Pacific Insects Monograph 2: 95–100 August 10, 1961

REMARKS ON THE DISTRIBUTION OF THE MACHAEROTIDAE

(Hemiptera: Cercopoidea)

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The Machaerotidae represent probably the most highly advanced group of the Cercopoidea or spittle bugs. They have been little collected and studied and according to our present knowledge are comprised of 2 subfamilies, 4 tribes, 28 genera and a few more than 100 species (including 6 new genera and 34 new species to be published elsewhere). They feed on woody dicotyledons and their distributional range is mainly restricted to rain forests of the Palaeotropics. Therefore they do not constitute an appropriate example to illustrate the generalized geographical distribution of the Cercopoidea or higher taxa. In certain respects, however, the distribution pattern of the family is fairly interesting and worthwhile discussing.

The names of the zoogeographic subregions in the paper are from Bartholomew, Eagle Clark and Grimshaw's Atlas of Zoogeography (Bartholomew's Physical Atlas, vol. 5, 1911), but their "Indo-Malayan" subregion is here divided, by the Wallace's Line (as revised by Dickerson *et al.*) into Malaysian and Philippine subregions, and their "Austro-Malayan" subregion, by a line between the Moluccas and New Guinea, into Wallacea and Papuan subregions. To avoid confusion, the names Indo-Malayan, Indo-Australian and Austro-Malayan of authors are not used.

(1) Distributional Centers and Eccentric Deviation

The Machaerotidae are of rather recent origin and no fossil forms assignable to this family have been discovered. Insofar as the "modern" forms are concerned, the primary distributional center is in the Malaysian and Indo-Chinese subregions (table 1, fig. 1). The number of genera and species and the percentage of endemicity gradually diminish in all directions from those centers. On the other hand, the different genera and species-groups each has its own secondary distributional center. For instance, the centers of the genera *Chaetophyes*, *Hindola* and *Machaerota*, respectively, are in E. Australia, N. Borneo and Indo-Chinese Peninsula. Half of the 28 genera are known from one species each, whereas several other genera each have few scattered species which fail to indicate a distributional center. The faunal affinities of such genera can only be measured by their phylogenetic affinities.

An example of replacement occurs in Borneo which has the richest machaerotid fauna–9 genera, 2 of which are endemic; 14 species, 10 endemic–but lacks any representative of the tribe Hindoloidini and of the genus *Machaerota*. The absence of Hindoloidini may

perhaps be attributed to lack of intensive collecting, but there occurs the peculiar genus *Parahindoloides* (Ibini, Clatopterinae) which probably occupies the ecological niche suitable for *Hindoloides*. The genus *Machaerota* is well represented in the neighboring countries of Borneo, with 3 species each in Malaya, Sumatra and Java, 1 each in Palawan and Celebes, 5 in Mindanao and 2 in S. Vietnam. It is evidently replaced by its close relatives *Platymachaerota* and *Grypomachaerota* in Borneo notwithstanding that the latter two are not restricted to that island. Replacement on a larger scale is seen in the Neotropical Region where the family as a whole is replaced by the cercopid subfamily Clastopterinae.

Related to the tribal and generic replacements as mentioned above, the phenomenon of eccentric deviation or "fringe speciation" of the species within a genus is common amongst the machaerotids. As examples, *Machaerota takeuchii* Kato of Japan, *M. punctatonervosa* Signoret of Ceylon, *M. pugionata* Stål and *M. finitima* Jacobi of NW Australia all show much higher degree of differentiation than do species occurring in or near the distributional center or main dispersal route. The further from the center or the route, the higher is the effect of isolation and the degree of differentiation. The same theory is also applicable to the speciation of the members of any generic complex in the machaerotids.

(2) Wallace's and other Lines

The distributional range of the Machaerotidae spans about 160 longitudinal degrees (5° W. at Ivory Coast to 155° E. at Woodlark I.) and 85 latitudinal degrees (43° N. at Kirin to 42° S. at Tasmania). It covers the phytogeographic division, Old World Intertropical Region (M. I. Newbigin, 1948, Plant and animal geography, 2nd edition, fig. 33) except the Bismarck Archipelago and Solomon Islands, but extends both north and southward near its eastern extremity. On the other hand, it covers the zoogeographical divisions, Ethiopian, Oriental and Australian regions (in the sense of Bartholomew *et al.*) excluding East African (northern part), South African (southern part), Indian (northwestern part), Polynesian and New Zealand subregions. The number of genera and species occurring at the east and south of the Indo-Chinese-Malaysian center is greater than those at the west and north, but their dispersal routes in general are in west-east, rather than north-south. The isothermal line plays an important role in delimiting the distributional ranges of their host-plants and this in turn affects the range of the insects involved. The southward penetration of the machaerotids along coastal areas of Australia has been mainly governed by the range of their preferred host-plants, *Eucalyptus* and the adult bugs are found only in favorable season, not throughout the year as in the tropics. This means that there they can meet unfavorable conditions and that the climate does not reach the limiting extreme and thus does not prevent their existence and dispersal. A similar explanation may be applied to the northward extension of one odd species, *Taihorina geisha* Schumacher, into Central Manchuria and Korea, where they feed on *Quercus*, a temperate plant. The continental climate in those countries is so severe at times, however, that the bugs cannot withstand and spread as far as their host-plants can.

The absence of machaerotids in the Bismarck Archipelago and Solomon Islands suggests the possibility that their ancestors established at NE New Guinea after these islands were already separated. The diversity of the Australian forms indicates, on the other hand, that the ancestors reached there at least in two different dispersal routes, (and at different times), one through the Torres Strait in the northeast (ancestors of *Chaetophyes* and *Pec-*

tinariophyes), another through the Molucca-Timor-Key Is. chain in the northwest (ancestors of *Machaerota pugionata* group). Both Wallace's and Weber's Lines form weak barriers in delimiting the ranges of the tribes and genera. Three of the 4 tribes are found on both sides of both lines; the fourth tribe, Maxudeini, is restricted to the Malaysian subregion. Of the 12 genera occurring in the Indo-Chinese and Malaysian subregions (not counting 2 additional ones of N. Thailand and Assam), only *Pectinariophyes* and *Machaerota* were able to cross both lines and reach far down to Australia; 3 of the 6 Australian and Papuan genera crossed Weber's Line; 2 of the 5 genera of the Philippine and Wallacea subregions are endemic.

The 5 African genera, except the widely distributed *Pectinariophyes*, are endemic. They were derived from two ancestral stocks, represented by this genus and *Aphrosiphon* respectively. All except the latter genus form a fairly compact generic complex.

The most interesting discontinuous distribution in Machaerotidae is exemplified by the genus *Pectinariophyes*. There are 3 species in the Australia-Papuan area which are closely related to one another and represent the most archaic forms of the genus. Another pair of closely related discontinuous forms is in S. India and the N. Philippines. The 3 remaining species are rather isolated in phylogeny and in distribution, one each in S. Africa, N. Borneo and the S. Philippines. Another example of discontinuous distribution is the genus *Machaeropsis* which has one species each in Ceylon, NW Thailand and NE Borneo, representing 3 different subregions.

Aside from morphological evidences, the distribution pattern of the machaerotids shows that they are undergoing active differentiation. Out of the 28 genera, 12 are known from 2 or more subregions, and only *Machaeropsis*, *Pectinariophyes* and *Machaerota* are known from 3, 6 and 9 subregions respectively; and only 5 of the 116 species are found in 2 or more subregions. Such strong localization is partly due to their relatively short history on the earth, and partly to their inactive, secretive habits and their sensitivity to microenvironments. The scarcity of these bugs in museum collections more or less indicates their rarity in nature. The commoner species have been known to form small colonies on one or two certain trees but never uniformly distributed to the same host-plant over a large area. Under such circumstances, chances for interbreeding between colonies are slim but the tendency toward localization or isolation is strong. Even within the same zoogeographical province, the machaerotid fauna may be quite localized. In the Philippines, for example, the faunae of Luzon in the north and of Mindanao in the south are markedly different. Each of the 2 islands has 7 species, but except *Serreia notabilis* Baker (genus and species endemic to the Philippines) and *Machaerota ensifera* Burmeister (lowland species, widespread in the Philippines), all the remaining 12 species are not present on the other side of the subregion.

The means of dispersal of the machaerotids are not clear but their dispersal ability is certainly limited. As mentioned above, most of the species dwell in the palaeotropic rain forests. The only records of accidental dispersal are *Hindola viridicans* Stål into Amboina, *Machaerota rastrata* Walker into Java and *M. ensifera* Burmeister into Palawan (which belongs to the Malaysian subregion). All of them are dwellers of lowland open forests, which are more likely to be widely spread than rain forest dwellers.

The number of the machaerotid genera and species are so small and their distribution is so localized that the relative faunal affinities of the subregions are much obscured and

cannot be properly evaluated. For the 4 Ethiopian subregions, Malagasy is comparatively remote from the 3 others. For the Oriental subregions, the present-day geographical proximity does not exercise influence evenly to the faunal elements. From fig. 1, the Indian subregion appears closer to Manchurian and Indo-Chinese rather than Ceylonese, which shows more affinities to Malaysian and Indo-Chinese than to Indian and is with a little Ethiopian element. The affinities of the Philippine subregion toward Indo-Chinese, Malaysian and Wallacea are weaker than toward Papuan. The Papuan subregion in turn is slightly closer to Australian than to Philippine or Wallacea.

(3) Dispersal Routes of the Tribes and Genera

For brevity, the dispersal routes of only the largest genus for each tribe are narrated below.

(a) *Hindoloides* Distant (Enderleiniinae, Hindoloidini). Of its 4 species, 1 is localized at the Ganges delta, 2 localized at NW Fukien and 1 spread over southern portion of Manchurian subregion, from Szechwan to S. Japan *via* Fukien and Taiwan. The first and last species, respectively, represent the most archaic and the most specialized form of the genus, and the route appears running northeastward and closely along N. border of Indo-Chinese subregion although the ancestor of this genus probably came from further south.

(b) *Hindola* Kirkaldy (Enderleiniinae, Enderleiniini). Six of the 12 species including the most archaic and most specialized of the genus, are found in Borneo; few species in Java, Sumatra, Malay Penin., Tenasserim, Vietnam and Taiwan, and one doubtful species in S. India. The main route of their dispersal probably runs from Borneo northward to Taiwan *via* Malay Penin. and Vietnam and secondary routes run south and westward.

(c) *Maxudea* E. Schmidt (Machaerotinae, Maxudeini). One species is known from

Table 1. Number of genera and species of Machaerotidae in different zoogeographic subregions.

	Total number		Number of endemics	
	Genera	Species	Genera	Species
W. African	1	2	0	1
E. African	3	4	1	3
S. African	3	3	0	3
Malagasy	1	1	0	1
Ceylonese	5	6	1	6
Indian	2	3	0	3
Manchurian	3	3	0	1
Indo-Chinese	11	30	4	27
Malaysian	12	31	5	29
Philippine	3	12	1	11
Wallacea	4	8	1	7
Papuan	4	11	1	10
Australian	5	10	2	9
Total	28	116	—	—

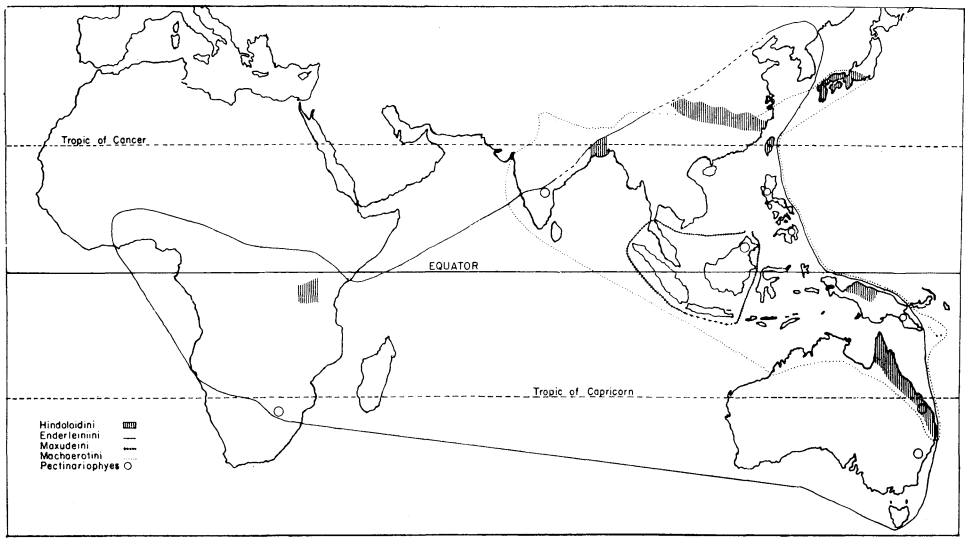

Fig. 1. Distribution of the four tribes and the genus *Pectinariophyes* of Machaerotidae.

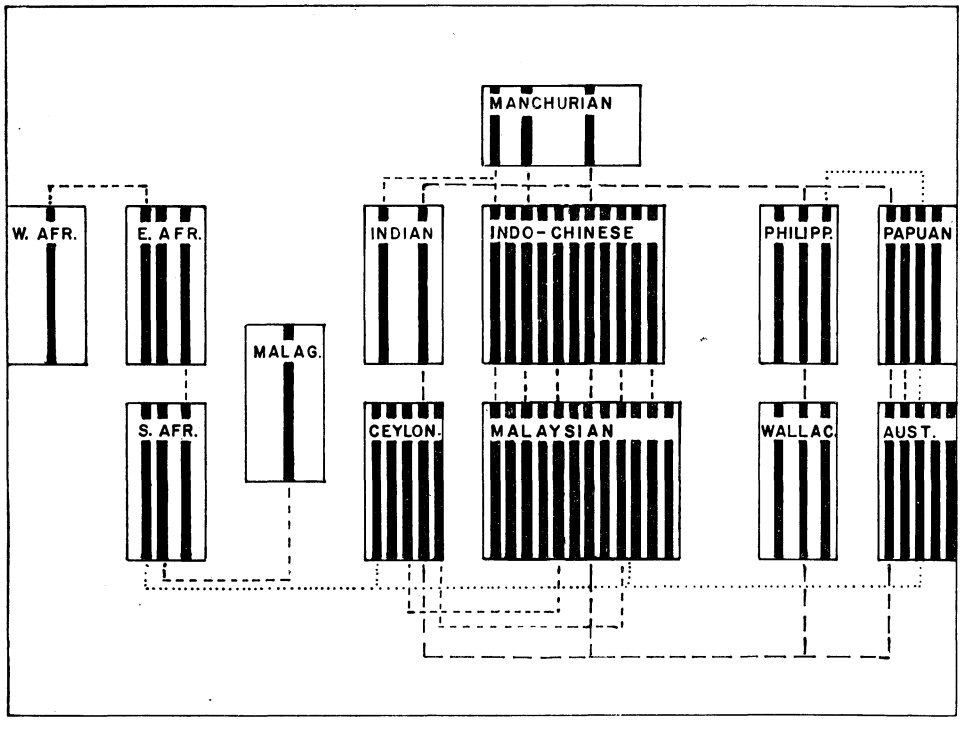

Fig. 2. Distribution of the machaerotid genera in different zoogeographic subregions. (Each solid line represents one genus; genus spreading over two or more subregions is connected by dotted or broken lines).

Sumatra and Malaya. The only other member of the tribe is an undescribed and more archaic genus (and species) found in Borneo. The dispersal is rather similar to that of *Hindola* but far less extensive.

(d) *Machaerota* Burmeister (Machaerotinae, Machaerotini). Altogether 48 species: 3 in Australian province, 4 Papuan, 5 Wallacea, 9 Philippine, 7 Malaysian, 15 Indo-Chinese, 2 Indian and 2 Ceylonese. Many of them form together into species groups which have been recognized by some authors as distinct genera. The *siebersi*-(Papuan) and *rastrata*-groups (Australian-Wallacea) probably represent the most archaic forms. Members of other species-groups deviate in various directions in morphological detail. They probably have specialized at different speed, and spread along several routes and at different times, since highly specialized forms are found here and there and species of different groups often occur in one country.