MILLIPEDES AND CENTIPEDES AS SOIL ANIMALS

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The distribution of British millipedes and centipedes in relation to soil type and soil stratum is briefly reviewed. The presence of water in the soil, in creating problems of endosmotic uptake, oxygen lack and immobilization by surface tension, is considered an important factor determining this distribution. Geophilomorph centipedes have solved these problems by waterproofing their cuticle with a superficial film of lipoid; Iulid millipedes are similarly waterproofed but, unlike geophilomorphs, lay unprotected eggs; lithobiomorph centipedes and flat-backed millipedes have imperfectly waterproofed cuticles and are thereby restricted to positions from which water drains rapidly, for example under leaves and stones at the surface of the soil. Despite their hydrofuge cuticle most myriapods loose water rapidly through their spiracles—most rapidly in centipedes which have imperfect spiracular closing devices. Desiccation is avoided in geophilomorphs and Iulids by burrowing deep into the soil; lithobiomorphs and flat-backed millipedes are not mechanically adapted to burrow and thus their surface retreats must provide shelter from drought in addition to flood. The economic status of these animals in the woodland floor is discussed.

INTRODUCTION

In many of the major quantitative works on soil arthropods millipedes (Diplopoda) and centipedes (Chilopoda) are not identified beyond families or even orders. Since the work of Diem (1903) no European survey of forest soils in which these animals are identified appeared until the recent work of Drift (1951). In Great Britain most quantitative work refers to grass and arable land but only in some of these surveys (Buckle, 1921; Morris, 1922, 1927; Thompson, 1924; Edwards, 1929; Baweja, 1939) have the Diplopoda and Chilopoda been identified. Our knowledge of the Myriapoda fauna of British woodlands has been accumulated largely by systematists and amateur naturalists but notwithstanding the absence of precise data there have emerged from the literature certain gross generalizations as, for instance, the concept due to Bornebusch (1930) that millipedes and lithobiid centipedes together with lumbricoid worms characterize brown forest soils in contrast to the fauna of podzols which consists largely of geophilomorph centipedes together with dipteran and Elaterid larvae. Another important generalization is that millipedes are humus-forming agents of considerable importance (Bornebusch, 1930; Jacot, 1940; Drift, 1951).

This paper is divided into three sections. First there is a brief statement of the distribution of the common centipedes and millipedes in Great Britain. In the second section several of the more important relations of these animals to their physical environment are reviewed to indicate some of the factors governing their distribution and lastly the role which millipedes play in the forest soil is considered and discussed.

DISTRIBUTION OF MILLIPEDES AND CENTIPEDES IN GREAT BRITAIN

Millipedes

Millipedes are essentially animals of the forest floor. As Verhoeff (1928) has pointed out, many species frequently found in non-wooded areas are no doubt relics of the fauna of the forest which once covered these areas.

In the quantitative surveys of grass and arable land in England previously mentioned only two species appear regularly, namely *Blaniulus guttulatus* (Bosc) and *Brachydesmus superus* Latzel. In addition *Cylindroiulus londinensis* var. *caeruleocinctus* (Wood) and *Archeboreoiulus pallidus* (Brade-Birks) were found by Morris (1922, 1927) on the chalk at Rothamsted but these species are usually confined to calcareous soils. *Brachyiulus pusillus* (Leach) was common in the soil at Aberystwyth (Edwards, 1929)—its distribution in Great Britain being mainly coastal. All these species, with the exception of *A. pallidus*, are also frequently associated with farmland on the continent (Verhoeff, 1928). Most millipedes can be found under stones and in the miniature woodland floor at the base of the hedgerows around farmland, but *Blaniulus guttulatus* is the most frequent in agricultural soils and often reaches the proportions of a pest (Brade-Birks, 1930; Cloudsley-Thompson, 1950). From the work of Morris (1922, 1927) and Edwards (1929) it would appear that arable land supports larger populations of millipedes than grassland, especially where there has been a liberal application of farmyard manure. A large population of millipedes has recently been recorded from grassland however (Salt and his collaborators, 1948), but the animals were not identified.

In woodland three main habitats can be distinguished: (1) *on* the floor and in the aerial parts of vegetation, (2) *in* the floor (litter and soil layers), and (3) under the bark and in the rotten wood of

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old tree stumps, fallen logs *etc*. The Iulids *Tachypodoiulus niger* (Leach) and *Schizophyllum sabulosum* (Linné) are typical of the first category and can be seen during the day and night, feeding on vegetation. *Tachypodoiulus* is very common on bramble during the autumn, feeding on the fruits. Most millipedes, however, are occasionally to be seen browsing upon the aerial fructifications of fungi *etc* and thus may be included as temporary members of this category of surface feeders.

Every species of millipede may be found in the third category but in most cases, in Great Britain, these subcortical species appear to be true soil and litter animals which have been deprived of their optimum habitat by deforestation. The Iulids, *Cylindroiulus britannicus* (Verhoeff) and *C. parisiorum* (Brölemann and Verhoeff), and the Blaniulids, *Isobates varicornis* and *Proteroiulus fuscus* (Stein), are, however, typically subcortical although the latter species does occur as a common litter animal in some regions. *Cylindroiulus punctatus* (Leach) (= *silvarum* Meinert) although often considered to be in its natural habitat beneath bark is in fact the most characteristic species of the floor of British oak woods.

Common millipedes of the deciduous floor (ii) in Great Britain are the pill millipedes, *Glomeris marginata* Villers and the variety (?) *perplexa* Latzel, the flat-backs, *Polymicrodon polydesmoides* (Leach), *Brachydesmus superus* Latzel, *Polydesmus angustus* Latzel and *P. denticulatus* Latzel, and the Iulids, *Cylindroiulus punctatus*, *Iulus scandinavius* Latzel and *Ophyiulus pilosus* (Newport). Undoubtedly *C. punctatus* and *Glomeris* are the dominant species of climax oak woodland, and of the flat-backs, *Polydesmus denticulatus* is often more common than *P. angustus*. *Iulus scandinavius* and *O. pilosus* appear to prefer mixed woods rather than pure oak, especially where the litter contains some of the more slowly decaying leaves such as beech. By contrast, in a floor where litter decomposition is rapid (for example ash), *Glomeris* alone appears capable of maintaining itself in large numbers. In coniferous woods the large Iulid, *Schizophyllum sabulosum*, is often frequent, especially in Scotland, although there is some doubt as to its status as a true floor animal. Also common are *C. punctatus* and *I. scandinavius* which also predominate in the fauna of deciduous woods where mor conditions prevail—*cf*. Drift (1951) who records these two species from beech mor in Holland.

Although millipedes are much more abundant in both numbers of species and individuals on calcareous soils there are but few instances of species being confined to such soils. In Great Britain the large black *C. londinensis* Leach (var.) and the Blaniulid *Archeboreoiulus pallidus* appear to be truly calcicole. They are known to occur extensively only in regions where the underlying rock is a limestone or chalk, although there is no information on the actual base-status of the soils in which they live. It is important to note that it is the former species which provided the basis for Lyford's conclusion that millipedes choose the leaves with the highest calcium content (LYFORD, 1943). Some millipedes are notably more frequent in calcareous soils such as *Glomeris*, *Polymicrodon* and *Polydesmus denticulatus* whereas others, such as *Cylindroiulus punctatus*, are less dependent on calcium.

There is a typical vertical distribution of millipedes in the floor. Flat-backs such as *Polymicrodon* and *Polydesmus* are most frequent in the litter whereas Iulids are found mainly in the soil beneath. *Glomeris* occupies an intermediate position in this respect. Lastly it may be noted that woods with a good supply of ground debris such as stones, old stumps and fallen logs, support a more varied and larger fauna than do the more 'tidy' habitats.

'Refugee' millipedes

It has been pointed out that some millipedes are characteristically subcortical. Some of these are living in this situation due to the destruction of their optimum habitat by deforestation (for example *C. punctatus*), others, such as *C. britannicus*, *C. parisiorum* and *Isobates varicornis*, are rarely found away from such a habitat, but it seems possible that they may eventually be found as true soil animals in some hitherto uninvestigated woodland.

A number of millipedes are often associated with sandy soils. *Schizophyllum sabulosum*, *Cylindroiulus latestriatus* (Curtis) (=*frisius* (Verhoeff)) and possibly *Iulus scandinavius* are of this type. *C. latestriatus* is almost confined to the coast in Great Britain, but has also occurred inland on sandy soils, at Nantwich on the New Red sandstone and in the East Anglian breckland. *Schizophyllum*, though common on the coast, is often found inland; it is exceptionally common on the Triassic sandstone of the Wirral peninsula, and throughout Scotland it is a common animal in coniferous forest. Possibly the coast represents another type of retreat, perhaps for species once widely distributed in the native conifer forests.

Centipedes

Like millipedes, centipedes are pre-eminently woodland animals but seem better able to re-adapt themselves to the new conditions of a deforested country. In arable land and grassland, *Necrophloeophagus longicornis* (Leach) is almost invariably present and appears in most of the previously mentioned surveys of this biotope. *Lithobius* *duboscqui* Brölemann is the most frequent lithobiid in such habitats. Unlike millipedes, centipedes have become adapted to moorland conditions and survive there in large numbers, as, for example, do the geophilomorphs, *Brachygeophilus truncorum* (Bergsoe and Meinert) and *Geophilus carpophagus* Leach, and the lithobiids, *L. variegatus* Leach, *L. calcaratus* Koch and *L. lapidicola* Meinert. As may be expected, the species frequent in moorland and heaths are often associated also with woodland soils tending towards mor conditions, whereas the species most often found in grassland and arable land are associated with mull soils.

According to Bornebusch (1930) lithobiids are frequent in mull soils and geophilomorphs in mor soils. While this is no doubt a valid generalization with respect to lithobiids there is a characteristic fauna of geophilomorphs in both mull and mor. *Geophilus carpophagus* and *Brachygeophilus truncorum* are common in poorer mull soils and in mor. In richer mull soils *G. insculptus* and *G. electricus* are most frequent. *Necrophloeophagus longicornis* is not often frequent in woodland soils. It will be recalled that this species is characteristic of grassland. It may be an exception to the general statement that all centipedes are pre-eminently woodland species.

As with millipedes, a distinction must be drawn between true soil and litter species and 'surface roamers' which rest beneath stones *etc* during periods of inactivity. The larger lithobiids come into the latter category, especially *L. forficatus*. *L. variegatus*, although frequently seen on the surface and on aerial vegetation, is a true soil species. The most common British soil and litter lithobiids are *L. crassipes* and *L. duboscqui*. Generally speaking lithobiids are most frequent in the litter whereas geophilomorphs are mainly inhabitants of the soil beneath. Nothing can be usefully said as yet about the relation between centipedes and the calcium content of the soil except that which may be implied by their preferences for either mull or mor.

SOME ASPECTS OF THE BIOLOGY OF MILLIPEDES AND CENTIPEDES IN RELATION TO DISTRIBUTION

Water relations

It is well known that centipedes and millipedes are very susceptible to desiccation and are consequently to be found only in places where they are assured of humid and moist conditions. Recent work on millipedes has subscribed to this view (Edney, 1951; Cloudsley-Thompson, 1950a). Centipedes are even more susceptible to desiccation than millipedes (Blower, 1954). It would appear, however, that the presence of water may prove, in several ways, as dangerous to these soil animals as its absence. Many small species and immature stadia of the larger species are completely immobilized by a film of water and are not able to overcome the surface tension which imprisons them. Water may also cut off the oxygen supply to the animal unless their surface is sufficiently hydrofuge to allow a film of air to remain round the body; also a soil animal is confronted with the ever-present danger of water uptake by endosmosis. Some soil animals such as lumbricoid worms avoid the dangerous consequences of endosmosis by pumping water out as rapidly as it enters. The development of a hydrofuge and impermeable cuticle, however, provides a solution to all three problems; surface tension, oxygen lack and endosmosis. It is in this last respect that centipedes and millipedes exhibit positive adaptations to their life in the soil; their cuticle is covered by a surface film of lipoid which is produced continually by gland cells in the epidermis (Blower, 1952) and this film renders the surface impermeable and hydrofuge to varying degrees according to the species. In order to assess the effectiveness of the lipoid layer in this respect it is more useful to follow the passage of water into the body rather than its transpiration outwards; the tracheal system complicates the issue in the latter type of experiment. Verhoeff (1928, 1932) studied the behaviour of various centipedes and millipedes when immersed in water. The author has repeated these experiments and extended the range of species examined (Blower, 1954) and the following conclusions have emerged. Iulid millipedes and geophilomorph centipedes are able to survive immersion for much longer than 24 hours (exact times depending on the species and the amount of air in solution). In both these groups air is held at the surface—in Iulids the space between the hind edge of the metazonite and the ring duplicature is used as a reservoir. There is no perceptible endosmosis of water after 24 hours. By contrast, lithobiid centipedes and the flat-backed millipedes (*Polymicrodon* and *Polydesmus*) are only able to survive immersion for a few hours—about six in *Polydesmus angustus* and less in *Polymicrodon*. The amount of air held at the surface of these species is negligible and there is considerable endosmosis of water. The intersegmental membranes are revealed due to the partial de-telescoping of the body rings and the extrusible parts such as the gonopods and vulvae are thrust out. That water enters across the cuticle is made quite evident in the case of *Lithobius*. If the latter is desiccated to the extent of a 20 per cent loss of weight it becomes quite motionless and apparently dead, but will regain its original weight within six hours if placed with its dorsal surface in contact with moist filter paper. The possibility of water entering at the mouth or other local site has not been fully excluded, but the resistance to water uptake is clearly correlated with the amount of lipoid secreted on to the surface of the cuticle; the lipoid at the surface and in the epidermal glands is much more readily demonstrable in the Iulids and the geophilomorphs than in the other groups.

Since Iulids are more resistant to wetting and water-uptake than Polydesmids and *Polymicrodon*, it may be expected that they will also be more resistant to water loss. This is, in fact, the case. Geophilomorphs however do not show an appreciably greater resistance to desiccation than lithobiomorphs, notwithstanding the considerable differences in the permeability of their cuticles. This is no doubt due to the imperfect spiracular closing devices of both orders of centipede, for a hydrofuge surface will prevent water entering the spiracle but cannot limit its transpiration outwards. By contrast all millipedes except *Glomeris* and its relatives possess efficient tracheal closing mechanisms and in Iulids and *Polymicrodon*, in addition, the spiral reflex gives added protection to the tracheal openings. The rolling-up of *Glomeris* will, of course, serve as a functional tracheal closing mechanism. Polydesmids are not able to spiral, and in any case the spiracles, being lateral, would gain little protection from such a habit.

Burrowing

It has recently been shown (MANTON, 1952, 1954) that the structural features which have provided systematists with a basis for distinction between orders of chilopod and of diplopod are directly correlated with the mode of progression of these animals on or through their substrate. Of the centipedes Manton (1952) distinguishes between the swift-running lithobiomorphs which are not able to burrow and the geophilomorphs which burrow rather like earthworms by means of body-wall musculature. Millipedes have developed slow powerful gaits and push their way through the substrate like a ' bull-dozer ' (Iulids and *Glomeris*), or somewhat like a wedge (Polydesmids and *Polymicrodon*) (Manton, 1954). The distinction she draws between the ' flat-back ' type of pushing and that of the Iulids and *Glomeris* is important here. In the former the head end is narrower than the mid-trunk region and it is insinuated into a crack which is then pushed open by the flat back. They are thus adapted ' to push a way through matter which splits open along one plane, as does the damp layered mass of semi-decayed leaves on a woodland floor . . . ' (Manton, 1954). The Iulids push with the first trunk segment (the collum) which overlaps the head in front and the second segment behind. In *Glomeris* the fused second and third tergites serve this purpose.

Nest building and moulting requirements

The eggs of geophilomorphs are well protected by a shell of tanned protein on emergence from the oviduct. They are laid in clusters and receive the protection of the mother until shortly after hatching. The eggs of lithobiomorphs and millipedes are not so well protected on leaving the genital opening and receive further protection in the form of a sticky secretion which hardens on exposure and to which soil particles adhere. This protection may take the form of a shell, an egg case or a nest. Lithobiomorphs lay eggs singly; the female coats the egg, while still at the exit of the oviduct, with a secretion to which soil particles adhere as she rotates the egg between her gonopods. *Glomeris* coats the egg in a similar way but in this animal the soil comes from the rectum; each case may contain more than one egg. All other millipedes lay a cluster of eggs and build a complex nest to protect them either before or after laying. EVANS (1910) reviews the literature and cites his own observations of these processes in millipedes. Iulids build their nest in the soil and their product is the least elaborate. Polydesmids build a more complex structure on the undersurface of a leaf, a piece of wood or a stone. *Polymicrodon* and other Nematophora (for example *Microchordeuma*) spin a silken nest which has been aptly termed a tent (MAIN, 1931) and is built invariably on the underside of a stone or other more solid object than is necessary for the earth nest of *Polydesmus*.

In addition to nest building *Polymicrodon*, *Polydesmus* and iulids construct a cell in which to moult. *Polymicrodon* spins a silken moulting chamber whereas Polydesmids and Iulids build an earthen chamber similar to the Iulid nest. As in nest building, special requirements are evident in the choice of site. On one occasion the author observed large numbers of *Cylindroiulus punctatus* undergoing apparently synchronous moults beneath moss on stones in an oak wood. This species is usually common in the litter which, however, had been almost completely abandoned on this occasion. *Glomeris* does not use any special cell in which to moult.

The choice of site for nest building and moulting will depend in part on the type of nest or cell which is constructed. It is also evident, however, that other considerations besides those purely mechanical, such as the potential dangers of desiccation or water-logging, must influence these animals in their choice.

Relation to mineral soil type

Although it has been pointed out that at least one millipede, *C. londinensis* (var.), may be truly calcicole, it would be premature to refer to *Schizophyllum* and *C. latestriatus* as calcifuge because of their frequent association with sandy soils. A sandy soil will prove advantageous to millipedes in being an easy medium for the diplopod type of burrowing; however, a clay soil with good crumb structure will offer the same advantages. Most millipedes are in fact influenced to a certain extent by calcium in the soil. This may be due to the fact that calcium ions in the soil water may exert a beneficial effect by limiting the permeability of the epidermis and thus restricting any water intake by endosmosis. This factor would be important to lithobiids and flat-backed millipedes and in fact to all species at times of egg-laying and moulting where there is a temporary susceptibility to water uptake. On the other hand the preference of millipedes for calcareous soils may reflect some nutritional requirement.

Résumé

In conclusion it will be convenient to comment on each of the major groups in the light of the foregoing. Lithobiomorph centipedes will tend to be confined to the litter since they cannot burrow and their susceptibility to wetting and water intake will make the soil inimical to them during periods of rainfall. In view of their susceptibility to water loss, however, a litter sufficiently thick to retain moisture in the lower layers during dry periods will be an advantage. Alternatively, a floor well strewn with stones, old logs and other ground debris will offer similar shelter to thick litter.

Polydesmid millipedes will tend to live at the surface for the same reasons as given above for lithobiomorphs but their nesting and moulting requirements place an additional premium on a thick litter or a floor covered with extensive macro-debris. *Polymicrodon* has the same limitations as *Polydesmus* but its greater susceptibility to wetting and its habit of weaving a silken nest make solid objects on the floor even more imperative.

Iulids and geophilomorphs are not so much affected by the comings and goings of water in the soil. However, the eggs of a Iulid and, during moulting, the animal itself will have none of the independence conferred by a hydrofuge and impermeable cuticle and thus these stages will have similar habitat requirements during part of their life as have been listed above for the other myriapods. The vulnerable species and the vulnerable stages of the more well-protected species may, as has been suggested, gain some protection from endosmotic uptake of water by living in a soil where the water is rich in calcium ions. The Iulid, *Cylindroiulus punctatus*, however, takes its vulnerable stages into positions free from liquid water (under moss on tops of stones) and in this way may free itself of dependence on the calcium content of the soil.

The pill-millipede *Glomeris* is a special case. Although it burrows in the same manner as a Iulid it is less powerful since it has a shorter body and fewer pairs of legs (see Manton, 1954); it thus tends to live more at the surface of the soil, and yet, because of its predilection for rapidly decomposing litter, it is rarely provided with the shelter afforded by a thick carpet of leaves. It is more numerous where a herb and/or shrub layer limits evaporation from the surface layers of the soil. It was no doubt this knowledge which led Verhoeff (1932) to include *Glomeris* in his category of ' fern-animals ' although there appears to be little difference in the shelter afforded to these animals by bracken and, say, bramble.

Geophilomorphs are well adapted to life within the soil. They are mechanically fitted to burrow and their waterproof cuticle ensures their survival in periods of temporary flooding. Their susceptibility to desiccation is of little importance since they are able to avoid drought by descending deeper into the soil. These same considerations apply also to Iulids with the qualification discussed above concerning their unprotected stages. By contrast lithobiids and flat-backed millipedes are neither mechanically nor physiologically adapted to life within the soil and are thus mainly confined to the litter or to suitable surface retreats (under stones, beneath moss and bark *etc*) which offer protection from flood and drought.

The above considerations are important in relation to sampling technique. Drift (1952) notes that the Iulid *C. punctatus* was sometimes left behind in the desiccated litter during Tullgren funnel sorting. Polydesmids may be left behind in even greater numbers since they are not active animals and are more susceptible to desiccation than Iulids. Again, in view of the differential wettability of the cuticle as discussed above, the consequent selectivity of certain flotation methods may prove misleading. Lastly, it will be evident that the retreats used by the surface-dwelling species should be sampled along with the soil and litter.

ECONOMICS OF MILLIPEDES AND CENTIPEDES IN THE SOIL

The economics of millipedes and centipedes in arable land and grassland has been discussed by Brade-Birks (1929, 1930) and Cloudsley-Thompson (1950) and nothing further will be added here. Of the part played by centipedes in the community of the woodland floor little can be said in view of our comparative ignorance of their feeding habits. Millipedes, however, are known to make an important contribution to the process of soil formation in woodland. Examples of the mull-forming activity of millipedes are given by ROMELL (1935) and EATON (1943). They break down litter and other organic material and effect a mixing of these with the mineral soil particles. Whether or not they channel the soil will depend on the nature of the mineral substrate. In heavy clay soils their effect in this respect will no doubt be small although they may channel indirectly in the manner suggested by Jacot (1940) by eating out dead and decaying root systems.

FRANZ and LEITENBERGER (1948) considered that the litter ingested by millipedes was subjected to an appreciable amount of chemical breakdown, but Drift (1952) questioned the validity of their conclusions, having shown that *Glomeris* merely comminutes the litter and facilities rather than initiates chemical breakdown by micro-organisms. The latter author points out the difficulty of estimating quantitatively the effectiveness of millipedes in the breakdown of litter. While not reaching any conclusion on this point he indicates that since the quantity of food extracted from litter by *Glomeris* is small, the amount of litter they consume must be considerable.

It may be wise to consider the effect of deforestation on the millipede population of Great Britain. It has been suggested above that some British millipedes may at present be refugees from the erstwhile indigenous woodlands, especially the coniferous forests. How many of these have recolonized the State forests is a matter of some interest. Baweja (1939) has indicated that millipedes are slow to recolonize soils from which they have been excluded although DIMBLEBY (1952) records the re-appearance of typical woodland millipedes under small islands of 14-year old birch on heather moor.

Jacot (1940) advocated the active re-stocking of new plantations with suitable mull-forming species. Apart from the spectacular example described by Romell (1935) there is little evidence that millipedes do in fact form mull. The nature of their influence on the soil is still largely unknown; that their influence is great, however, is suggested by the size of the populations encountered (100–400 per m^2) and by the amount of food they need to eat (Drift, 1952). Furthermore, little is known regarding the types of environment wherein certain associations of millipedes could contribute maximally to soil improvement. Certain of the edaphic factors important in determining their distribution have been mentioned but these fall far short of explaining the known facts of their habitat preferences. Practically nothing has or can be said regarding the complex biotic factors which are operative.

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DISCUSSION

PROFESSOR W. KÜHNELT: Referring to subcortical species it may be said that the general behaviour of the group appears to define the habitat. Many arthropods (myriapods, mites, etc) are often subcortical in moist atmospheres, but are found in the litter in drier atmospheres. This difference may be observable in adjacent areas with differing micro climates, or geographically as one passes for instance from the moister parts of Northern Europe southwards to drier regions.

Concerning *Isobates varicornis*, I have never found this elsewhere than under bark: I should appreciate Mr. Blower's opinion, please !

MR. BLOWER: Yes ! It is confined to subcortical habitat in Great Britain also—as is *Cylindroiulus britannicus*—but the number of species thus confined gets fewer as more habitats are investigated, and even these species may be found eventually in litter.

PROFESSOR KÜHNELT: I would expect the behaviour of *Craspedosoma rawlinsi* to differ from other flat-backs since it occurs in river woods sometimes subject to flooding.

MR. BLOWER: *Craspedosoma rawlinsi* is rare in Great Britain and was not available alive during the conduct of my water immersion experiments. As in Europe generally, in Great Britain too, this species is often associated with flowing water, but usually in well-drained situations.

PROFESSOR W. TISCHLER: I should like to mention the investigations

* See the speaker's own papers.

of Krüger (1952)* who worked quantitatively at the species level in arable land. Very considerable numbers of myriapods of several different species were shown to exist in cultivated fields. Furthermore, most of the woodland species were trapped on the surface of the soil (by means of sunken jars) throughout the whole area of the fields. I am of the opinion that fields may provide optimum biotopes for many species of millipede.

Mr. Blower: The question is still open regarding the typical fauna of arable land and grassland. In Great Britain about ten species of myriapod are common in these environments which never constitute optimum habitats except perhaps for *Blaniulus guttulatus* which is slender enough to use the small spaces. However, in plagues, millipedes may occur in large numbers away from their normal habitat, but the absence of surface debris in non-wooded *agricultural* regions may preclude such regions from consideration as optimum.

Professor Tischler: There may be some differences between England and North Germany in regard to the occurrence of myriapods in fields. As many as 100–200 millipedes or centipedes have been found per m^2 in the latter. Such numbers were not obtained in woods, so they may have been true grassland species.

Mr. Blower: I have tried to compare woodland with other habitats but the matter is still open to investigation since the data from different surveys are not truly comparable. One British species (one which is new to science) may be a true grassland form; it has only been found in wire-worm samples. Verhoeff (1928) also regarded all but a few millipedes in non-wooded areas as relicts of the woodland which used to cover these places.

Professor Tischler: I agree that the former woodland character of fields might explain the existence of myriapods in such biotopes.