are from two to four islands, and the remainder from single islands only. Luzon and Mindanao are the principal contributors but species have been collected on all the major islands. Many more species are anticipated with more adequate collecting, but this should only accentuate the belief that Philippine Tabanidae were chiefly derived through Borneo and Wallacea with a possible contribution from Papua.

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