THE CLASSIFICATION AND DISTRIBUTION OF THE SIMULIIDAE (DIPTERA) WITH PARTICULAR REFERENCE TO THE GENUS AUSTROSIMULIUM

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Summary

The affinities and distribution of *Austrosimulium* Tonnoir are examined in relation to those of other genera in the Simuliidae, especially those represented in the Southern Hemisphere. It is concluded that *Austrosimulium* is not clearly derivable from or closely related to *Gigantodax* Enderlein but shows greater affinities with *Simulium* Latreille. The South American species, *A. anthracinum* Bigot is distinctly separated from the Australian and New Zealand species and is doubtfully ascribable to *Austrosimulium*. The doubtfully disjunctive distribution, the affinities of *Austrosimulium* with *Simulium*, and the relationships between the Australian and New Zealand species-groups, suggest that the genus is of northern origin and route of entry into New Zealand, and probably into Australia also.

INTRODUCTION

A study of the New Zealand simuliid fauna was undertaken because of the intrinsic interest of the group and its bearing on medical and veterinary entomology. The formal taxonomy of the fauna which is the basis for the present contribution will be presented as a separate paper. *Austrosimulium* Tonnoir, the only genus present in New Zealand, is represented elsewhere in Australia and, more doubtfully, in South America. The present paper deals with the more general questions of classification and dispersal which have arisen from an attempt to integrate the genus with the rest of the family.

CLASSIFICATION AND DISTRIBUTION OF THE GENERA OF SIMULIIDAE

The family Simuliidae is a discrete group, there being no annectant species which give evidence in the adult stage of strong affinities with any other of the families included in the Nematocera. There are some suggestions of affinity in the larval stage with those of the nematocerous families in which the premandibular organs or messores are present. This is especially true of the Chironomidae which also show similarities in the cocoon (Shewell, 1958). Downes (1958) has discussed the view (which is not accepted here) that the primitive Diptera were biting species and that the adult mouthparts are reduced in the Chironomidae. Larval affinities with other families in which the larval head is of rectangular form are not apparent. The affinities of the family have been discussed by Grenier and Rageau (1960) who concluded, on grounds of adult morphology and larval anatomy, that it is a highly evolved nematocerous family and a precursor of the Brachycera.

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The classification of the family has been discussed by Smart (1945) and more recently by Rubcov (1959 *et seq.*). The divergence in the classifications into subfamilies and tribes which have been proposed may be seen from the comparison in Table 1. The classification adopted here differs from that of Grenier and Rageau only in relegating *Gigantodax* and *Cnephia* (s.l.) to the Prosimuliinae.

There is a similar absence of agreement concerning the limits of the older genera and the validity and status of segregates from these genera which have been proposed. Smart (1945), Mackerras and Mackerras (1949), and Freeman and de Meillon (1953) have recognised Edwards' (1931) sub-genera as of generic status but there is no general agreement as to the status of many genera proposed by Enderlein, though many of them are recognised by Rubtzov (1959 *et seq.*).

A conservative interpretation of generic limits is adequate for the purposes of this paper though it is recognised that a soundly based phylogeny must await the segregation of well defined sub-generic taxa from within *Cnephia* and *Simulium* and a better understanding of the relationships between them. Further study may show that some segregates of *Cnephia* (s.l.) could be placed in the Simuliinae.

SUBFAMILY PARASIMULIINAE

This is considered by Shewell (1958) and Grenier and Rageau (1960) to be warranted, because of the distinctness of the adult of the Californian species *Parasimulium furcatum* Malloch. It is based however on a single species known only in the adult stage, the unique specimen being a possible gynandromorph. Its affinities remain to be elucidated.

SUBFAMLIY PROSIMULIINAE

The subfamily appears to be broadly separated from the Simuliinae by the character of the cocoon, though gradations between the two exist in *Cnephia (Astega)* (Shewell, 1958).

The tribe Prosimuliini includes species with normal filter-feeding larvae. *Prosimulium* is considered to be the most primitive of the unmodified filter-feeding forms which constitute the majority of the species in the family. The apparent homology of the premandibular organs (messores) in the larvae of other families with the mouth-brushes of larval Simuliidae is the basis for the assumption that the ancestral Simuliidae possessed larval mouth-brushes, at least in the fourth instar. Davies (1960) has shown, however, that they are not present in the first-instar larva in at least one species of *Prosimulium*.

The genus *Cnephia* has affinities with both *Prosimulium* and *Simulium* (Shewell, 1958) and the gradation in characters betwen these three suggests that they mark the approximate main line of evolution of the filter-feeding forms. The few species of *Cnephia* investigated (Davies, 1960) have mouth-brushes present in the first-instar larva. Rubtzov (1959) has pointed out the affinities between *Prosimulium* and the disjunct Southern Hemisphere groups at present referred to *Cnephia*. The South African species *C. damarensis* (de Meillon and Hardy) was originally placed in *Prosimulium*.

TABLE 1—Classification of SIMULIIDAE

Subfamilies, Tribes, and Genera

(– = genus not existing at that time; x = not represented in fauna considered)

Genus	Smart (after Edwards) 1945	Stone & Jamnback 1955	Shewell 1958	Rubcov 1959 *et seq.*	Grenier & Rageau 1960
Parasimulium Malloch	PARASIMULIINAE	x	PARASIMULIINAE	x	PARASIMULIINAE
Gymnopais Stone	–		PROSIMULIINAE	GYMNOPAIDIINAE	PROSIMULIINAE GYMNOPAIDIINI
Twinnia Stone & Jamnback	–	PROSIMULIINAE	PROSIMULIINAE	GYMNOPAIDIINAE	PROSIMULIINAE GYMNOPAIDIINI
Prosimulium Roubaud	SIMULIINAE PROSIMULIINI	PROSIMULIINAE	PROSIMULIINAE	SIMULIINAE	PROSIMULIINAE PROSIMULIINI
Cnephia Enderlein	SIMULIINAE PROSIMULIINI	SIMULIINAE	PROSIMULIINAE	SIMULIINAE	SIMULIINAE CNEPHIINI
Gigantodax Enderlein	SIMULIINAE	x	x	SIMULIINAE	SIMULIINAE AUSTROSIMULIINI
Austrosimulium Tonnoir	SIMULIINAE AUSTROSIMULIINI	x	x	SIMULIINAE	SIMULIINAE AUSTROSIMULIINI
Simulium Latreille	SIMULIINAE SIMULIINI	SIMULIINAE	SIMULIINAE	SIMULIINAE	SIMULIINAE SIMULIINI

Gigantodax is more distinctly separated from the main line of the family but its strongest affinities are with *Cnephia* (Edwards, 1931; Rubtzov, 1959) and *Prosimulium*. The condition of the mouth-brushes in the first-instar larva in this genus is unknown.

The tribe Gymnopaidiini includes the few species, about 1% of the family, in which the mouth-brushes are absent and the mandibles modified in the last-instar larva. The condition in the first-instar larva is not so far reported. The larvae are mobile browsers on the substratum in slower waters. The species are distinct from those of other genera in the larvae but less so in the adult stage, and Shewell (1958) has suggested that *Twinnia,* in particular, could be considered as a subgenus of *Prosimulium*. If *Prosimulium* is truly representative of an ancestral stock of the family which possessed mouth-brushes in the fourth-instar larva, then the absence of mouth-brushes in the larvae of the closely allied *Gymnopais* and *Twinnia* is presumably a secondary condition due to loss. Grenier and Rageau (1960) and Dumbleton (1962a) have discussed the reduction of the mouth-brushes and the modification of the mandibles in the fourth-instar larva of *Simulium oviceps* Edwards, and the latter author has discussed the modification of both mandibles and mouth-brushes in *Cnephia crozetense* Womersley, the adults of both these species being normal members of their genera. It was concluded that these were cases of caenogenesis, which is defined by Rensch (1959) as a deviation consisting of an hereditary adaptation to the environment affecting the intermediate stages (larval) in the ontogeny and not necessarily affecting the structure of the adults. The deviation of the larvae of *Twinnia* and *Gymnopais* from the *Prosimulium* condition may also be viewed as a caenogenesis, but as one which affecting an older stock and having had a longer time in which to operate has also, especially in *Gymnopais,* produced differentiation in the adults. The condition of the mouth-brushes in the first-instar larva of *S. oviceps* may provide interesting evidence as to how much it has been affected by the process which caused their reduction in the last instar. If the absence of mouth-brushes in the first-instar larva of *Prosimulium* is the unmodified primitive condition their presence in *Cnephia, Simulium* and *Austrosimulium* may represent a shift of ontogenetic stages relative to the time of hatching.

SUBFAMILY SIMULIINAE

Included here are the two genera *Simulium* and *Austrosimulium,* the affinities of the latter being discussed in a later section.

Simulium is the largest single genus and has the widest distribution, extending from the Arctic to the cool-temperate of the southern continents. While a few species of *Cnephia* and *Gigantodax* occur at high altitudes in Southern Mexico and species of *Gigantodax* occur along the Andean chain, *Simulium* is the only genus present throughout the lowland tropics. The diversity of habitats occupied by species of *Simulium* is apparently the result of a radiation which was both later in time and more extensive than in any other genus. It is the only genus of which some species act as vectors or intermediate hosts of at least one virus and of several pathogenic protozoa and filarial worms. Other species have developed phoretic associations with mayfly nymphs and freshwater crabs. The genus is probably polyphyletic and it cannot be discussed with advantage until it is split into more clearly defined segregates. It appears to be most readily derivable from *Cnephia*.

The world distribution of the genera of Simuliidae is shown in Fig. 1. The principal features to be observed are:

(1) The restriction to the Northern Hemisphere of a group of genera (*Prosimulium. Parasimulium, Gymnopais,* and *Twinnia*) which is considered to include the most primitive genera in the family.

(2) The cosmopolitan distribution, including the lowland tropics, of the genus (*Simulium*) which is considered to be the most specialised, and the indication of its relatively late invasion of at least the Australian and South Pacific areas.

(3) The junction of the purely Neotropical and predominantly Southern Hemisphere genus *Gigantodax* with Northern Hemisphere genera in Central America.

(4) The virtual absence from the tropics (except in Central America) of *Cnephia* which occurs in both hemispheres and has a disjunctive distribution in the more southerly areas of the three southern continents (tricentric austral distribution).

(5) The restriction of *Austrosimulium* to the Southern Hemisphere and its possession of an austral distribution which can be interpreted either as monocentric (if Australia and New Zealand are considered as constituting one southern centre) or, less certainly, as bicentric (with southern South America as the second centre).

SIMULIID GENERA OCCURRING IN THE SOUTHERN HEMISPHERE

KEY TO GENERA OF SIMULIIDAE IN THE SOUTHERN HEMISPHERE

(1) Adult with 11-segmented antennae, vein Cu_2 curved or straight, pedisulcus absent; pupa with large horns on dorsum of 9th abdominal segment, basal rows of spines on abdominal tergites, segments 5–8 sclerotised; cocoon loosely woven, of indefinite shape; larva with or without semicircular sclerite and backward struts on anal segment, often with the frons angulate postero-laterally .... (2)

Adult with 10- or 11-segmented antennae; vein Cu_2 with double curve, pedisulcus well developed; pupa with small horns on 9th segment, with or without basal row of spines on abdominal tergites, segments 5–8 not sclerotised; cocoon closely woven, of definite shape; larva with or without semicircular sclerite and backward strut, never with frons angulate postero-laterally .... (3)

(2) Adult with Cu_2 curved (except *umbratorum* (Tonnoir)); larva with semicircular sclerite and backward strut absent, frons often angulate, ventral tubercles usually absent, ventral incisure moderately to strongly developed .... *Cnephia.*

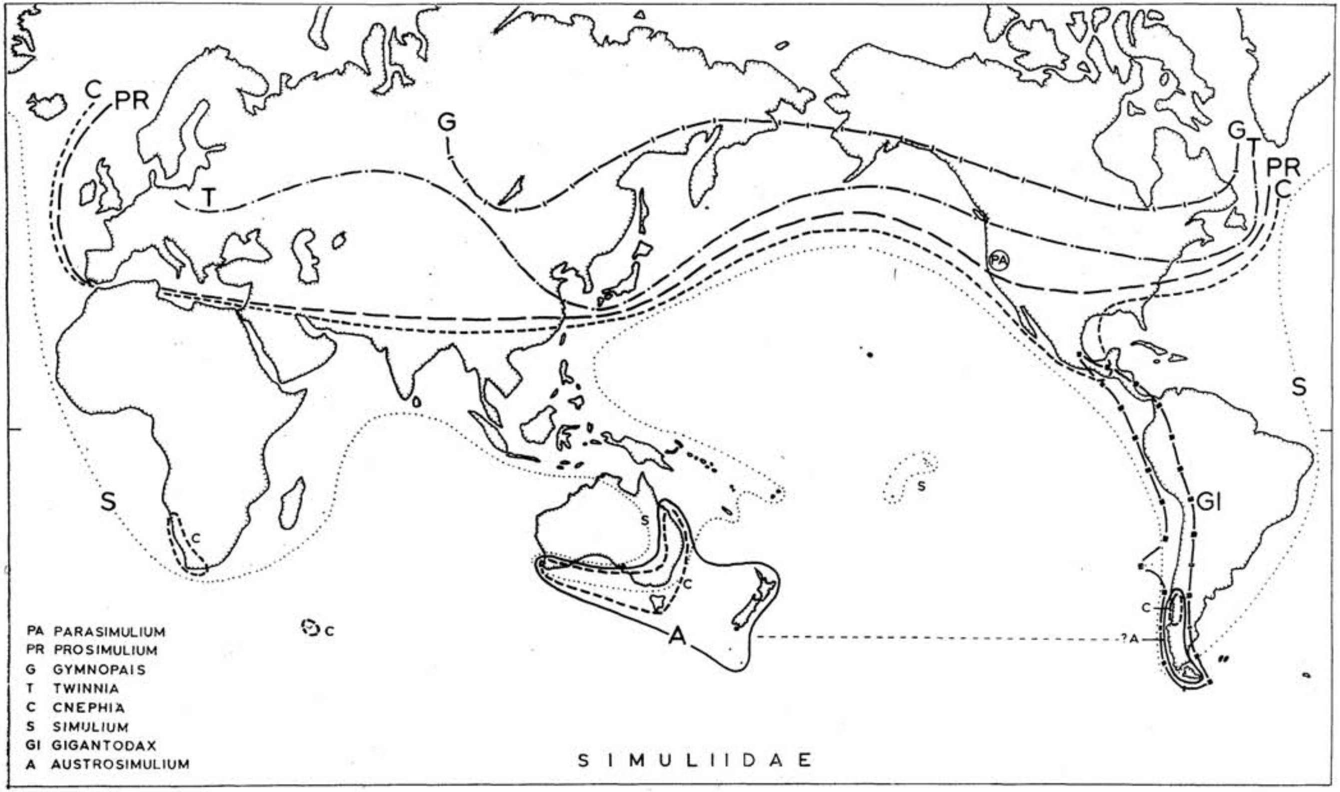

FIG. 1—The world distribution of the genera of Simuliidae.

Adult with Cu_2 straight; larva with semicircular sclerite and backward strut present, frons not angulate, ventral tubercles present (except *aquamarensis* (de Leon)), ventral incisure small or absent .... *Gigantodax.*

(3) Adult with 10-segmented antennae (9 in *bancrofti* (Taylor)), mandible toothed only on inner side of apex (except *anthracinum* (Bigot)), stem of genital fork broad tapering cephalad without thicker median rib (except *anthracinum*); pupa without basal row of spines on abdominal tergites (except *anthracinum*), breathing organ frequently horned, always with filaments (except *anthracinum*); larva with backward strut always present, ventral tubercles present or absent, semicircular sclerite present or absent, anal gills always simple .... *Austrosimulium.*

Adult with 11-segmented antennae (if 10, as in *varicorne,* larva with compound anal gills), mandible usually toothed on both sides of apex, stem of genital fork a narrow rib without lateral wings; pupa with basal row of spines on abdominal tergites, breathing organ never truly horned, often without fine filaments; larva without backward struts, ventral tubercles present or absent, semicircular sclerite present or absent (if present, as in *S. (S.) jacumbae* Dyar and Shannon and *S. (Hearlea)* spp., anal gills compound), anal gills simple or compound .... *Simulium.*

THE GENUS SIMULIUM

South Africa

The African Simuliidae have been monographed by Freeman and de Meillon (1953) who recognised two divisions and seven species-groups in *Simulium.* Crosskey (1960) found that the larval groups which he established for West African species of *Simulium* correlated satisfactorily with the groupings made by Freeman and de Meillon mainly on adult and pupal characters. Only *S. ruficorne* Macquart occurs outside Africa and there are no strong Oriental affinities. The *medusaeforme* group has affinities with the Palaearctic *S. (Wilhelmia) equinum* L. A number of species are widespread in the region and the extent of local endemism is not pronounced except in the East African highlands. On a numerical basis the centre of the fauna appears to be on or south of the Equator.

South America

There is no comprehensive review of the genus *Simulium* in South America or study of the segregates present and their affinities. *Simulium (Hearlea)* which is present in North and Central America is not reported as present. Some species lack the calcipala, many have branched pupal trichomes and some have the larval abdomen of *Cnephia*-form. An analysis of distributions in the southern part of the continent suggests a break in distribution near Mendoza. No species extends far to both north and south of this point. Several northern species have their southern limit here and eight southern species have their northern limit here or further south. This distribution is similar to that of *Cnephia.*

Australia

The Australian *Simulium* fauna has been studied by Tonnoir (1925) and Mackerras and Mackerras (1948, 1949, 1950, 1952, 1955) who distinguished three species-groups on the characters of the adults. The *ornatipes* group, includes only this species which is widespread in Australia and also in New Guinea and New Caledonia. The *peregrinum* group also contains only the one species which occurs in Queensland and has affinities with Edwards' (1934) C-group in Java. The *clathrinum* group contains seven species of which the majority occur in Queensland and New South Wales with two extending to Victoria. One species (near *clathrinum* M. and M.) occurs in New Caledonia. The genus is absent from Tasmania. The colonisation of Australia from the north is suggested by the relatively small number of species, with numbers decreasing towards the south, and affinities with those of the Malayan region. There is an absence of forms with strongly inflated breathing organ filaments, or branched pupal trichomes. Only *papuense* Wharton has a fenestrated cocoon and *peregrinum* M. and M. a latticed cocoon.

A single species *S. jolyi* Roubaud is present in New Hebrides and Fiji, two species are present in New Caledonia, while the Society Islands and Marquesas Islands each have three species. None have been found on intervening high islands such as Rarotonga and Samoa.

THE GENUS GIGANTODAX

This is the only genus other than *Simulium* which bridges the tropics though it barely reaches the Nearctic Region in Mexico and does not occur in the lowlands. The nineteen species which have been described are, in general, confined to the Andean chain and have been recorded at altitudes of from 3,000 m in southern Mexico to sea level in Tierra del Fuego. The distribution of the species is as follows: Mexico, 1; Guatemala, 2; Bolivia, 1; Peru, 3; Argentina, 2; Chile, 12.

For the purposes of comparison with *Austrosimulium* and other genera a brief review of morphological characters of *Gigantodax* is presented below. It is based in part on larval and pupal material of *G. antarcticum* (Bigot), *G. chilense* (Philippi), *G. femineum* Edwards, and *G. fulvescens* (Blanchard), which was supplied by courtesy of the British Museum. The principal publications containing descriptions are those of Edwards (1931); Andretta and Andretta (1947); Wygodzinsky (1949, 1951, 1952, 1958); Vargas and Najera (1951, 1957); and Dalmat (1955).

The adults tend to be of large size and yellowish, orange, or reddish coloration is common. The presence of ciliated setae in the adults of *G. horcotiani* Wygodzinsky has been noted by Wygodzinsky (1949). *G. femineum* Edwards is notable for the dichoptic eyes of the male but the type may be a gyandromorph. The tarsal claws have a basal tooth in all species for which the condition is stated. The calcipala is long and the pedisulcus absent. The wings have no basal cell and both Cu_2 and An are straight. Spiniform setae are present on the costa and, at least in a number of species, on the distal part of R_1 also. In the male genitalia the parameral hooks are strongly developed and the teeth on the dististyle vary from two to three. The stem of the female genital fork is narrow and not tapered.

The sculpturing of the integument of the pupa, where it is described, is of small circular platelets or asperities. On the head only the facial trichomes between the bases of the antennae are present, the frontal and epicranial trichomes are absent. On the thorax the two trichomes usually present in other genera on the propleural lobe are absent in the species examined. The pupal breathing organ varies in type. There are 18 filaments which are simple and bifurcated in *fulvescens* and *chilense,* and tend to be grouped into dorsal and ventral groups and coalesced at the bases in *antarcticum* and *femineum*.

There are thirteen filaments in *horcotiani* Wygodzinsky and *aquamarensis* (de Leon) and eight in *wrighti* Vargas, Martinez and Diaz, the filaments tending to be inflated and in some species with the terminal part of the filament much finer. The branches are inflated and reduced to four in *wittmeri* Wygodzinsky and three in *abalosi* Wygodzinsky and *bolivianum* Enderlein, with the finer filaments present or absent. Hooks are present on abdominal tergites three and four, hairs only on five, a basal row of spines on six to eight, and long dorsal horns on nine. Ventral hooks are present on segments five to seven. No anchor hairs or curly hairs have been seen on segment nine in the species examined or in those figured.

The body of the larva is of normal fusiform shape posteriorly. The frontal sclerite is widest posteriorly with the postero-lateral angles rounded. The post-frontal lobes are tapering and triangular, connected with the epicranium and nearly meeting in the median line. The antennae have segment one as long as or longer than two and one plus two sub-equal to three plus four. The mouth-brushes are normal, many rayed, with fine biordinal hairs. The mandible is normal without flattened apically-multifid bristles. The submentum is of *Prosimulium* type, parallel sided apically, with fifteen teeth. The submental setae are four or more, usually simple but bifid in *wrighti* and *aquamarensis*. The ventral incisure is absent or very slight, broad, and shallow. The posterior tentorial pits are not markedly elongate. Ventral tubercles are present, except in *aquamarensis*. The anal gills are simple trilobed. Anal scales or spines are present, except in *aquamarensis*. The anal sclerite is X-shaped. the median piece open or closed behind, enclosing a number of circular pigmented spots (cf. *Hearlea*); the posterior arms overlapping or articulated with the ends of the semicircular ventral sclerite which is always present; the expansions of the semicircular sclerite are further from the dorsal end than in *Austrosimulium* and may be horizontal or bent ventrad. Backward interarm struts are present. The crochet ring is normal.

The cocoon is loosely woven, of indefinite shape, some with a curtain over the aperture, not stalked, and apposed to the substratum over its whole length. In some of the northern species it may cover only part of the abdomen. In *bolivianum* and *abalosi* it is of more definite form and closer texture.

Enderlein's genus *Archinesia,* erected for *femineum,* was recognised by Vargas and Najera (1951) but not by Smart (1945). There appears to be no satisfactory basis at the present time for the recognition of species-groups in this genus. The restriction of the species with simple filamentous breathing organs to the Chilean area, contrasts with the northern and eastern distribution of the species with inflated and reduced filaments.

The Central American area has an interesting assemblage of unusual species of *Gigantodax, Cnephia,* and *Simulium* but it is not possible at the moment to discuss the centre of origin of *Gigantodax.* Edwards (1931) mentioned a number of resemblances to *Simulium* (*Eusimulium*) but believed that the species which approached *Gigantodax* most closely was *Cnephia umbratorum* (Tonnoir) which has Cu_2 only slightly curved. Mackerras and Mackerras (1949) considered that *Gigantodax* was closely related to *Prosimulium* and *Cnephia,* and *Rubcov* (1959) regarded it as a vicarious equivalent of the Holarctic *Cnephia.*

THE GENUS CNEPHIA

South America

Four species are recorded by Edwards (1931) from the Puerto Montt - Bariloche area, about 40° S. Unlike *Gigantodax* no species of *Cnephia* are recorded between here and Guatemala, and the Guatemalan species are unusual either in the type of pupal breathing organ (*C. aguirrei* (Dalmat), *C. roblesi* de Leon, *C. grenieri* Vargas and Najera and *C. pacheco-lunai* (de Leon)), or in the possession of ventral tubercles in the larva.

Of the Chilean species *C. dissimile* Edwards was compared by Edwards with the Australian *C. aurantiacum* Tonnoir in that vein Cu_2 is not strongly curved. The species was placed by Enderlein in the Holarctic genus *Stegopterna* Enderlein, which Rubcov (1959) considered to have affinities with both *Prosimulium* and *Austrosimulium.* Parameral hooks are present in the male genitalia of this species though they are absent in *C. atroparvum* Edwards, a species which Edwards stated was very similar to *Austrosimulium anthracinum* Bigot except in the number of antennal segments. The calcipala is absent in *C. montanum* (Philippi). *Cnephia gynandrum* Edwards was made the type of Eenderlein's genus *Cnesia,* which was recognised by Vargas and Najera (1951) but not by Smart (1945), since the type is a probable gynandromorph.

The immature stages of only *C. dissimile* are known. The pupal breathing organs have 30–35 filaments. The pupa is unusual in the genus in having no row of basal teeth on abdominal tergites five to eight but has four apical hooks on the eighth tergite. The larva has the *Cnephia*-form of abdomen and is without ventral tubercles. The submental teeth are small and the sides of the submentum not parallel. The frons is angulate posterolaterally.

South Africa

The *Cnephia* fauna has been reviewed by Freeman and de Meillon (1953) and by de Meillon (1955). Six species are known from Cape Province and two from South-West Africa. Rubtzov (1959) stated that the affinities of these species, in spite of the spiniform setae on the wing veins, were with *Prosimulium* rather than *Cnephia,* and that they should be placed in a separate genus.

Crozet Islands

The single species described from here, *C. crozetense* Womersley, though aberrant, appears to belong to the same stock as the South African *Cnephia* (Dumbleton, 1962b).

Australia

Six species of the genus *Cnephia* have been described, and Mackerras and Mackerras (1949) recognised two species groups—largely on the characters of the adults, since the larval and pupal stages of the *terebrans* group are unknown. The *aurantiacum* group was thought to show an almost perfect transition from *Cnephia* to *Gigantodax*. The species of the *terebrans* group were considered to resemble *Austrosimulium* in their smaller size, darker colour, and in palpal and abominal characters in the female. The genital fork of the female is not of *Austrosimulium* form however, and the mandible of *C. terebrans* (Tonnoir) is toothed on both sides of the apex. *C. fergusoni* (Tonnoir), also of the *terebrans* group, resembles *Prosimulium* in the absence of spiniform setae on the wing veins. The distribution of the species ranges from Western Australia to Tasmania and the southern and south-eastern states, but there are northern occurrences in both south and north Queensland.

Each of these three Southern Hemisphere *Cnephia* faunas has a restricted distribution in the south of its continent, though there are northern occurrences in South-West Africa and North East Australia.

Within the Simuliidae these groups are relatively primitive, certainly more so than *Simulium,* and their present distribution and faunal associates suggest that they are part of a distinct and relatively old faunal element. They appear to be humidity-dependent though the S.W. Africa occurrence is apparently inconsistent. Water temperatures may be an important factor, though they extend into warmer temperatures in N.E. Australia. The three distribution areas are largely bounded on the north by arid areas at the present time, though there is an eastern humid corridor to the north (which passes however to higher temperatures) in both South Africa and Australia. There is no evidence of extension along it in Africa though there is in Australia. The present distribution is probably mainly the result of historical factors of climate and faunal dispersal, possibly preserved by advantages in competition with *Simulium* in their characteristic habitats as is suggested by de Meillon (1955).

In so far as generalisations are permitted by the published descriptions and available material all three faunas show considerable diversity within themselves. This diversity applies to characters which are commonly used in the Simuliidae as indicators in classification and phylogeny. These include, for example, the presence or absence of scales in the mesonotal ventiture, the forking and setation of the wing veins, the form of Cu_2, the presence or absence of the calcipala and pedisulcus, the number of spines on the genital styles and the submentum-form in the larva. This diversity is of similar range in the Australian and African faunas and the limited information suggests it is present also in the South American fauna. The African and Australian faunas (and, discounting the aberrant larva, the species from the Crozets also) in particular would appear to be segments of the same genetic stock. This stock has strong *Prosimulium* affinities, which are perhaps strongest in the African fauna. Examples are the absence of the calcipala and of spiniform setae on the wing veins in some species, and the type of larval submentum in others.

Three characters in the larvae of the Southern Hemisphere *Cnephia,* while they are imperfectly clarified in *Prosimulium* itself, are suggestive. One is the sub-parallel apex of the submentum (as in *C. damarensis* etc.), another is the angulate character of the frontal suture postero-laterally, and the third is the strong development of the epicranium as post-frontal lobes rather than as isolated (cervical) sclerites.

Few characters separate the Australian and African faunas. In the African species the extremely short branching of the pupal breathing organ, giving in most cases the appearance of filaments arising directly from the common stem, and the larger number of spines or teeth on the style of the male genitalia are examples. No Australian species has the reduced dentition of the mandible and maxilla which is present in some South African species.

The Southern Hemisphere *Cnephia* differ from *Prosimulium* in the following characters: anterior gonapophyses in the female not produced between the anal lobes, not more than vestiges of branching in vein Rs, absence of modified 2- or 3-branched pupal breathing organs bearing fine filaments on the surface of the branches (e.g., as in *P. onychodactylum* D. and S.) and, in African forms, the larger number of teeth on the style of the male. The larvae differ from those of *Gymnopais, Twinnia,* and *Prosimulium,* and from those of *Cnephia (Astega),* in that all segments of the antennae (except in *C. (?) umbratorum* (Tonnoir)) are pigmented, and not the third only.

Fewer characters separate the Southern Hemisphere *Cnephia* and the Northern Hemisphere *Cnephia.* Except in *Cnephia (Astega)* which is well characterised, more especially in the larva, by the very deep ventral incisure, and the foliate apically-multifid setae on the mandibular brush, the segregates of Northern *Cnephia* are not strongly characterised. Posteriorly rounded frontal sutures and reduced prominence of the submental teeth appear to be more common in the Northern Hemisphere *Cnephia.* Development of the posterior arms of the X-sclerite tends to be stronger in the Southern Hemisphere *Cnephia.*

The northern *Cnephia (Mallochianella) dacotensis* D. and S. has a number of features in common with some of the Southern Hemisphere *Cnephia* species: larval antennal segments 1 and 2 pigmented, mandibles and maxillae in the female with dentition lacking (as in *C. turneri* Gibbins), frontal sutures more nearly angulate.

Unfortunately the South African *Cnephia* larvae are not described in detail and the larvae of the *terebrans* group in Australia are unknown. Only one of the Southern Hemisphere species (unnamed, Wharton, 1949) from Australia has ventral tubercles reported as present in the larva.

Cnephia is, in general, absent from the tropics, though somewhat aberrant species occur at higher elevations in Guatemala and Mexico.

There is little within these Southern Hemisphere *Cnephia* faunas to suggest their origins and dispersal routes. The absence of the genus from

New Zealand, which has many other reputed Palaeantarctic taxa, and their presence in South Africa, from which many other such taxa present in Australia and New Zealand (including *Austrosimulium* and *Nothofagus* and *Peloridiidae*) are absent, is difficult to explain in terms of southern origin and entry. The strength of the affinity, especially of the African *Cnephia* fauna, with the primitive Holarctic *Prosimulium* suggests rather strongly that they are of directly northern origin and entry. Certainly some segregates of Northern Hemisphere *Cnephia* such as *Astega* Enderlein, are not present in the Southern Hemisphere, nor does *Ectemnia* Enderlein appear to be, but while relationships with *Cnephia* (*Cnephia*), Enderlein are not clear, those with *C.* (*Mallochianella*) Enderlein are more suggestive.

Rubcov (1959 *et seq.*) has suggested that the Southern Hemisphere *Cnephia* species are not properly placed in that genus, and that they have strong *Prosimulium* affinities and should be in a distinct genus.* It has been shown above that the difficulty is in providing an adequate definition of such a genus until both the Northern Hemisphere and the Southern Hemisphere segregates are more closely studied.

THE GENUS AUSTROSIMULIUM

The genus *Austrosimulium* Tonnoir (1925) was segregated from the genus *Simulium* Latreille, at that time the only generally recognised genus in the family, solely by the ten-segmented antennae of the adult. The fauna studied by Tonnoir was restricted to Australia and New Zealand. Tonnoir mentioned that the larvae of all the New Zealand species possessed a strut (backward strut) between the anterior and posterior arms of the anal sclerite and figured it also in several Australian species.

Edwards (1931) treated *Austrosimulium* as a sub-genus of *Simulium* and remarked on the presence or absence of the tooth on the tarsal claw of the females and the horned condition of the pupal breathing organ.

Smart (1945) gave a brief diagnosis of the genus, mentioning the presence of the calcipala and the pedisulcus on the hind tarsus, the basal cell in the wing, the definite shape of the cocoon, and the presence of ventral abdominal tubercles and simple anal gills in the larva.

Mackerras and Mackerras (1949), as a result of their revision of the Australian species, gave a full characterisation of the genus, defined the three Australian species-groups and included the New Zealand species in their *mirabile* group.

The genus *Austrosimulium* includes, at present, nineteen species though there are at least three undescribed species in New Zealand which belong to New Zealand species-groups defined below. The typical sub-genus is represented only in Australia (10 species) and New Zealand (8 species),

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Footnote inserted in proof

*Rubcov has since (Simuliid genera in the fauna of Ethiopian Region. Zoological Journal, USSR 12 (10): 1488–1502. 1962. In Russian, English summary) erected a new genus *Paracnephia,* of which *Cnephia muspratti* Freeman and de Meillon is the type species. The genus includes six of the South African species of *Cnephia,* the two remaining species, *C. brincki* de Meillon and *C. thornei* de Meillon, not being mentioned.

the single South American species having been placed in a separate subgenus by Wygodzinsky and Coscaron (1962). The species included in each species group are listed in the following key.

Key to the Sub-genera and Species-groups of Austrosimulium

(1) Female mandible toothed on one side of apex only, spiniform setae not present on distal R_1 vein; stem of female genital fork broad, tapering cephalad, without narrow parallel-sided median rib; basal row of spines on abdominal tergites of pupa absent; pupal breathing organ never lamellar and pseudosegmented, always with filaments; anal spines absent in larva .... (Aust. and N.Z.) .... subgenus *Austrosimulium* .... (2)

Female mandible toothed on both sides of apex; spiniform setae present on distal R_1 vein; stem of female genital fork if broad and tapering with prominent narrow parallel-sided median rib; basal row of spines on abdominal tergites of pupa present; pupal breathing organ lamellar, pseudosegmented, without filaments; anal spines present in larva (Southern Chile) .... subgenus *Paraustrosimulium* Wygodzinsky and Coscaron. (Includes only *A. (P.) anthracinum* (Bigot)).

(2) Antenna of adult with segment 3 longer than 2 (except in *torrentium* Tonnoir), female tarsal claw without tooth (with only a small tooth in *magnum* M. and M.) pupa without ventral abdominal hooks; cocoon without floor; larva without semicircular sclerite, with or without ventral tubercles, antennae with segments 1, 2, and 3 subequal in length .... (*bancrofti* and *fusiosum* groups) .... (3)
Antenna of adult with segment 2 longer than 3, tarsal claws with or without tooth; pupa with ventral abdominal hooks present; cocoon with or without floor; larva with semicircular sclerite and ventral tubercles present, antenna with segment 2 short and 3 longer than 1 plus 2 .... (*mirabile, ungulatum,* and *australense* groups) .... (4)

(3) Antenna of adult with segment 3 much wider than 2 (except in *magnum*), abdomen with pale ashy patches or hairs; pupa with hooks or curly setae on abdominal tergites 5 to 8; larva without ventral tubercles (Australia) .... *bancrofti* group.

(Species included: *A. bancrofti* (Taylor), *A. magnum* M. and M., *A. pestilens* M. and M.)

Antenna of adult with segment 3 little wider than 2, abdomen dark; pupa without hooks or curly setae on abdominal tergites 5 to 8; larva with ventral tubercles (Australia) .... *furiosum* group.

(Species included: *A furiosum* (Skuse), *A. torrentium torrentium* Tonnoir, *A. torrentium hilli* M. and M., *A. victoriae* (Roubaud).)

(4) Female without tooth on tarsal claw; pupa without ocular spine; larva with dorsal ends of semicircular sclerite expanded or forked (New Zealand) .... *australense* group.

(Species included: *A. australense* (Schiner), *A. laticorne* Tonnoir, *A. longicorne* Tonnoir, *A. multicorne* Tonnoir, *A. tillyardi* Tonnoir.)

Female (except one N.Z. sp.) with tarsal claw toothed; pupa with ocular spine; larva with or without expanded ends of semicircular sclerite .... (*mirabile* and *ungulatum* groups) .... (5)

(5) Semicircular sclerite without dorsal expansions ....
.... New Zealand .... *ungulatum* group.
Species included: *A. ungulatum* Tonnoir, *A. vexans* (Mik.)
Australia .... *cornutum* section *mirabile* group).

(Species included: *A. cornutum* Tonnoir, *A. crassipes* Tonnoir.)
Semicircular sclerite with dorsal expansions ....
(Australia) .... *mirabile* section *mirabile* group.

(Species included: *A. fulvicorne* M. and M., *A. mirabile M. and M.*, *A. montanum M. and M.*).

The distribution of the species groups in Australia and New Zealand is shown in Fig. 2 in which the morphological identity of the *ungulatum* group (U) with the *cornutum* section of the *mirabile* group (Mc) is indicated by the employment of an unbroken line to show the distribution-areas of both groups.

South America

Edwards (1931) placed in *Austrosimulium* two species from Southern Chile, *Simulium anthracinum* Bigot and *S. moorei* Silva Figueroa. *A. moorei* was subsequently considered by Wygodzinsky (1953) to be a synonym of *A. anthracinum*. Wygodzinsky redescribed the female and gave the first description of the pupa and cocoon and Wygodzinsky and Coscaron later (1962) gave the first description of the male and created a new sub-genus for the species. The larva was first described by Dumbleton (1960) who considered that the species was not closely related to the other members of the genus.

The attribution to *Austrosimulium* of a disjunctive austral distribution therefore rests on the existence of a single South American species of debatable affinities. This species occurs from Tierra del Fuego to Angol in Southern Chile, the northern limit of distribution coinciding approximately with the northern limit for species of the genus *Cnephia* in South America and with the position of an apparent break in the distribution of species of *Simulium*. In addition to the foregoing two genera the faunal associates of *A. anthracinum* include *Gigantodax*.

The affinities of *A. anthracinum* are critical in any consideration of possible relationships, not only between *Gigantodax* and *Austrosimulium*, but also between the Australian - New Zealand and South American segments of *Austrosimulium*, and thus for the alternative hypotheses as to the evolution and dispersal of Southern Hemisphere Simuliidae. The problem in the generic placement of this species lies in the interpretation of those characters which set it apart from all other *Austrosimulium* species, and, in particular, those which are characteristic of *Simulium*. Whether these are to be regarded

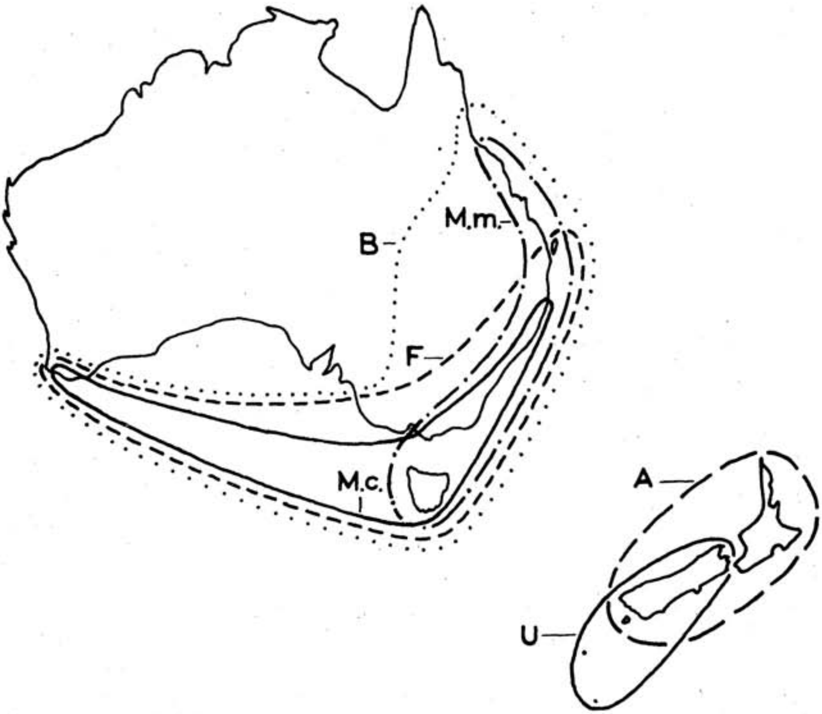


FIG. 2—The distribution of *Austrosimulium* species-groups in Australia and New Zealand.

A	*australense* group,
U	*ungulatum* group,
B	*bancrofti* group,
F	*furiosum* group,
M.c.	*Mirabile* group (*cornutum* section),
M.m.	*Mirabile* group (*mirabile* section).

as of continuous descent indicating close relationship, as chance segregations of ancestral characters, or as convergence in different stocks may be determinable by chromosomal evidence as to the genetic affinities of the species.

The attribution of *anthracinum* to *Austrosimulium* rests principally on two characters, the ten-segmented antennae of the adult, and the possession of a backward strut in the anal sclerite of the larva, which are characteristic of the genus as a whole. The relationships of several species in other genera which possess ten-segmented antennae may be briefly considered in the light of other characters. In *Simulium* these include an unnamed species (*Simulium* species J4) from Japan (Bentinck, 1955) and *S. varicorne* Edwards (1934) from Java. The larva of the Japanese species is unfortunately unknown. The larva of *S. varicorne* differs from that of *A. anthracinum* in the deep ventral incisure of the head, the presence of tubercles and spines on the body segments, the compound anal gills, and the absence of the backward strut of the anal sclerite.

The pupae of the three species are similar in that all have simple trichomes, small anal horns and a row of basal spines dorsally on some abdominal segments. The cocoons are closely woven with no anterior dorsal processes. The pupal breathing organ in the two *Simulium* species is not lamellar but 8-filamented. The ventral abdominal hooks, which are not described in *S. varicorne,* are simple in *A. anthracinum* but bifid in *Simulium* species J4.

The female of *S. varicorne* is not known but the tarsal claw of the females in the other two species has a basal tooth. The mandible of the female is toothed on both sides of the apex in *A. anthracinum* but in *Simulium* species J4 it is toothed on only one side.

The males of the two *Simulium* species have large and prominent parameral hooks in the genitalia and fine hair on the katepisternum. This latter is absent in *A. anthracinum* and the parameral hooks are less strongly developed.

These two *Simulium* species show some evidence of relationship but are probably unrelated deviant species of *Simulium*. Their relationship with *A. anthracinum,* if any, is more distant.

Of the other species with ten-segmented antennae *Prosimulium isos* Rubtzov and *Greniera fabri* Doby and David (1959) appear to be aberrant species of typically prosimuliine genera, though the long third segment in the larval antenna of *G. fabri* recalls the condition in some *Austrosimulium*.

The second character—the backward strut in the anal sclerite of the larva—is known to occur only in species of the simuliine genus *Austrosimulium* and the prosimuliine genus *Gigantodax*. Since *A. anthracinum* is simuliine in facies (cf. cocoon) and shows no evidence of any near affinity with *Gigantodax* this might be taken as confirming that it is congeneric with other *Austrosimulium* species, but neither the presumed derivation of *Austrosimulium* from *Gigantodax* nor the phyletic significance of the strut is so well established as to exclude the possibility of the latter occurring in species of genetic stocks other than these two. If the characters of *A anthracinum* are examined in relation to those of the existing species groups in the Australian and New Zealand faunas it is found to fit none of them. It comes nearest to the Australian *furiosum* group in the form of the antenna of the female, the absence of the semicircular sclerite, and the presence of the ventral tubercles in the larva. It differs, however, in the presence of a tooth on the tarsal claw of the female and the presence of ventral hooks on the abdomen of the pupa. These characters and the form of the larval antenna might suggest affinities with the *mirabile* and *ungulatum* groups, but it differs from these also in the absence of the ocular spine in the pupa, the processes on the cocoon, and the semicircular sclerite in the larva.

A. anthracinum presents a number of characters which are unique in *Austrosimulium* but occur in other genera including *Simulinum,* and strongly suggest affinity with that genus. Apart from the presence of backward struts in the anal sclerite of the larva none of the other characters, except possibly the form of the larval antennae, would be anomalous in a species of *Simulium*.

The mandible of the female was stated by Wygodzinsky (1953) to have normal dentition, but the disposition of the teeth was not given. A reared specimen from Tierra del Fuego was kindly supplied by Dr Wygodzinsky and Dr Coscaron and this proved to have the mandible toothed on both the outer and the inner sides of the apex—a condition which is unique in *Austrosimulium* and is further discussed below.

Wygodzinsky (1953) figured two examples of the female genital fork in *A. anthracinum,* but neither of these has the broad stem, tapering cephalad, which is characteristic of all three Australian species groups (Mackerras and Mackerras, 1948, 1949,), and of New Zealand species. Wygodzinsky and Coscaron (1962) stated that the stem of the genital fork is broad. Examination of a stained preparation of the genitalia of a female bred and supplied by these authors shows that on each side of the prominently sclerotised median element, which is parallel-sided and widened apically, there is a thin transparent membrane which is probably not evident without staining. This may be present in some form in all Simuliidae, but in the Australian and New Zealand species of *Austrosimulium* it is thicker and more evident, and the median thickening or rib is absent. The presence of spiniform setae on the distal part of the R_1 vein in the wing of *A. anthracinum,* the type of pupal breathing organ, and the presence of a basal row of spines on the abdominal tergites of the pupa, are also unique in *Austrosimulium*.

The stronger development of the parameral spines in the genitalia of the male and the presence of anal spines in the larva are also anomalous in a species of *Austrosimulium*.

While a similar form of the breathing organ appears to be characteristic of *Simulium (Hearlea)* the dentition of the mandibles and the development of the spiniform setae shows intra-generic variation in *Simulium* without being characteristic of any particular segregate.

If *anthracinum* is to be placed in *Austrosimulium* these characters must be regarded as subject to intra-generic variation and the species itself as demanding the subgeneric status which Wygodzinsky and Coscaron have given it. There remains some doubt, however, as to whether this gives full weight to its affinities with *Simulium*.

Australia and New Zealand

The views which have been put forward on the classification of the family Simuliidae, based largely on the characters of the adults, have been briefly reviewed above. The taxonomic characters of the pre-adult stages have been discussed elsewhere (Dumbleton, 1962b).

When Tonnoir separated *Austrosimulium* from *Simulium,* he expressed no opinion as to its affinities. The genus was associated with *Gigantodax* in the tribe Austrosimuliini by Smart (1945), following his intepretation of Edwards' views. Mackerras and Mackerras (1949) stated that its relationships, while obscure, appeared to be with the *Prosimulium* complex (presumably referring especially to *Gigantodax*) rather than with *Simulium.* They remarked on the resemblance between *Austrosimulium* species and those of the *Cnephia terebrans* group. Rubcov (1959) considered *Austrosimulium* to have distinct relationships with *Prosimulium* and *Helodon* Enderlein in respect of the structure of the pupal thorax and breathing organs, but it is doubtful if these are reliable generic indicators. He also considered that the antennae and submentum of the larvae indicated affinities with *Stegopterna.* The species which he refers to *Stegopterna* (*mutatum* Malloch, *permutatum* Malloch and *dissimile* Edwards) appear, however, to have much clearer relationships with *Cnephia* and *Prosimulium.* Grenier and Rageau (1960) also associated *Austrosimulium* with *Gigantodax* in the tribe Austrosimuliini. The basis for this association of *Austrosimulium* and *Gigantodax* appears to be (a) the common possession of backward struts and a semicircular ventral sclerite in the anal sclerite of the larva, (b) wing vein Rs being convex with macrotrichia distally on the upper surface. These characters (except the backward strut) appear however in some species or segregates of *Simulium.* Edwards (1931) himself stated that "apart from the reduction in the number of antennal segments the species of *Austrosimulium* are similar to those of *Eusimulium,* having the calcipala well developed, pedisulcus present and usually distinct, small basal cell rarely distinguishable, basal section of radius hairy, a row of hairs on the surface of Rs distally, costa with the usual minute spinules, R_1 and Rs ending close together, and Cu_2 with a distinct double bend".

The significance of the most prominent character, the similarity of the larval anal sclerites in *Austrosimulium* and *Gigantodax* is uncertain. It could be due to either parallel evolution in more recently separated lines or to convergence in older lines.

A number of characters bearing on the relationship between *Simulium* and the species of *Austrosimulium,* other than *anthracinum,* are considered below.

Relationships

Adult

The antennae are 10-segmented in *Austrosimulium* and 11-segmented in *Simulium,* but a similar difference separates *Prosimulium* from the closely related *Gymnopais* and *Twinnia.* The species with ten-segmented antennae occurring in *Simulium* have been discussed earlier.

The mandibles in the females of all *Austrosimulium* species which have been examined are toothed only on the inner side of the apex. Rubcov (1959) stated that in the family Simuliidae the mandibles are usually toothed on both sides, and seldom on one side only. Rubcov (1940) figured the mandible of *Simulium* (*Eusimulium*) *angustitarse* (Lundstr.) which is toothed on only one side. Freeman and de Meillon (1953) stated that in the majority of species the mandibles are toothed on both sides, but that the outer teeth are absent in a number of species. Gibbins (1938) stated that the outer teeth are absent in *S. (S) damnosum* Theobald and in *S. (E) neavei* Roubaud. Bentinck (1955) figured the mandibles of two unnamed Japanese species of *Simulium* (J4, and J14) as lacking the outer teeth. In the South African species of *Cnephia* the mandibular dentition is vestigial in several, but it is present on both sides in *C. turneri* Gibbins (Freeman and de Meillon, 1953). The mandible of *C. crozetense* Womersley is toothed on both sides (Seguy, 1940), as is that of *C. terebrans* Tonnoir. Dr Wygodzinsky (in litt.) informs me that it is toothed on both sides in the South

American *C. dissimile,* and in species of *Gigantodax, Austrosimulium* (with the exception of *anthracinum*) is exceptional in that the absence of the outer teeth is characteristic of the genus. While the same condition occurs in some species of *Simulium* the information available is insufficient to indicate whether it occurs more commonly in species of *Simulium (Eusimulium).*

The basal cell in the wing, noted by Edwards (1931) as being small or indistinguishable in *Austrosimulium,* is absent in *Simulium.*

The calcipala is present in all *Austrosimulium,* but not in all *Simulium* or *Cnephia* (Smart, 1945).

The parameral structures in the male genitalia are simple and not strongly developed in *Austrosimulium,* and also in *Simulium (Eusimulium)* (Freeman and de Meillon, 1953). They are also poorly developed in southern *Cnephia* (with the exception of *C. dissimile*) but are strongly developed in *Gigantodax.*

Pupa

The breathing organ is horned in most *Austrosimulium,* but the filamentous condition occurs and both types may be present in the same species group. None of the species has completely lost the fine filaments. In *Simulium* a rudimentary horn occurs in *S. (E) hisseteum* Gibbins, (Freeman and de Meillon (1953). The somewhat similar form in *Prosimulium ferrugineum* (Wahlberg) is doubtfully identical, and in some other *Prosimulium* species the horn is usually obviously branched.

Some other characters common to *Austrosimulium* and *Simulium,* such as the small horns on the ninth segment, and the weak sclerotisation of the integument on abdominal segments five to eight, appear to be correlated with the type of cocoon.

The absence of the basal row of spines on the abdominal tergites sets *Austrosimulium* apart, but in some species at least there are faint basal bands of spinule combs such as occur with the spines in species of *Simulium* such as *downsi* V. M. and D., *microbranchium* Dalmat, and *jacumbae* Dyar and Shannon (Dalmat, 1955).

Cocoon

Austrosimulium and *Simulium* are the only two genera which, as a whole, are characterised by cocoons that are closely woven, usually thin and always of definite shape, though some *Cnephia* (*Astega*) approach the same condition. Dorsal anterior processes are present in some segregates of both genera. In both genera they may be single or paired. Many of the *Simulium* species whose cocoons have processes have been attributed to *Eusimulium.* In *S. (E) bicorne* Dor. & Rub. they are paired, while in *S. (E) geniculare* Shiraki, *S. (E) latipes* (Meigen), *S. (E) croxtoni* Nicholson and Mickel, and *S. (E) gouldingi* Stone and Jamnback, they are single. There is a single process in a number of species of *S. (Simulium),* such as *S. (S) jacumbae* D. and S.

Larva

The ventral incisure is similar in many *Austrosimulium* and *Simulium* species, but is not shallow or absent as in some *Gigantodax.*

The proportions of the antennal segments in the *mirabile, ungulatum,* and *australense* groups of *Austrosimulium* are characterised by the unusual length of the third segment, while those of the *bancrofti* and *furiosum* groups are similar to those of most *Simulium* and *Cnephia.*

The submental teeth in *Austrosimulium* and *Simulium* are smaller than in most Prosimuliine species (except for some *Cnephia*), and the lateral teeth are not produced so as to give a parallel-sided appearance to the anterior margin of the submentum.

The ventral tubercles are present or absent in both genera.

The anal gills are always simple in *Austrosimulium* as in *Simulium (Eusimulium) aureum* Fries. Compound anal gills occur only in some segregates of *Simulium.*

The backward struts in the anal sclerite are present in all *Austrosimulium,* as they are also in all *Gigantodax.* They were reported to be present in *Simulium nili* Gibbins and *S. ruwenzoriensis* Gibbins (= *S. dentulosum* Roubaud) from Africa (Gibbins 1934), but Crosskey (1960) did not find them to be present in *S. dentulosum.*

The anal spines or scales which are present in *Gigantodax* are absent in *Austrosimulium,* except in *anthracinum.*

The semicircular ventral sclerite is always present in *Gigantodax,* but may be present or absent in both *Austrosimulium* and *Simulium.* It is present in some species of *Simulium (Hearlea)* and in *Simulium (Simulium) jacumbae.* In both *Austrosimulium* and *Simulium* it is, when present, distinctly separated from the posterior arms of the X-sclerite, but in *Gigantodax* its ends articulate with, or overlap, the ends of the posterior arms of the X-sclerite.

It is considered that the affinities discussed above support the view that *Austrosimulium* has a closer relationship with *Simulium* than with *Gigantodax.*

Species-Groups

It is necessary for the purposes of the following section to consider the probable relationships between the species-groups within the genus *Austrosimulium.* The morphological evidence bearing on this is scanty. The *mirabile, ungulatum,* and *australense* groups appear to have more characters which could be regarded as primitive than do the *furiosum* and *bancrofti* groups. These characters are the absence of coloration (except in the *mirabile* section), the more generalised form of the adult antenna, the presence of ventral abdominal hooks in the pupa, the presence of filamentous non-horned breathing organs in the pupae of some species, and the presence of the semicircular sclerites and the ventral tubercles in the larvae. On this interpretation the absence, in the *furiosum* and *bancrofti* groups, of the ventral abdominal hooks in the pupa, and the semicircular sclerite and the ventral tubercles in the larva, is due to loss, and the *Simulium*-like larval antenna is due to convergence. The distinctive larval antennae and the ocular spine in the pupa are however not known in other genera. This and the southern bias in the distribution of the *mirabile* and *ungulatum* groups suggest that these are derived groups, owing their present development to conditions in the Pleistocene.

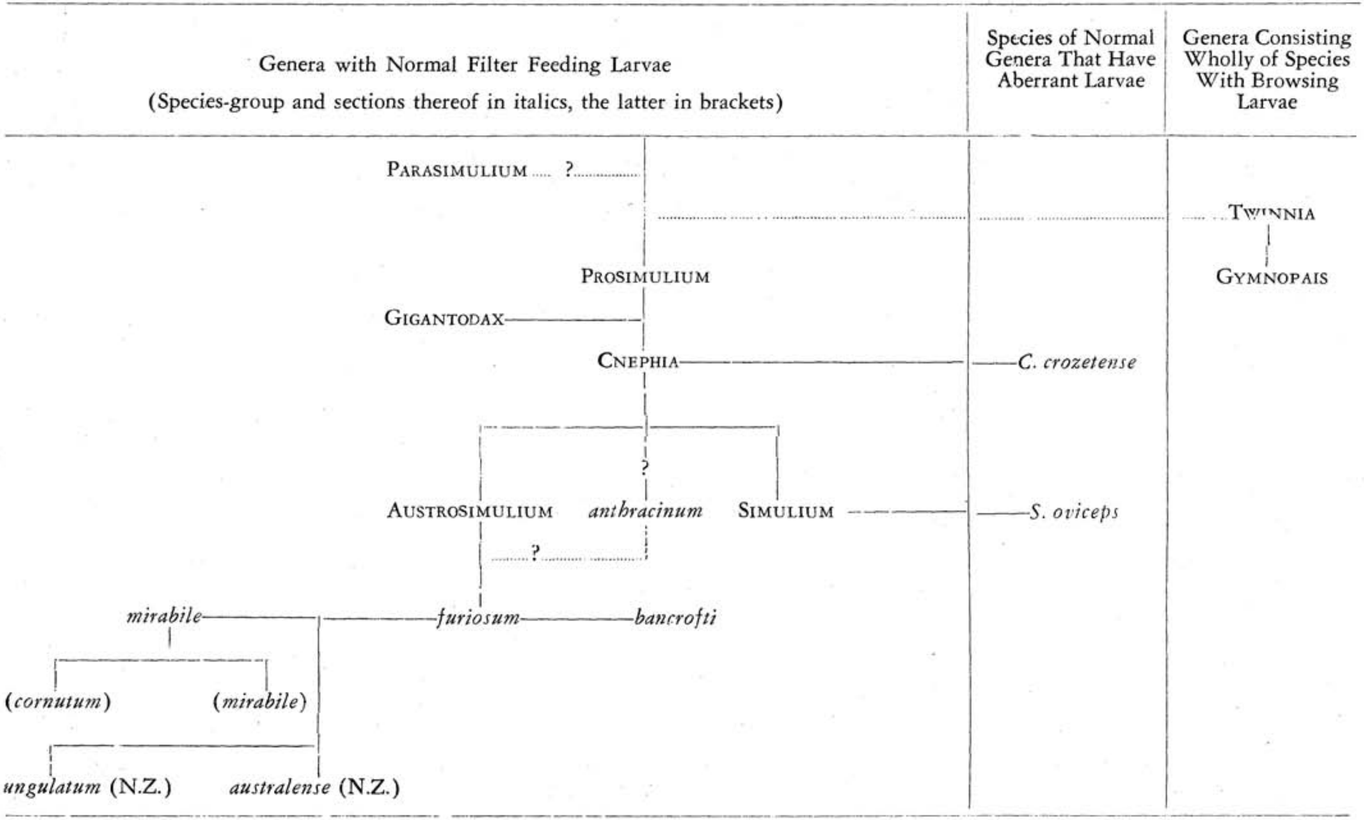
Morphologically, the *furiosum* group occupies a more nearly central position than any of the other groups. The *mirabile-ungulatum* groups are ecologically specialised towards colder habitats and the *bancrofti* group toward habitats of higher temperature or greater aridity, and they may be regarded as derivative segregates of a stock which was close to the present day *furiosum* group. The *bancrofti* group is less widely separated from the *furiosum* group than is the *mirabile* group. The species *A magnum* of the *bancrofti* group, which incidentally has the most northerly distribution of all species of the genus, possesses the ocular spine which is characteristic of the pupae of the *mirabile* and *ungulatum* groups. The fact that the New Zealand *australense* group is intermediate between the *furiosum* and *ungulatum-mirabile* groups suggests that the New Zealand fauna derived from the same *furiosum*-like stock as did the *mirabile* group, but not from a genetically-identical segment of it. The *furiosum* group, with the exception of the unresolved origin of the backward strut in the larva, is most like *Simulium* in the larva. The ventral tubercles are present and the semicircular sclerite is absent. It differs, however, in the pupa. The *furiosum* group is also closest to the South American *A. anthracinum,* which is quite distinct from all other *Austrosimulium* species. The very slender semicircular sclerite in *A cornutum* of the *mirabile* group suggests an earlier stage in the acquisition of the more strongly developed sclerite which is present in the *mirabile* section of the group and in the *australense* group. The absence of the ventral tubercles in the larvae of the *bancrofti* group is presumably due to loss, since they are present in more primitive genera.

The distinctness of the gap which separates the *furiosum* and *bancrofti* groups from the other three groups suggests that it is due to a relatively ancient divergence, and that the *furiosum-bancrofti* stock was in existence when Australia and New Zealand were still connected and is not a product of later evolution in Australia.

The separation of the two sections of the Australian *mirabile* group is only incipient compared with the larger gaps which separate the *australense* group from both the *ungulatum* group and the *mirabile* section of the *mirabile* group. These three groups must derive from a common stock and the divergence in the end products suggests that the segments isolated in Australia and New Zealand were not identical and diverged to some extent in their subsequent evolution. On this reasoning the equivalence of the *ungulatum* group and the *cornutum* section of the *mirabile* group is a parallelism and the *australense* group probably segregated in New Zealand.

An outline of the possible relationships between the genera of the Simuliidae, and of the derivation of *Austrosimulium* and of its species groups is shown diagrammatically in Table 2.

TABLE 2—Relationships in SIMULIIDAE



THE ORIGINS OF THE GENUS AUSTROSIMULIUM

The present distribution of the genera and species of Simuliidae in the world is the current stage in a continuing process of dispersal. The possibility of tracing earlier stages in the evolution and dispersal of the family is limited by the complete absence of fossil evidence in Australia and New Zealand, its virtual absence elsewhere, and the uncertainties inherent in the interpretation of phylogeny.

According to Tillyard (1935) the order Diptera has existed since the Permian, and Rubcov (1959) considered that the genera of Simuliidae were probably segregated by the Jurassic.

Dispersal

It is believed that for these freshwater insects dispersal overland is the most important mode of dispersal, and that the world pattern of distribution could scarcely be as well defined as it is if aerial dispersal over the oceans were not a relatively minor factor, affecting only the details of distribution. There would seem to be little doubt that aerial dispersal does occur. Glick (1939) recorded the capture of Simuliidae in the atmosphere up to 5,000 ft, and even overland mass flights of 50–100 miles are known.

The occurrence of species of Simuliidae on isolated oceanic islands, which are mostly volcanic and of late Tertiary age, would appear to be explicable only in terms of aerial dispersal, either over existing water gaps or via now-submerged archipelagoes. The existence of several species of Simuliidae in both the Marquesas and the Society Islands, with no known occurrence nearer than South America or Fiji, is an example. So also is the occurrence of a species in the Crozet Islands, which are equally distant from both Australia and South Africa. Another possible case is the occurrence of *Gigantodax kuscheli* Wygodzinsky on Juan Fernandez Island, though Wygodzinsky (1952) believed that it was attributable to an ancient land connection. The widespread African species *Simulium ruficorne* Macquart occurs not only on Madagascar but also on Mauritius and Reunion. The species on the Seychelles Islands, *S. speculiventre* Enderlein, is possibly a form of the East African *S. johannae* Wanson (Freeman and de Meillon, 1953). The occurrence of *Austrosimulium vexans* in the Auckland and Campbell Islands is also presumably due to Post-Pleistocene aerial dispersal. The absence of Simuliidae from the Chatham Islands is surprising, but even more paradoxical is the failure of the southern species in New Zealand to cross the twenty-mile barrier of Cook Strait.

While there can be no certainty that New Zealand was not colonised by the aerial dispersal of *Austrosimulium* from Australia it is considered to be unlikely, more especially as no species has reached New Caledonia. The presence of *Simulium ornatipes* Skuse and *S.* sp. near *clathrinum* in New Caledonia and of *S. jolyi* in the New Hebrides and Fiji is possibly due to dispersal via the Melanesian arc, since *ornatipes* at least is present in New Guinea.

It is most probable that *Austrosimulium* reached New Zealand by overland connection, and geological evidence (Benson, 1923; Fleming, 1957) suggests that this was not significantly later than the Cretaceous.

Floral and Faunal Elements in New Zealand

Zonation of the insect fauna within New Zealand is not marked and appears to be primarily an altitudinal or latitudinal effect on the whole fauna. Because of the relative uniformity of the climate there are no faunal elements which are indigenous in the sense of being clearly characterised entities developed within distinctive climatic zones or regions since the isolation of New Zealand. A non-indigenous element is a group or class of taxa whose characteristics are consistent with their being, or being derived from, immigrant components of a fauna which exists elsewhere, or is known from fossil evidence to have existed elsewhere. Implicit in the recognition of such an element is its derivation from a specific source and by a route of entry which, if overland, was a geological probability and indicates the approximate time of entry. In attempting to determine the affiliations of any taxon consideration must be given to its morphological affinities and phylogenetic position relative to related taxa occurring elsewhere, and the distributions of these latter. Physiological or ecological characteristics such as cold-adaptation or time of flight may provide supporting evidence. The views of some of the authors who have considered the biotic elements, of presumed overland entry, which may be present in New Zealand may be briefly reviewed here.

Oliver (1925) and Cockayne (1928) recognised three floral elements, an older Palaeozelandic element and two younger elements, the Antarctic (Oliver) or Sub-Antarctic (Cockayne), and the Malayan (Oliver) or Palaeotropic (Cockayne). Tillyard (1926) recognised in the insect fauna three elements which he named Gondwanan, Antarctic, and Austro-Malayan.

Three elements apparently equivalent to the above were recognised by Jeannel (1942) and named the Palaearctic, Palaeantarctic, and Australian respectively. Mackerras (1950), dealing specifically with the Australian Diptera, recognised two elements of Mesozoic age, an older autochthonous element and a younger Bassian (Antarctic) element, but later (Mackerras, 1962) mentioned a third element, of possible northern origin, apparently corresponding with the Malayan of other authors. There is thus substantial agreement as to the probable existence in New Zealand of three elements of Mesozoic age though there is some difference of opinion as to the periods during which they first appeared in New Zealand. The geological history of New Zealand in the Triassic would suggest that the oldest element is of Jurassic rather than Triassic age. Within the limits of the Cretaceous period the two younger elements are suggested as being contemporaneous.

Jeannel (1942) implied a Palaearctic origin for the oldest element, but it may have developed *in situ* in the larger southern land areas and most authors are noncommital as to its ultimate origin. Of the two younger elements one is suggested as being of tropical or Palaearctic origin and northern route of entry to New Zealand, and the other as having entered from the south, even if it did not originate there.

No author has recognised an element reaching New Zealand by dispersal overland at a period significantly later than the Cretaceous with the exception of Jeannel (1942), who suggested that an element which was ancient in Australia reached New Zealand between the Eocene and Oligocene.

This emphasises the difficulty that dispersals of morphologically primitive taxa may occur either early or late in the existence of the taxon so that primitiveness is not necessarily an indication of earlier arrival. With the exception of taxa which may be considered to have arrived over ocean barriers in later times the principal elements suggested as being present in New Zealand are of not later than Cretaceous age.

Some elements have been recognised as being present in Australia but absent from New Zealand. The Second Antarctic element which Tillyard recognised as reaching Australia in the Late-Tertiary has little evidence to support it, and appears to be a rationalisation designed to explain anomalous distributions. There appears to be no clear evidence for the existence of possible overland dispersal routes between New Zealand and Australia or New Guinea in the Tertiary. The Late-Tertiary Austro-Malayan or Indo-Malayan element, which Tillyard and Mackerras recognised as present in Australia, is absent from New Zealand because of its prior isolation. Mackerras cited the Dipterous genera *Simulium* and *Anopheles* as members of this element.

The relatively small proportion of the total insect fauna which has been referred to one or other of these elements is evidence of the difficulty of identifying their members. It would be especially difficult to recognise the members of two distinct elements—the Gondwanan and the Austro-Malayan of Tillyard—both of northern route of entry into New Zealand. Mackerras (1950) has instanced the Trichoceridae (Dipt.), which occur in Australia and New Zealand but not in South America, as belonging to an autochthonous (ancient, of undeterminable origin) element which would apparently include both of Tillyard's elements. In terms of relationships and distribution the characteristics of taxa referred to the element of presumed southern route of entry (Antarctic, Bassian) are more convincing, but on closer analysis some may be capable of a different interpretation. It is not clear, for instance, what criteria can be used to separate an older Gondwanan from a younger Palaeantarctic element, that is, how one can distinguish between relict Gondwanan taxa which are *in situ* and immigrant Palaeantarctic taxa.

The dispersal to New Zealand of many taxa—particularly freshwater insects and those which are of poor vagility because of flightlessness or for other reasons—would require an earlier continuity with, or contiguity of, adjoining land areas. Geologically it is perhaps easier to make a convincing case for northern connections to Australia and New Zealand than it is to make one for southern connections. The physical explanations which have been proposed for the disjunctive distributions of presumed Palaeantarctic taxa involve either land bridges between stable (? continental) land areas or continental drift. According to Blackett (1961) the latter is consistent with the palaeomagnetic and palaeoclimatic evidence.

Two hypotheses have been advanced to explain the disjunctive distributions in the Southern Hemisphere of segments of the same taxon, or of taxa which are apparently closely related and considered to be monophyletic. Both hypotheses, however, because of the probable isolation of New Zealand since at least the Cretaceous, imply that the subsequent evolution of the isolated segments of the same taxon was either extremely conservative or closely parallel.

The Hypothesis of Southern Origin or Route of Entry

The first hypothesis considers these taxa to be, if not of Palaeantarctic origin, at least of Palaeantarctic route of entry. It has to explain dispersal over present day oceans and in some cases the derivation of these taxa from more primitive taxa which are confined to the Northern Hemisphere.

The Tabanidae for example is one of the few New Zealand taxa of presumed Palaeantarctic origin which have been subjected to recent examination in relation to the Australian and other faunas. Mackerras (1957) stated that none of the three ancient genera which are represented in New Zealand showed any continuity with Austro-Malayan faunas or other evidence of a northern origin. The more recent Chrysopinae and Tabanini are absent from both New Zealand and Tasmania. The New Zealand Tabanid fauna was considered to be derived from an extensive "Antarctic" radiation.

The subfamily Tabaninae is represented by *Dasybasis* Macquart (tribe Diachlorini) which occurs also in South Africa, South America, Australia, and Tasmania. In New Zealand there are 9 species of the subgenus *Protodasyommia* Enderlein as contrasted with the 92 species in the same tribe in Australia. The subgenus is confined to New Zealand with the exception of two species in New Caledonia.

The subfamily Pangoniinae is represented in New Zealand by one species belonging to *Paranopsis* Mackerras, an endemic subgenus of the primitive Australian genus *Ectenopsis* Macquart (tribe Pangoniini), as against 18 species in the same tribe in Australia.

The tribe Scionini is represented by one genus, *Scaptia* Walker which occurs also in South America, Australia, Tasmania, and New Guinea. Of the six subgenera of *Scaptia*, three are confined to Australia, one to Chile, and one to South America and Australia. The subgenus *Pseudoscione* Lutz Araujo and Fonseca is widely distributed in South America, Australia, Tasmania, and New Guinea, as well as in New Zealand. It has six species in New Zealand as against 25 in Australia. The tribe Scionini has 69 species in Australia.

The genus *Scaptia* was regarded by Mackerras (1960) as adapted to mild-temperate conditions, and the New Zealand fauna as originating from renascent relics within a limited range of environments and with limited opportunity to escape Pleistocene glaciation. Mackerras recognised three Australian species-groups (plus two ungrouped species) of *Pseudoscione*. The Australian, New Zealand, and South American Scionini were regarded as having arisen from a common stock. Neither of the two species groups which he recognised (Mackerras, 1957) in New Zealand was identical with any Australian group and the only suggested affinity was that between the (ungrouped) Tasmanian species *S. (P.) ianthina* (White) and *S. (P.) adrel* (Walk) from New Zealand.

The distributions of the species of *Scaptia* in New Zealand show no southern bias and would support Mackerras' opinion that the genus was adapted to mild-temperate conditions. One species occurs in the North Island only and one in the South Island only, while four occur in both islands. *Dasybasis,* with seven species confined to the North Island and only two occurring in both islands, is more biassed towards the north.

There is an apparent parallel between the Tabanidae and the Simuliidae. The New Zealand faunas of both are much reduced, as compared with those of Australia, in both size and components. The absence of the Tabanini from New Zealand may be compared with the absence of the genus *Simulium,* but there is no obvious parallel for the absence of *Cnephia.* The absence from New Zealand of the three endemic Australian subgenera of *Scaptia* (*Myioscaptia* Mackerras, *Plinthina* Walker, and *Palimmecomyia* Taylor) may be compared with that of the *bancrofti* and *furiosum* groups of *Austrosimulium.* The Australian and New Zealand *Pseudoscione* is equivalent to the *mirabile* (part) and *ungulatum* groups. The parallel is not exact in that while the same taxon (*Pseudoscione*) occurs in South America the South American *Austrosimulium anthracinum* does not fit any of the Australian or New Zealand species groups and differs at least at a subgeneric level.

The parallel may be entirely fortuitous but it would be of interest to determine whether similar interactions of phylogenetic pattern and distribution are observable in other taxa common to Australia and New Zealand.

Palaebotanical evidence from Southern Hemisphere countries, including Antarctica, indicates that there was a characteristic Gondwanan (*Glossopteris*) flora, long separated from that of the Northern Hemisphere and possibly significant in relation to the origin of the Angiosperms (Plumstead, 1961). It suggests that the Antarctic was a route of dispersal, without however determining the direction of movement, or the actual origin of the taxa concerned. Fossil evidence of the occurrence in Antarctica of *Nothofagus* Blume and other southern plant taxa (Cranwell, 1959) is consistent with a southern route of entry into New Zealand, but the significance of the occurrence of *Nothofagus* pollen in Eocene deposits in England (Ma Khin Sein, 1961) has yet to be determined.

It may be inferred that there was a large and varied insect fauna associated with this flora, but while there is a considerable body of information on Australian fossil insects there is little if any on those of South America and South Africa, and none on those of Antarctica and New Zealand. Tillyard (1935) considered that the order Diptera might have evolved in the south, and Jeannel (1949) that the Culiciformes (which includes the Simuliidae) may have done so. Alexander (1958) stated that on present evidence the family Blepharoceridae originated in the Southern Hemisphere, to which the Edwardsininae, the most primitive existing subfamily, is restricted. Tillyard (1926) included the Simuliidae amongst the cold-climate and aquatic insects reaching New Zealand and Australia from the south in the Cretaceous, but did not differentiate between *Simulium* and

Austrosimulium. Mackerras (1950) included *Austrosimulium* and the *aurantiacum*-group of *Cnephia* as members of the Bassian element in Australia, and believed that the evidence pointed to their entry from the south. Some comments on the criteria used by Mackerras for recognition of taxa to be included in the Bassian element of the Australian Diptera are given below in relation to *Austrosimulium*.

PRIMITIVENESS All attempts to rank or relate taxa in order of primitiveness by the use of morphological criteria involve some degree of subjectivity and it is doubtful whether it is always possible to distinguish true primitiveness from secondary regressions or deviations. In the case of *Austrosimulium,* however, far from being primitive, it appears to have reached much the same level of specialisation as the admittedly highly evolved *Simulium,* though possibly by parallel evolution or convergence in different lines. The generic diversity in the whole family is not great, however, and it does not seem probable that *Simulium* and *Austrosimulium* are widely separated. Both genera appear to be less primitive than *Cnephia* and *Gigantodax,* and are certainly less so than *Prosimulium, Twinnia,* and *Gymnopais,* which are confined to the Holarctic region. This distribution of simuliid genera is, in respect of primitiveness, the exact opposite of that in the Blepharoceridae.

It might be assumed that the species groups of *Austrosimulium* which are common to New Zealand and Australia would be the most primitive ones if the Australian and New Zealand faunas were derived from a common source by a southern route of entry. It has been shown in an earlier section, however, that the stock which reached New Zealand can be regarded as derived rather than primitive.

AUSTRAL DISTRIBUTION This refers to occurrence in Australia and at least in South America, often in New Zealand, and occasionally in South Africa.

Several explanations for the absence of certain taxa from South Africa have been proposed. Plumstead (1961), assuming that continental drift did occur, explains the absence of *Nothofagus* by its evolution after Africa had separated from Gondwanaland. *Austrosimulium* might be thought to fall in the same category. Darlington (1957) suggested that those austral taxa which are also present in South Africa did not enter Australia and New Zealand from the south. On this criterion the recent discovery of *Paulianina* Alexander in Madagascar (Alexander, 1958) would exclude the much quoted Edwardsininae (Blepharoceridae) as an example of a southern taxon. Brinck (1960) stated that South Africa was not subjected to Pleistocene glaciation and considered that while its invertebrate fauna exhibited affinities with those of almost every major part of the world these were mainly due to colonisations from the north. The southern cold temperate taxa present in cold wet habitats in South Africa show affinities with either South America or with Australia and rarely with both, while a few "Antarctic" taxa were believed not to have arrived overland.

Hennig (1960) concluded that systematic studies of southern Diptera had not so far revealed a pattern of phylogenetic relationships which would support the thesis of an Antarctic centre of evolution, or even of an Antarctic migration route. He suggested that taxa which are present in Australia, New Zealand, and South America, must have originated between the Oligocene and the Miocene at the latest.

In the Simuliidae, among those of possible southern origin, the genus *Cnephia* occurs in all the southern regions except New Zealand, while *Austrosimulium* occurs in Australia and New Zealand but not in South Africa and is represented in South America by a single species of problematical affinities, belonging at least to a distinct subgenus. The absence of certain other insect taxa from New Zealand is discussed in a later section.

SOUTHERN BIAS IN INTRA-REGIONAL DISTRIBUTION Distributions which are biassed toward the south in New Zealand are pronounced in such presumed Palaeantarctic taxa as the Blepharoceridae (Dumbleton, in press) and in the carabid tribes Pterostichini and Broscini (Britton, 1940, 1949). In many other reputed southern taxa, however, the bias is absent or not pronounced.

The explanations offered for southern-biassed distributions tend to stress by implication the cold-temperature relations of the taxa concerned. Even if such cold-adaptation as exists is not wholly a result of conditions in the Pleistocene there is little reason to suppose that there was, prior to the Pleistocene, greater cold-adaptation in Paleantarctic than in Palaearctic taxa. The cooler southern areas also coincide with the areas of higher rainfall and humidity and greater reliability of stream flow, and it is difficult to isolate the effects of these factors.

There are a number of ways in which a southern bias could have been produced in New Zealand. One is by the extinction in the North Island of some components of an originally uniform fauna by unfavourable temperatures, aridity, volcanism, or differential submergence. There is no direct evidence of such extinction for the insects, but in the plants, *Nothofagus* of the *brassi* group, which were present in New Zealand before the Pleistocene, are now restricted to New Caledonia and New Guinea (Couper, 1960).

While some taxa such as *Choristella* (Mecoptera) and Thaumaleidae (Diptera) are not known to be present in the North Island, other taxa such as Peloridiidae (Hemiptera), which are equally humidity-dependent and of poor vagility, occur in both islands. High temperatures and aridity would appear not to have been as important in New Zealand as they were in Australia.

A second explanation is that it is a persisting original bias, which may have been accentuated by concentration in a diminishing area and by greater relief and greater stability in the South Island. This does not necessarily imply that the colonising fauna was a cool-adapted one or of southern origin and entry to New Zealand. Geological reconstructions (Fleming, 1957) show the land extension towards New Guinea in the Jurassic and mid-Cretaceous as making a connection to the south-western half of the South Island, rather than directly with the North Island.

A third explanation is that there was more active speciation in the South Island, perhaps accentuated in the Pleistocene, but not necessarily confined to that period.

The southern bias which is pronounced in the New Zealand Simuliidae is, at least in part, the result of such Pleistocene speciation but whether there was a pre-existing (pre-Pleistocene) bias is not clear. Subsequent dispersal has not obscured the bias because of geographic discontinuity (not always complete) at Cook Strait, and perhaps limited time, since there appears to be no ecological reason why some at least of the South Island species should not establish in the North Island.

The Hypothesis of Northern Origin and Route of Entry

This proposes that many taxa with disjunctive southern distributions may be regarded as peripheral or end-of-peninsula relicts of dispersals which colonised the Southern Hemisphere directly from the north. It has, however, to explain their absence (except in the Simuliidae, for *Gigantodax*) from higher elevations in the tropics.

As an example of an insect taxon which appears to conform with this hypothesis the recent study by Ross (1956) on the evolution and zoogeography of the Trichoptera may be cited. He considered that the cool-adapted condition was primitive in all families and that these insects required cool fast water in areas which are forested and at least hilly if not mountainous. The persistence of these insects in any area over long geological periods was considered to be evidence for the continued existence of the necessary ecological and topographical conditions. Three families were studied in detail. The family Philopotamidae is represented throughout the world by nine genera of which eight are cool-adapted. The cool-adapted genus *Sortosa* Navas, which is represented throughout the world by seven regionally-isolated subgenera, is of particular interest. Species of the subgenus *Hydrobiosella* Tillyard (occurring in Australia, New Zealand, and New Caledonia) are very similar to those of the Chilean subgenus *Sortosa* Navas, and a third subgenus *Thylakion* Barnard occurs in South Africa. *Hydrobiosella* and the warm-adapted genera of the Rhyacophilidae (Hydrobiosinae) were considered to have entered New Zealand from the north, from an Asian centre of evolution, in the Cretaceous, though the possibility of a connection between South America and Australia and New Zealand could not be excluded. The warm-adapted genera *Chimarra* Stephens (Philopotamidae) and *Apsilochorema* Ulmer (Rhyacophilidae) which did not reach New Zealand, were believed to have reached Australia and Fiji in the Miocene.

An examination of Australian and New Zealand Simuliidae in relation to this hypothesis suggests that the absence of the genus *Simulium* from New Zealand is explicable by its failure to reach Australia until after the isolation of New Zealand, as happened with many other higher groups of insects (Tillyard, 1926). The Australian and New Zealand *Austrosimulium* faunas have no species in common, and while both have endemic species groups there is one taxon, not at present accorded the same categorical rank in both, which is common to both countries (Fig. 2). The interpretation which has, on morphological evidence, been suggested above is that the the New Zealand fauna originated from a derived rather than a primitive Australian group, the isolated segments of which have diversified in slightly different directions. This would be consistent with a northern route of entry of the *Austrosimulium* stock into Australia. The present day absence of such stock from Malaysia or Asia is paralleled by the same condition in other taxa which, however, have fossil representatives in the Northern Hemisphere.

The absence from New Zealand of the more primitive *Cnephia* is paralleled by the absence of other presumed Palaeantarctic insect taxa such as *Pelecorhynchus* Macquart and *Edwardsina* Alexander in the Diptera, the Choristidae in the Mecoptera, and the Thynnidae in the Hymenoptera. It is notable that above the generic level there are extremely few insect taxa other than the Mnesarchaeidae (Lep) which are present in New Zealand but absent from Australia. In addition, in several groups which are poorly represented in New Zealand, such as the Blepharoceridae and the Mecoptera, the taxa actually present in New Zealand are less primitive than some of those in Australia and elsewhere. Jeannel (1942) considered that the Australian taxa which had South American affinities were older than the New Zealand ones.

The poor representation in New Zealand of many taxa which are well represented in Australia is consistent with their derivation from Australia, or a common northern source, as a filtered or impoverished selection. So also is the absence from New Zealand of some of the more primitive forms which (if the possibility of subsequent extinction is discounted) would seem more likely to have been present in both countries if they derived from a common southern source.

Any attempt to explain the differences or anomalies in the distributions of austral taxa in southern countries is faced with the task of determining whether the absence of any taxon is the result of failure to reach the country, failure to establish, or of subsequent extinction.

It is possible that the absence of certain older taxa from New Zealand is a chance result of the hazards of access to, and dispersal along, the available dispersal route. The filtering effect would be greatest if the connection were narrow and either permanently incomplete or subject to periodic interruptions. Even if New Zealand is essentially continental in crustal thickness (Thompson and Evison, 1962) its shape and limited area suggest that any connection with Australia may have been just such a precarious one. If, as Tillyard (1926) and Ross (1956) believed, and as Fleming (1957) shows, the connection between Australia and New Zealand in the late Cretaceous was through New Guinea or to Northern Queensland, it suggests that the common stock from which the taxa colonising the two countries was derived was situated in and derived from the north rather than from the south. On the other hand any connection with Antarctica may necessarily have been a much broader one if it was common to both Australia and New Zealand. The spatial relationship of New Zealand to the other and larger components of the now-dismembered Gondwanaland and the time of separation are matters of some uncertainty. Du Toit (1937) regarded New Zealand, with other islands to the north, as originally forming part of the eastern margin of Australia though he shows it as separated, even in the Palaeozoic, by the Samfrau geosyncline.

Tillyard (1926) has explained these absent taxa as the result of a number of connections with Antarctica which existed at different times, not all of them being common to both Australia and New Zealand. Benson (1923) also suggested that there were significant differences between the connections of Australia and New Zealand with Antarctica.

Since many reputed southern taxa which are predominantly humidity-dependent (e.g., Peloridiidae) both reached New Zealand and survived until the present, and since these included not only taxa adapted to cold or cool temperatures but also some adapted to mild temperatures, there is no reason to suppose that New Zealand was ecologically unsuitable, at the time of connection, for the establishment of the absent taxa.

Chance extinctions after the isolation of New Zealand might result from reductions in its area or from periodic partial submergences. Paramonov (1959) and Mackerras (1957, 1960) have suggested that the Pleistocene cold climate was responsible for the extinction of some taxa in New Zealand. Ross (1953), however, stated that the Pleistocene glaciation in the Nearctic region caused neither wholesale extermination nor wholesale migration of insect faunas, but increased speciation in some taxa, reduction in the area of distribution of others, and expansion of the area of distribution of yet others. Though the Pleistocene ice sheets were much larger in the Northern Hemisphere the correspondingly larger land areas gave greater scope for faunal retreat and the existence of refuges than the small and circumscribed area of New Zealand.

It would be surprising, however, if the *furiosum* group of *Austrosimulium* was once present in New Zealand but left no survivors for this reason, since it is little if any less cool-adapted than the *mirabile* and *ungulatum* groups. One would expect some survivors to remain, as did the mild-temperature adapted Tabanidae (Mackerras, 1960).

CONCLUSION

The alternative origins of *Austrosimulium* would appear to be the following:

(1) That it is a derivative of *Gigantodax,* originating in South America or in Antarctica and entering Australia and New Zealand from the south. There are, however, few morphological affinities between the two genera, except one of uncertain significance in the larva, and there is no evidence of annectant or transitional forms. *Gigantodax* itself is not wholly southern in distribution, and only a single species of uncertain affinities is attributed to *Austrosimulium* in South America.

(2) That it is a derivative of Southern Hemisphere *Cnephia,* originating either in Australia or in Antarctica, and only in the latter case of southern route of entry to New Zealand. Affinities with the adults of the *terebrans* group of *Cnephia* in Australia have been suggested, but the larvae of this group are unfortunately unknown. The close affinities of African *Cnephia* with *Prosimulium* and with the Australian *Cnephia* suggests a direct northern rather than a southern contact.

(3) That it is a derivative of *Simulium* stock originating in the Northern Hemisphere, and of northern route of entry into Australia and New Zealand. This is considered to be the most probable origin. The affinities of *Austrosimulium* with *Simulium* have been discussed earlier. The critical point is whether these are due to convergence. The relationships of *Austrosimulium* with other genera as revealed by comparison of chromosome structure may provide more reliable evidence on this point.

That *Simulium* itself was apparently much later in reaching Australia would be explicable only if there had been a very early segregation of the genera. Rubcov (1959) believed that this had occurred by the Jurassic and considered that the vicarious relationship of *Austrosimulium* with the Holarctic genera *Prosimulium* and *Stegopterna* resulted from a Mesozoic separation. It is not clear, however, whether this implies that *Simulium* and *Austrosimulium* were the culminations of two distinct lines of descent. If on the other hand they segregated in the Northern Hemisphere from the same immediate ancestral stock then *Simulium* (*Hearlea*) and possibly *Austrosimulium anthracinum* also might be regarded as representatives of collateral segregates.

The distribution of Southern Hemisphere *Cnephia* and of *Austrosimulium,* and the taxonomic distinctness of the latter, indicates that they have long been isolated in the Southern Hemisphere. There is no evidence, however, to suggest whether *Austrosimulium* is as old as other monocentric austral taxa such as *Sphenodon* Gray (Rynchocephalia) in New Zealand, and the Choristidae (Mecoptera) and Tettigarctidae (Hemiptera) in Australia, all of which have fossil representatives in the Palaearctic region (Martynova, 1961; Evans 1959).

The origin of *Austrosimulium* in respect of both phylogeny and dispersal remains problematical but there is sufficient evidence to throw some doubt on its confident attribution to a Palaeantarctic element.

The fossil evidence which may be indispensible for the elucidation of southern distributions in insects is likely to be slow in accumulating. Until the distribution of many more taxa of reputed southern origin have been subjected anew to critical examination attempts to find a single widely-applicable and unifying explanation for all the multifarious variations in type of distribution exhibited by such taxa seem unlikely to succeed. A narrower field of investigation seems likely to be more productive. In particular, analyses of the distributions and interrelationships of additional insect taxa which are common to both Australia and New Zealand may provide evidence bearing not only directly on the probable derivation of some elements in the New Zealand fauna, but also indirectly on the wider question of the origins of taxa which have a bicentric or tricentric austral distribution.

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REFERENCES

ALEXANDER, C. P. 1958: Geographical Distribution of the Netwinged Midges (Blepharoceridae, Diptera). *Proc. 10th int. Congr. Ent., 1*: 813–28.

ANDRETTA, M. A. V. D'; ANDRETTA, C. D'. 1947: Redescricao de *Gigantodax wrighti* (Vargas, Martinez, & Diaz, 1944) (Diptera : Simuliidae). *Pap. Dep. Zool. Sec. Agric. S. Paulo, 8 (2)*: 23–37.

BENSON, W. N. 1923: Palaeozoic and Mesozoic Seas in Australasia. *Trans. Proc. N.Z. Inst. 54*: 1–62.

BENTINCK, W. C. 1955: The Black Flies of Japan and Korea. (Diptera : Simuliidae). Contr. Dep. Ent. 406th med. gener. Lab. Far East med Res. Unit, pp. 1–23, 33 figs.

BLACKETT, P. M. S. 1961: Comparison of Ancient Climates with the Ancient Latitudes Deduced from Rock Magnetic Measurements. *Proc. roy. Soc. A, 263 (1312)*: 1–30.

BRINCK, P. 1960: The Relations between the South African Fauna and the Terrestrial and Limnic Animal Life of the Southern Cold Temperate Zone. *Proc. roy. Soc. B 152*: 568–71.

BRITTON, E. B. 1940: The Carabidae (Coleoptera) of New Zealand. Part I. Pterostichini. *Trans. roy. Soc. N.Z. 69*: 473–508.

——— 1949: The Carabidae (Coleoptera) of New Zealand. Part III. A Revision of the Tribe Broscini. *Ibid., 77*: 533–81.

COCKAYNE, L. 1928: XIV The Vegetation of New Zealand *in* "Die Vegetation der Erde," ed. A. Engler and O. Drude, Leipzig.

COUPER, R. A. 1960: Southern Hemisphere Mesozoic and Tertiary Podocarpaceae and Fagaceae and Their Palaeogeographic Significance. *Proc. roy. Soc. B 152*: 491–500.

CRANWELL, L. M. 1959: Fossil Pollen from Seymour Island, Antarctica. *Nature, Lond., 184*: 1782–5.

CROSSKEY, R. W. 1960: A Taxonomic Study of the Larvae of West African Simuliidae (Diptera : Nematocera) with Comments on the Morphology of the Larval Blackfly Head. *Bull. Brit. Mus. (nat. Hist.), Entom., 10*: 1–74.

DALMAT, H. T. 1955: The Black Flies (Diptera : Simuliidae) of Guatemala and Their Role as Vectors of Onchocerciasis. *Smithson. misc. Coll. 125 (1)*: 1–425.

DARLINGTON, P. J. 1957: "Zoogeography." John Wiley, New York; Chapman and Hall, London. pp. 1–675.

DAVIES, L. 1960: The First-instar Larva of a Species of *Prosimulium* (Diptera : Simuliidae). *Canad. Ent. 92*: 81–4.

DOBY, J. M.; DAVID, F.: 1959: *Greniera* Genera Noveau de Simuliidé (Diptères Nematocères) Discussion de la Position Systématique. *C.R. Acad. Sci., Paris. 249*: 763–5.

DOWNES, J. A. 1958: The Feeding Habits of Biting Flies and Their Significance in Classification. *Ann. rev. ent., 3*: 249–66.

DUMBLETON, L. J. 1960: Larval Simuliidae (Diptera) from Navarino Island, Tierra del Fuego. *N.Z. J. Sci. 3*: 543–8.

——— 1962a: Aberrant Head-structure in Larval Simuliidae (Diptera). *Pacif. Insects., 4*: 77–86.

——— 1962b: Taxonomic Characters in the Pre-adult Stages of Simuliidae (Diptera). *N.Z. J. Sci. 5*: 496–506.

——— in press: The New Zealand Blepharoceridae (Diptera-Nematocera). *N.Z. J. Sci.*

DU TOIT, A. L. 1937: "Our Wandering Continents." Oliver and Boyd, Edinburgh and London. pp. 1–361.

EDWARDS, F. W. 1931: Simuliidae, Ceratopogonidae. *In* "Diptera of Patagonia and South Chile," pt. II, fasc. 4, pp. 121–232.

——— 1934: The Simuliidae (Diptera) of Java and Sumatra. *Arch. f. Hydrobiol. (Suppl. 5), 13*: 92–138.

EVANS, J. W. 1959: The Zoogeography of Some Australian Insects. *In* "Biogeography and Ecology in Australia." Monog. Biol, 8: 150–63 (Ed. A. Keast, R. L. Crocker and C. S. Christian) W. Junk, Den Haag, pp. 1–640.

FLEMING, C. A. 1957: Trans-Tasman Relationships in Natural History. *In* "Science in New Zealand," ed. F. R. Callaghan, Wellington, A. H. and A. W. Reed, pp. 228–46.

FREEMAN, P.; DE MEILLON, B. 1953: "Simuliidae of the Ethiopian Region." British Museum (Natural History) London. pp. 1–224.

GIBBINS, E. G. 1934: Further studies on Ethiopian Simuliidae. *Trans. R. ent. Soc. Lond., 82*: 51–105.

——— 1938: The Mouth-parts in the Female of *Simulium damnosum* Theobald, with Special Reference to the Transmission of *Onchocerca volvulus* Leuckart. *Ann. trop. Med. Parasit., 32*: 9–20.

GLICK, P. A. 1939: Distribution of Insects, Spiders, and Mites in the Air. *Tech. Bull. U.S. Dep. Agric. 673*: 1–150.

GRENIER, P.; RAGEAU, J. 1960: Simulies (Dipt., Simuliidae) de Tahiti. Remarques sur la Classification des Simuliidae. *Bull. Soc. Pat. exot., 53*: 727–42.

HENNIG, W. 1960: Die Dipteren-Fauna von Neuseeland als Systematisches und Tiergeographisches Problem. *Beitr. Ent. 10 (3/4)*: 221–329.

JEANNEL, R. 1942: "La Genese des Faunes Terrestres." Presses Universitaires de France. Paris. pp. 1–513.

——— 1949: Les Insectes; Classification and Phylogénie, les Insectes Fossiles, Evolution and Géonémie. *In* P. Grassé ,"Traité de Zoologie," 9. pp.1–110.

MACKERRAS, I. M. 1950: The Zoogeography of the Diptera. *Aust. J. Sci., 12*: 157–61.

——— 1957: Tabanidae (Diptera) of New Zealand. *Trans. Roy. Soc. N.Z., 84*: 581–610.

——— 1960: The Tabanidae (Diptera) of Australia. III. Subfamily Pangoniinae, Tribe Scionini and Supplement to Pangoniini. *Aust. J. Zool., 8*: 1–152.

——— 1962: Speciation in Australian Tabanidae. *In* "The Evolution of Living Organisms," Melbourne University Press, pp. 328–57.

MACKERRAS, M. J.; MACKERRAS, I. M. 1948: Simuliidae (Diptera) from Queensland. *Aust. J. sci. Res. (B), 1*: 231–70.

MACKERRAS, I. M.; MACKERRAS, M. J. 1949: Revisional Notes on Australasian Simuliidae (Diptera). *Proc. Linn. Soc. N.S.W., 73*: 372–405.

MACKERRAS, M. J.; MACKERRAS, I. M. 1950: Notes on Australasian Simuliidae (Diptera), II. *Ibid., 75*: 167–87.

MACKERRAS, I. M.; MACKERRAS, M. J. 1952: Notes on Australasian Simuliidae (Diptera), III. *Ibid., 77*: 104–13.

MACKERRAS, M. J.; MACKERRAS, I. M. 1955: Notes on Australasian Simuliidae (Diptera). IV. *Ibid., 80*: 105–12.

MA KHIN SEIN. 1961: *Nothofagus* Pollen in the London Clay. *Nature, Lond., 190*: 1030–1.

MARTYNOVA, O. 1961: Palaeoentomology. *Ann. Rev. Ent. 6*: 285–91.

MEILLON, B. DE. 1955: Diptera (Nematocera): Simuliidae and Phlebotominae. *In* Brinck, "South African Animal Life," 2 pp. 344–60. Uppsala.

OLIVER, W. R. B. 1925: Biogeographical Relations of the New Zealand Region. *J. Linn. Soc. (Bot.) 47*: 99–140.

PARAMONOV, S. J. 1959: Zoogeographical Aspects of the Australian Dipterofauna. In "Biogeography and Ecology in Australia." Monog. Biol. 8: 164–91. (Ed. A. Keast, R. L. Crocker and C. S. Christian.) W. Junk, Den Haag, pp. 1–640.

PLUMSTEAD, E. P. 1961: Ancient Plants & Drifting Continents. *S. Afr. J. Sci., 57*: 173–81.

RENSCH, B. 1959: "Evolution Above the Species Level." Methuen, London. pp. 1–419.

ROSS, H. H. 1953: On the Origin and Composition of the Nearctic Insect Fauna. *Evolution, 7*: 145–58.

——— 1956: "Evolution and Classification of the Mountain Caddisflies." Univ. of Illinois Press, Urbana. pp. 1–213.

RUBCOV, I. A. 1940: Family Simuliidae. (In Russian.) *Fauna SSSR* (*Diptera, 6 (6)*) *n.s. 23*: 1–532.

——— 1959–: Simuliidae (Melusinidae) *in* Lindner, "Die Fliegen der Palaearktischen Region," Bd. 3 (14) Lief. 203. pp. 1–48; Lief. 206. pp. 49–96; Lief, 211. pp. 97–160 (1960). Stuttgart.

SÉGUY, E. 1940: Diptères. Croisière du Bougainville aux iles Australes Françaises. *Mem. Mus. Hist. nat., Paris (n.s.), 2*: *14* :203–67.

SHEWELL, G. E. 1958: Classification and Distribution of Arctic and Subarctic Simuliidae. *Proc. 10th int. Congr. Ent. 1*: 635–42.

SMART, J. 1945: The Classification of the Simuliidae (Diptera). *Trans. R. ent. Soc. Lond., 95*: 463–532.

STONE, A.; JAMNBACK, H. A. 1955: The Black Flies of New York State. *Bull. N.Y. St. Mus. 349*: 1–144.

THOMPSON, A. A.; EVISON, F. F. 1962: Thickness of the Earth's Crust in New Zealand. *N.Z. J. Geol. Geophys. 5*: 29–45.

TILLYARD, R. J. 1926: "The Insects of Australia and New Zealand." Angus & Robertson, Sydney. pp. 1–560.

——— 1935: The Evolution of Scorpion-Flies and Their Derivatives (Order Mecoptera). *Ann. ent. Soc. Amer. 28*: 1–45.

TONNOIR, A. 1925: Australasian Simuliidae. *Bull. ent. Res., 15*: 213–55.

VARGAS, L.; NAJERA, A. D. 1951: Notas Sobre Sistematica y Morfologia de Simulidos. *Rev. Soc. mex. Hist. nat., 12*: 123–72.

——— 1957: Simulidos Mexicanos *Rev. Inst. Salubr. Enferm. trop., Mex. 17*: 143–399.

WHARTON, R. H. 1949: New Species of Simuliidae from New South Wales. *Proc. Linn. Soc. N.S.W., 73*: 406–12.

WYGODZINSKY, P. 1949: Contribuciones al Conocimento de los Simuliidae Argentinos. II. *Gigantodax horcotiani* sp. n. de la Provincia de Tucuman (Diptera). *An. Inst. Med. region., Tucuman, 2 (3)*: 325–33.

——— 1951: Sobre *Gigantodax horcotiani* Wygodzinsky, 1949 y *Gigantodax wittmeri* sp. n. *Ibid. 3 (2)*: 199–206.

——— 1952: Los Insectos de las Islas Juan Fernandez, 6. Simuliidae (Diptera). *Rev. chil. Ent. 2*: 81–5.

——— 1953: Sobre Algunos Simulidos Argentinos (Diptera). *An. Inst. Med. region. Tucuman,* 3: 293–320

——— 1958: Notas y Descripciones de Simuliidae Patagonicos y Andinos (Diptera). *Acta zool. lilloana, 16*: 121–48.

WYGODZINSKY, P.; COSCARON, S. 1962: On the Relationships and Zoogeographical Significance of *Austrosimulium anthracinum* (Bigot), a Black Fly from Southern South America. *Pacif. Insects, 4*: 235–44.