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THE ZOOGEOGRAPHY OF WESTERN PACIFIC TABANIDAE (Diptera)

By I. M. Mackerras

QUEENSLAND INSTITUTE OF MEDICAL RESEARCH, BRISBANE, AUSTRALIA

The Tabanidae are a comparatively small element in the Pacific insect fauna. Those on the periphery are marginal representatives of the adjacent regional faunas. The Philippine Tabanidae have been discussed by Philip (1959), and the present review will therefore be limited to the south-western quadrant, where extension to oceanic islands has been greatest. The sectional faunas have been revised recently (of Australia by Mackerras, 1956a, 1956b, 1959, 1960, 1961b; of New Zealand by Mackerras, 1957; of New Guinea by Oldroyd, 1947, 1949; and of the south-western Pacific by Mackerras and Rageau, 1958), so the time is opportune to collate the information.

GENERAL CONSIDERATIONS

The Tabanidae are an important group of blood-sucking flies, which have been collected fairly thoroughly in most parts of the world. They are therefore useful for analysis of distributional problems. The subfamilies and tribes that concern us are shown in Table 1. The primitive division of the Pangoniini, Scionini, Bouvieromyiini and Diachlorini are ancient, and have a predominantly southern distribution, which suggests that they might have evolved in, and radiated from, a temperate Antarctica. The Philolichini appear to have evolved from (and replaced) scionine ancestors in southern Africa. The more modern Chrysopini and Tabanini evolved mainly in Holarctica, whence they have radiated into the southern hemisphere. The remaining major tribes, Rhinomyzini and Haematopotini, were derived, respectively, from bouvieromyiine and diachlorine ancestors; neither has crossed Wallace's line.

It is necessary to understand the Oriental fauna in order to appreciate how the Pacific fauna originated. It lacks primitive Pangoniini and Scionini, and the ancestors of all its existing groups of Tabanidae appear to have been derived in a fairly advanced state of evolution from other regions. They include two distinct elements. The smaller, older element consists of Philolichini, Rhinomyzini, Bouvieromyiini and Diachlorini, which came from Ethiopian ancestors and swept in a series of waves around the Indian Ocean. By far the larger element consists of more modern *Chrysops*, *Tabanus* and *Haematopota*, which appear to have flooded into an almost empty Oriental region from both the Palaearctic and Ethiopian regions. It is difficult to data this diffusion, but it may be significant that the first of the major arid barriers, which would have cut off Africa and northern Asia from southern Asia, appears to have developed in mid-Pliocene (Axelrod, 1948).

The significance of this situation, from the point of view of Pacific invasion, is that the more vigorous Chrysopini and Tabanini have had less time to extend their range to the eastward than some of the more primitive, earlier groups.

The Moluccan division, lying between Borneo and New Guinea, but excluding the southern chain from Lombok to Timor, has 44 known Tabanidae (Table 1). It has been poorly collected, and the absence of Bouvieromyiini may be due to that fact. Nevertheless, it does appear to have served as a zone both of filtration and of local evolution.

The Australian fauna (Table 1), which is the other possible source of the western Pacific Tabanidae, is nearly as large as the Oriental. It includes four elements: 184 ancient southern (presumably Mesozoic) Pangoniinae, Bouvieromyiini and Diachlorini; 31 older northern (presumably Tertiary) Bouvieromyiini and Diachlorini, at least some of which were offshoots from the Ethiopian-Oriental arc; 19 younger northern (probably Pleistocene) *Chrysops* and *Tabanus*, not all of whose ancestors appear to have arrived via New Guinea; and about 6 late Pleistocene-postglacial immigrants from New Guinea.

The capacity of Tabanidae to disperse and to colonize new areas also needs to be considered. Excluding such widely ranging species as the Oriental *Tabanus ceylonicus* and the Australian *T. innotabilis*, to which normal barriers appear to offer little impediment, the available evidence suggests that ocean gaps of the order of 100 miles in favourable climates are generally sufficient to permit speciation to occur (Mackerras, 1961a). This implies that effective recolonizations probably do not occur more than once in every 50,000 or more years.

Limitations to colonization are difficult to define. It is likely that all the Tabanidae that have extended into the Pacific require vertebrate sources of blood, and they also need vegetation for shelter in a reasonably humid microclimate. These conditions would be found everywhere, except on the lowest atolls. Their breeding grounds are diverse. All of the few Pangoniini, Scionini and Diachlorini of which the early stages are known breed in situations ranging from damp soil, rot-holes in trees, and axils of *Pandanus* (Barrett, personal communication), to quite dry sand. Some Tabanini have terrestrial larvae, but many are aquatic, as are the larvae of *Chrysops* and of the single bouvieromyiine studied. Available food for the larvae does not present a problem, and any of the higher Pacific islands should provide suitable breeding grounds for groups that are available to colonize them. One group of *Dasybasis* breeds in the sand of ocean beaches, an environment which is probably fairly uniform everywhere. It is distributed in a deep curve from the south coast of New South Wales through southern New Guinea and the Melanesian arc to New Caledonia, and has become divided into four species which illustrate the retarding effect of ocean gaps on gene flow.

COMPOSITION OF SECTIONAL FAUNAS

The sectional faunas (including unpublished records) are dissected in Table 1. Samoa marks the known limit of the family to the east. *Tabanus insularis* Walk., supposedly from " Sandwich Is. ", was shown by Oldroyd (in Mackerras and Rageau, 1958) to have been mislabelled, and, in spite of reasonable collecting, no Tabanidae have been reported from any of the island groups between Samoa and the Galapagos Is., where a Neotropical species appears (Bequaert, 1933). To the south, none has been found in Lord Howe and Norfolk Is., and none in the subantarctic islands, the most southerly records being 46°28′ S in New Zealand and about 53° S in the Strait of Magellan.

Table 1. Distribution of Pacific Tabanidae—number of species.

Subfamilies	Tribes and Genera	New Zealand	Australia	Moluccan	New Guinea	Melanesian Arc	New Caledonia and Loyalty Is.	Fiji	Samoa	Micronesia
		Geographical Divisions								
PANGONIINAE	Pangoniini (primitive divn.)	1	18	—	—	—	—	—	—	—
	Scionini	6	69	—	12	—	—	—	—	—
	Philolichini	—	—	1	—	—	4	—	—	—
CHRYSOPINAE	Bouvieromyiini									
	Mesomyia (*Pareucompsa*)	—	—	—	2	—	—	—	—	—
	(*Perisilvius*)	—	1	—	5	—	—	—	—	—
	(*Pseudotabanus*)	—	19	—	1	—	—	—	—	—
	Others	—	16	—	—	—	—	—	—	—
	Chrysopini—*Chrysops*	—	1	2	2	—	—	—	—	—
TABANINAE	Diachlorini									
	Neobolbodimyia	—	—	1	1	—	—	—	—	—
	Paracanthocera	—	1	1	—	—	—	—	—	—
	Japenoides	—	—	—	1	—	—	—	—	—
	Cydistomyia (*Lissimas*)	—	—	2	—	—	—	—	—	—
	(*Parabolbodimyia*)	—	—	—	2	2	—	1	—	—
	(*Chalybosoma*)	—	2*	—	4	—	—	—	—	—
	(*Chasmia*)	—	—	—	12	—	—	—	—	—
	(*Cydistomyia*)	—	25	7	32	3	10	3	—	—
	Dasybasis	9	68	1	5	2	3	—	—	—
	Tabanini—*Tabanus*	—	20	29	40	6	—	1	1	2
	Totals:	16	240	44	119	13	17	5	1	2

* Subgeneric allocation doubtful.

New Zealand

All the species belong to southern components, and their relationships seem to lie more closely with those of South America than of Australia. Each tribe is represented by a single subgenus, one being precinctive, one with a limited extension to New Caledonia, and the third—*Scaptia* (*Pseudoscione*)—shared with South America, Australia and New Guinea. The absence of Bouvieromyiini, and the evidence of divergence between relatively few species-groups, suggest that there was probably much extinction during Pleistocene glaciations, with limited survival in isolated pockets, which would produce the present rather confusing mixture of closely related forms within the groups. New Zealand lacked a pathway for recolonization after glaciations, and this would account for its limited, renascent fauna.

New Guinea

A great deal of evolution at generic and specific levels has occurred here and in the associated Moluccan division. That does not necessarily imply great antiquity of the fauna, because the occurrence of isolating mechanisms is as essential as time in the development of genetically isolated segregates; while the occurrence of available niches in varied and rapidly changing environments is correspondingly important in producing selection pressures that could lead to wide morphological divergence of the genetically separated populations. Th arc of islands to the north of Australia has been an area of instability, and most of the major tectonic and climatic changes in it took place in the late Tertiary and Pleistocene. It seems likely, therefore, that most of the evolution of which we see the results also occurred during that period.

Three faunal elements are indicated in the Tabanidae. The unequivocally Australian element (18 species) comprises *Scaptia* (*Pseudoscione*), *Mesomyia* (*Pseudotabanus*) and *Dasybasis*, and includes a few recent immigrants. The younger Oriental element is represented by 2 species of *Chrysops* and 40 of *Tabanus*, although some of the *Tabanus* may have been derived via Australia rather than directly through the Moluccan division. Their detailed relationships with Malayan or Philippine elements have not yet been adequately studied.

The third element includes 7 Bouvieromyiini and 52 Diachlorini. The subgenera *Pareucompsa* and *Perisilvius* belong, fairly clearly, to the Ethiopian-Oriental arc (Mackerras, 1961b). In the Diachlorini, the first five genera and subgenera listed in the Table are the result of a Moluccan-Papuan burst of evolution in stock which extends back at least to Ceylon and diverges to the Philippines. On the other hand, the ancestry of the subgenera *Chalybosomas*, *Chasmia* and *Cydistomyia* is not so clear. They have developed a distinctive Papuan facies, and there is little to indicate whether their ancestors came from the same northern arc as the others or from Australia. Certain recurrent morphological trends, and parallel distributions in other groups of insects, support the hypothesis of northern origin.

If these indications prove to be correct, we may visualize a relatively early influx of Ethiopian-Oriental Bouvieromyiini and Diachlorini, for which the Cyclopean ridge postulated by Miss Cheesman (1951) might have formed an effective path and initial home, and two later invasions, one from the Oriental region, the other from Australia, into the southern part of New Guinea when it became habitable.

Melanesian Arc

This area (in the sense of Mackerras and Rageau, 1958) has been inadequately collected, but, even so, there is strong indication of a filtration effect operating against several of the major groups. The analysis below, which may be useful to workers in the field, also shows that there is a sharp break between the New Hebrides, where there is close relationship with Fiji, and the remainder of the arc, which shows local speciation in an impoverished Papuan fauna.

Admiralty Is.: *T. ceylonicus* Schin.; *D. mellicallosa* M. & R. (littoral group).

New Britain: *C.* (*C.*) *nana* M. & R.

New Ireland: *T. ceylonicus*, *T.* sp. nov.

Solomon Is.: *T. ceylonicus*, *T. innotabilis* Walk., *T.* sp. nr. *lenticulatus* Oldr., *T. leveri* M. & R.; *C.* (*P.*) *ratcliffei* M. & R.; *C.* (*C.*) sp. ?nov.; *C.* (*C.*) *lorentzi* (Ric.), *C.* (*C.*) *nana* M. & R., *C.* (*C.*) *solomensis* (Ric.); *D. anomala* M. & R., *D. mellicallosa.*

Santa Cruz Is.: *T. innotabilis*, *T. leveri*; *D. mellicallosa.*

New Hebrides: *T. expulsus expulsus* Walk.; *C.* (*P.*) *veitchi* (Bezzi) ?subsp. nov.

New Caledonia and Loyalty Islands

The fauna of this area is remarkable for possessing Philolichini and lacking *Tabanus.* The species of *Philoliche* are of unequivocally Ethiopian origin. They belong to a distinctive group which has its nearest relatives in Mauritius (Oldroyd, personal communication), rather than in the series of Oriental species which ends in *P. amboinensis* (Fabr.) of Amboina and Timor, and they provide the only plausible indication in the family for diffusion across, as well as around, the Indian Ocean.

Five of the species of *Cydistomyia* represent three different Papuan species-groups. The other five are large, distinctive species more like a group that occurs in eastern New South Wales than any in New Guinea. They may have followed the same pathway as the ancestors of *Dasybasis rubricallosa* (Ric.), which belongs to the group of littoral species referred to earlier. The other two species of *Dasybasis* represent the *sarpa* and *truncata* groups of the subgenus *Protodasyommia,* and show that there must have been a connection which allowed some traffic from New Zealand, probably at the beginning of the Pleistocene. *D. rubricallosa* and one of the large species of *Cydistomyia* are known also from the Loyalty Is.

The absence of *Tabanus* suggests that these islands have been isolated from the north for much, if not all, of the Pleistocene, which would indicate, in turn, that the intruding Papuan groups of *Cydistomyia* had evolved earlier than might have been expected.

Fiji

T. expulsus fijianus Ric. and *C.* (*P.*) *veitchi* (Bezzi) are conspecific with, or closely related to, the corresponding species in the New Hebrides. The remaining species of *Cydistomyia* are small and nondescript. They are probably derivatives of rather ancient stock, and would not be out of place in the Papuan or Moluccan fauna. All the species represent separate colonizations, except possibly *C.* (*C.*) *pacifica* (Ric.) and *C.* (*C.*) *bezzii* M. & R. These might have been segregated locally from a common ancestor, although the isolating mechanism is not clear.

Samoa

The affinities of *T. samoensis* Ferg. are obscure, but it too would not be out of place among the New Guinea species.

Micronesia

Two species are recorded by Stone (1960). *T. palauensis* Tak. from Palau is precinctive, and may have Philippine affinities, whereas *T. striatus* Fabr. from Guam is evidently an immigrant.

CONCLUSION

The evidence from the Tabanidae supports the view that the western Pacific was colonized mainly by a stream of older Ethiopian-Oriental species, most of which swept past the north of Australia. The morphological evidence is conclusive for *Philoliche*, strong for some Bouvieromyiini and Diachlorini, and largely inferential for the remainder. This main stream was supplemented by two smaller, probably later, streams of Oriental and Australian elements, and by a limited extension from New Zealand to New Caledonia. That *Tabanus* extends further into the oceanic islands than the older *Cydistomyia* is probably an expression of superior capacity to disperse.

There has been considerable filtration at the Melanesian arc, and further breaks in continuity at the New Hebrides and New Caledonia. The fauna of New Zealand stands apart in its exclusive relationship with South America and southern Australia.

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