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Soil Fauna Studies Illustrated by Collembola

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Soil fauna studies illustrated by Collembola

By P. N. Lawrence and Penelope J. M. Greenslade

Part I. Taxonomy and geographical distribution of the Collembola

By P. N. Lawrence
British Museum (Natural History)

[Plate 47]

Introduction

The first Collembola from the Solomons appear to be those collected by J. D. Bradley, British Museum (Natural History) in 1954. The first published record of Collembola in the Solomons, by Yosii (1960) is based on thirty-six specimens.

The Expedition collections have been studied with those made by Dr and Mrs P. J. M. Greenslade, the Zoological Museum, Copenhagen, and the Bernice P. Bishop Museum, Hawaii which together number over 50000 specimens.

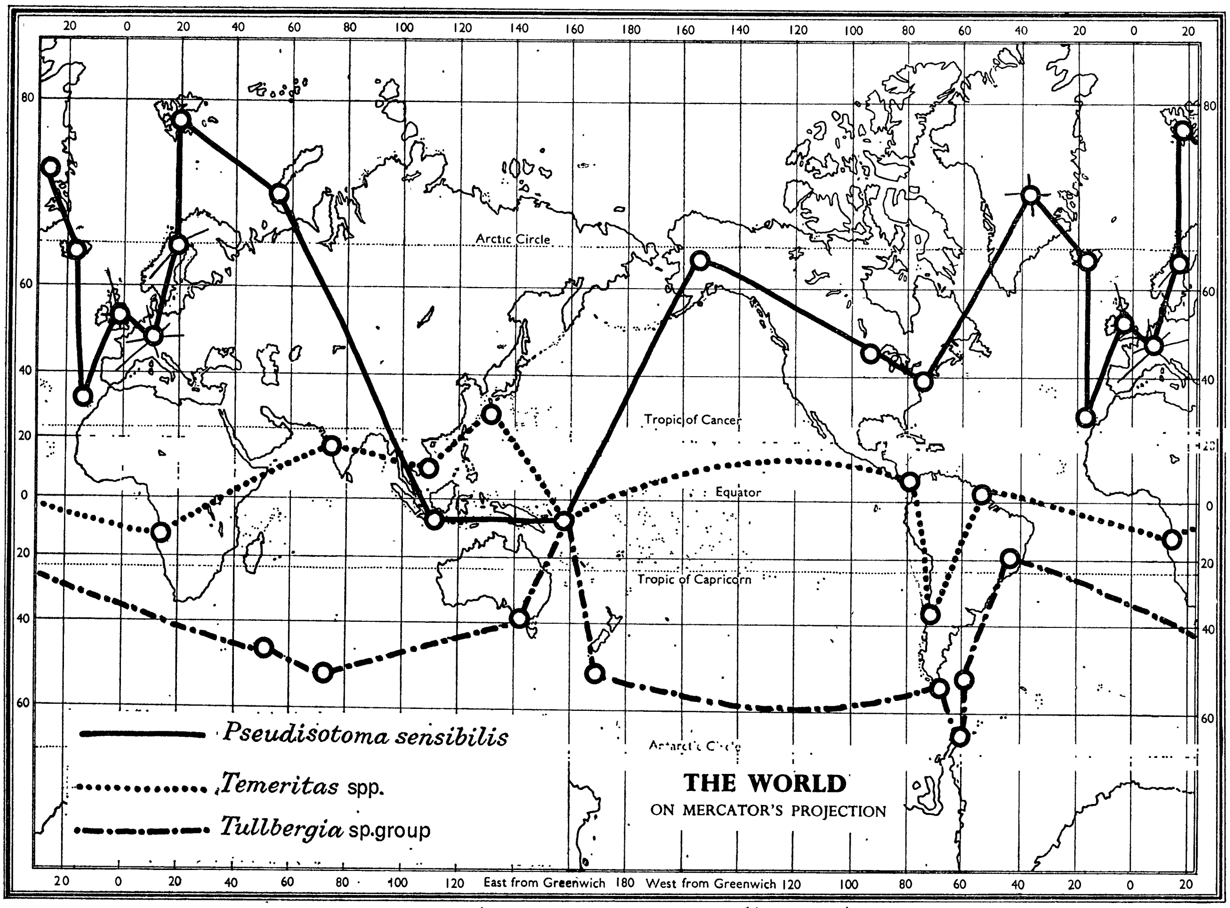
Geographical distribution

Collembola have been comparatively lightly collected in the tropics, although substantial contributions have been made to the knowledge of the fauna of some areas, for example Costa Rica and Angola.

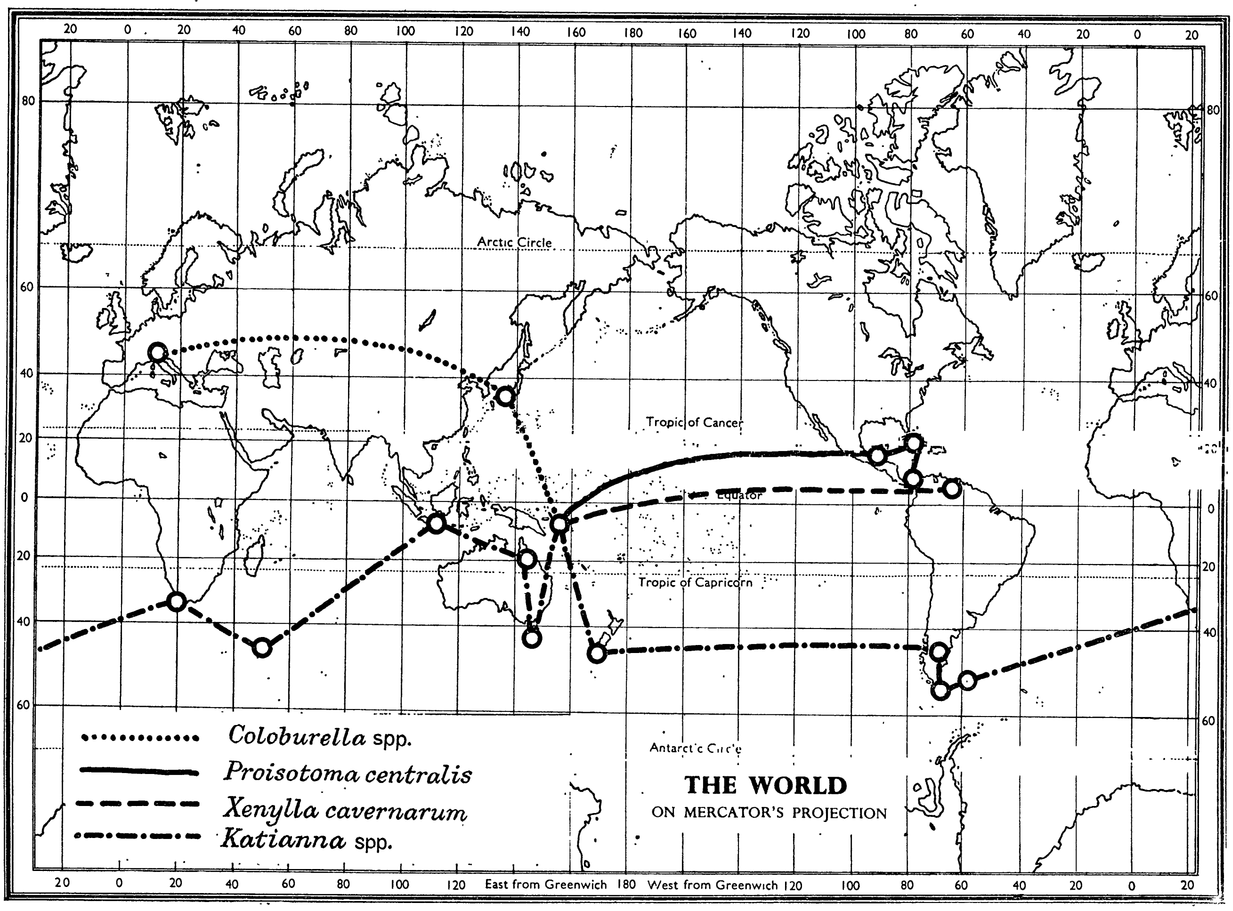
Among the most abundant Solomons Collembola are four species of widely distributed Isotomidae: *Isotomiella minor* described from Germany, common through Europe, known from U.S.A., Hawaii, Japan and New Zealand; *Folsomides exiguus* described from Hawaii, recorded from Malaya, Australia and perhaps identical with European and American species; *Proisotoma minuta* described from Sweden and found in Siberia, U.S.A., Egypt, Brasil, China; *Isotomina thermophila* described from Finland, recorded from Poland, Australia and Costa Rica.

One of the most conspicuous Symphypleona in the Solomons belongs to the genus *Temeritas* which might be described as pan-tropical with representatives in Angola, Argentina, Bombay, China Sea, Costa Rica and Dutch Guiana.

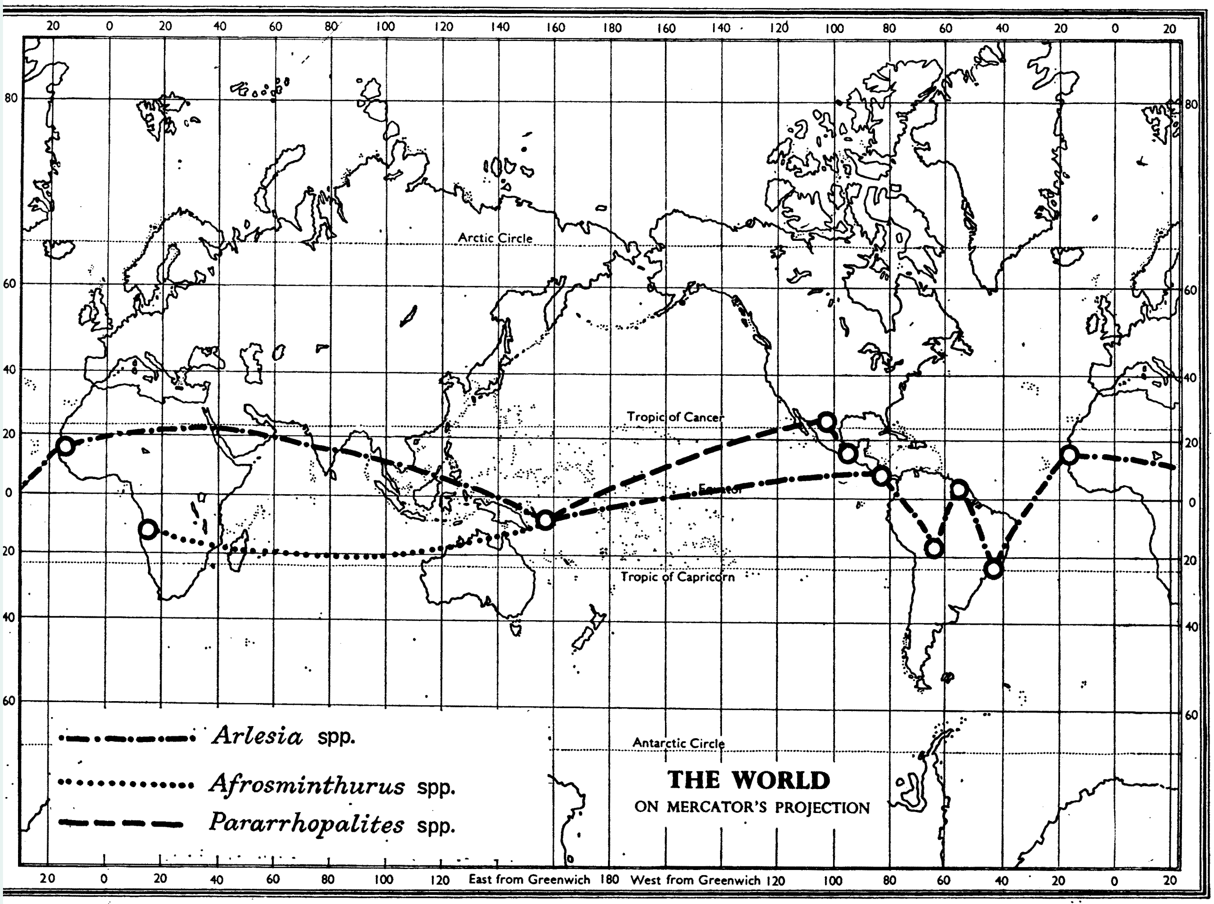
Three of the Solomons Symphypleona also occur in South East Asia. These comprise *Sphyrotheca santiagoi* hitherto known from a single Singapore specimen, now recorded from thirteen islands; *Sphyrotheca dawydoffi* previously known from an isolated Indochinese individual and now also redescribed on the basis of adequate Solomons specimens (Lawrence 1968*b*); *Neosphyrotheca fasciata* described from Singapore under two different names (Lawrence 1969). A difference appearing to separate animals described under these names arises from different diagrammatic representations by their authors of lines of small scales on the setae. These are difficult to resolve with the light microscope and to reproduce on a small-scale line illustration (figures 31*a–c*, plate 47).


Pseudisotoma sensibilis
Temeritas spp.
Tullbergia sp.group
THE WORLD
ON MERCATOR'S PROJECTION
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
East from Greenwich
West from Greenwich

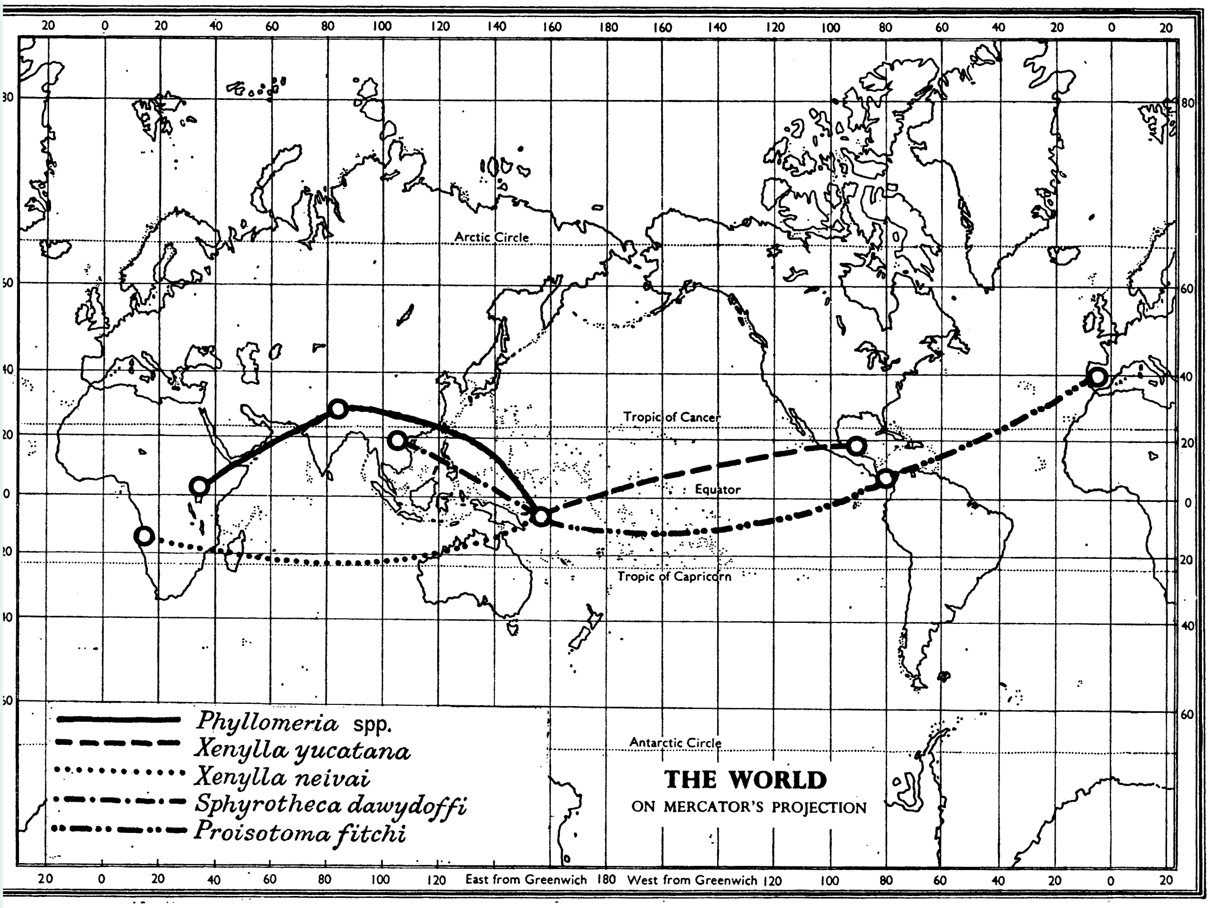
(*a*)


Coloburella spp.
Proisotoma centralis
Xenylla cavernarum
Katianna spp.
THE WORLD
ON MERCATOR'S PROJECTION
Arctic Circle
Tropic of Cancer
Equator
Tropic of Capricorn
East from Greenwich
West from Greenwich

(*c*)



(b)



(d)

FIGURE 29. *a–d*. Distribution maps of Collembola.

Discontinuous distributions westwards are apparent for *Xenylla neivai* which has a subspecies in Angola and the Bismarcks and a new subspecies *X. neivai lawrencei* (da Gama 1967) in the Solomons. The genus *Afrosminthurus*, hitherto known from seven Angolan specimens, is now adequately represented by a new Solomons species. The genus *Bovicornia*, previously exclusively African, is represented by a new Solomons species, *B. greensladei* Massoud & Delamare Deboutteville (1967). Since the original description of this species, it has been studied in detail by Betsch (1967) and lately has been found to be common in Madagascar (Z. Massoud, personal communication). A slightly less discontinuous distribution westwards from the Solomons is shown by *Phyllomeria* (Neanuridae) which is also recorded from Sudan and Nepal.

Eastward discontinuities are provided by the occurrence in the Solomons of two new species of *Pararrhopalites*, a genus hitherto confined to Mexico and specimens of *Arlesia* (Neanuridae) related to those represented in Surinam, Bolivia, Brazil and Costa Rica. A common Solomons Isotomid, *Proisotoma centralis*, is known from Costa Rica and Cuba, while *P. fitchi*, also described from Costa Rica, is now recorded from Spain and the Solomons. Another eastern affinity is the presence in the Solomons of a new subspecies, *Xenylla cavernarum salomonensis* (da Gama 1967) of a species restricted to oil bird caves in Trinidad.

Discontinuities extending northwards are apparent in the genus *Coloburella*, known from Europe, Japan and the Solomons, largely restricted to mountains. An exclusively montane distribution in the Solomons, as well as in the Bismarcks and New Guinea, is maintained by *Pseudisotoma sensibilis*. This species was described from Sweden, extends into Arctic Siberia and has previously been recorded from mountains in Java. There is no tropical record of the species below 3000 ft. Above this altitude, the climate and mossy vegetation most nearly approximates that of the European sites, where it numbers among the dominant animals. It is possible that the tropical, montane populations of *P. sensibilis* represent a relic fauna or are the results of long-distance dispersal by air of a species only able to survive in the tropics under montane conditions.

Southerly distributions are shown by a group in the genus *Parisotoma* which has its most northern species in the Solomons. This species appears to be new but is not, at present, identifiable because members of this genus have been separated on the size and number of ocelli. These characters are largely a matter of opinion due to the fact that ocelli are at different stages of degeneration (figure 31 *d*, plate 47). The genus *Katianna* is also predominantly of southern distribution with twenty species south of the Solomons and only one to the north, in Java. The two Solomons species occur on Mount Popamanaseu but insufficient were collected to ascertain their identity.

An additional Southern distribution is shown by a *Tullbergia* species which represents a group known from Kerguelen, South Shetlands, Tierra del Fuego, Campbell Island, New Zealand, Australia and a Brazilian mountain. Specimens from the summit of Popomanaseu appeared to be identical with a species from a subantarctic penguin rookery. However, comparison of a series from different altitudes on Popomanaseu, collected by Dr Greenslade, with material from Nuhu at 1000 ft. showed a range of variation, especially in the lengths of specialized setae lateral to the pseudocelli (figure 30). Examination of the types or fresh topotypes of the four species involved suggests that only one

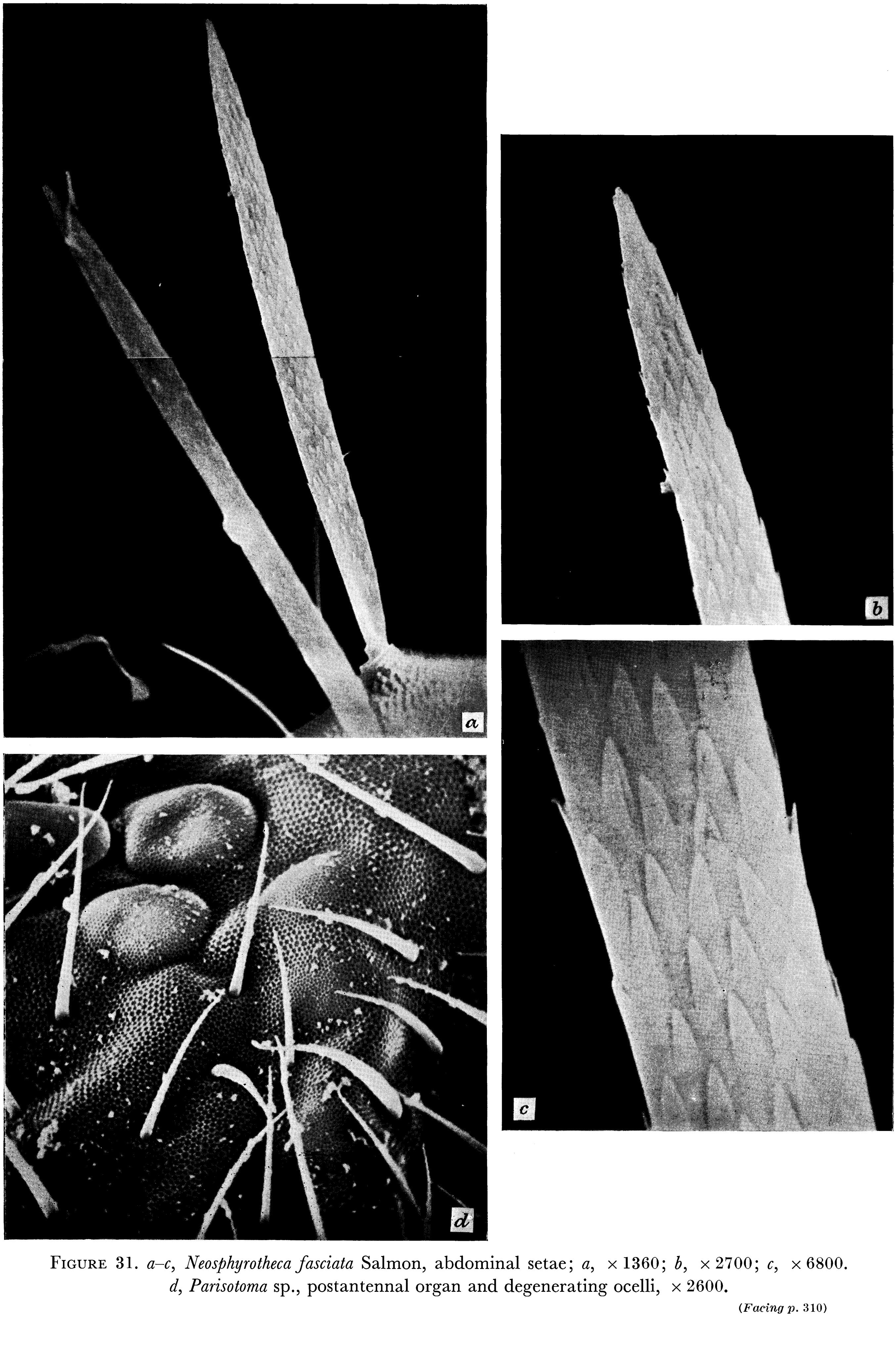


FIGURE 31. *a–c*, *Neosphyrotheca fasciata* Salmon, abdominal setae; *a*, ×1360; *b*, ×2700; *c*, ×6800. *d*, *Parisotoma* sp., postantennal organ and degenerating ocelli, ×2600.

(*Facing p.* 310)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

variable species is present. It appears that this species is tending to form ecotypes or subspecies at some isolated points of its distribution. This interpretation is supported by the known plasticity of other Collembola under different conditions of temperature and humidity. Further experimental, ecological work will be necessary to test the validity of the above conclusion.

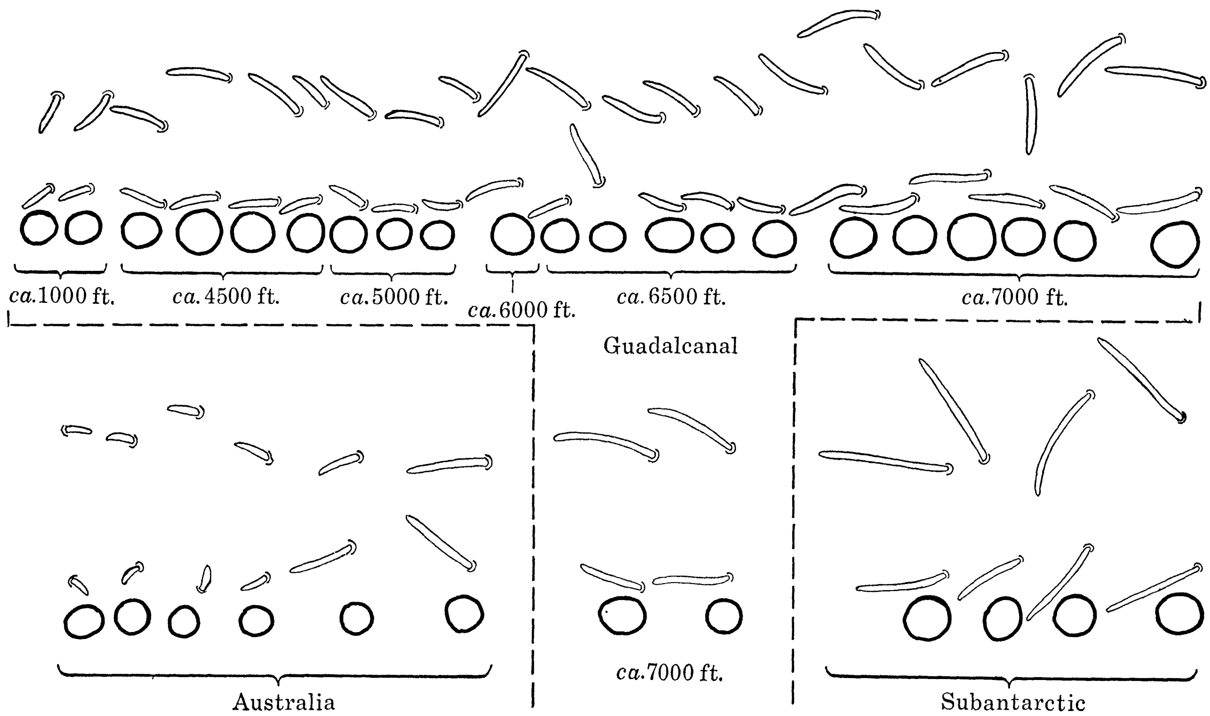


FIGURE 30. 1–33, *Tullbergia* sp., variation of specialized abdominal setae. (Stereoscan photograph.)

Conclusions

It is apparent that little can be deduced from the geographical distribution of Solomons Collembola until more collecting has been carried out in intervening areas. It must also be emphasized that substantial parts of the collection, for example the Paronellidae and Entomobryidae, are as yet completely unworked. The conspicuous genus *Temeritas* was described as being pan-tropical on the basis of only 16 specimens. It is clear that had a few less been collected, it might have been recorded as having a discontinuous distribution to the east or west, similar to that at present known for less conspicuous animals mentioned in this paper. Some of the curious distributions mapped do not necessarily reflect places to which Collembola have drifted but perhaps only those to which Collembologists have been driven.

The taxonomic work on the above material has been carried out or is being prepared by the following specialists: Dr M. M. da Gama, Portugal (*Xenylla*); Professor C. Delamare Deboutteville; Dr Z. Massoud and Dr J. Betsch, Museum d'Histoire Naturelle, Paris (*Bovicornia*); Dr Z. Massoud (Neanuridae and Neelidae); S. K. Mitra, Zoological Survey of India, Calcutta (Paronellidae); D. H. Murphy, Singapore (*Sminthurides*); Professor R. Yosii, Kyoto, Japan (Dicyrtomidae). The author has been responsible for the remainder of the Symphypleona, the Isotomidae and the Tullberginae.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Part II. Ecology

By Penelope J. M. Greenslade*

Introduction

It is clear from part I of this paper that rather little published information on tropical Collembola is available. Data from collections and ecological studies in the Solomon Islands are used here in a first attempt to characterize a tropical fauna. Comparisons are made between the Solomons Collembola and a relatively well known temperate fauna, that of the British Isles, and the habitat and local distributions of Collembola in the Solomons are compared briefly with those of other groups there. This is necessarily a preliminary account as taxonomic work on the expedition's and my own collections are not yet completed. Therefore in the case of certain families provisional determinations have to be used.

Size and composition of the fauna

Table 11 shows that at present fewer species of Collembola are recorded from the Solomon Islands than from the British Isles, although there are no doubt further species yet to be collected in the Solomons. Even so the total fauna may well not be so large as that of Britain and certainly it does not appear to be greater. It is possible therefore that the Collembola contradict the usual rule that tropical faunas are much larger than temperate ones. However, the smaller land area of the Solomon Islands must be remembered.

Table 11. Composition of temperate and tropical collembolan faunas

	British Isles		Solomon Islands	
	no. of species	%	no. of species	%
Poduridae:				
Hypogastrurinae	34	11·1	7	5·0
other subfamilies	29	9·5	45	32·1
Onychiuridae:				
Onychiurinae	50	16·4	4	2·9
Tullberginae	15	4·9	5	3·6
Isotomidae	77	25·2	24	17·1
Entomobryidae	50	16·4	> 25	17·9
Sminthuridae	50	16·4	30	21·4
total	305	—	> 140	—

Without complete species' lists little can be said now about species diversity and local fauna sizes. However, there appears to be less difference here when the British Isles and Solomon Islands are compared. Around 50 to 70 species were recorded from Mt Austen, the most intensively worked lowland forest site, and from the north ridge of Mt Popamanaseu, a montane locality. These totals are of the same order of size as lists obtained in comparable temperate collections, for example by Hale (1966) in Britain and by Petersen

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(1965) in Denmark. In lowland tropical rain forest the litter layer is thin and there is no great depth of soil which is rich in organic material and has a well-developed crumb and pore structure. Therefore only a relatively small habitat volume is available to Collembola, so that in terms of number of species per volume of habitat, faunal diversity is high in rain forest.

In a comparison of the proportions of the total species contributed by each collembolan family table 11 shows distinct temperate–tropical differences (a simple classification is used in this part of the paper to allow comparisons at the family level of lists given by authors using various different systems). The Hypogastrurinae in the Poduridae, the Onychiuridae and to a lesser extent the Isotomidae form a smaller percentage of the total species in the Solomons than in Britain. On the other hand, Poduridae other than Hypogastrurinae, especially *Neanura* species and members of allied genera, appear to be best represented in the rain forest. This comparison can be extended to colder climates with Hammer's (1953) survey of the collembolan faunas of Canada and other cold temperate and Arctic areas. Their composition is similar to that of the British Isles but shows a continuation of the trends in table 11. Sminthuridae and Entomobryidae are slightly less well represented than in Britain and form respectively 21 and 18 % of the species in the Solomons (table 11), 16 to 17 % (both groups) in the British Isles and 13 and 11 % in Hammer's list for Canada. In a collection from more extreme northern conditions in Jan Mayen (Macfadyen 1954) Isotomidae reached 40 % of the total list and Entomobryidae were absent. Near the polar limits of Collembola in Antarctica, isotomids predominate and neither Symphypleona nor Entomobryidae occur (except one sminthurid species as an introduction) (Wise 1967). Therefore the present Solomons' list suggests that on passing from tropical rain forest through temperate to boreal climates there is a continuous decline in the representation of Entomobrydae and Sminthuridae and a corresponding increase in Isotomidae. The relative numbers of species in Poduridae and Onychiuridae is similar in temperate and colder areas, although there is considerable variation between sites and habitats. Therefore the diversity of *Neanura* and allies and the low numbers of onychiurid species and other Poduridae, notably in *Hypogastrura* and related genera (but not *Xenylla*, da Gama 1967) seem peculiar to tropical rain forest and perhaps other warmer climates.

Habitats of lowland species

In table 12 data summarized in table 11 are regrouped with the species classed according to life form. The relation between this and vertical distribution in the soil is discussed by Gisin (1943), Delamare Deboutteville (1951) and others. Occurrence at lower levels in the profile is associated with lack of pigmentation, simplification of the chaetotaxi, reduction of the appendages and eyes and greater development of olfactory sense organs. It is in agreement with litter and soil with a high organic matter content being shallow in lowland rain forest that the more exclusively soil inhabitant Collembola are poorly represented compared with a temperate fauna. Conversely, surface active and upper litter species, that is Entomobryidae, including *Paronella*, most Sminthuridae and Isotomidae which have long appendages are relatively numerous. Species with very long appendages, in the Solomons for example *Paronella* species and in the Sminthuridae *Temeritas womersleyi*, are peculiar to the tropics. There is, in addition, a structurally intermediate group here which appears to have many Solomon Islands species, although they have yet to be identified in detail. These are species of *Neanura* and allied genera which occur in litter, sticks and logs where there are indications that the species are segregated according to habitat (P. J. M. Greenslade & P. Greenslade, in preparation).

TABLE 12. NUMBER OF SPECIES CLASSED ACCORDING TO LIFE FORM IN A TROPICAL AND A TEMPERATE FAUNA

Calculated for differences between observed number of species in the Solomon Islands fauna and expectation derived from proportions in the British fauna

	no. of British species	no. of Solomons species	χ^2	P
blind, white, reduced appendages	101	22	12·7	$<0{\cdot}001$
reduced appendages ± eyes	101	70	12·1	$<0{\cdot}001$
longer appendages	103	41	0·7	$>0{\cdot}3$
appendages very long, longer than body	0	7	—	—
total	305	140	—	—

TABLE 13. SMINTHURIDAE AND ISOTOMIDAE OF TWO HABITATS OTHER THAN SOIL AND LITTER. NUMBER OF OCCURRENCES OF EACH SPECIES RECORDED

habitat	compost heaps	trees	litter
total collections	6	5	190
species			
Xenylla welchi	1	.	0*
X. yucatana	1	.	8**
X. thibaudi	.	1	24***
Proisotoma fitchi	2	.	1*
Isotomina thermophila	4	.	39***
Folsomides exiguus	1	.	56***
Parisotoma sp.	1	.	8**
Temeritas womersleyi	.	1	25***
Sphyrotheca santiagoi	.	2	58***
Ptenothrix sp.	.	2	30***
Dicyrtomidae sp. 1	1	1	14***
Dicyrtomidae sp. 2	.	1	18***
Dicyrtomidae sp. 3.	.	1	11**

Status in litter: *, rare; **, occasional; ***, common

Turning to the distribution of species in different types of habitat, the Solomons Collembola seem to include few specialists adapted to situations other than soil and litter. The only undoubted specialists collected appear to be an *Isotomurus* species and a *Sminthurides* associated with fresh-water surfaces and *Bovicornia greensladei* on grasses. Other specialized or local habitats are occupied mainly by those Collembola which are also most abundant in open soil and litter. This is illustrated in table 13 where the Isotomidae and Sminthuridae of trees, that is bark and accumulations of litter and humus above the ground, and of compost heaps are contrasted with the forest floor fauna. It is possible that a *Paronella* and a *Willowsia* species may be restricted bark inhabitants, but final specific indentifications have not been made in these genera. The Collembola of carrion, including insect carrion, were also investigated but again no characteristic species occurred which were not frequent in the surrounding litter.

Therefore the main feature of the Collembola of the lowland tropical rain forest is a rather large number of species on any site, and of individuals (Greenslade & Greenslade 1968) living together in a thin zone of litter and surface soil. Here little evidence could be found of division of the species horizontally between different habitats. There is however vertical segregation according to life form. As the depth involved is small the litter surface is proportionally important. It is significant then that the specially tropical groups occur mainly at the surface. These are Entomobryidae (including *Paronella*) and Sminthuridae, notably those with very long appendages, and certain Poduridae. That they are inhabitants of the top of the soil profile was shown by their abundance in pitfall traps and by hand collections from sticks and wood fragments on the forest floor, and logs. It is also noteworthy that these two groups differ in structure. The species with long appendages contrast with poduromorph species. In the latter the appendages are reduced and pigmentation is often light; at the same time they are poorly adapted to the mineral soil in such characters as abundant long setae, and body processes. In addition, they may possess eyes and some of them taken from sticks and logs are very large. It can be suggested that a factor involved in the division of resources amongst tropical rain forest Collembola is this morphological divergence which contributes to the coexistence of numerous species in a thin litter layer.

The montane fauna

The remarks above apply to lowland forest Collembola. References to the mountain species makes it possible to examine the altitude-endemism relation in Collembola and compare it with findings from other groups. The mountain ground fauna was studied mainly on Mt Popomanaseu and here climatic limitation of Collembola was indicated at high altitudes (P. J. M. Greenslade & P. Greenslade, in preparation). With increasing height the density of individuals, the number of species and the diversity of the fauna all declined. This was accompanied by the entry of a group of montane species. About 10 to 20 Sminthuridae and Isotomidae were represented, some of them only by one or a few specimens so they cannot be identified specifically. Among these montane species there were further altitudinal changes; Lawrence has already commented on the continuous trend of increasing setal length with altitude in a *Tullbergia* species which appears to be related ultimately to some aspect of climate.

In some groups other than Collembola it has been suggested that certain types of distribution pattern are best explained by a continuing process of establishment of new species and extinction in others (P. J. M. Greenslade, in this Symposium). One such set of patterns is characteristic of island distributions within the archipelago and it can be noted that these are not yet recorded for Collembola. Another pattern is a correlation between endemism and altitude with the most recent arrivals occurring in disturbed habitats at low elevations.

From the data available now it is immediately clear that this relationship does not hold throughout the Collembola, since some of the most geographically widespread species

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

occur at high altitudes. Among the most frequent Isotomidae in the Solomons there are wide-spread species, for example *Isotomiella minor*, *Folsomides exiguus*, *Proisotoma minuta* and *Isotomina thermophila*; these are unlikely to be recent introductions as they are not associated with coastal or disturbed habitats and occur on mountains. The montane fauna in addition includes the widespread species *Pseudisotoma sensibilis* and the *Tullbergia* to which reference has already been made. Together these widespread Isotomidae form a substantial proportion of the montane species.

The origin of wide-spread montane distributions presents a problem. Considering the areas involved and the chances of dispersal from different habitats, mountain-top to mountain-top movement is unlikely compared with spread between coasts or lowlands. A possible solution is provided first by reference to two Ponerine ant species. One of them, *Amblyopone australis* occurs in Melanesia on mountains and is found above 2000 ft. in the Solomons. The other, *Myopopone castanea*, closely allied and ecologically very similar, is a lowland species in the Solomon Islands but extends into the montane zone in islands east of New Guinea where the *Amblyopone* is absent. This suggests competitive displacement

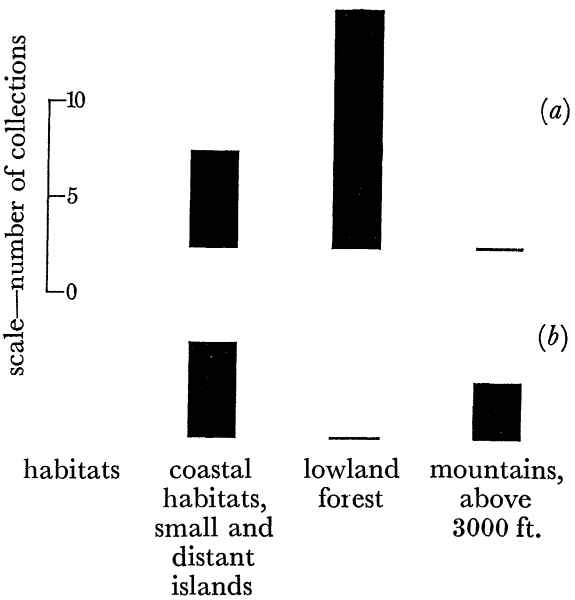

FIGURE 32. Habitat distribution of (*a*) *Folsomina onychiurina* and (*b*) *Folsomina* sp.nov.

between the species (Brown 1960), *M. castanea* being restricted in its altitude range by *A. australis* which is excluded from the lowlands by one or a combination of the factors: presence of *M. castanea*, climate, or the rich fauna of other lowland ant species. A very similar case is found in the Collembola in *Folsomina onychiurina* and *Folsomina* sp.nov. *F. onychiurina* appears to have a wide geographical distribution and occurs in the Solomon Islands in the lowlands, especially in forest (figure 32) while the new species is found on mountains, in disturbed situations on the coast and on small and isolated islands. These are all habitats in which it is reasonable to suggest that there is little competition. Again competitive exclusion is indicated; in this case of the new species from the lowland rain forest either by *onychiurina* or by other Collembola. It is possible to account for the present montane distribution of *Pseudisotoma sensibilis* in similar terms. Therefore widespread montane distributions are not incompatible with cycles of expansion and replacement although they are unaccompanied by the divergence on individual islands which is common in other groups such as birds and higher insects.

Discussion

Differences between the Collembola of the Solomon Islands and those of temperate climates can be considered first in terms of ecology. The Solomons fauna is appropriate to the single major vegetation type, tropical rain forest, other habitats without a tree cover being confined to its coastal margins or occurring as small enclaves within it. In contrast in colder climates there are tree lines due to latitude and at relatively low elevations, to altitude, so that forest is interspersed with other habitats, often influenced by man. The main temperate–tropical differences, in collembolan faunas can be related in part to forest development, so that the groups which are especially numerous in species in the tropics are inhabitants of the litter, (many Entomobryidae, Sminthuridae and some Poduridae), while moving to colder regions with declining importance of forest, the fauna includes mineral soil species to a greater extent. In temperate climates there is a wide range of habitats occurring as a mosaic and differing in soil and litter type and vegetation cover. Here the distribution of Collembola presents many problems. Poole (1961) and Wood (1966) point out that the factors responsible for pattern on a small scale may be obscure and complex, while Hale (1966) and Petersen (1965) show that many species are widespread in respect to habitat and others are inconsistent in their occurrence. Even so these authors are able to attribute characteristic habitats to some species in their studies. This has not proved possible on the floor of lowland tropical rain forest, except in the case of vertical stratification.

To some extent Collembolan distributions can be related to the moisture content of the environment (Murphy 1955) and in classifications by life form, a xerophile type, occurring in exposed situations and another associated with water can be distinguished (Christiansen 1964). But a broad intermediate category remains between these extremes and it is this with which studies in rain forest are concerned. With the rapid evaporation rates of the tropics, soil moisture appears to be a major factor in habitats with no tree cover (see Choudhuri & Roy 1967, for example) but in forest protection is afforded by the canopy. However, the poor collembolan fauna of temporary decay habitats in the Solomons can be related to the desiccation risk on open sites, and perhaps also to the ephemeral nature of some of these habitats at high temperatures.

Salmon (1949) has drawn attention to what he describes as an archaic element of almost cosmopolitan distribution in the Collembola and the world-wide occurrence of some species present in the Solomons has been shown by Lawrence. Although wind dispersal cannot be entirely disregarded, reference to any suction trap sample of airborne arthropods will show that this is much less important among Collembola than in many other groups. As there was no indication in the Solomons that these widespread patterns are caused by human introduction it seems that in these species, area may well be correlated with age.

If so the wide-spread species must be closely adapted to their niches in order to persist, and have little potential for variation in that they can be recognized as the same species over different parts of their range. In this context it is of interest that the Popamanaseu–Campbell Island *Tullbergia* species shows the same changes in seta length in response to climatic variation over a wide area.

Both the ecological and geographical distributions of the Solomon Islands Collembola which have been examined suggest, in the terminology used elsewhere in this Symposium, that they are the product of *K*-selection. It appears that in the favourable environment of the rain forest floor, many species coexist and a relatively high proportion of the available species occur on any one site. Conversely, the same species tend to be found in different areas and on different islands. This absence of the restricted island pattern which suggests expansion and replacement, indicates a rather stable fauna.

It will be of interest to see how further taxonomic work on Solomon Islands material and later collections support this preliminary discussion. Other points on which information is required include the details of the specializations which allow the coexistence of species in rain forest. Murphy (1966) has found ecological differences between co-existing *Sphaeridia* species in Singapore showing how ecological segregation is likely to be achieved by other factors besides the contrasts in life form mentioned here. Rates of increase in different habitats and climates also require attention since Salmon (1949) comments on the ability for rapid increase shown generally by introduced species. Finally no information is available yet on the role of the very large fauna of predators in rain forest in maintaining the diversity of Collembola there.

I should like to thank Mr P. N. Lawrence for his help in the course of my work on these Collembola. I am also grateful to Dr Z. Massoud for information on the material from the Solomon Is. which he is studying.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

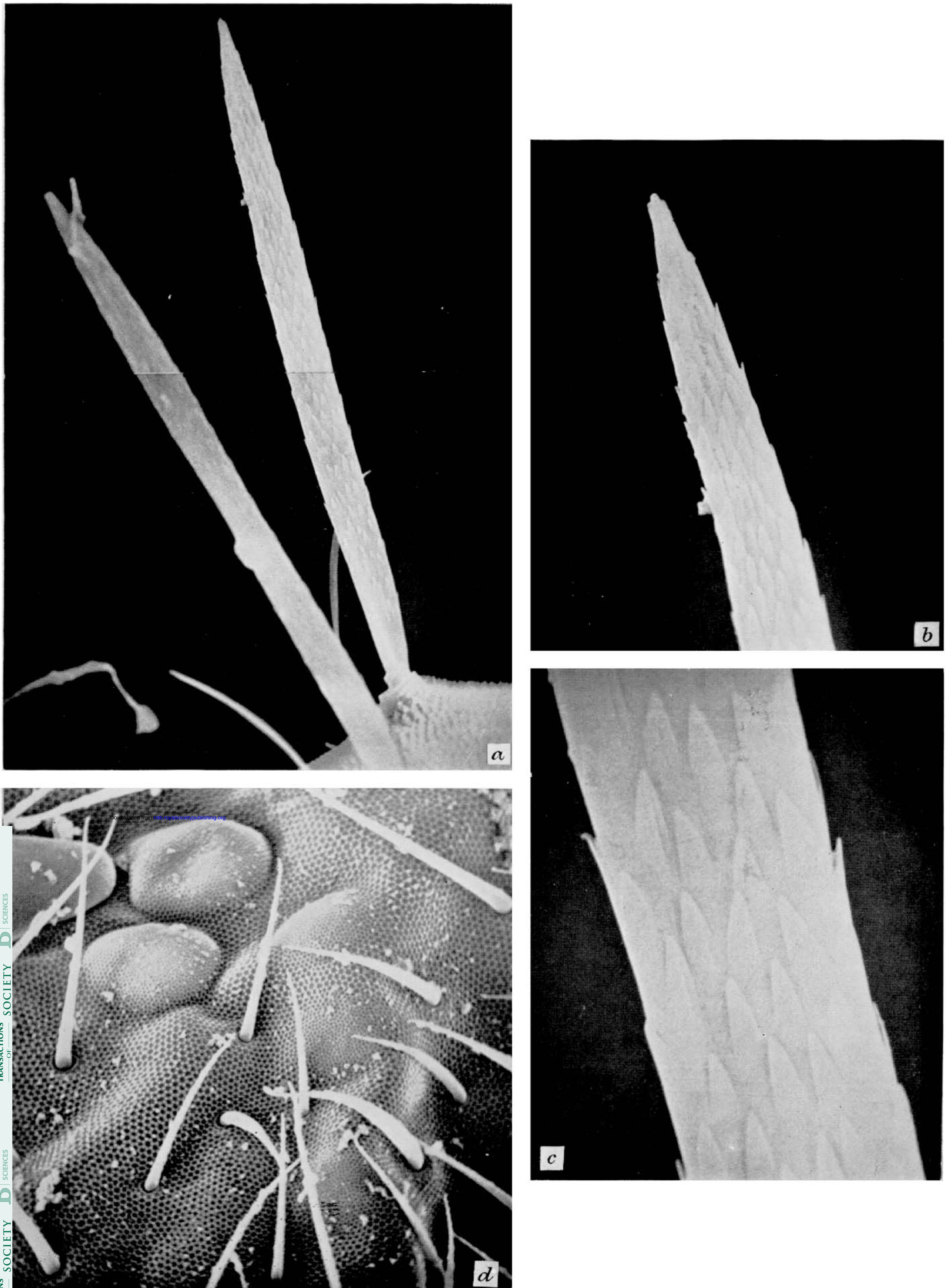

FIGURE 31. *a–c*, *Neosphyrotheca fasciata* Salmon, abdominal setae; *a*, × 1360; *b*, × 2700; *c*, × 6800. *d*, *Parisotoma* sp., postantennal organ and degenerating ocelli, × 2600.