STUDIES ON THYSANURA. III. SOME FACTORS AFFECTING THE DISTRIBUTION OF SOUTH AFRICAN THYSANURA

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INTRODUCTION

Wygodsinsky (1955) has suggested that, on the available evidence, the machilid component of the South African Thysanura is confined in its distribution to those regions of the subcontinent which have an assured rainfall of between 500 and 750 mm. per annum. Lawrence (1953) comes to a similar conclusion, regarding the genus *Machiloides*, which is the dominant machilid genus in South Africa, as a "forest indicator", its presence being either correlated with the presence or previous location of an indigenous forest plant community.

Figure 1 shows the distribution of known species of Thysanura in southern Africa excluding the termitophilous Nicoletiidae. The Lepismatida occur throughout the subcontinent, but the Machilida, with the exception of *Machiloides solitarius* Silvestri, are confined to the more equable conditions below the Great Escarpment in the zone which Lawrence (1953) describes as the "discontinuous forest belt".

The broad correlations made by Lawrence (1953) and Wygodzinsky (1955) therefore appear to be correct, but no critical study of the ecology of any of the South African Thysanura has, as yet, been undertaken. The present investigation is an attempt to interpret the distribution of these animals in terms of the autecology of *Machiloides delanyi* Wygodzinsky and *Ctenolepisma longicaudata* Escherich, two species whose water economy and orientations to their physical environment have already been studied (Heeg 1967 a and b) and whose ecological requirements are thus more readily understood. Evidence gleaned from other species is also included, but it must be stressed that the conclusions reached here can only be regarded as tentative, since they are based largely on the findings for the two species mentioned only. Conflicting or contrary evidence may follow when other species are studied in detail.

THE AUTECOLOGY OF *Machiloides delanyi* AND OF *Ctenolepisma longicaudata*

M. delanyi and other species of *Machiloides*, although geographically restricted to the discontinuous forest belt, are not confined to the remnants of indigenous forest within this region. Not one of the five species of *Machiloides* collected in the Grahamstown area occurs exclusively in forest. At least one hitherto unnamed species has only been found outside the shelter of forests, and *M. delanyi*, the most abundant species in the Grahamstown area has been found in numerous localities, ranging from forest to the open scrub of the semi-arid "False Karroo" to the north-west. In the latter region it is only found in the proximity of streams and stock watering dams, in which respect it resembles species of *Machilinus* which

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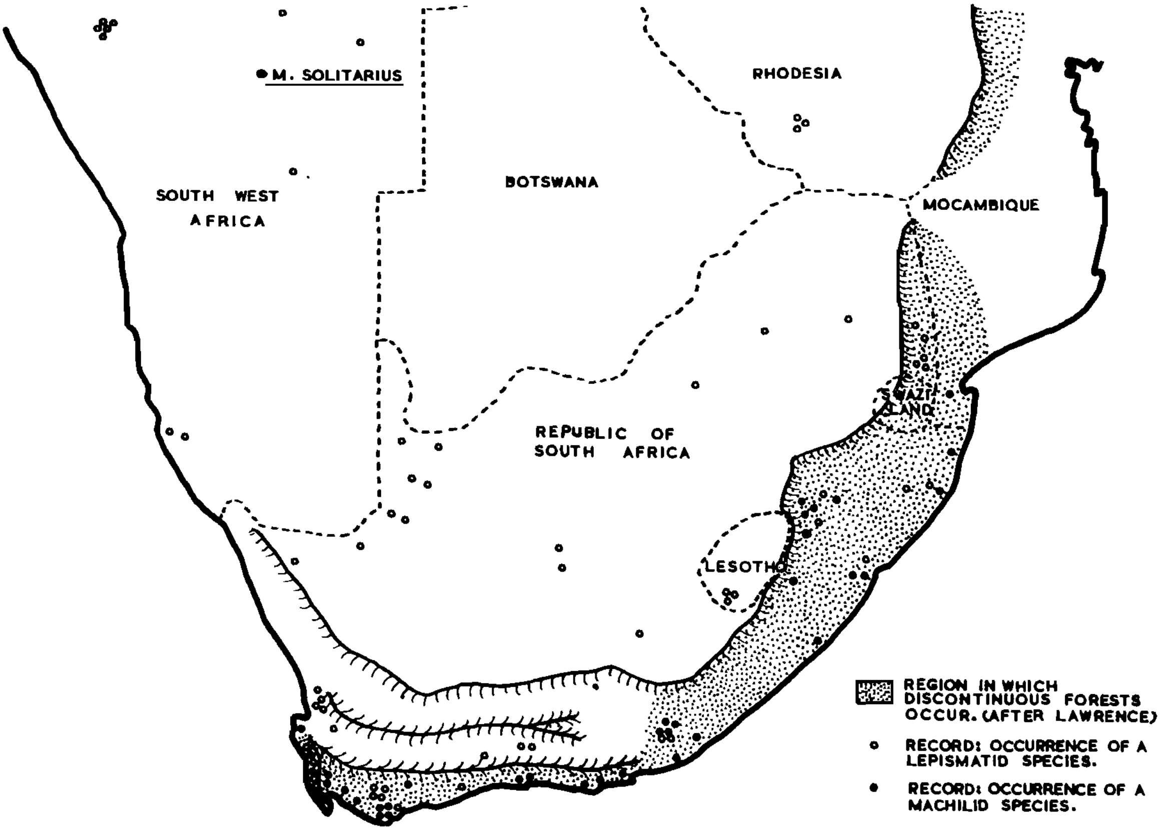

FIGURE 1
Distribution of the Machilida and Lepismatida in southern Africa (compiled from data in Wygodzinsky, 1955, and from personal collections).

have invaded the more arid regions of South America (Wygodzinsky 1955). A feature of the localities where Machilida have been collected in the present study is that moisture in some form, whether as condensation in mist belts, frequent precipitation, or as permanent bodies of water in more arid regions, is usually readily available. However, in spite of the above generalisation, the actual microhabitat occupied by the animals is almost invariably dry. Kuhnelt (1961) describes the Machilida as "... found regularly in dry forests between leaves and stones". Those species of Machiloides studied, and which are found in indigenous forest, show a similar avoidance of the wetter parts of their habitat. They are seldom found in the moister litter layers but occur in their greatest abundance among loose rock rubble, clinging to stones or the boles of trees at a level where only dry surface litter covers them, or under bark. Rock rubble, such as the talus at the foot of a cliff is a particularly favoured shelter, and such loose rocks also seem to be the characteristic habitat of *Petrobius brevistylus*

Carpenter in Great Britain (Delany 1959) and of various species of *Machilis*, *Dilta* and *Trigoniophthalmus* in Switzerland (Wygodzinsky 1940).

C. longicaudata, as a widespread household pest, inhabits an atypical habitat, being found in almost any sheltered locality in human dwellings. It has been encountered out of doors, but then invariably near human habitation, and its original microhabitat is thus difficult to determine. Other Lepismatida, including species of *Ctenolepisma*, have been collected from a number of localities ranging from open grassland to the semi-desert Karroo. These were always found under stones. It is not uncommon, within the geographical range of the Machilida, to find lepismids and machilids sharing the same shelter. Lepismids are seldom encountered in forests; while collecting in this habitat I have found only an unidentified species of *Lepisma* under the bark of a dead tree in the coastal forest surrounding Lake Sibayi in northern Zululand.

Three microhabitats, which were found to house Thysanura, were studied in order to determine the physical conditions to which the animals would normally be subjected. These were:

(i) A talus slope in a well-wooded stream valley. The interstices between the rocks forming the slope housed numerous specimens of *M. delanyi*, and, although this species was found in many other localities, its abundance here would indicate that the microhabitat afforded it favourable conditions.
(ii) Reprint filing boxes in the laboratory, from which many *C. longicaudata* were collected and which could be regarded as typical of its normal habitat.
(iii) A pile of concrete rubble located in open grassland, which was found to house specimens of *M. delanyi* together with a hitherto undescribed species of *Machiloides* and a species of *Ctenolepisma*.

The study was largely confined to microclimates in these habitats, but observations on biotic factors were also made.

Climatic conditions in the microhabitats and their surroundings.

Temperature and relative humidity within the microhabitats were recorded twice weekly over a period of three months (Jan. to March, 1962) at 1400 hours, when the most extreme conditions prevailed. For comparative purposes the climatic conditions of the surroundings were recorded at the same time, and, in the case of the habitat of *M. delanyi*, conditions in the adjacent humus and litter layers of the valley floor were measured as well.

Temperature was recorded by means of mercury thermometers, the sizes of the actual microhabitats being such that heat loss by conduction along the mercury column would not markedly affect the result. Relative humidity was determined using wet and dry bulb thermometers as well as suitably calibrated Edney paper hygrometers. These two methods gave almost identical results for a given microhabitat, but the wet/dry bulb thermometers had the advantage of not requiring a lengthy period of equilibration; such thermometers, used singly, could also be inserted into the interstices between rocks with a minimum of disturbance to the habitat. Evaporation from the wet bulb does not appear to have significantly affected the humidity of the microhabitat as shown by the good correspondence with the paper hygrometers. Edney hygrometers, calibrated at 90% and 96·5% respectively were found to give more reliable results in determining the relative humidity of the humus and litter layers, since it is difficult to keep the wet bulb from contact with the substratum here. Equilibration periods of up to six hours were necessary for these instruments.

A summary of the climatic conditions in the three microhabitats and their immediate surroundings is given in Table 1. This shows conditions in the humus and litter layers and in the interspaces between the rocks of the talus slope to have a remarkable degree of constancy when compared with their surroundings. Whilst these all owe their stability in part to the protection of the canopy of vegetation, edaphic factors would play a major role in maintaining this constancy. Humus has marked water retaining properties conferred on it by its colloidal nature, thus it soaks up moisture during rain showers and releases this water very slowly as water vapour. The litter forms a covering blanket over the humus, and, as such, reduces the rate of evaporation thus giving rise to near saturation in the complex. The litter also serves to insulate the underlying layers from the ambient temperature. These factors, together with the protection afforded by the vegetation canopy and by physical features of the terrain, give rise to climatic conditions in the humus and litter layers which are subject to only small fluctuations in response to substantial weather changes in the surroundings. The interstices between the boulders of the talus slope also owe their stability to an underlying humus layer; the substratum at the bottom of these interspaces usually contains a quantity of humus formed from leaves which have filtered through from above, but, presumably owing to the larger air spaces and consequent better air circulation between the rocks, the relative humidity here is usually lower than that of the humus/litter complex. Indeed, it was at times found to be lower than that of the surroundings, since very light showers do not penetrate into the interstices.

Conditions in the microhabitat of *C. longicaudata* were found to be more variable than those discussed above. This was particularly marked in the case of relative humidity. However, the habitat in which both lepismids and machilids were found showed even greater fluctuations in response to changes in ambient climatic conditions. This habitat lacks the stabilising effect of a humus layer, and its exposed position gives rise to more extreme temperatures.

Biotic factors in the microhabitats.

M. delanyi shares its microhabitat with relatively few other organisms. Cribellate spiders, and, less commonly, a species of reduviid bug of the sub-family Emisinae were the only predators found occupying the same horizon. Other than these, aggregations of a gregarious psocopteron and a few mosquitoes form the total associated fauna. Thus the animals are comparatively free from both competition and predation when their microhabitat is compared with the surroundings. The litter layer of the valley floor houses numerous spiders, chilopods, and an occasional onychophoran, in addition to large numbers of Collembola and Acarina. The humus layer accommodates an even more diverse fauna, the amphipod *Talitrioides eastwoodae* and the introduced polydesmid diplopod *Orthomorpha gracillis* comprising the larger phytophagous species, whilst predators include Japygidae and various chilopods.

TABLE 1

SUMMARY OF THE CLIMATIC CONDITIONS OBTAINING IN THE MICROHABITATS AND SURROUNDINGS OF *M. delanyi*, *C. longicaudata* AND AN UNIDENTIFIED SPECIES OF *Ctenolepisma*, BASED ON RECORDINGS MADE TWICE WEEKLY, AT 1400, OVER A PERIOD OF THREE MONTHS

	Temperature (°C)		*Relative Humidity (%)*		*Saturation Deficit (mm. Hg.)*	
Species	*Mean*	*Range*	*Mean*	*Range*	*Mean*	*Range*
M. delanyi.						
Microhabitat	19·3	14 - 23	85·0	72 - 94	2·7	0·7 - 8·0
Surroundings	22·5	15 - 32	75·6	55 - 98	5·7	0·2 - 16·0
Litter (A, oo)	19·1	14 - 21	94·8	83 - 100	0·93	0·0 - 3·2
Humus (A, o)	18·5	14 - 21	99·2	96 - 100	0·14	0·0 - 0·6
C. longicaudata.						
Microhabitat	22·4	19 - 25	64·5	50 - 85	7·4	2·6 - 11·8
Surroundings	23·4	18 - 31	64·0	40 - 90	8·2	1·7 - 19·4
Ctenolepisma sp.						
Microhabitat	23·3	15 - 30	74·8	49 - 98	5·8	0·3 - 15·4
Surroundings	24·6	18 - 37	62·5	35 - 100	10·3	0·0 - 27·6

Most of the tree trunks and stones in the habitat of *M. delanyi* support a considerable growth of microflora, which, owing to the equable conditions under the canopy, persists even under drought conditions. This is not true for the more exposed habitats in which the animals are also found, but they feed on fallen leaves (Kuhnelt 1961) as well as small thallophytes (Wygodzinsky 1940; Heeg 1967 a) and thus food is unlikely to constitute a limiting factor in their distribution.

Biotic factors in the habitat of *C. longicaudata* are difficult to assess. Spiders seem to be the only obvious predators, and the omnivorous habit of *C. longicauta* ensures an adequate food supply. Indeed, a dearth of predators and abundant food may well be largely responsible for the success of this species as a household pest. Other species of *Ctenolepisma* have been found in association with various arthropod species, both phytophagous and carnivorous, but too little is known of their biology for any discussion.

DISCUSSION

M. delanyi, and, on the available evidence, other Machilida, have abandoned the equable conditions prevailing in the humus/litter complex of forest floors for a drier, but nonetheless climatically stable microhabitat. Their present environment not only reduces competition for food and space, but also minimises the risk of predation and of fungal attack. The animals are extremely susceptible to fungal infections under saturation conditions. In response to these drier conditions, the animals have developed a moderate resistance to water loss, but the degree of resistance is variable, being dependent, at least in part, on the stage within an instar (Heeg 1967 a). Conditions within its microhabitat are such that *M. delanyi* is not subject to the risk of too great a water loss, and temperature extremes also never occur. These conditions are attained by the animals as a result of their orientation behaviour to physical conditions in the environment (Heeg 1967 b).

The habitat of *C. longicaudata* shows greater fluctuations in its climatic conditions, and this is even more marked in the microhabitat of other lepismid species. Here the cover of the stones provides shelter from temperature extremes, but the humidity is very variable. Greater resistance to water loss correlates with *C. longicaudata's* indifference to ambient relative humidity (Heeg 1967 b), and, while temperature will limit its choice of microhabitat, it finds shelter largely by means of its light responses.

However, the behavioural and physiological adaptations demanded by the environment regarded here as typical for *M. delanyi* are such that they will permit the animals to survive outside of the shelter of the forest canopy, and this indeed they do. Within their geographical range they maintain substantial populations and, as witnessed by the presence of very young individuals, reproduce in areas far removed from the more typical habitat described above. Three factors must be considered as of some importance in governing the distribution of the Thysanura on a wider scale, namely temperature, humidity and availability of water.

C. longicaudata has a higher temperature range than *M. delanyi*, both in its preferendum and its avoidance temperature, but it hardly seems likely that temperature alone has been the limiting factor in restricting the distribution of the machilids. Delany (1954) reports a higher temperature tolerance than that shown for *M. delanyi* in the shore living machilid *Petrobius maritimus* (Leach) on Lundy. Field measurements of the temperatures under stones inhabited by this species were as high as 28·6°C, an example of a machilid species which has abandoned the more sheltered environment common to most Machilids and which presumably has had to adapt both its temperature tolerance and its temperature responses to suit the new environment.

This is not, however, to minimise the importance of *accepting* higher temperatures on leaving the shelter of the forest. If other factors permit the invasion of harsher conditions, and the animal is unable to adapt to temperature conditions obtaining in the new surroundings, the invasion is doomed to failure. However, it has been shown that, while temperatures above the eccritic result in avoiding or escape behaviour, these conditions are not necessarily lethal. *M. delanyi* survives prolonged exposure to a temperature of 30°C (Heeg 1967 b) and, clearly, if the population pressure were sufficiently strong to force an invasion of an area where temperatures of this order prevailed in the typical microhabitat, this species, like *Petrobius maritimus*, should be able to adapt to the new temperature conditions. The higher temperature tolerance of *C. longicaudata* is a necessary adaptation to the conditions under which it lives, but cannot be regarded as the factor which has allowed it to invade these conditions. Such tolerance must have evolved under the conditions demanding it.

Humidity, particularly when coupled with temperature and expressed as saturation deficit, is more likely to be a factor limiting the distribution of the Machilida. Disregarding

M. solitarius, their range coincides almost exactly with that region of South Africa where the mean saturation deficit at 1400 hours is less than 15 mb (= 11·25 mm Hg) (Schulze 1965). A high ambient saturation deficit must impinge to some extent on the microhabitat of the animals, as shown in the present investigation, and it seems that the relatively high rate of water loss suffered by *M. delanyi* limits it to regions where this would not be excessive. However, *C. longicaudata* loses water faster than do the Pterygota and other arthropods which have invaded more arid regions and we have, therefore, to elucidate why, despite this physiological shortcoming, the Lepismatida are so widely spread.

If an animal is to invade a dry region, the risk of a high rate of water loss being fatal is not great if the loss can be made good before the internal water store has been depleted to a degree where cellular function is impaired. Such an invasion usually requires the organism to have an eccritic humidity that is below saturation, and, consequently, when its water content falls to a critical level, a positive response to regions of high humidity must be elicited. However, a source of replenishment must be readily available if the animals are to survive, and it is here that the difference between the Machilida and Lepismatida is to be sought. *M. delanyi* and all other Machilida studied are able to utilise transient water sources not usually available to animals. By means of eversible vesicles located on their abdominal coxosternites, they are able to absorb water from such sources as thin films of condensation moisture and soil capillary water (Heeg 1967 a), thus in mist belts the only essential requirement enabling the animals to leave the shelter of the forest is the acceptance of a somewhat higher temperature range. In spreading from these mist belts, their general inability to curb water loss would only seem to limit the distribution of the Machilida insofar as it necessitates frequent replenishment of the internal water store, thus the chief limiting factor is the availability of water. Wygodzinsky's (1955) suggestion that the South African Machilida are confined to regions where the assured rainfall is between 500 and 750 mm. per annum can, therefore, be partially substantiated but only inasmuch as that these regions include areas subjected to an influx of moist air giving rise to frequent mists and/or a mean monthly precipitation greater than 10 mm. *throughout the year*. These are also the conditions under which the remnants of indigenous forests occur (Lawrence 1953).

It would seem, then, that *M. delanyi* and at least one other species of *Machiloides* have penetrated the more arid regions of the False Karroo to the north-west of Grahamstown by following water courses, since the watershed of the streams flowing through this region, the Highlands Ridge, lies in a mist belt supporting remnants of indigenous forests. This would enable them to establish themselves around permanent bodies of water, such as stock watering dams. The occurrence of species of *Machilinus* in comparable microhabitats in semi-arid regions of Argentina can be explained in the same way; the animals may, in all probability, have invaded these semi-arid regions by following the courses of rivers down from the more equable conditions of the Andes. The absence of mist belts, and forest, and thus of distribution centres, could account for the absence of Machilida in South Africa west of the Drakensberg and north of the Langeberg-Outeniqua-Winterhoek ranges.

C. longicaudata shows an advance over *M. delanyi* in at least two aspects of its water economy. It has acquired both a higher resistance to water loss and the ability to absorb water from a subsaturated atmosphere down to a relative humidity of 60% (Heeg 1967 a). The former reduces the need for frequent replenishment and the latter enables the animals to effect such replenishment under conditions where *M. delanyi* loses water. Even in the most arid regions, humidities from which the lepismids can absorb water occur far more frequently than actual precipitation, and the widespread distribution of the Lepismatida can, therefore, be attributed to the water gaining mechanism which has made them independent of the presence of water in its liquid state.

In considering the distribution of the Thysanura in South Africa mention must, however, still be made of *Machiloides solitarius*. The presence of this species at Okahandja in South West Africa upsets the view expounded here. While there is no doubt about its correct identification as a machilid, it must be stressed that, to date, only the type specimen, a solitary female, has been collected. The Swedish South Africa Expedition of 1950-1951, which added 26 new species of Thysanura to the recorded South African fauna (Wygodzinsky 1955) failed to collect any specimens of this species in spite of having collected in the Okahandja area. It seems possible that an error in labelling may have occurred when the type specimen was described. If further specimens confirm its distribution, not only will it prove to be an animal of great physiological interest, but the present hypothesis may require significant modification. However, to develop a more complex picture of Thysanuran distribution upon a unique specimen does not now appear justified.

SUMMARY

An analysis of the distribution of the South African Thysanura, excluding the termitophilous Nicoletiidae, shows the Lepismatida to have spread over the whole of the sub-continent, while all except one species of the Machilida are confined to the discontinuous forest belt below the Great Escarpment, and to seaward of the mountain ranges of the southern and eastern regions. The Machilida are not, however, confined to the actual forests within their geographical range, some species having invaded regions of considerable aridity. Studies on the microhabitats of *M. delanyi*, *C. longicaudata* and other machilids and lepismids, when considered in conjunction with the physiological and behavioural adaptations of the animals concerned, lead to the conclusion that the chief factor limiting the distribution of the Machilida is the availability of water in a form in which the animals can absorb it. The Lepismatida are not thus restricted, having the ability to absorb water in the form of water vapour from sub-saturated atmospheres.

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