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Studies on the ecology of *Proteroiulus fuscus* (AM STEIN, 1857) (*Diplopoda, Blaniulidae*)

[With Pls. XVIII—XXV, 17 figs.]

Studia nad ekologią *Proteroiulus fuscus* (AM STEIN, **1857**) (*Diplopoda, Blaniulidae*)

Abstract. This study deals with the biology and biocenotic role of the species *Proteroiulus fuscus* (*Diplopoda*) and its aplicability in soil zooamelioration. Its distribution in Poland, tolerance and preference as regards temperature, light, humidity and food, and the morphology and duration of particular developmental stages (especially periodomorphosis) are discussed. The dynamics and spatial distribution of populations relative to the age of the stand are described in detail and the biocenotic role of *P. fuscus* and the possibility of its introduction into new environments, i.e. into formerly arable soils designed for forestation, are also dealt with.

CONTENTS

I. INTRODUCTION

An investigation carried out by a team of the Institute of Forest and Wood Protection, SGGW-AR, on the composition and groupings of the soil macrofauna in pine stands growing in the biotopes of fresh coniferous forests on wood soils and formerly arable soils showed that the millipede *Proteroiulus fuscus* (AM STEIN 1857) forms its high proportion

(SZUJECKI et al. 1974). This species occurs under the bark of dead tree-stumps and in logs and branches left lying, mostly of pine, less frequently in those of birch, willow, alder and ash. It can also often be met with in litter of deciduous trees. In decaying wood of the above-named species of trees it occurs in very large numbers, living, e.g. in pine stumps as a member of one of the last stages of succession of the soil invertebrate fauna contributing to their decay (MAMAEV, 1960, 1961; KOZARZHEVSKAYA and MAMAEV, 1962; SCHIMITSCHEK, 1952).

The introduction of *P. fuscus* on to formerly arable soils as a zooameliorative procedure, after their being supplied with slowdecaying organic remains, could prompt the biological activation of the top layer of soil, while covered by plantations and young woods. However, the successful utilization of any animal species for regulation of the function of an ecosystem is possible only after enough knowledge of its development and ecology has been acquired. The studies carried out so far on *P. fuscus* (BROOKES, 1974; RANTALA, 1970, 1974; PEITSALMI, 1974) were concentrated nearly exclusively on certain aspects of the biology of this species.

The main purpose of the work here presented was to get to know some selected problems of the developmental biology of *P. fuscus* and to determine its requirements as to the environment it inhabits and important ecological agents. Its objective was also to study the nature of occurrence of *P. fuscus* in fresh pine forests and to characterize the food conditions it finds and the biocenotic role it plays in the ecosystems of pine woodland. The choice of these issues was dictated by the role this species plays in the procedures of land zooamelioration.

Here I wish to express my heartfelt thanks to Prof. Andrzej SZUJECKI for help and all methodological instructions I received from him in the course of this work; I am also grateful to Assist. Prof. Kazimiera GROMYSZ-KAŁKOWSKA and Dr Andrzej GRZYWACZ for help with some of the laboratory experiments.

II. STUDY AREA

A field study was carried out in the Niedźwiady forest-range in the Słupsk Province. In this forest-range a number of experimental plots were set up on wood and formerly arable soils in stands of pines in fresh forest habitats for research purposes of the Institute of Forest and Wood Protection. The Niedźwiady forest-range is situated at the western edge of the Tuchola Forest in the Krajeńsko-Pomeranian District of the 3rd Wielkopolska-Pomeranian vegetation-forest province of Poland (MROCZKIEWICZ, 1952).

A phytosociological examination of the study plots showed that they lay in typical habitats of fresh forest and, within this type, in rather

Table I

Phytosociological and soil characteristics of the study plots

Plot No.	Age in years	Forest site type	Forest association	Subassociation	Soil type	Litter	Genetic horizons
16/2	4	Fresh coniferous forest	*Leucobryo-Pinetum* MAT.	*Leucobryo-Pinetum Typicum*	Brown podzolic soil on coarse sand	Rohhumus	A_l, A_f, A_h, A_1
17/2	8						
20/2	6						
22/2	12						

poor subtypes resembling dry forests. The suboceanic pine forest *Leucobryo-Pinetum* MAT. 1962 is the dominant association and *Leucobryo-Pinetum typicum* the subassociation.

The abundant occurrence of *P. fuscus* in the earliest developmental stages of a forest on wood soils necessitated a close investigation of the nature of occurrence and development of this species in tree nurseries and young stands. For this purpose four plots, 30 × 30 m in area, were chosen from the existing groups of experimental plots of forest on wood soils, similar in respect of biotopic conditions (Table I).

The field study was conducted during two vegetation seasons from May to October in 1975—1976.

III. OCCURRENCE OF THE SPECIES

Proteroiulus fuscus occurs in the regions situated round the North Sea and the Baltic (Great Britain, Ireland, Iceland, European part of the U.S.S.R., Poland, Czechoslovakia, Germany, Denmark, Netherlands, Belgium, France, Luxemburg, Austria and Italy (VERHOEFF, 1928, 1932; SCHUBART, 1934; LANG, 1954; STOJAŁOWSKA, 1961b; LOKSHINA, 1969). It is very common in Scandinavia and LOHMANDER (1925) considers it a characteristic species of the Baltic area. *P. fuscus* is the only diplopod species that ranges beyond the Polar Circle (SCHUBART, 1931; PALMEN, 1949). SCHUBART (1931) explains the wide distribution of this species to the north by its capability of quick adaptation to conditions prevailing after the retreat of the ice-sheet and the relatively easy colonization of areas covered by shrubby and arboreous plants. PALMEN (1952) records this species — after JAWŁOWSKI (1930, 1939) and SCHUBART (1934) — from the eastern region of North America and New Foundland, where, in his opinion, it was brought by man.

P. fuscus, which inhabits the regions bordering upon seas, rivers and lakes, can readily be carried by water on drifting wood to various places

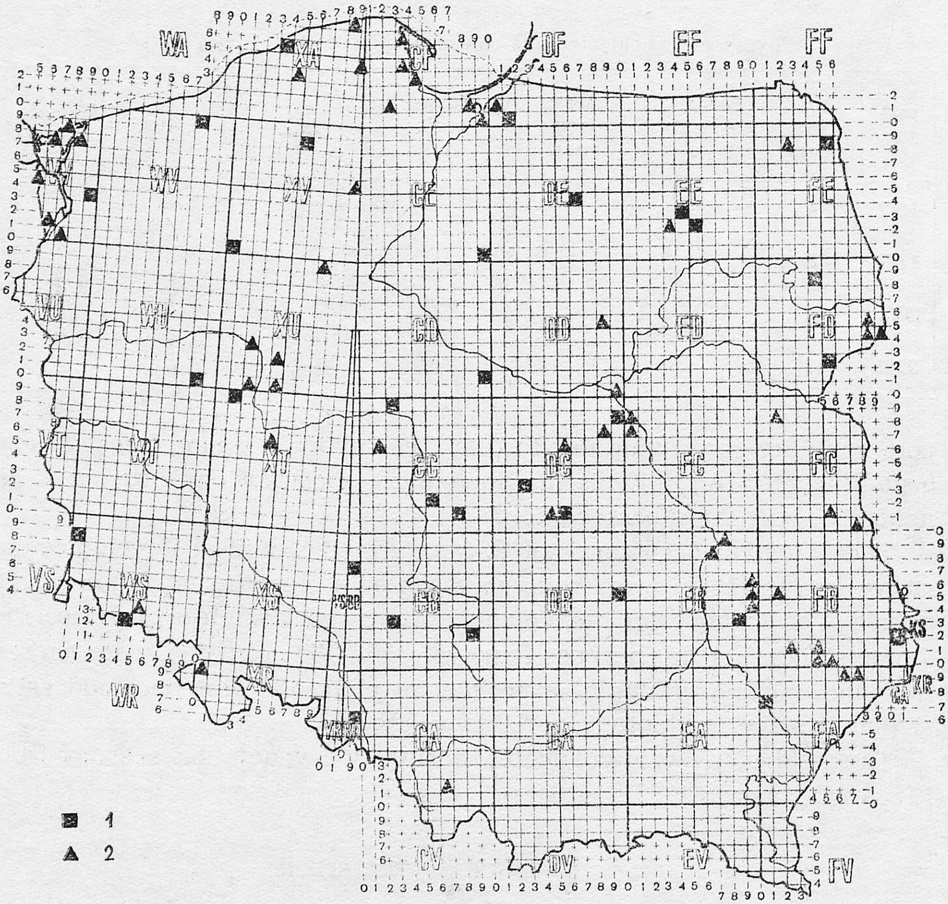


Fig. 1. Distribution of the localities of *Proteroiulus fuscus* on the basis of own observations (1) and the data from literature (2) after STOJAŁOWSKA & STARĘGA, (1974)

and this probably accounts also for its appearance on the islands in the Baltic Sea (PALMEN, 1949).

In Poland it occurs most frequently in lowlands, from the Baltic coast up to the highlands (Fig. 1). In the Sudetes specimens of *P. fuscus* were found in a mountain mixed coniferous forest with pine at an altitude of 600 m. The fact that it lives under bark and mosses and in decaying wood makes this species to a certain degree independent of the now prevailing environmental conditions. In consequence, it may appear, as one of a few diplopods, both in poor and dry pine forests and moorlands as well as in peatbogs and fertile habitats of alder swamps. It, besides, often happens in anthills, bird nests and tree-holes. In autumn it can frequently be met with on the fructifications of fungi growing out of litter and treestumps. This inhabitant of woodlands may occur both in shady forests and in open and sunny clearings, tree nurseries, etc.

Table II

The list of *Proteroiulus fuscus* in Poland prepared on the basis of the author's own observations

Locality	Forest site type	Habitat characteristics	Number of individuals	Males	UTM-System
1	2	3	4	5	6
Ustka	Fr. Con. F.	2 y. old stand, 7 y. old stand Pn: under bark of stumps, 300 m from sea line	4 juvenile 6 mature	—	XA-4,5
Manowo	Fr. Con. F.	2 y. old stand, 90 y. old stand Pn: in stumps under bark and under moss	16 mature	—	WV-8,9
Młynary	Fr. Mix. Con. F. Hu. Con. F.	4 y. old stand, Sp, Pn, Br, under bark of Pn stumps	4 mature	—	DF-2,0
Głęboki Bród	Fr. Con. F.	70—80 y. old stand Pn, in Pn stumps, under bark	9 mature 7 juvenile	—	FE 5-8,9
Niedźwiady	Fr. Con. F. Fr. Mix. Con. F. Al. F. Mix. F.	young and mature stands, Pn: in stumps under bark, in rotten wood, in litter composed of Br, Wl, Al, leaves, ant nests, fungi, outer bark	specimens collected during the study period	2,07%	FE-6,8
Goleniów	Fr. Con. F.	1 y. old stand Pn: under bark of stumps, 90 y. old stand Pn: in old stumps, under litter	8 juvenile 5 mature	—	VV-3,0
Olsztynek	Fr. Con. F.	8—10 y. old stand Pn: in a stump	2 juvenile 4 mature	—	DE-7,4
Pisz (Uściany, Zdunowo)	Fr. Con. F.	4—5 y. old stand Pn: under bark of dead stumps	6 juvenile 7 mature	—	EE-5,3 6,2
Wałcz	Fr. Con. F.	3 y. old stand Pn: under bark of stumps 0,8 m above ground	9 juvenile 30 mature	—	XV-1,0
Kłodawa near Gorzów Wlkp.	Fr. Con. F.	7 y. old stand, Ok, L, Be, Pn, under bark of a stump, under moss on a stem	5 juvenile 3 mature	—	WU-2,4

1	2	3	4	5	6
Smolarz near Drezdenko	Fr. Con. F. Fr. Mix. Con. F.	2 y. old stand, 90—100 y. old stand, under bark of stem, 5 y. old stand complete ploughing, Pn: stump wood under bark	16 juvenile 36 mature	—	WU-7,5
Brodnica	Fr. Mix. F.	13 y. old stand, Wl, Hz, Br, Al, Wl stump, under moss	5 juvenile	—	CE-0,0
Dojlidy near Białystok	Fr. Mix. Con. F.	12 y. old stand, Pn with Br admix. in Br litter	2 mature	—	FD-5,8
Trzciel	Fr. Con. F.	4 y. old stand, Pn, under bark of stumps, 100 y. old stand on stumps covered with moss	6 juvenile 42 mature	2,3%	WU-9,0
Wielkopolski National Park near Stęszew	Fr. Mix. Con. F.	90 y. old stand, Pn understory of Br, Ma, Ok, under bark of a stump	25 mature	—	ĘT-2,9
Konin	Fr. Mix. Con. F.	90 y. old stand, Pn, understory of Br, Ma, Ok, on stump under litter	6 juvenile 15 mature	—	CC-3,9
Łąck	Fr. Con. F.	5—6 y. old stand, Pn, under bark of a stump	2 mature	—	CD-0,1
Bielsk Podlaski	Hu. Mix. Con. F.	10 y. old stand, Pn, in a stump, under bark	2 mature	—	FD-6,2
Kampinos National Park	Fr. Mix. Con. F.	80 y. old stand, Pn with admix. Br, Ok, under bark of stumps	9 mature	—	DC-0,8
Experimental Forest, Rogów	Fr. Mix. Con. F.	hollow in maple tree, nest of *Lasius brunneus*	2 mature	—	DC-3,3
Kolumna near Łask	Fr. Con. F.	15 y. old stand, on a stump under moss	9 mature	—	CC-8,1
Sieradz	Fr. Con. F.	80—90 y. old stand, in a stump under moss	3 mature	—	CC-6,2
Spała	Fr. Mix. Con. F.	8 y. old stand, Pn, Ok, Br, in a Pn stump, nest of *Formica fusca*	6 mature	—	DC-6,1

1	2	3	4	5	6
Bralin near Kępno	Fr. Mix. Con. F.	80—100 y. old stand, Pn with admix. Br, Ma, in a stump under bark	6 juvenile 7 mature	—	BB-0,7
Ruszów	Hu. Mix. Con. F.	11 y. old stand, Pn, Sp, Br, Al, Ok, L, marshy area, in a stump, under moss	5 juvenile 4 mature	—	WS-1,8
Olesno	Fr. Mix. Con. F.	12 y. old stand, Pn, Ok, Br, in Br litter, in stumps, under bark and in wood, in stump fungi	53 73 135 122 58	— — — 0,82%	CB-3,3
Złoty Potok near Częstochowa	Hu. Mix. Con. F.	80 y. old stand, Pn, Br, Al, wet area, on stumps under moss	7 juvenile 5 mature	—	CB-9,2
Starachowice	Fr. Con. F.	100 y. old stand, Pn with Jp understory, under bark and in rotten wood of stumps	3 juvenile 8 mature	—	DB-0,5
Kraśnik	Fr. Mix. Con. F.	100 y. old stand, Ok, Br, under bark of stumps	8 mature	—	EB-9,3
Karkonosze National Park (Chojnik Reserve near Sobieszów)	Mnt. Mix. Con. F.	120 y. old stand, Sp, Be, Br, Pn, in a Pn stump under bark, on a 3 m long Pn log, under bark of Br dead wood	8 juvenile 12 mature	—	WS-5,2
Rudy Raciborskie	Fr. Mix. Con. F.	5 y. old stand, Ok, Pn, Sp. L, under bark of of Pn stumps	6 juvenile 5 mature	—	BA-0,6
Leżajsk	Fr. Con. F.	4 y. old stand, Pn, under bark of stumps, in nests of *Formica fusca*	4 juvenile 5 mature	—	FA-1,7

Literature (PALMEN, 1949; HEYDEMANN, 1956) reports also the occurrence of *P. fuscus* in cultivated fields, gardens, in the proximity of human settlements, wherever there are pieces of decaying wood, rubble covered by mosses, and the like. In Finland it was also found in greenhouses, which would indicate the synanthropic nature of its occurrence. POCKER'S (1956) finds from Luxemburg are interesting. He observed large numbers of specimens of this species in the wooden lining of the shafts of old mines of gypsum and silicates.

In Poland *P. fuscus* occurs in abundance in pine forests, in tree nurseries, young and fairly young stands, where in consequence of cutting it comes to the accumulation of large amounts of organic remains, like bark, sawdust, chips, branches and decaying wood of stumps and logs. It may occur in such an environment as the only member of the *Diplopoda*.

The utter lack of this species in young stands on formerly arable soils makes one of the essential differences between the fauna of these soils and that of wood soils in the first forest generation. It is chiefly due to the lack of suitable food supplies, presumably also to different microbiological relations in soils used for agricultural purposes, but, above all, to the absence of this species from fields and its slow dispersal.

In formerly arable, wooded areas *P. fuscus* does not occur until the final phase of the production cycle of the stand (SZUJECKI et al., 1974). It is generally observed that the inhabited environments are greatly differentiated, which may indicate that this species is very tolerant as regards the choice of sites for colonization and suggests its eurytopic nature.

The occurrence of *P. fuscus* in the territory of Poland is shown in Table II, providing a list of localities.

IV. TOLERANCE AND PREFERENCE AS REGARDS ENVIRONMENTAL AGENTS

A. Temperature preferendum

Reactions of millipedes to thermal stimuli were examined using a HERTER apparatus by the method described by GROMYSZ-KAŁKOW-

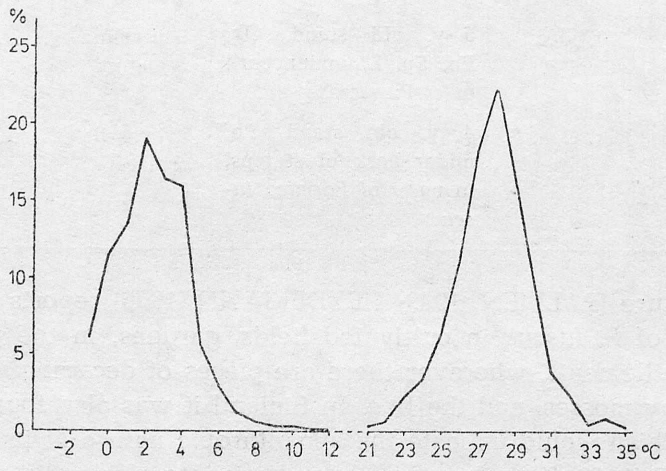


Fig. 2. Retreats of *Proteroiulus fuscus* (%) at low and high temperatures (T)

Table III

Thermic behaviour of *Proteroiulus fuscus*

Temperature in °C	Retreats under low temperature		Mean terminal temperature	Retreats under high temperature		Temperature in °C	Mean terminal temperature
	Numbers	%		Numbers	%		
−2	0			0	0	36	
−1	41/4*	6,0/0,6*		3	0,4	35	
0	80/11*	11,6/1,6*		5	0,8	34	
1	93/12*	13,5/1,7*		3	0,4	33	
2	131/12*	19,0/1,7*		16	2,3	32	
3	112/5*	16,3/0,7*		27	3,9	31	
4	110/3*	15,9/0,4*		70	10,2	30	
5	38	5,5		113	16,4	29	
6	19	2,8		156	22,6	28	
7	8	1,2	+2,6°C	127	18,4	27	+27,7°C
8	4	0,6		78	11,3	26	
9	2	0,3		45	6,5	25	
10	3	0,4		24	3,5	24	
11	1	0,1		16	2,3	23	
12	1	0,1		5	0,7	22	
13	0	0		2	0,3	21	
14	0	0		0	0	20	
15	0	0		0	0	19	
16	0	0		0	0	18	
17	0	0		0	0	17	
Total	643/47*	93,3/6,7*		690	100		

Note: millipedes which were struck by cold and could not turn back after reaching a certain temperature

SKA (1967). The temperature gradients used in the experiment ranged from −2 to +17° and from +17 to +35°C. The lower and upper extreme temperatures were determined by reading the substratum temperatures at which millipedes changed the direction of motion by 180° or showed symptoms of thermical stroke. The substratum temperature at which a specimen was observed to come to a stop spontaneously was assumed to be a measuring unit of preferential temperature.

The observations of the behaviour of *P. fuscus* at various temperatures are summarized in Table III and Fig. 2. An analysis of the minimum temperatures showed the most retreats at +2—+4°C. Cases of cold stroke were recorded starting from +4°C. The mean lower extreme temperature was +2.6°C.

Preferential

Temperature in °C	6	7	8	9	10	11	12	13	14	15	16	17	18
Number of individuals resting	4	1	17	53	53	41	57	36	43	39	44	37	29
% of individuals resting	0,7	0,2	2,8	8,8	8,8	6,8	9,5	6,0	7,2	6,5	7,3	6,2	4,8

Mean preferential temperature is +15°C.

As regards the maximum temperature, most retreats — as many as 78.9% of the total of observations — occurred at temperatures between 26 and 30°C. The mean upper extreme temperature was +27.7°C.

The range of preferential temperatures at which most specimens of *P. fuscus* (81.2% of those used in the experiment) stop for rest is wide (9—20°C). The mean preferential temperature of this species is +15°C. (Table IV).

As can be seen from the foregoing, *P. fuscus* has a wide range of thermal tolerance. Considering activity, this species is active from −1 to +35°C, which values are the minimum and maximum temperatures of activeness. The range of lower extreme temperatures is the range within which not all specimens and not each time are able to withdraw by themselves. And so 6.7% of the *P. fuscus* specimens became torpid at temperatures between +4 and −1°C (Table III, dotted figures). As for high temperatures, the millipedes examined never delayed their retreat until the temperature prevented them from accomplishing it. To be sure, *P. fuscus* tolerates fairly high temperatures but, on the other hand, it is adapted to marked 24-hour fluctuations in air temperature. These facts are supposed to be responsible for the lack of strokes at high temperatures and their very small number at low temperatures.

The fact that *P. fuscus* is able to tolerate a wide range of temperatures inclines us to consider it a eurythermal species.

B. Light preferendum

Four different intensities of light were used to observe its effect upon the behaviour of millipedes and their staying in definite areas of the experimental vessel. A detailed description of the method is given in the

Table IV

temperatures

19	20	21		23	24	25		27	28	29	Total observations	Number of individuals
25	30	19	22	15	17	7	7	3	0	1	600	30
4,3	5,0	3,2	3,7	2,5	2,7	1,2	1,2	0,5	0	0,1	100	

author's previous paper (TRACZ, 1979). Twenty mature specimens of *P. fuscus* were used for this study. One experimental run took about 2.5 hrs, next the bedding (sand) and millipedes were changed. Every 15 minutes the millipedes were counted in particular parts of the vessel. Altogether 30 runs were made and the mean values were calculated from the results obtained. The differences between particular means were examin-

Table V

Mean number of individuals in illumination divisions (Klx)

16,6—24,5	3,7—4,4	1,4—1,6	0
0,8	3,4	6,5	9,3

	1	2	3	4
1		+	+	+
2	$t_{obl.}$ 11,69		+	+
3	$t_{obl.}$ 27,17	$t_{obl.}$ 15,22		+
4	$t_{obl.}$ 30,21	$t_{obl.}$ 18,31	$t_{obl.}$ 8,30	

Significance of differences at
at $p_{\alpha} = 0{,}01$
$t' = 2{,}66$

ed by STUDENT's t test at the 0.01 level of significance. *P. fuscus*'s preference of definite light intensities is presented in Table V.

The significance of the differences between the means was determined. The results indicate that the millipedes preferred the most shaped region, corresponding to the conditions of darkness. The occurrence of millipedes also in the other regions, those partly shaped or lit directly from light sources of various intensity, corresponding to the conditions of cloudy and sunny days, suggests that, preferring darkness, this species may appear also in lighted places.

These results are also confirmed by field observations of *P. fuscus,* which is met with both in thick shady woods and in its more open places, e.g. in clearings, young plantations, etc. More often than not, however, in the daytime, especially on fine days, millipedes take shelter in soil or in deeper portions of stumps to avoid the direct action of the sun's rays. In the night-time they move into the surface layers of litter and may more frequently be encountered on the surface of stumps. This is probably connected also with higher air humidity at that time.

C. Dampness preferendum

The preferential dampness of surroundings of *P. fuscus* was determined on the basis of the presence of its specimens in particular compartments of the experimental vessel, in which a humidity gradient was maintained. A detailed description of the method is given in the author's previous paper (TRACZ, 1979). One experimental run lasted 12—15 hrs and during this period the occurrence of 20 adult millipedes in particular compartments, easily accessible to them, was observed at intervals of 0.5—1.0 hr. After the run the bedding (sand) and millipedes were changed and the experiment was repeated. It was run in a thermostat at a temperature of 22—24°C. Altogether 20 runs were performed and the results obtained were reduced to mean values and statistically analysed.

Table VI gives the preferential dampness of surroundings for *P. fuscus*. The results obtained suggest that this millipede prefers dampness corresponding to that of very moist sand, i.e. 20%. As the dampness of the bedding diminished in successive compartments, the number of specimens found in them was also smaller. These results are confirmed by field observations on the behaviour of *P. fuscus* in relation to the dampness of surroundings.

PEITSALMI (1974) described the behaviour of *P. fuscus* against various levels of air humidity. She found that its vertical migrations and formation of aggregations are closely dependent on air humidity. At various gradients of air humidity millipedes always choose the zone with saturated air (100% relative humidity) and their aggregations can pers-

Table VI

Mean number of individuals in humidity divisions

0%	1,25%	2,5%	5%	10%	20%
0,5	1,2	1,9	3,3	5,9	7,2

	1	2	3	4	5	6
1		+	+	+	+	+
2	$t_{obl.}$ 3,59		− 0,01 + 0,05	+	+	+
3	$t_{obl.}$ 4,71	$t_{obl.}$ 2,16		+	+	+
4	$t_{obl.}$ 9,15	$t_{obl.}$ 6,35	$t_{obl.}$ 3,50		+	+
5	$t_{obl.}$ 16,05	$t_{obl.}$ 10,58	$t_{obl.}$ 9,44	$t_{obl.}$ 6,05		+
6	$t_{obl.}$ 24,06	$t_{obl.}$ 20,01	$t_{obl.}$ 14,14	$t_{obl.}$ 10,22	$t_{obl.}$ 3,20	

Significance of differences
at $p_\alpha = 0{,}01$
$t' = 2{,}704$
at $p_\alpha = 0{,}05$
$t' = 2{,}021$

ist as long as the air is saturated. Their orientation towards the preferential air humidity consists in formation of small groups, which other specimens join next (it may well be that we are here concerned with the influence of tigmokinetic reactions — PEITSALMI, 1974).

The 24-hour rhythm of *P. fuscus* is closely associated with its responses to such factors as light, temperature and humidity in the daytime and by night. Observations made on the behaviour of the specimens of this species kept for 7 days and nights in jars filled from top to bottom with layers of litter, A_l, humus, $A_{f/h}$, and mineral soil, A_1, show that millipedes react evidently to the time of day and night. In the evening, throughout the night and early in the morning most millipedes were observed on the surface of the moss or litter (in the 0—2 cm layer — A_f), on the glass wall of the vessel and the covering net or on the surface of stumps grown over by algae and mosses. On the other hand, in the daytime, especially at noon, when the sun was beating down, the specimens were observed to descend into the soil profile to a level of 4—8 cm, $A_{f/h}$, A_h and to mineral soil.

Hence it follows that, out of the environmental agents under consideration, humidity plays the most important role in the life of this species. Light and temperature have a minor effect on the behaviour of millipedes. STOJAŁOWSKA (1949, 1961a), basing herself on laboratory and field studies, arrives at similar conclusions with regard to other millipede species. She believes that the phenomenon of mass migrations observed in these animals indicates positive phototaxis and tolerance of lower levels of humidity, whereas BARLOV (1957) thinks that changes in the intensity of light may be a signal informative of the occurrence of changing levels of humidity and temperature, which affect millipedes.

It may be supposed on the basis of laboratory and field observations that *P. fuscus*, capable to tolerate various levels of humidity, light and temperature, in consequence shows more plasticity in relation to colonized habitats and can adapt itself relatively easily to various conditions. This character of the species may be very advantageous in trials of its introduction into various environments.

V. FOOD

A. Analysis of alimentary-canal contents and excrement

In order to gather information as to the type of organic matter and the set of micro-organisms occurring in the alimentary canal and excrement of *P. fuscus*, their microbiological analysis was carried out. Mature specimens of *P. fuscus*, representing three different environment of occurrence, i.e. wood of decayed pine stumps, pine bark from stumps (or the zone between the bark and wood) and dead birch leaves in litter.

Two series of experiments were set up. The composition of the micro-organisms in the alimentary canal was investigated in one of them and in excrement of living millipedes in the other. Three kinds of media, a bacterial, a wort-agar and a glucose-potato, were used to isolate as wide a spectrum of micro-organisms occurring in the substrate examined as possible (STRZELCZYK, 1968). Removed from the body of a millipede, 1 mm sections of the mid- and hind-guts were placed directly on the media under conditions of utmost sterility. Twenty-seven petri dishes with appropriate media (3 repetitions) were used in this series.

Table VII

Relationship between the number of colonies of bacteria and fungi and the kind of substratum

Kind of substratum (habitat)	Number of colonies		Ratio bacteria/fungi
	bacteria	fungi	
birch leaves	52	24	2 : 1
pine bark	14	43	1 : 3
pine rot	44	47	1 : 1
Total	110	114	1 : 1

In the second series of experiments two living millipedes were placed, after their being cleaned first, in each petri dish with the same media as before. Twenty-seven petri dishes with media were used also in this series. The millipedes, moving about on the medium, inoculated the dishes by defecating.

The petri dishes with living millipedes were incubated for 2 weeks at 22°C and those with gut sections on the bacterial medium at 35°C and on the wort-agar and glucose-potato media at 25°C. After two weeks of incubation the micro-organisms present in the petri dishes were determined (STRZELCZYK, 1968). Specific determination of fungi was carried out by Dr A. GRZYWACZ of the Institute of Forest Phytopathology and Wood Protection, SGGW-AR.

The results of these analyses showed the occurrence of verious groups of micro-organisms in the alimentary canal. Many bacterial colonies, 3 species of ray-fungi and about 50 species (or other systematic groups) of fungi were isolated. Various species of the *Protozoa, Flagellata, Nematoda* and *Acarina* were numerous in the alimentary canal. Of this abundant group of micro-organisms only the fungi have been studied more closely.

Out of 135 inoculants (1 mm sections of alimentary canals) from millipedes living in three different environments, on three different media, 224 colonies of micro-organisms were isolated (Table VII).

The ratio of the number of bacterial colonies to that of fungi living in an environment (substrate) is a simplified but commonly applied microbiological measure. As regards the alimentary canal of *P. fuscus*, these ration reflected some general regularities prevailing in the substrates making up its nourishment (RUSSEL, 1958; DOMSCH and GAMS, 1970). Fungi predominate quantitatively in decaying bark and bacteria in decaying leaves. Wood at the final stage of decay is colonized by both fungi and bacteria, which is also confirmed by the flora found in the alimentary canal of *P. fuscus*.

The fungi of the genera *Mucor, Penicillium, Aspergillus* and *Gliocladium* were the most numerous in the alimentary canals. A list of the fungi isolated from the alimentary canals is presented in Table VIII, according to the habitats from which the millipedes used in the study were derived.

The most fungi (qualitatively) were isolated from the alimentary canals of millipedes inhabiting the decomposed wood of pine stumps. They were common pedogenic fungi, encountered in various substrates and characterized by a wide range of occurrence (GILMAN, 1959). Hence, they occurred commonly in the alimentary canals of the millipedes examined.

The common nature of the occurrence of *Trichoderma viride* in the alimentary canal of millipedes is a fairly interesting finding (DOMSCH

Table VIII

Fungi isolated from digestive tract of *Proteroiulus fuscus*

No.	Fungus species (group)	Kind of substratum		
		rot	bark	leaves
	Actinomycetes			
1.	*Actinomyces* spp.	+		
2.	*Streptomycetes* spp.	+	+	
3.	*Actinomycetes* nr 1			+
	Phycomycetes			
4.	*Mucor griseo-ochraceus*		+	
5.	*Mucor hiemalis*	+	+	
6.	*Mucor luteus*			+
7.	*Mucor mucedo*	+		
8.	*Mucor racemosus*	+		
9.	*Mucor silvaticus*		+	
10.	*Mucor* spp.	+	+	+
11.	*Rhizopus nigricans*	+	+	
12.	*Cunninghamella* sp.		+	
13.	*Thammidium elegans*	+		
	Basidiomycetes			
14.	Strain Bm1	+		
15.	Strain Bm2		+	
16.	Strain Bm3	+		
	Deuteromycetes			
17.	*Acremonium* sp.	+		
18.	*Aspergillus flavus*			+
19.	*Aspergillus fumigatus*		+	+
20.	*Aspergillus glaucus*	+	+	+
21.	*Aspergillus ochraceus*	+		
22.	*Aspergillus ornatus*		+	
23.	*Aspergillus versicolor*	+		
24.	*Aspergillus* sp.		+	
25.	*Botrytis cinerea*	+		+
26.	*Chrysosporium pannorum*			+
27.	*Cephalosporium* sp.	+		
28.	*Cylindrocladium* sp.	+		
29.	*Dimorphospora folicola*		+	+
30.	*Gliocladium* sp.	+	+	+
31.	*Meria* sp.	+		
32.	*Monocillium* sp.			+
33.	*Monosporium* sp.	+	+	+
34.	*Myrothecium verrucaria*	+		
35.	*Oidiodendron* sp.			+
36.	*Oedocephalum* sp.	+		
37.	*Paecilomyces elegans*	+	+	
38.	*Paecilomyces* sp.	+		
39.	*Penicillium* spp.	+	+	+
40.	*Stysanus microsporus*			+
41.	*Trichoderma viride*	+	+	+

Tab. VIII cd.

No.	Fungus species (group)	Kind of substratum		
		rot	bark	leaves
42.	*Verticillium* sp.	+		
43.	*Alternaria tenuis*	+		+
44.	*Cladosporium cladosporioides*			+
45.	*Cladosporium herbarum*			+
46.	*Graphium* sp.	+		
47.	*Hormiscium* sp.	+		
48.	*Humicola* sp.	+	+	+
49.	*Aurobasidium pullulans*	+		
50.	*Torula herbarum*	+		
51.	*Rhizoctonia solani*	+		
	Total	34	19	20

and GAMS, 1970). This fungus is particularly important in reducing the number of *Fomes annosus*, which induces a severe disease of wood tree roots, especially pines on formerly arable soils.

The composition of the mycoflora of the excrement of *P. fuscus* was markedly poorer than that of the mycoflora in the alimentary canal. The most frequent forms found in it were *Penicillium* spp., *Monocillium* sp., *Aspergillus glaucus, Aspergillus ochraceus, Gliocladium* sp. and *Meria* sp. The genus *Meria* is closely associated with some nematodes and, as nematodes were very numerous in the excrement of millipedes, it may be assumed that his genus was indirectly connected with millipedes. The fact that the composition of the mycoflora of excrement was poorer than that of the alimentary canals seems to have due to various causes:

— some species of fungi are digested by millipedes, make their food up or are digested to such a degree that they lose their capability of germination and so did not appear on the media in our experiment;

— some species may be integral components of the flora of the alimentary canals of millipedes and so they are not excreted but take part in digestive processes.

B. Food preference

Since literature gives only vague and fragmentary information about the food consumed by millipedes (DUNGER, 1958a,b; GERE, 1956, 1962a, b; KOZLOVSKAYA, 1976; MÜLLER, 1965; STRIGANOVA, 1967, 1969a, 1970, 1971; SOKOLOV, 1955, 1957), studies on food preference in *P. fu-*

scus were started with an analysis of the alimentary canals of these animals so as to fix the sort of food on which further studies were to be carried out.

As was shown by microbiological and microscopis studies (scanning electron microscope — Pl. XXIII—XXV), there were various numerous species of fungi, bacteria and other micro-organisms and remains of various organic substances in the contents of the alimentary canal of *P. fuscus*. In order to find whether some species of fungi, sorts of substrates or particular carbohydrates are taken by millipedes more often than the others, the following three experiments were conducted.

a. Wort-agar medium was put in 63 small glass vessels, 20 mm in diameter, 3 ml in each. It was next inoculated with 20 species of fungi (each in 3 repetitions) such as may occur in the biotope of *P. fuscus*. After seven days' growth of mycelium, the vessels were distributed at random in damp sand, flush with the surface of the sand so that the millipedes, moving about, could easily get on to the mycelium.

Three ecological groups were represented by the test species of fungi i.e., group I — species inducing different types of decomposition of wood, including that of stumps, group II — species inducing the discoloration of wood, those making up an association that causes the grey (mouldy) decomposition of wood and occurring as pathogenic agents on weakened plans, and group III — common species of soil fungi participating in the

Table IX

Selectivity (consumption frequency) of various substrata

No.	Kind of substratum	Consumption frequency
1.	Mycelium of *F. annosus* on pine bark	+++
2.	Mycelium of *P. gigantea* on pine sawdust	+++
3.	Mycelium of *P. gigantea* on pine bark	++
4.	Pine bark	++
5.	Mycelium of *P. gigantea* on spruce sawdust	++
6.	Pine bark decomposed by *P. gigantea*	++
7.	Mycelium of *F. annosus* on alder sawdust	+
8.	Pine bark decomposed by *F. annosus*	+
9.	Mycelium of *F. annosus* on birch sawdust	+
10.	Mycelium of *T. versicolor* on alder sawdust	+
11.	Spruce sawdust decomposed by *P. gigantea*	+
12.	Pine sawdust decomposed by *T. viride*	·
13.	Spruce sawdust decomposed by *T. viride*	·
14.	Alder sawdust decomposed by *T. versicolor*	·
15.	Mycelium of *T. versicolor* on alder sawdust	·
16.	Alder sawdust decomposed by *T. versicolor*	·

Note: +++ very frequent consumption, ++ frequent consumption, + consumption of medium frequency, · sporadic consumption.

decay of litter, leaves and in final stages of wood decomposition. The first group includes *Fomes annosus* (FR.) COOKE, *Peniophora gigantea* (FR.) MASS, *Schizophyllum commune* FR., *Gloeophyllum sepiarium* (WULF. ex FR.) P. KARST., *Armillaria mellea* (VAHL. ex FR.) P. KARST., and *Lentinus edodes* (BERGH) SING (epidendral mashroom, absent from Poland). In the second group we number *Aurobasidium pullulans* (DE BARY) ARNUND., *Chaetomium globosum* KUNZE ex FR., *Discula brunneo-tingens* MAYER, *Alternaria tenuis* NESS., *Paecilomyces variati* BAINIER and in the third group *Trichoderma viride* PERS ex FR., *Rhizoctonia solani* KÜHN., *Penicillium brevi-compactum* DIERCKX, *Cylindrocarpon didymum* (HARTIG) WOLLENW., *Penicillium cyclopium* WESTLING, *Aspergillus niger* VAN TIEGHEM, *Fusarium oxysporum* (SCHLECHT.) SNYD. et HANSEN, *Pythium debaryanum* HESSE and *Myrothecium verrucaria* (ALB. et SCHW.) DITMAR.

Twenty adult millipedes, starved for 2 days, were placed in each vessel with test fungi. The consumption frequency was estimated on the basis of the number of specimens in particular vessels with mycelium at a given moment, the amounts of mycelium eaten up and the amounts of excrement left on it.

b. Food preference in relation to 37 natural substrates was examined in a manner analogous to that used in the preceding experiment. The substrates were pine, spruce, alder and birch sawdust and pine bark and the same materials subjected previously to decay by the fungi *Fomes annosus, Peniophora gigantea* and *Trichoderma viride* (pine and spruce sawdust and pine bark) and *Trametes versicolor* (alder and birch sawdust and pine bark). The substrates were being decomposed for a period of 3 weeks, next dried up and crumbled; one-week-old mycelium of the above mentioned test species of fungi was also used on the same substrates in this experiment. Thirty-seven small vessels, each with about 2 g of one of these substrates were distributed in three receptacles with sand. The method and duration of this experiment were like those described above.

c. This study of food preference included also some of the carbohydrates occurring in wood (PROSIŃSKI, 1969): monosaccharides — pentoses: 1-arabinose, anal. pure (Fluka AG, Buchs SG), D-xylose, anal. pure (Fluka AG, Buchs SG); hexoses: anhydrous D-glucose, anal. pure (P.O. CH), D-fructose, pure (P.O.CH), D-mannose, pure (VEB Berlin-Chemie), D-galactose, anal. pure (Xenon); polysaccharides: starch, pure (P.O.CH), cellulose, pure (Whatman), lygnine (induline C, alkalygnine —OCH_3 West Virginia Paper Company). The experiment was repeated seven times. Observations were made 3—4 times daily for 10 days. The consumption frequency was determined as in the previous experiments.

The objective of these experiments on food preference was to find the answer to the question what sort of food is preferred by *P. fuscus*,

Table X

Fungous selectivity (consumption frequency) of *Proteroiulus fuscus*

No.	Fungus species	Consumption frequency	Ecological groups of fungi
1.	*Trichoderma viride*	+++	III
2.	*Alternaria tenuis*	+++	II
3.	*Rhizoctonia solani*	+++	III
4.	*Penicillium brevi-compactum*	+++	III
5.	*Cylindrocarpon didymum*	+++	III
6.	*Schizophyllum commune*	++	I
7.	*Penicillium cyclopium*	+	III
8.	*Aspergillus niger*	+	III
9.	*Fusarium oxysporum*	+	III
10.	*Aurobasidium pullulans*	+	II
11.	*Pythium debaryanum*	+	III
12.	*Paecilomyces variati*	+	II
13.	*Discula brunneo-tingens*	+	II
14.	*Chaetomium globosum*	+	II
15.	*Gloeophyllum sepiarium*	+	I
16.	*Peniophora gigantea*	·	I
17.	*Fomes annosus*	·	I
	Wort-agar medium (control)	·	
18.	*Myrothecium verrucaria*	—	III
19.	*Armillaria mellea*	—	I
20.	*Lentinus edodes*	—	I

Note: +++ very frequent consumption, ++ frequent consumption, + consumption of medium frequency, · sporadic consumption, — lack of consumption.

this being of great consequence to the estimation of its role in the processes of soil formation and the possibilities of its utilization in zooameliorative procedures on formerly arable soils.

The three experiments described above show that *P. fuscus* is a polyphagous species. However, the various foodstuffs offered differ in attractiveness they present for this species. In the experiment in which *P. fuscus* was given 36 combinations to choose from: fresh mycelium of four species on various substrates (pine, spruce, birch and alder sawdust and pine bark), the same substrates after their being decomposed by the tested species of fungi, and the fresh substrates without mycelium, it appeared that the mycelium of *Fomes annosus* growing on pine bark and that of *Peniophora gigantea* on pine sawdust and bark were most frequently consumed (Table IX). Other substrates were taken less often,

Table XI

Carbohydrate selectivity (consumption frequency) of *Proteroiulus fuscus*

No	Carbohydrate	Consumption frequency
1.	D — glucose	+++
2.	D — galactose	+++
3.	Starch	+++
4.	D — xylose	++
5.	D — fructose	+
6.	L — arabinose	+
7.	D — mannose	+
8.	Cellulose	—
9.	Lignine	—

Note: consumption frequency marked as in previous tables.

still others only sporadically if they were taken at all. Hence it follows that mycelium itself is a more attractive foodstuff than sawdust or bark, whether fresh or partly decayed by fungi. *F. annosus* and *P. gigantea* belong to rather frequently occurring species which bring about the decay of wood of coniferous tree stumps (MAŃKA and PRZEZBÓRSKI, 1974) and so the result of this test confirms the observations of the frequent occurrence of this species in the decayed pine stumps.

In natural conditions *P. fuscus* was also fairly often seen to consume fruit-bodies of mushrooms. The most often eaten caps and stems belonged to *Leccinum scabrum* (BULL. ex FR.) S. F. GRAY, *Leccinum duriusculum* (SCHULZ) SING., and *Paxillus involatus* (BATSCH ex FR.) FR.

In the experiment on food preference in relation to 20 species of fungi it was shown that the mycelium and conidia of common soil species, which also take part in the decay of wood but in the final stages of this process, were taken most readily (Table X).

Peniophora gigantea and *Fomes annosus*, which were eaten up more readily in the previous experiment, were now taken only sporadically. There seems to be no inconsistency between these results, for if *P. fuscus* has sawdust, bark and mycelium to choose from, it takes mycelium, whereas as regards different species of mycelium, it gives preference to those it encounters more frequently in its biotope.

The mycelium of various species may present various nutritive and calorific values for *P. fuscus*. Some evidence in this respect is provided by the results of studies on respiratory metabolism (GROMYSZ-KAŁKOWSKA and TRACZ, 1977), which show that *P. fuscus* feeding on mycelium of *Trichoderma viride* takes more oxygen (calculated for 1 g body weight over an hour) than it does while consuming *Schizophyllum commune*. A comparison of the respiratory metabolism of adult specimens fed on litter with that of these animals fed on fungi from pure cultures of *Trichoderma viride* and *Schizophyllum commune*, revealed that in the case in which fungi were consumed the respiratory metabolism increased on the average by about 32.6%.

The choice of mycelium of one or another species by *P. fuscus* as its food is certainly influenced by still other factors not studied here: the colour of mycelium, its smell and antibiotic properties. For instance, in preliminary studies on this problem high mortality was observed in *P. fuscus* in the presence of the mycelium of *Aspergillus niger* (in consequence, this species was not used in further studies on food preference).

It may be stated that in general *P. fuscus* readily takes mycelium, and then the mycelium of a wide spectrum of species belonging to various ecological groups.

Since it has been found that *P. fuscus* consumes decayed and undecayed wood, bark, leaves and other vegetable parts of various species, an examination was carried out in which its food preference was tested in relation to particular (pure) carbohydrates of which those substances are built up.

It appeared that out of the rich group of carbohydrates, *P. fuscus* often consumed monosaccharides and, as regards polysaccharides, starch; however, it did not eat cellulose or lignin, because it seems to have had at its disposal more easily assimilable carbohydrates (Table XI). Consumption of filter paper (pure cellulose) despite the presence of other foodstuffs in the culture (e.g. bark and rotten wood) was observed many a time in course of other experiments. This experiment may confirm the field observations which show that *P. fuscus* often occurs in old decayed stumps, which contain more simple carbohydrates produced in the process of fungi-induced wood decay, or, in fresher stumps, between the bark and xylem, in places where there is still a lot of simple carbohydrates in the phloem.

Both laboratory studies on food preference in *P. fuscus* and many field observations suggest that, as regards this species, it is hard to find preference for one definite foodstuff. As has already been mentioned, a wide range of tolerance in relation to the habitats colonized makes it possible for this species to utilize dead organic matter in conditions in which it occurs at the given time. This property may be very interesting in so far as the utilization of this species in zooameliorative procedures for, among others, formerly arable soils is concerned.

VI. REPRODUCTION AND DEVELOPMENT

A. Methods

Observations were made in the course of laboratory cultures and in field. The living specimens gathered in field were arranged in appropriate developmental stadia according to the methods described by HALKKA (1958), RANTALA (1970) and BROOKES (1974).

In the field cultures, conducted for two years, 60 specimens were kept in two bottomless glass vessels, with a soil profile formed in them. The vessels were secured with bolting-cloth at both sides and placed in pits flush with the soil surface. Various combinations of substrates were used as culture media in petri dishes in the laboratory cultures:

I — rotting wood,
II — humous parts from humification layer,
III — litter (leaves of alder, birch and willow, needles of pine),
IV — sawdust,
V — touchwood +bark, humous parts, litter and sawdust (distributed proportionally to the surface of the dish), and
VI — touchwood, bark, humous parts, litter and sawdust (also distributed proportionally).

The cultures, run for 2 years, were observed at a week's intervals. The development of *P. fuscus*, its method of egg laying, differences between stages, periodomorphosis, preferential food and the increase in the biomass were observed in such conditions. Some of the living specimens were used as material for miscroscopic studies and to take scanning electron microphotographs.

B. Reproduction and fertility

Studies made by many authors indicate a low proportion of males in the populations of *P. fuscus* in natural conditions. They form 0.64—0.71% in Finland (PALMEN, 1949; RANTALA, 1970, 1974), up to 2—3% in the other Scandinavian countries (LOHMANDER, 1925) and 2.3% in the former Eastern Prussia (SCHUBART, 1934). In Poland, according to STOJAŁOWSKA (1961b) the males formed 4.3% in the Roztocze Uplands. In occasional collections the proportion of males may appear considerably higher, e.g. LOHMANDER (1925) observed 3 ♂ to 8 ♀ in Sweden and 5 ♂ to 7 ♀ in Denmark. In the populations of *P. fuscus* under study, coming from the pine forests of the vegetation-forest provinces of the Tuchola Forest, Lubusz Lakeland and Opole Basin, the proportions of males varied from the pine forests of the vegetation-forest provinces of the Tuchola conditions the proportion of males is larger and may reach above 10%, even 20% (VERHOEFF, 1933; RANTALA, 1974).

Table XII

Characteristics of the developmental stages of *Proteroiulus fuscus**

Stadium	Body segments	Pairs of walking legs	Pairs of defence glands	Number of new segmens	Ocelli	Body length mm	Biomass in mg
I	4	3	—	2	—	1,0—1,1	0,05
II	6	7	1	4	1	1,3—2,1	0,06—0,22
III	10	15	5	4	2	2,0—2,9	0,14—0,31
IV	14	23	9	4—5	3	3,0—3,9	0,28—0,51
V	18—19	31—33	12—14	4—5	4	3,9—5,1	0,33—0,88
VI	22—24	39—43	16—19	4	5	5,2—6,8	0,99—1,98
VII	26—28	47—51	20—23	3—4	6+	6,6—8,6	1,77—2,76
VIII	29—31	53—57	24—26	2—3	7+	8,6—10,3	2,35—4,52
IX	32—33	59—61	27—28	2	8+variable	9,4—11,1	3,20—5,07
X	34—36	63—67	29—31	2	-,,-	10,8—12,1	3,90—6,95
XI	36—38	67—71	31—33	2	-,,-	12,0—13,6	5,63—7,40
XII	38—39	71—73	33—34	2	-,,-	13,5—14,4	7,10—7,80
XIII	40—41	75—77	35—36	2	-,,-	14,3—14,8	7,60—8,10
XIV	41—43	78—81	36—37	2	-,,-	15,0—15,7	8,20—9,30
XV	43—45	81—83	38—40	2	-,,-	16,3—16,8	8,40—9,60

* On the basis of material collected in pine forests of Niedźwiady Forest Division (District of Bory Tucholskie).

POCKER (1956) found exclusively females in Luxemberg and he thinks — after SCHUBART — that in some geographical conditions parthenogenesis may be the only way of reproduction in this species. The slight proportion of males in the populations of *P. fuscus* indicates that besides bisexual reproduction (copulating specimens can be seen in laboratory cultures) parthenogenetic reproduction also takes place in this species. This is also supported by the author's own observations of specimens reared in isolation under laboratory conditions and producing progeny. Similar results have been obtained by RANTALA (1974).

Before laying eggs the females are easy to distinguish for their thickened body and intenser brown colour. They lay 8 to 15 eggs; RANTALA (1974) claims that a female lays as many as 30 eggs, though. The eggs, which are white-cream globules, 0.5—0.6 mm in diameter, are laid in damp touchwood, bark fissures or a fairly thick layer of litter to eliminate fluctuations in humidity. The season of egg-laying extends from the end of June to Mid-September in Poland.

C. Morphology of developmental stages

Postembryonic development of *P. fuscus* is of anamorphic type. The developmental stages, starting from the youngest forms, are distinguished by the number of body segments, pairs of legs, defence glands and eyes (HALKKA, 1958; RANTALA, 1970; BROOKES, 1974) (Table XII).

The larvae at stage I are white in colour, transparent and extremely sensitive to light and dryness. This stage lasts about 2—3 weeks, after which the larva moves to deeper layers of the litter or the stump to moult unaffected by fluctuations in humidity and temperature. The moult takes about 2—3 weeks. In this period the larva is curled in a characteristic manner, enclosed in a cradle of decayed touchwood, bark and excrement, and remains motionless until it has shed the old cuticle, leaving it in the cradle. A young larva of stage II, at first very poorly sclerotized, has its legs stretched to the sides, an increased number of segments and a characteristic defence gland, red in colour, on either side of body on the middle segments. A few days after the ecdysis the larva of stage II is able to leave its cradle and begin feeding.

Under favourable weather conditions, i.e. with relatively long and warm autumn, the specimens of stage II may undergo a further moult and winter as larvae of stage III. For winter millipedes descend into deeper parts of the stump of deeper layers of the soil profile.

Early in the spring of the next year the larvae begin active life. A successive moult of the larvae belonging to the generation of the previous year occurs at the end of June and at the beginning of July or, in the conditions of a pine plantation or a fairly open young wood, somewhat earlier. The body of at stage IV larva is usually darker than at younger stages. The second moult in the vegetation season falls in August or September. After overwintering for the second time, at stage IV or V, and going through a moult, already in the third year of life, these millipedes encountered in mid-summer are at stage V or VI.

Stage VI is the last larval stage and the body colour of the larva becomes still darker. In the autumn of the third year of development the specimens observed after a successive moult are at stage VI or VII. Stage VII, of adulthood, is not often reached before the summer of the fourth year. Millipedes at this stage are light brown in colour and able to lay eggs. Older specimens, in addition to the increasing number of the body segments (from stage VII onwards more often than not by two segments each moult), pairs of legs and defence glands, have a dark-brown body and the distinctness of the defence glands on the body sides is increasingly blurred. However, the eyes are of a compound nature and arranged in a branched row.

Males differ from females in body size, they are as a rule smaller and narrower. E.g., at stage VIII the male is 9.2 mm long and 0.3—0.4 mm broad and the female is 9.6 mm long and 0.5—0.6 mm broad.

The morphological characters which differ females from males are presented in the form of a key:

1. First pair of walking legs normal, untransformed. Cheek lobe not

Table XIII

Male forms developed as a result of consecutive molts

No.	Developmental stages					
	VI	VII	VIII	IX	X	XI
1	L	C	S	S	—	—
2		C	S	—	—	
3		L	C	S	S	—
4	L	C	S	S	C	—
5		C	S	—	—	—
6	L	L	C	S	—	—
7	L	C	S	S	C	—
8	L	C	S	—	—	—
9	L	C	S	C	—	—
10	L	L	L	C	—	—
11	L	L	C	S	S	—

rounded. Between the second and the third pair of legs there is a short distance in which the vulvae are situated . . . . females ♀♀

—. First pair of walking legs transformed into hooked or short appendages. No vulvae between second and third leg pair. Cheek lobe rounded 2

2. Penes behind second pair of legs and gonopods on seventh body segment visible . . . . mature males (C ♂♂)

—. Penes and gonopods invisible . . . . larval and schalt males (L and S ♂♂)

Proteroiulus fuscus, like other members of the families *Julidae* and *Blaniulidae* (VERHOEFF, 1933, 1939; STOJAŁOWSKA, 1961b), is marked by a peculiar phenomenon, namely, the prolongation of life of males by the so-called periodomorphosis. A sexually mature male can return, even several times, to the stage of sexual immaturity, assuming the form of the "status medius" of male (Schaltmännchen). Such specimens are characterized by a smaller number of joints in the first pair of walking legs and the atrophied copulatory organs (no gonopods on seventh segment and no visible penes behind second pair of legs). On the other hand, the cheek lobe is like that in sexually mature males.

Observations of the males reared confirm the results of earlier investigations carried out by RANTALA (1970, 1974) on this phenomenon. The following forms of males have been distinguished on the basis of these results:

1. larval (L-♂) — with narrow bulges instead of legs on 7th segment; the first-pair legs have, besides, a smaller number of joints;

2. mature (C-♂) — characterized by
   a) rounded cheeek lobe,
   b) hook-shaped legs of first pair,
   c) penis visible behind second pair of legs,
   d) gonopods, anterior and posterior, on 7th segment, and
   e) lanceolate setae on legs of middle segments;
3. backward (S-♂) — similar to L-♂, is characterized by
   a) lack of external gonopods on 7th segment, there are only delicate bulges,
   b) reduced number of joints of the first pair of legs,
   c) penis imperceptible, and
   d) setae on legs of middle segments imperceptible.

The sexually backward males (S-♂) appear as a rule starting from the VIIIth stage. The larval males (L-♂) are usually observed in stages VI—VII. Successive moults most frequently cause the following transformations of these forms of males (cf. Table XIII):

L-♂ — C-♂ after 7th moult
C-♂ — S-♂ after 8th moult
S-♂ — C-♂ after 9th moult
C-♂ — S-♂ after 10th moult

Males go through 2 moults yearly and periodomorphosis occurs in all moulting specimens. The moults oftenest fall in the spring and autumn. It never happens that two consecutive moults bring about the rise of the same forms: C-♂ — C-♂. The phenomenon of periodomorphosis thus permits the prolongation of life of adult specimens.

RANTALA (1970) observed also the shape of the vulvae (reproduction organs), changing in females with age. She distinguished a) larval vulvae, b) intermediate vulvae in young females, and c) vulvae of adult females. VERHOEFF (1939) also thought that the existence of sexually immature females (S-♀) is possible. After all, in the present work females have not been studied closely.

Some morphological characteristics of the two sexes are shown in Plates XX—XXI.

VII. DYNAMICS AND SPATIAL DISTRIBUTION OF POPULATION

A. Introduction

Litter-soil samples, 0.0625 m^2 in area (25×25 cm) SZUJECKI et al., 1974), extracted in funnel eclectors, were used for study of the spatial

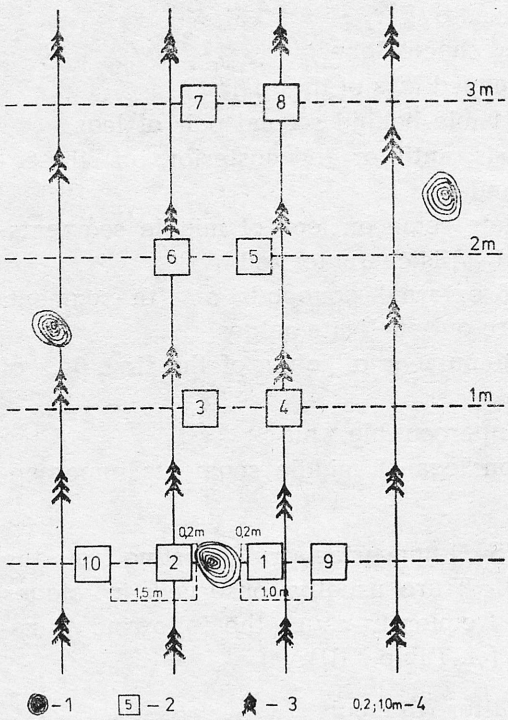


Fig. 3. Diagram showing the collection of litter-soil samples: 1 — stump, 2 — place of sampling, 3 — seedling, 4 — distance from stump

distribution of *P. fuscus*. They were collected in such a way as to make is possible to trace the density of millipedes in relation to the distance from the nearest stump (Fig. 3). At sampling temperature was measured in particular layers with a thermistor thermometer and parts of the samples were used to determine humidity by the drying-gravimetric method. Altogether 4 series of litter-soil samples were used from the areas selected, each series consisting of 10—12 samples taken at an interval of a month. A total of 164 samples were taken.

In order to evaluate the vertical distribution of *P. fuscus* in stumps and roots during a vegetation season, 10 pine stumps, on the average 10—15 cm in diameter, were collected in eclectors. The stumps were divided into sections, about 10 cm thick, over- and underground parts being distinguished. Altogether 67 samples (sections) were obtained.

The study carried out shows that *P. fuscus* was present in fresh pine forests throughout the cycle of standing timber production on wood soils and in cutting stands on formerly arable soils (SZUJECKI et al., 1974).

The process of condensation of the population of this species against the background of the stand growth is presented in Fig. 4. The rapid increase in the density of the population in plantations and young woods is noteworthy; there it averages more than 100 specimens per square metre, whereas in older stands it is hardly 1.0 specimen or less. In some samples the density of the population exceeded 1300—1500 specimens per square metre in 5—7-year-old plantations and, according to earlier studies (SZUJECKI et al., 1974), 2000 specimens per square metre in a 4-year-old plantation.

In the youngest period of the timber production cycle *P. fuscus* is the most important component of the soil macrofauna. The index of domination of this species in the group of soil saprophages was 70% in 2—3--year-old plantations and nearly 50% in 8—9-year-old plantations. This would indicate a quick increase in the size of the population as a reaction to the accumulation of large amounts of felling debris, i.e. bark, branches and sawdust, in which (just as under the bark of dead stumps and lying logs) they find food and shelter. Parthenogenesis occurring in this species is also conducive to the colonization of new habitats and to a rapid increase in the size of the population under favourable conditions.

On the other hand, the complete lack of *P. fuscus* in plantations and young stands on formerly arable soils is characteristic and it makes one of the essential differences between the fauna of wood soils and that of formerly arable soils in a forest of first generation. This is chiefly due to the lack of appropriate food supplies and presumably also to a different microflora.

P. fuscus, dominant in the first period, is gradually ousted from its litter-soil habitats with the age of the stand, its occurrence being restricted to old stumps or their nearest surroundings. This is so probably owing to the progressing process of humification and mineralization of organis residues in soil, the great development of understorey in the forest floor, an increase in the external pressure exerted by natural enemies and a general change in the arrangement of microclimatic conditions favouring the development of other groups of the fauna.

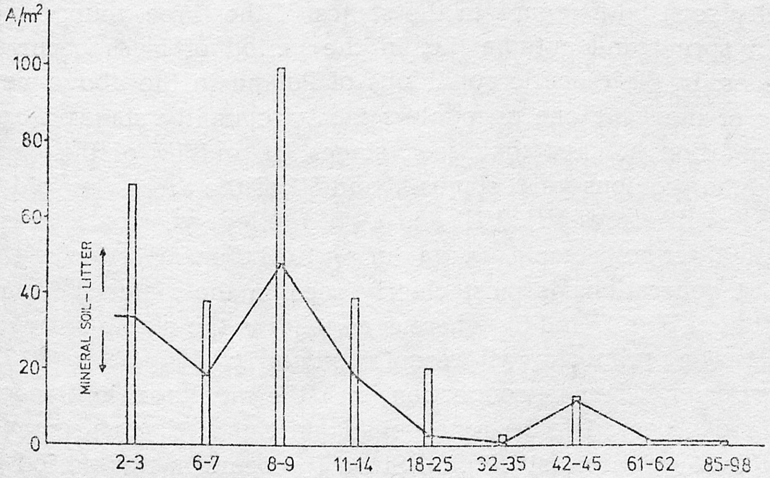


Fig. 4. Density of population (A/m²) of *Proteroiulus fuscus* in wood soils under stands of pines varying in age

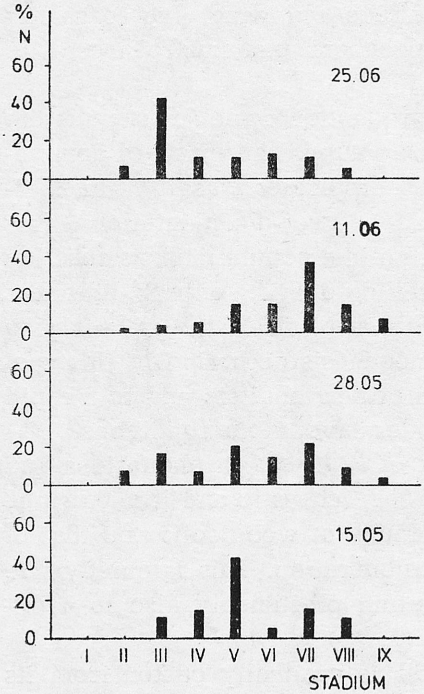


Fig. 5. Proportion of developmental stages in litter-soil samples — spring

B. Age distribution of the population in the annual cycle

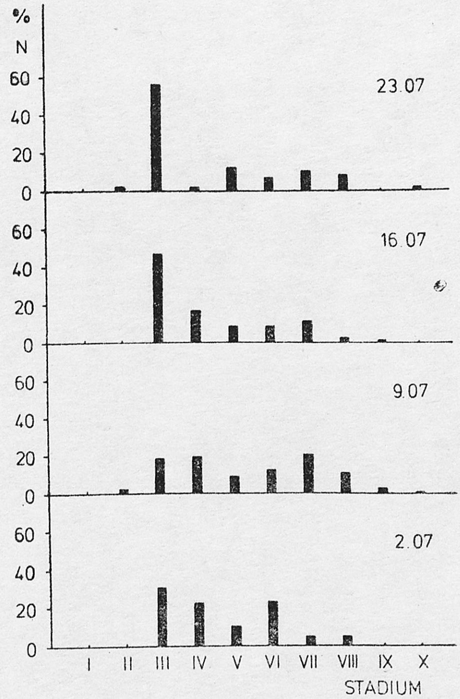
The prolonged period of egg-laying and the relatively long time of development are responsible for the fact that nearly all developmental stages of *P. fuscus* can be met with during one vegetation season. This notwithstanding, the domination of specimens belonging to particular generations can be observed in definite seasons of the year. This is most distinctly seen with regard to the stages of the three youngest generations in spring and autumn, i.e. in the period of mass occurrence of millipedes. In the climatic conditions of Poland in the above-mentioned periods of the year one encounters most frequently stages I and II of the generation hatched that year, stages III and IV of the generation hatched the previous year, stages V and VI of the three-year-old generation and adult stages VII, VIII and IX of the four-year-old generation.

In the litter-soil samples taken during 1975 the proportion of the three youngest generations is most clearly seen in the material from spring and autumn (Figs. 5 and 6), whereas as regards the stump samples taken in autumn this proportion is presented similarly in Figs. 9 and 10.

In summer, when in connection with the moults of millipedes, their stages are observed to be regrouping and the distinct spring peaks of particular stages are lost (Fig. 6). Stage I appears in this period (Fig. 7).

The year 1974, according to the data obtained from the local meteorological office at Niedźwiady, was marked by a long vegetation period

Fig. 6. Proportion of developmental stages in litter-soil samples — summer



and a high annual rainfall (982 mm). Hence, in the spring of 1975 stage III prevailed in the youngest generation. On account of less favourable weather conditions in 1975 stage II was dominant in the youngest generation in the litter-soil and stump samples in autumn (Figs. 8 and 9).

In the stump samples taken in 1976 (spring, summer and autumn) a distinct culmination of the three generation was observed in autumn, when the specimens had completed their second moult and would winter at the stages attained. The one-stage difference in the generation from before two years (i.e. stage VII against VI — Fig. 10) was brought about by favourable weather conditions in 1974.

The percentage structure of the *P. fuscus* population in respect of particular stages in the annual cycle in 1975 is given on the basis of litter-soil samples in Fig. 11. Stages III, V and VII prevail in the first period of sampling. During the vegetation season the developmental stages undergo a regrouping, which runs faster in younger stages. The first moulting season (June/July) is poorly marked in the graph, whereas the second one (August/September) is distinct, as some of the stages were not represented in it at all. Towards the end of the vegetation season most specimens were at stages II, IV, VI and VII and they wintered at these stages.

According to the data of the local meteorological office at Niedźwia-

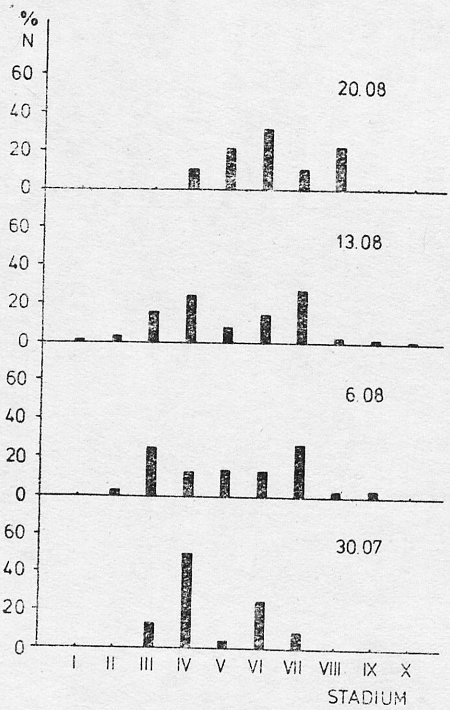


Fig. 7. Proportion of developmental stages in liter-soil samples — summer

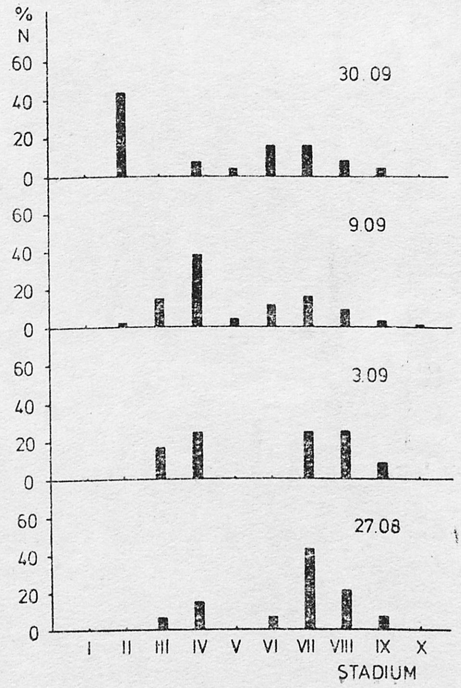
dy, the vegetation season in 1976 was shorter and the annual rainfall was only 516 mm. In consequence, the most specimens of the generation of that year were at stage II.

The reproductive potential and possibilities of *P. fuscus* in particular areas may be indicated by the proportion of adults in the litter-soil samples and the ratio of the number of adults to that of juveniles (Figs. 12 and 13).

It can be seen that both these characteristics assume the highest values in spring and autumn, which is connected with the mass occurrence of millipedes in these very seasons of the year. Similarly the greatest differentiation of both characteristics is observed for the population of *P. fuscus* in the period of the youngest plantations. At that time the generation arising from the eggs laid by millipedes at the time when the plantations were started is already in the adult stage and in this connection the next generation may have already appeared or will soon appear.

Hence, there exist great possibilities for this species to reproduce in these areas (the 5-year-old plantation shows the highest density of population (Table XIV). A gradual levelling of these characteristics is observed in older (8-year-old) plantations and young woods, in which the density of the population also begins to decrease, and this is particularly well seen in young woods. Probably, in this period of growth of the

Fig. 8. Proportion of developmental stages in litter-soil samples — autumn



stand the reproductive explosion of the species has already subsided and most specimens have been migrating into adjacent clearings and plantations.

C. Spatial distribution

The occurrence of particular developmental stages of *P. fuscus* in the study areas according to the litter-soil samples is presented in Table XIV and the average number of specimens from a sample in Fig. 14.

As can be seen, the annual average number of specimens from a sample and the mean density of population (37 specimens/m^2) are the lowest in a four-year-old plantation. The population will presumably grow in the following years when the adult specimens of the first generation that has taken rise in this area produce offspring. The mean density of population in the 5-year-old plantation and the number from a sample are the highest, the former amounting to 168 specimens/m^2. In the 8-year-old plantation the mean density of population comes to 123 specimens/m^2 and in the young (12-year-old) wood to 86 specimens/m^2.

Field observations in the study area showed that in the 4-year-old plantation millipedes occurred in the largest numbers 0.2—1 m away from a tree-stump and only sporadically at greater distances. The maximum density of population was about 330 specimens/m^2. In the 5-year-old plan-

Table XIV

Occurrence of the developmental stages of *Proteroiulus fuscus* in the experimental plots according to litter-soil samples

Age in years	Sample collecting date	Developmental stages I	II	III	IV	V	VI	VII	VIII	IX	X	Total	Number of samples	Mean number of specim.	Mean density/ /m²	Percentage of mature individuals	Ratio of mature individuals to juvenils
4 years old stand	15.V.1975			2	3	8	1	3	2			19	12	1,7	37	26,3	0,35
	2.VII.1975			12	9	4	9	2	2			38	10	3,8		10,5	0,11
	30.VII.1975			3	12	1	6	2				24	10	2,4		8,3	0,09
	27.VIII.1975			1	2		1	6	3	1		14	10	1,4		71,4	2,50
8 years old stand	28.V.1975		10	22	10	27	19	29	11	5		133	10	13,3	123	33,8	0,45
	9.VII.1975		2	15	16	8	10	17	9	3	1	81	9	8,9		49,4	0,97
	6.VIII.1975		2	19	9	10	10	20	2	2		74	10	7,4		32,4	0,48
	3.IX.1975			2	3			3	3	1		12	10	1,2		58,3	1,40
5 years old stand	11.VI.1975		3	5	6	17	19	44	17	8		119	12	9,9	168	57,9	1,40
	16.VII.1975			32	12	6	6	8	2	1		67	10	6,7		16,5	0,19
	13.VIII.1975	1	5	25	41	13	24	45	5	3	1	163	10	16,3		33,1	0,49
	9.IX.1975		2	14	36	4	10	15	8	3	1	93	10	9,3		29,1	0,40
12 years old stand	25.VI.1975		11	64	16	16	18	16	8			149	11	13,5	86	16,3	0,19
	23.VII.1975		1	27	1	6	3	5	4		1	48	10	4,8		26,3	0,26
	20.VIII.1975				1	2	3	1	2			9	10	0,9		33,3	0,50
	30.IX.1975		11		2	1	4	4	2	1		25	11	2,3		28,0	0,38
2 years old stand	26.VI.1975			3	9	1	3	3				19	5	3,8		15,8	0,18

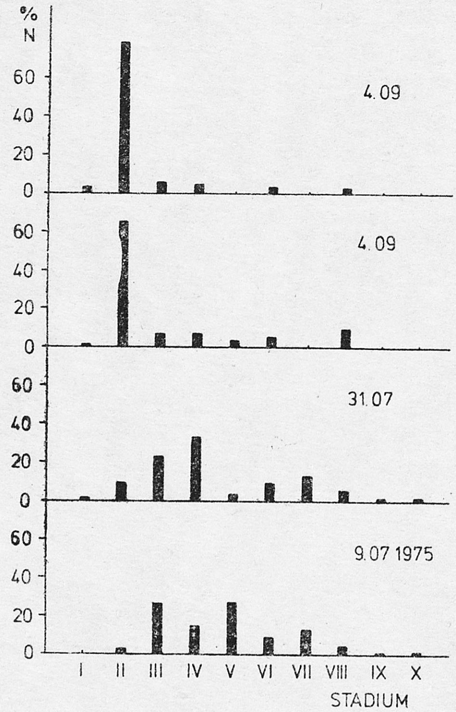


Fig. 9. Proportion of developmental stages in stumps (1975)

tation the occurrence of millipedes was observed farther from a stump. The maximum density of population, about 1300 specimens/m², was found at a distance of 1.5 m from it. In the 8-year-old plantation the maximum density of 1300 specimens/m² was observed at a distance of 1 m from stumps. In the 12-year-old wood the highest density was met with in a sample taken at a distance of 2 m from a stump and it was about 1070 specimens/m².

In studying the distribution of *P. fuscus* in the aisles between three--rows, we observed that the farther from the stumps along the aisles, the more the density of population decreases, which fact shows various intensities in particular study areas. This is best seen in clearings and youngest plantations or in fairly old young woods. In the first case the expansion of *P. fuscus* has not involved the whole area yet, whereas in the second case it is already too weak and, with small exceptions, begins increasingly to confine itself to stumps.

Generally speaking, a great irregularity can be seen in the spatial distribution of a population, less distinct in older plantations, because these have the most specimens, which occur in great concentrations also at greater distances from stumps. The collective nature of the occurrence of *P. fuscus* in the vertical and horizontal systems is connected with the irregular distribution of felling debris and with the varied degree of its decay.

Table XV

Relationship between numbers of *Proteroiulus fuscus* and depth of humus layer in a profile, temperature in substratum and distance from tree stems

Plot	$r_{1y(2,3)}$ humus layer	$r_{2y(3,1)}$ tempera-ture	$r_{3y(1,2)}$ distance from tree stems	coefficient of multiple correlation
4 years old stand	0,4704	0,4091	−0,1024	0,6139
8 years old stand	0,2153	−0,4688	−0,3295	0,5360
5 years old stand	0,4393	−0,2499	0,1169	0,4718
12 years old stand	0,0570	0,2514	0,0834	0,2767

The results obtained permit the statement that the process of invasion of an area by millipedes begins with their colonization of places marked by the greatest accumulation of felling debris. Such places are the main sources of organic matter in wood soils and are characterized by the

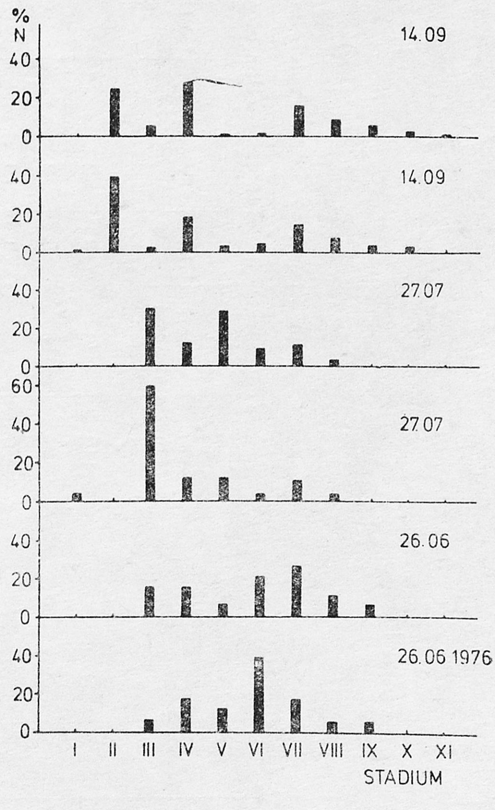


Fig. 10. Proportion of developmental stages in stumps (1976)

Table XVI

Inhabitance levels of *Proteroiulus fuscus* in pine stumps

Age in years	Sample collecting date	Number of individuals in 10 cm section of a stump							Total	Section inhabited most numerously	Notes
		I over-ground	II under-ground	III	IV	V	VI	VII			
8	5.VII.1975	113	48	8	2	—			171	I	stumps of average diameter 10—13 cm, rotten partly with bark frequently covered with mosses and lichens
5	31.VII.1975	34	16	5	2	—			57	I	
8	4.IX.1975	6	13	9	10				38	II	
4	4.IX.1975	17	28	40					85	III	
5	25.VI.1976	8	6	1	2	1	—	—	18	I	
	25.VI.1976	8	5	3	2	1	—	—	19	I	
9	27.VII.1976	32	34	15	1	—	—		82	II	
	27.VII.1976	11	10	2	2		—		26	I	
13	14.IX.1976	34	46	43	—	10	8		141	II	
	14.IX.1976	23	22	27	24	8	—		104	III	

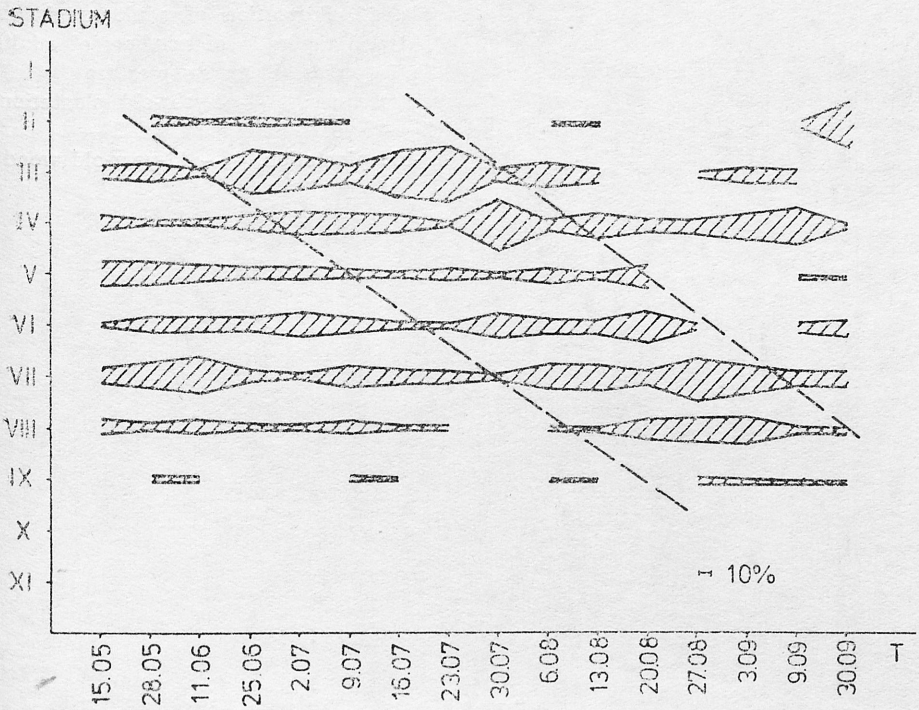


Fig. 11. Proportion of developmental stages in annual cycle (T)

least variable thermal and moisture conditions. The stumps of the trees felled constitute the main source supplying the area with new progeny of millipedes throughout the cycle of standing timber production and it is where the migration of *P. fuscus*, through the dead roots and litter to the aisles between the tree-rows, begins. Moreover, stumps, which present more stabilized thermal and moisture conditions, provide convenient shelter to these animals in unpropitious periods of life (moult, long droughts and hibernation).

During our collection of litter-soil samples, reaching a depth of 15—20 cm, in areas characterized by a similar temperature and humidity, it turned out that there is a relationship between the occurrence of *P. fuscus* and the thickness of the humus layer A_f and layer A_h in the soil profile and the dampness of the substratum. The layer of litter A_l is colonized by a small number of millipedes, probably because of great fluctuations in its dampness. In the genetical horizon A_1 of the mineral soil single specimens were met with at a depth of 12—15 cm and then, more often than not, near stumps.

The coefficient of partial correlation r_y (Table XV) was used to illustrate the dependence of the number of millipedes on the thickness of layer $A_{f/h}$ in the soil profile, the temperature of the substratum and the distance from a stump. In computing this dependence we successively

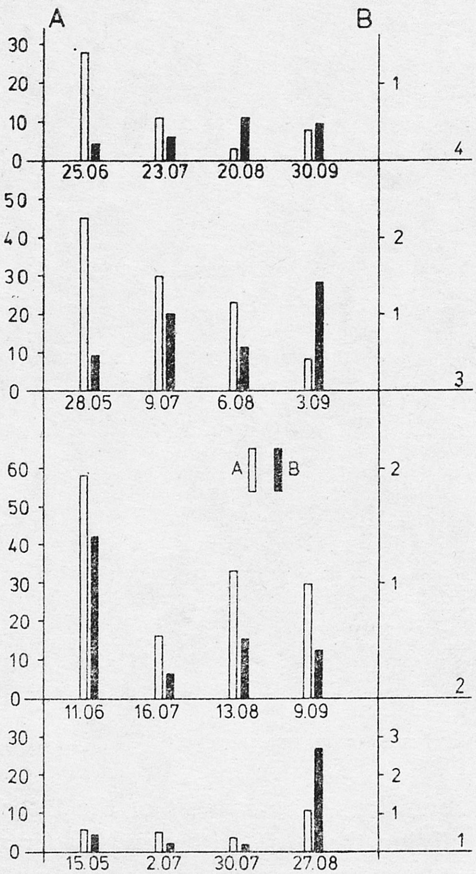


Fig. 12. Proportion of adult specimens (A) and the ratio of numbers of adults to juveniles (B) in samples from particular areas: 1 — 4-year-old plantation, 2 — 5-years-old plantation, 3 — 8-year--old plantation, 4 — 12-year-old wood

excluded the influence of the remaining factors. The number of millipedes shows a fairly distinct tendency to increase with the growing thickness of the humus layer in 4-, 5- and 8-year-old plantations. No such tendency is observed in 12-year-old woods, in which the process of decay of organic residues is presumably more advanced and a partial humification and mineralization have already occurred. Moreover, the succession of understorey in the aisles between the tree-rows in this area is more vigorous. It may therefore be supposed that, in general, the number of millipedes in the mineral soil rises with the increase of the thickness of humus (Fig. 15). This would mean that having exceeded a certain level of density of the population in the humus layer, millipedes may exert ecological pressure, manifested by their capability to move not only horizontally but also in vertical planes, and hence they appear also in the underlying mineral soil.

The important role that millipedes play is connected with their presence in the soil, where they transport organic matter, burrow underground passages, thus aerating the soil, and enrich it in excrement, etc.

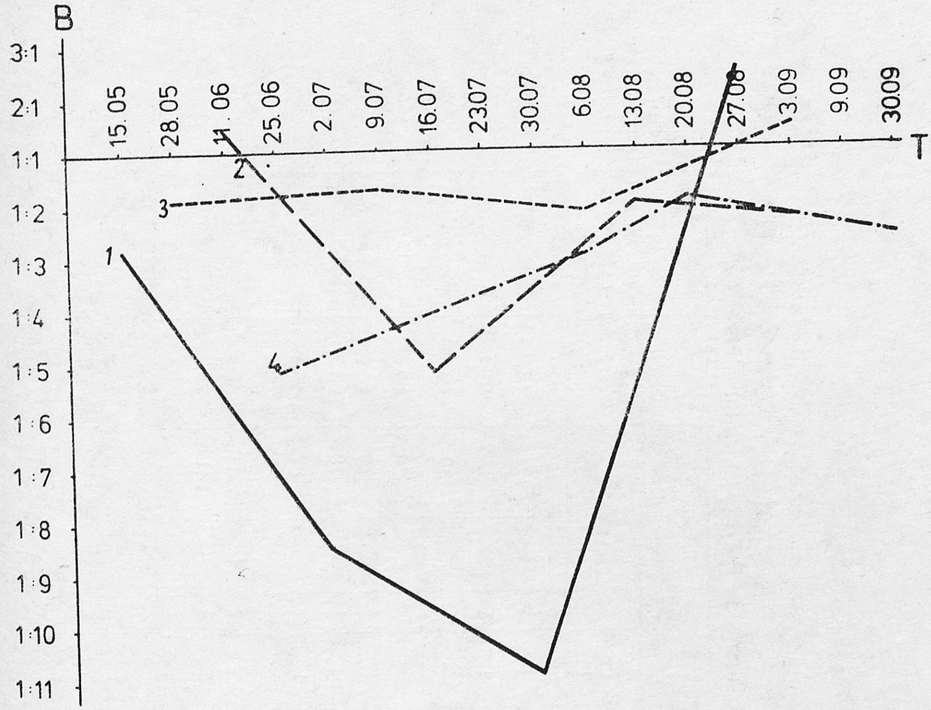


Fig. 13. Ratio of numbers of adults to juveniles (B) in annual cycle (T): 1 — 4-year-old plantation, 2 — 5-year-old plantation, 3 — 8-year-old plantation, 4 — 12-year-old wood

D. Colonization of stumps

An analysis of the colonization of pine stumps by millipedes with respect to their vertical distribution shows that in the vegetation season the first overground section of the stump (10—13 cm) and the second underground section (10 cm) are frequented most numerously, namely, by about 77—94% of the total number of specimens. Towards the end of the vegetation season, in September, the percentage occurrence of millipedes in these zones drops to about 43—54% (Table XVI). Single specimens may occur at a depth of 40—50 cm (Table XVII). The proportion of adult specimens in rotting stumps is relatively low and juvenile specimens usually prevail in this environment.

The vertical distribution of millipedes in the soil profile and in stumps is also dependent to a great extent on the substratum moisture, air humidity and time of day. During a rainy spell, at the time of high air humidity and in the night-time millipedes are very often encountered on the surface of stumps grown over by algae, lichens and mosses. This is also connected with the nature of the 24-hour cycle of *P. fuscus*, whose activeness, as in other diplopod species (HAACKER, 1967), increases in the night-time.

Table XVII

Occurrence of *Proteroiulus fuscus* in pine stumps in the experimental plots

Age in years	Sample collecting date	Developmental stage											Total	% mature	Ratio of mature to juveniles	% of inhabitance in stump section I and II
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI				
8	9.VII.1975		4	46	27	47	15	22	7	1	2		171	18,7	0,23	94,1
5	31.VII.1975	1	5	13	19	2	5	7	3	1	1		57	21,1	0,26	87,7
8	4.IX.1975	1	30	2	3	—	1	—	1	—	—		38	26	0,02	50,1
4	4.IX.1975	1	56	6	6	3	5	—	8	—	—		85	94	0,10	52,9
5	25.VI.1976	—	—	—	1	3	2	7	3	1	1		18	66,6	2,0	77,7
	25.VI.1976	—	—	—	3	3	1	4	5	2	1		19	63,2	1,7	81,2
9	27.VII.1976	—	—	25	11	24	8	10	1	1	2		82	17,1	0,2	80,5
		1	—	14	3	3	1	3	1	—	—		26	13,4	0,2	80,8
13	14.IX.1976	—	26	6	32	1	1	17	9	7	4	1	104	36,5	0,6	43,3
	14.IX.1976	2	56	3	27	5	6	22	11	5	4	—	141	29,7	0,4	53,8

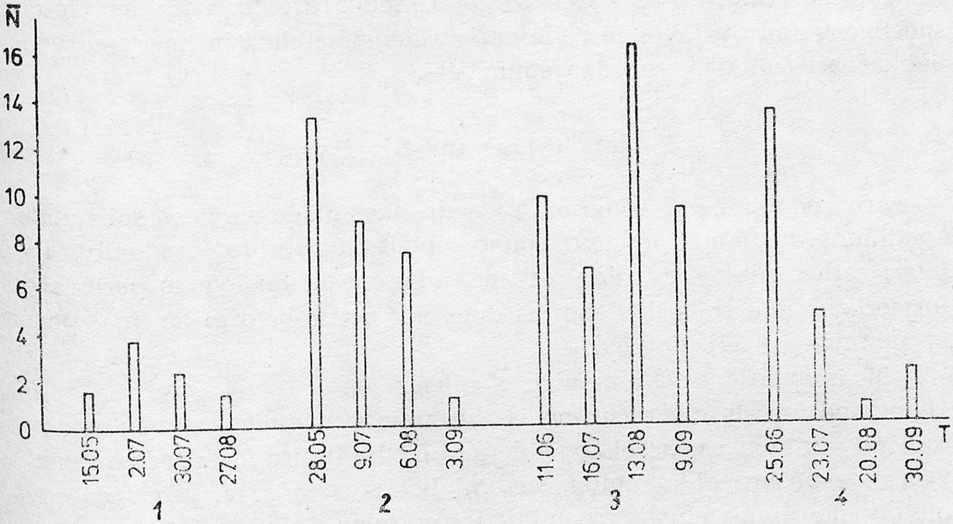


Fig. 14. Average number (N) of specimens of *Proteroiulus fuscus* from one sample in study areas: 1 — 4-year-old plantation, 2 — 8-year-old plantation, 3 — 5-year-old plantation, 4 — 12-year-old wood

Dead pine stumps removed from a 50-year-old pine stand on formerly arable soils on to wood soils (plantations and young woods), were colonized by millipedes. Table XVIII shows the degrees of colonization and the proportions formed by the developmental stages of *P. fuscus* after 2 and 14 months of experiment. In both cases the stumps were found for the most part to be colonized by juvenile specimens, which most likely took origin from eggs laid by mature animals in the touchwood of the stumps. Two months after the beginning of the experiment the colonization of the stumps was rather poor and not all the developmental stages were represented, whereas after 12 months the coloniza-

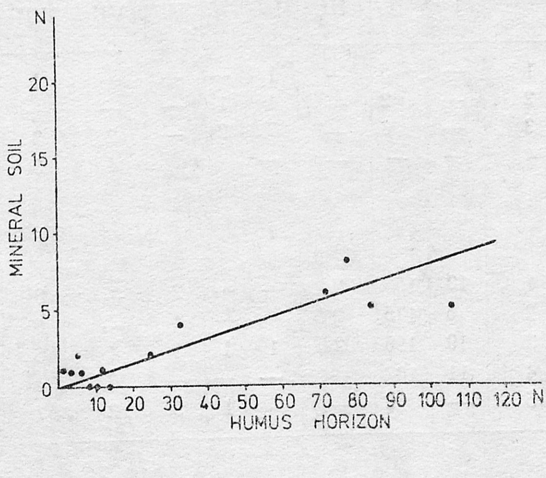


Fig. 15. The dependence of the occurrence of *Proteroiulus fuscus* in soil upon its occurrence in the humus layer

tion of the stumps was observed to be much greater both by mature specimens and by juveniles, the early stages, hatched in the some year, being represented by very large numbers.

E. Conclusions and Discussion

A reproductive explosion of *P. fuscus* takes place on wood soils under conditions of plantations and young woods; it subsides gradually, and, later, rather rapidly in older stands, whereas in analogous periods on formerly arable soils this species does not occur before the final phase of the timber production cycle.

This is so besause of a number of causes:

1) in pine forests clear cutting is the main economic intervention that radically influences the biological state of the future forest ecosystem.

2) The exposure of a region, several hectares in area, produces completely new microclimatic conditions; extreme values of temperature, humidity and exposure to the sun's rays eliminate the species which find such environmental conditions unsuitable and, on the other hand, they afford the populations of species having a broad range of tolerance with respect to those factors the possibility to exist, develop and spread.

3) In consequence of cutting large amounts of organic residues are left lying about as a get-at-able food source for the saprophagic micro- and macrofauna, in which a whole complex of microorganisms may develop.

4) Disturbances caused by environmental changes in clearings in pine

Table XVIII

Inhabitance of *Proteroiulus fuscus* in pine stumps transferred from post-agricultural to forest site after 2 months (1976)

Stump	Developmental stages												Total	Ratio mature/ juvenile
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII		
1	—	5	—	1	—	—	—	1	1	—	—	—	8	0,33
2	—	2	—	1	1	—	—	—	—	—	—	—	4	—
3	—	6	—	7	2	—	2	3	—	2	1	—	23	0,53
4	—	—	—	—			4	3	2	—	—	—	9	—
after 14 months (1975—1976)														
1	10	156	2	—	—	2	—	8	2	2	1	1	184	0,08
2	6	175	2	—	—	4	—	6	6	2	1	—	202	0,08
3	19	196	2	1	1	1	4	6	2	—	—	—	232	0,05
4	11	107	—	—	—	—	6	4	2	1	—	—	131	0,11
5	—	25	—	—	1	3	2	7	6	2	1	—	47	0,62

forests may bring about a reduction in the external pressure of natural enemies and the creation of new competitive conditions, which decline with the age of the stands.
5) Environments spoilt by man and by natural disasters, and newly arising natural environments (forestation of steppes and wasteheaps and dumps revealing initial soil-forming processes) probably favour millipedes, which are characterized there by their huge developmental dynamics.

Here are some causes of these changes:
a) The main places of reproduction of *P. fuscus* are dead pine stumps left after silvicultural procedures throughout the cycle of timber production. After the cutting of a stand and the renewal of the area millipedes begin to migrate from stumps to the aisles between the tree-rows. In the first years of the timber production cycle the parthenogenetic reproduction of *P. fuscus* induces the explosion of its population in the existing conditions and its rapid spread to new plantations. In view of very low mortality, the concentrate nature of occurrence, and three years' period of development of a generation, it seems possible for a population to attain the level of density observed in some of the litter-soil samples, i.e. 1300—2000 specimens/m² in 4—5-year-old plantations.

In order to determine theoretically what size a population of *P. fuscus* developed from one female will reach in the second generation (i.e. after 3 years), the formula for biotic potential in the form of an exponential equation (TROJAN, 1975) has been used:

$$N_t = r^T$$

where N_t is the number of offspring produced by a female in one generation of *P. fuscus*

$$r = 15—30 \text{ eggs}$$
$$T = 2$$

N_t = 225—900 specimens

Assuming that the initial density of populations was 2 specimens/m², we receive a density of 500—1800 millipedes/m² after the 3—4-year existence of the plantation.
b) Seeing that millipedes can also immigrate from the adjacent older plantations and young woods, the local population of *P. fuscus* may be reinforced and so its density in the study areas may have increased still sooner.

On cloudy, foggy, and rainy days millipedes can migrate for short distances, but it is not known whether light (in open areas) is, or not, the factor that informs them of the existing conditions. Literature mentions mass migrations of some diplopod species, connected with their seasonal sexual activity and also induced by changes in the climatic

Table XIX

Annual biomass, excrement production and respiratory metabolism of *Proteroiulus fuscus* population on 1 m^2 and 1 ha in fresh pine forest

Age	Population density		Mean biomass of 1 individual	Population biomass		Mean excrement production (1 ind)	Weight of excrements		Mean respiration of 1 idividual	Population respiration (kcal)	
	1 m^2	1 ha		1 m^2(g)	1 ha(kg)		1 m^2(g)	1 ha(kg)		1 m^2	1 ha
4	37	370000	2,15 mg	0,0795	0,795	0,08 mg 37,2 mg/ /g/day	0,591	5,91	195 mm^3/ /g/h	0,350	3500
8	123	1230000		0,264	2,64		1,964	19,64		1,144	11440
5	168	1680000		0,36	3,6		2,678	26,78		1,584	15840
12	86	860000		0,185	1,85		1,376	13,76		0,814	8140
mean values for young stands											
	103,5	1035000		0,22	2,221		1,652	16,52		0,973	9730
18—25	20	200000	2,15 mg	0,043	0,430	0,08 mg 37,2 mg/ /g/day	0,3	3,20	195 mm^3/ /g/h	0,1892	1892
32—35	2,5	25000		0,0054	0,054		0,04	0,4		0,0237	237
42—43	12,5	125000		0,0312	0,312		0,22	2,2		0,1373	1373
61—62	1	10000		0,0022	0,02		0,016	0,16		0,0097	97
85—98	1	10000		0,0022	0,02		0,016	0,16		0,0097	97

1 mm^3 O_2 = 0,0047 cal (KLEIBER 1968, DUNGER 1968).

conditions (VERHOEFF, 1900; SCHUBART, 1940; CLOUDSLEY-THOMPSON, 1949; JAEKEL, 1954; STOJAŁOWSKA, 1949; HELB, 1975).

Similarly, it cannot be stated definitively on the basis of observation of animals reared in field and the data obtained from literature that microclimate and accumulation of a large amount of food may favour an increase in the fertility of female millipedes, the shortening of the development period and the earlier attainment of sexual maturity.

It may be concluded in general that the initial phase of the cycle of forest growth on wood soils, the presence of old tree-stumps, and the accumulation of a large amount of felling debris constitute a base for the reproductive explosion of *P. fuscus* and its spread to other areas. Abundant food resources, microclimatic conditions within the range of tolerance of this species, reduced external pressure of natural enemies and parthenogenetic reproduction influence the development of *P. fuscus*, which prevails in the populative systems that have come to be.

VIII. BIOCENOTIC ROLE AND POSSIBILITIES OF UTILISATION OF THIS SPECIES IN SOIL ZOOAMELIORATION

A. Biocenotic role

Respiratory metabolism, the biomass of a specimen and population, and the production of excrement can be used, among other data, to evaluate a given ecosystem. The respiratory metabolism of each stage of the postembryonic development of *P. fuscus* is presented in a work by GROMYSZ-KAŁKOWSKA and TRACZ (1977).

The dependence of the biomass on the body length has been calculated on the basis of the measurements taken on 380 specimens representing all the developmental stages of *P. fuscus*. The biomass of adult specimens ranges from 1.77 to 9.6 mg and the body length from 6.6 to 16.8 mm, the mean biomass being 2.15 mg and the mean length 7.0 mm. The coefficient of variation of the biomass (V_y) is 79.7% and the index of correlation (R) between the biomass and body length of a specimen is 0.9872. Hence, the coefficient of variation of biomass, obtained from the equation $V_{y \cdot l} = V_y \sqrt{1-R^2}$ from which the effect of the body length ($V_{y \cdot l}$) has been excluded, is 12.7%. This means that the biomass of a specimen determined on the basis of the quadratic equation given above is charged with a mean error of 12.7%. The dependence of the biomass (y) of *P. fuscus* on its body length (x) is best defined by the quadratic equation

$$y = a + bx^2 \quad \text{(Fig. 16)}$$

Hence $y = -0.00009745 + 0.00003807x^2$

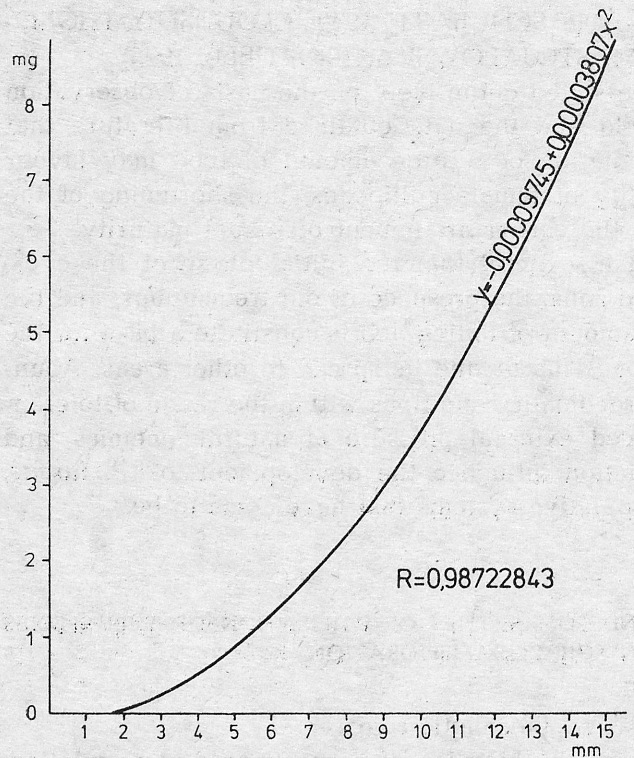


Fig. 16. The dependence of biomass (mg) on body length (mm) of *Proteroiulus fuscus*

The above values for *P. fuscus* in fresh pine forests are characterized in Table XIX. A comparison of the data shows that these values are the highest in the earliest developmental period of the stand, i.e. in plantations and young woods, where the mean biomass of population comes to 0.22 g/m^2 and 2.2 kg/hectare, the mean weight of excrement produced to 1.65 g/m^{2}yr and 16.5 kg/hectare/yr, and the mean metabolism of population to 0.973 kcal/m^2/yr and 9730 kcal/hectare/yr.

As regards the remaining developmental stages, these values decrease gradually to reach a minimum during the final phase of the productive cycle. It may therefore be supposed that the role of *P. fuscus* will be the greatest in the youngest period of the timber production cycle in connection with the highest density of its population at that time. This might be of great importance, because, among other things, millipedes prompt a slow decomposition, followed by humification and mineralization of organic debris accumulated in consequence of timber cutting. Thus this debris makes up a source of food for pines, the nutritional requirements of which are the highest in the period of the intensest growth of trees, usually in the second group of age (GUNIA, 1967).

The amount of excrement discharged by 1 specimen daily averages 0.08 mg, which forms 3.7% of its body weight.

Bark and wood, besides litter, constitute the main source of organic matter in wood soils and, at the same time, are food for *P. fuscus*, less diversified in fresh pine forests than in mixed forests. Millipedes ingest coniferous litter reluctantly because of resins, polyphenols, etc. that it contains.

Bark can constitute a source of food only for a small number of organisms, including micro-organisms. This is so on account of its being hard to decompose and the poor assimilability of its constituent substances. Nevertheless, bark can make indirect and direct sources of food for *P. fuscus*, which therefore becomes particularly important in the decyaing processes of this organic matter, commonly met with in nature and slow to decompose.

Wood cannot be consumed by millipedes until it is in the state of decay resulting from the activity of fungi and other micro-organisms. In general, the consumption of wood depends to a great extent on its psysical and chemical properties (state of decay).

P. fuscus gives some preference to the litter of various deciduous species, of which it most willingly consumes leaves of the alder, elder, ash and birch. This may be explained — in accordance with DUNGER'S (1958b) study — by their higher nitrogen content, lower C:N ratio and lower humic-acid content in leaves than in the leaves of, e.g. the maple, beech and oak.

Moreover, after the winter season this foodstuff has better properties for consumption by millipedes. This is connected with the activity of micro-organisms, which are the first to become active and also with the fluctuations of climatic factors leading to its maceration. In the first stages of wood decay in pine stumps and felling debris *P. fuscus* inhabits the subcortical zone, presumably because of the presence of storage substances, readily assimilated by this species, in the bast and better moisture

Table XX

Occurrence of *Proteroiulus fuscus* in plots in zooamelioration area in 1975 (in the first year of treatment), according to soil samples

Sample collecting date	Plot		Fertilization variant	Number of individuals
	No.	Symbol		
14.V.1975	20	D	sawdust + bark + fauna	5
14.V.1975	11	C	sawdust + bark	1
21.V.1975	11	C	sawdust + bark	1
9.VII.1975	15	D	sawdust + bark + fauna	1
9.VII.1975	29	E	soil + fauna	1
24.IX.1975	22	G	bark	1
				10

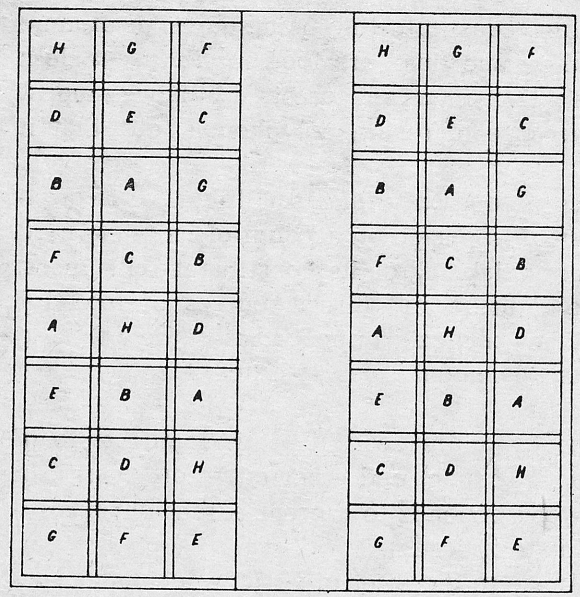


Fig. 17. Arrangement of the randomized blocks of zooameliorated areas (left block — plantation after potatoes, middle — isolating strip of ground, right block — plantation after lupin)

conditions in this zone. Gradually, as fungi and other micro-organisms cause the decay of wood, *P. fuscus* penetrates into the inner zones (containing more simple carbohydrates), being — in the terminal stage of wood decay — one of the main members of the soil fauna. It then plays an importante role in mixing humus and mineral parts together. These observations are supported by data given by SCHIMITSCHEK (1952), MAMAEV (1960, 1961) and KOZARZHEVSKAYA and MAMAEV (1962).

During their passage through the alimentary canal of *P. fuscus* litter, bark and wood all break up mechanically but hardly part of food becomes digested and assimilated. According to GERE (1956), about 80—90% of the food taken by millipedes may be discharged in the form of excrement, in which structural fragments of organic remains can sometimes be distinguished (Pl. XXII—XXV).

The composition of food is probably subject to small chemical changes, which are dependent upon the sort of food and degree of its decay. The excrement discharged consists of broken-up organic matter and is deposited in various parts of the soil profile or on the surface of the soil. Mixed with the mineral substances of the soil it improves its structure and enriches it in compounds easier to decompose. The occurrence of the population of *P. fuscus* in aggregations is connected with the accumulations of organic debris and exerts an ecological pressure on these animals, causing them to move to the layer of mineral soil, thus influencing the aeration of the soil (burrowing of passages).

Out of the alimentary canal excrement becomes a place for the concentration and vigorous activity of microorganisms, which is greater at

Table XXI

Occurrence of *Proteroiulus fuscus* in plots in zooamelioration area in 1976 (in the second year of treatment), according to soil samples

Sample collecting date	Plot		Fertilization variant	Number of individuals
	No.	Symbol		
4.VI.1976	12	B	bark + fauna	1
4.VI.1976	17	B	bark + fauna	1
4.VI.1976	22	G	bark	1
16.VI.1976	7	B	bark + fauna	1
16.VI.1976	22	G	bark	3
16.VI.1976	24	E	soil + fauna	1
16.VI.1976	46	G	bark	1
14.VI.1976	17	B	bark + fauna	1
14.VI.1976	20	D	sawdust + bark + fauna	1
20.VII.1976	15	D	sawdust + bark + fauna	4
20.VII.1976	22	B	bark	1
20.VII.1976	20	D	sawdust + bark + fauna	2
1.IX.1976	4	D	sawdust + bark + fauna	2
1.IX.1976	28	D	sawdust + bark + fauna	2
				22

this coprogenic phase than in soil. The processes of humification and mineralization of remains are also much intenser at this phase.

The formation of a definite complex of microorganisms in the alimentary canal of *P. fuscus* depends on the kind of organic matter consumed and the composition of the microflora of the soil. A change in the nutritional conditions or that resulting from the introduction of the species to other environments may bring about a change in the nature of mutual relations with microorganisms.

P. fuscus, harbouring such soil fungi in its alimentary canal as *Trichoderma viride*, *Aspergillus* sp. and *Penicillium* sp., which are also known to be antagonistic towards *Fomes annosus* (inducing a severe disease of forest trees, especially pines on formerly arable soils), contributes to their propagation while colonizing pine stumps and may play an important role in forest protection.

A microbiological analysis showed that in the alimentary canal of *P. fuscus* saprophytic soil fungi and antagonistic fungi form a greater proportion than to fungi producing tree diseases. This is also confirmed by tests for its food preference, in which these first fungi were consumed more frequently than the fungi of the class *Basidiomycetes* inducing tree diseases. It follows from that that *P. fuscus* not only contributes to the spread of fungi in general but, what is more, it spreads such species as play a beneficial role in the forest environment as regards pedogenesis and the resistance of its habitats to diseases.

In the alimentary canal of *P. fuscus* there are besides more favourable conditions for ligno- and cellulolytic activity of microorganisms than in the external surroundings, which indirectly accelerates the decay of organic residues. A series of further biochemical studies would make it possible to decide whether the cellulolytic enzymes are produced by millipedes themselves or by the microorganisms existing in their bodies and would provide more information about the role of this species in pedogenesis.

It is, in addition, hard to find if the protozoa, saprophytes, and nematodes present in the alimentary canal of *P. fuscus* are in a constant connection with it and, if so, what consequences may follow. *P. fuscus* is certain to be instrumental in propagating them in the soil environment.

It may be stated in general that the relatively long developmental period (attainment of sexual maturity takes 3 years, adult specimens may live still longer), the long period of activeness in the year (March—November), the great concentration of specimens of a population, their tolerance for a wide range of habitats and temperatures, the lack of strictly defined food preference and the beneficial role in the litter-soil environment place *P. fuscus* in the row of species which are interesting with a view of their use in the biological activation of formerly arable soils grown over by woods.

B. Possibilities of zooamelioration

The results of earlier studies (SZUJECKI et al., 1974) on the succession of the macrofauna in wooded and formerly arable soils show that the lack of organic remains in wooded areas of formerly arable soils and the distance, considerable for flightless members of the macrofauna, from other wooded areas hinder the occurrence of those animals, including *P. fuscus*, which is common on wood soils, especially in plantations and young woods. In order to check the possibilities of development of this species and its capability to spread on formerly arable soils, an area used previously under crop and specially selected for this purpose was top-dressed with bark and sawdust.

A system of 8 randomized blocks (A—H) were set up in each of the three plots, 15×15 m in area, in each of the two equal parts of the zoameliorated area (one after potatoes and the other after lupin, separated by a 30-metre strip of ground). The plots were isolated from each other by strips of ground, 5 m in width (Fig. 17).

The blocks present the following experimental conditions:

A — soil (control)

B — bark + fauna

C — sawdust + bark

D — sawdust + bark + fauna
E — fauna
F — sawdust
G — bark
H — sawdust

One plot was uniformly top-dressed with 6 m^3 of bark (variants B and G), 4 m^3 of bark and 2 m^3 of sawdust (variants C and D) or 4 m^3 of sawdust (variants F and H). In the surface thus prepared furrows were made at 1.5-metre intervals using a double-mouldboard plough, to concentrate the organic matter on the surfaces. Next the area was planted with pines 1.5 m apart. In addition, in 24 squares of appropriate variants three groups of 50 adult specimens of *P. fuscus* each were placed in specially prepared holes (30×30×30 cm) with pieces of decaying bark and wood. A total of 3600 specimens of this millipede were introduced. The preparatory work was completed in 1974.

In the vegetation season of 1975 the experimental squares were checked for development and spread. Soil samples to a depth of 10 cm were taken by means of eclectors from each square in three periods of the vegetation season (May, July and September), altogether 144 samples. In the autumn of the same year the previously planted squares were again supplied with millipedes, 50 specimens per hole, altogether 3600 specimens. The development and spread of the species was observed also in the vegetation season of 1976, soil samples being taken, as in the preceding year, twice in three periods of the vegetation season. A total of samples taken in two seasons was 432.

The soil samples taken in the first year of experiment (1975) show a slow spread of *P. fuscus* in 4 out of the 24 squares in which these millipedes had been introduced, i.e. 16.6% (Table XX). This species was represented by the largest number in variant D in the plot dressed with sawdust and bark (80 specimens/m^2). Besides, in one case of variant G (with bark but no millipedes introduced) *P. fuscus* was also found present.

Observation of the colonization of wood dust and bark in the holes of appropriate variants shows the occurrence of adult and juvenile specimens in most cases, which would indicate the procreation of offspring under new conditions. In 7 out of the 72 holes examined, in which millipedes had been introduced, no specimens of *P. fuscus* were found, which was probably due to unfavourable conditions of development. A rather long drought in 1975 caused the drying-up of the substratum and the millipedes may have been in resting condition. The colonization of wood dust and bark by adult and juvenile specimens was observed in the remaining cases.

In the second year of the experiment a further slow spread of the species introduced was observed in 21% of all the plots (after 1 year —

10.4%). Taking into consideration the plots in which millipedes had been introduced in different variants, 33.3% of them were colonized at that time, their greatest density, reaching 64 specimens/m^2, being found in variant D (bark and sawdust — Table XXI). The occurrence of millipedes becomes noticeable also in plots dressed only with bark in which they have not been introduced.

During the two years of this experiment 7200 adult specimens of *P. fuscus* were introduced in the zooameliorated area. Taking into account its size, i.e. 1.08 hectares, the theoretical density of the population was 0.66 specimens/m^2, whereas the theoretical density of the population in the area of 24 plots where millipedes had been introduced was 1.33 specimens/m^2.

Twenty-two millipedes were found in the soil samples taken from the whole zooameliorated area in 1976 and so the empirical density in this area was 1.22 specimens/m^2 against the theoretical density of 0.66 specimens/m^2, and so increasing by nearly 100%. As regards the plots in which millipedes were found (22 specimens), the empirical density reached a level of 5.87 specimens/m^2 against the theoretical results of 1.33 specimens/m^2, i.e. more than four times as many. In variant D (bark and sawdust), as has already been mentioned, the density of the specimens of *P. fuscus* was the greatest and reached 64 specimens/m^2. On the basis of these considerations it may be inferred that the species *P. fuscus*, introduced in the area put to zooamelioration, had been adapted to its new habitat and started a slow spread out of the holes on to the surface of the plots, as was proved by the soil samples, which showed the presence of adults and juveniles even in the area where the millipedes had not been introduced. Besides, the higher the initial density of the millipedes introduced in an area was, the higher was their empirical density, owing to the ecological pressure exerted on them and to their horizontal migration.

It may also be supposed that the young generation arising from the eggs laid by millipedes in the zooameliorated area, having attained sexual maturity (in 3 years' time), will contribute to the intenser development of the population of *P. fuscus*.

Translated into English
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STRESZCZENIE

W wyniku przeprowadzonych badań stwierdzono, że *Proteroiulus fuscus* (AM STEIN) jest gatunkiem eurytopowym, występującym na obszarze całej Polski z wyjątkiem Karpat. Wykazane 32 stanowiska gatunku dowodzą, że najchętniej zasiedlanymi środowiskami są bory sosnowe, co wiąże się ze zrębowym sposobem zagospodarowania lasu oddziałującym bezpośrednio na zasobność bazy pokarmowej.

Z czynników abiotycznych (światło, temperatura, wilgotność) największe znaczenie ma wilgotność. Światło odgrywa mniejszą rolę, natomiast największą tolerancję gatunek ten wykazuje względem temperatury, której tolerowany zakres wynosi od $-1°C$ do $+35°C$.

Rozwój postembrionalny *P. fuscus* przebiega jako anamorfoza. Dojrzałość płciowa osiągana jest w VII stadium rozwojowym w trzecim roku życia osobnika. Część osobników VII stadium po złożeniu jaj ginie, natomiast pozostałe po przejściu kolejnych linień mogą osiągać wiek 5—6 lat, sporadycznie nawet 7 lat (w XIV i XV stadium rozwojowym). W cią-

gu wzrostu osobnika zależność między jego biomasą a długością ciała charakteryzuje model równania kwadratowego

$$y = -0{,}00009745 + 0{,}00003807\, x^2$$

Niewielki udział samców w populacjach *P. fuscus* (0—5,4%) wskazuje na występowanie partenogenezy, co potwierdziły badania laboratoryjne. Zjawisko to sprzyja zasiedlaniu nowych środowisk i szybkiemu wzrostowi liczebności populacji w korzystnych warunkach. Ponadto u samców obserwuje się osobliwe dla krocionogów zjawisko tzw. peridomorfozy, pozwalającej przedłużać życie oraz zdolność rozmnażania płciowego. Przedłużony okres składania jaj oraz stosunkowo długi czas trwania rozwoju sprawiają, że w ciągu sezonu wegetacyjnego spotyka się niemal wszystkie stadia rozwojowe *P. fuscus*. W okresie masowego pojawu krocionogów, tj. na wiosnę i w jesieni, występuje I i II stadium generacji tegorocznej, które dominuje w populacji w tym okresie, III i IV stadium generacji zeszłorocznej, V i VI stadium generacji trzyletniej oraz stadia dojrzałe VII, VIII i IX generacji czteroletniej.

O potencjale i możliwościach rozrodczych *P. fuscus* świadczyć może m.in. udział osobników dojrzałych oraz stosunek liczbowy osobników dojrzałych do juwenilnych. Obie te charakterystyki przyjmują największe wartości w okresie wiosny i jesieni.

Badania terenowe w borach sosnowych świeżych na gruntach leśnych wykazały, że *P. fuscus* występuje w całym cyklu produkcyjnym drzewostanu, natomiast na gruntach porolnych dopiero w drzewostanach rębnych. Wskaźnik dominacji tego gatunku na gruntach leśnych wynosi 70% w uprawach 2—3-letnich i prawie 50% w uprawach 8—9-letnich. Zagęszczenie populacji w uprawach i młodnikach wynosi około 100 osobników/1 m^2, podczas gdy w starszych drzewostanach zaledwie 1,0 i mniej.

Duża aktywność rozrodcza *P. fuscus* na powierzchniach upraw i w młodnikach gruntów leśnych łączy się z konsekwencjami gospodarki zrębowej w borach sosnowych. Wynikami jej są: zasobna baza pokarmowa w postaci resztek zrębowych, zmiana mikroklimatu eliminującego organizmy o wąskich przedziałach tolerancji wobec czynników ekologicznych, ograniczenie presji zewnętrznej wrogów naturalnych i wystąpienie nowych układów konkurencyjnych.

Fluktuacja w rozmieszczeniu poziomym na powierzchniach oraz w rozmieszczeniu pionowym na profilu glebowym, ponadto skupiskowy charakter występowania *P. fuscus* (miejscami zagęszczenie 1300—2000 osobników/1 m^2) związane są z nieregularnym rozmieszczeniem resztek zrębowych, zagęszczeniem pniaków oraz z grubością warstwy próchnicznej i jej wilgotnością. Stwierdza się dość wyraźną tendencję wzrostu liczebności krocionogów wraz ze wzrostem grubości warstwy próchnicznej na uprawach.

Wraz ze wzrostem grubości warstwy próchnicznej wzrasta na ogół także liczba osobników w glebie mineralnej. Można by sądzić zatem, że po przekroczeniu pewnego zagęszczenia w warstwie próchnicznej wzrasta glebotwórcza rola krocionogów w glebie mineralnej.

Fluktuacje w rozmieszczeniu pionowym w pniakach łączą się ze stopniem ich rozkładu, wilgotnością podłoża, rytmem dobowym gatunku oraz porą dnia i nocy.

W przewodzie pokarmowym *P. fuscus* stwierdzono liczne kolonie bakterii, 3 gat. promieniowców, ok. 50 gatunków i innych grup systematycznych grzybów. Liczne też były różne gatunki pierwotniaków, nicienie i roztocza. Skład flory przewodów pokarmowych *P. fuscus* jest potwierdzeniem pewnych ogólnych prawidłowości odzwierciedlających stosunki mikrobiologiczne w substratach stanowiących jego pożywienie. Grzyby: *Mucor* spp., *Aspergillus glaucus, Gliocladium* sp., *Monosporium* sp., *Penicillium* spp., *Trichoderma viride, Humicola* sp. występowały w przewodach pokarmowych krocionogów z wszystkich badanych środowisk i są one pospolitymi gatunkami glebowymi. Powszechnie w przewodach pokarmowych *P. fuscus* występuje *Trichoderma viride*, gatunek o szczególnym znaczeniu antagonistycznym wobec *Fomes annosus.*

Skład mykoflory ekskrementów P. fuscus był znacznie uboższy od mykoflory przewodów pokarmowych, z uwagi na możliwość niewydalania tych grzybów, które stanowią integralną część składową flory przewodów pokarmowych tych zwierząt, a także z uwagi na trawienie grzybów lub utratę przez nie zdolności kiełkowania.

Z badań nad wybiórczością pokarmową *P. fuscus* wynika, że jest to gatunek polifagiczny posiadający w rzeczywistości dość szerokie spektrum troficzne, w skład którego wchodzi też kora sosnowa o różnym stopniu rozkładu. Grzybnia niektórych gatunków jest atrakcyjniejszym pokarmem niż trociny czy kora i to zarówno w stanie świeżym lub częściowo przez grzyby rozłożonym. W wypadku zaś grzybni różnych gatunków bardziej jest preferowana ta, z którą częściej w swoim środowisku życia się styka.

W badaniach nad preferencją węglowodanów będących składowymi spożywanego pokarmu, stwierdza się wybiórczość względem cukrów prostych: glukozy i galaktozy, a z polisacharydów skrobi.

Metabolizm oddechowy dojrzałych osobników *P. fuscus*, karmionych ściółką liściastą oraz grzybnią z czystych kultur, okazał się w przypadku konsumpcji grzybni średnio wyższy o około 32,6%.

Biomasa, produkcja ekskrementów oraz metabolizm oddechowy populacji *P. fuscus* w borze sosnowym świeżym są najwyższe w najmłodszych okresach rozwojowych drzewostanu. Średnio dla upraw i młodników stan biomasy wynosi 2,2 kg/ha, produkcja ekskrementów 16,5 kg/ha rocznie, a metabolizm oddechowy populacji 9730 kcal/ha rocznie. Stopniowo wraz z wiekiem drzewostanów wartości te zmniejszają się osiągając najniższy poziom w drzewostanach rębnych.

Na podstawie dokonanych badań można się spodziewać znacznej roli *P. fuscus* w rozkładzie mechanicznym szczątków organicznych (kory, drewna, ściółki) i w zmianach w składzie chemicznym pokarmu po przejściu przez przewód pokarmowy. Wydalane ekskrementy zawierają rozdrobnione szczątki organiczne i odkładane są w różnych częściach profilu glebowego (migracje pionowe) wzbogacając glebę w łatwiej rozkładalne związki i stają się przez to miejscami ożywionej aktywności mikroorganizmów, w których odbywają się przyspieszone procesy humufikacji i mineralizacji. Migracje pionowe i poziome gatunku wpływają na wymieszanie części organicznych z mineralnymi, drążenie chodników (aeracja), przenoszenie mikroorganizmów i w konsekwencji polepszanie właściwości i struktury gleby. Propagacja niektórych grzybów glebotwórczych jak: *Trichoderma viride, Aspergillus* sp., *Penicillium* sp., będących antagonistycznymi wobec *Fomes annosus*, stanowi przy zasiedlaniu martwych pniaków sosnowych ważny element w biologicznej ochronie lasu przed tą groźną i pospolitą chorobą korzeni.

Introdukowany na powierzchnię zoomelioracyjną (gleba zasilona mieszaniną kory i trocin) *P. fuscus* zaadaptował się do nowego środowiska i rozpoczął powolne rozprzestrzenianie się z miejsc umieszczenia odkładów na działki. W drugim roku trwania zabiegu obserwowano prawie 100% wzrost zagęszczenia wyjściowego na całej powierzchni. Przy uwzględnianiu działek ze stwierdzonymi na nich krocionogami praktyczne zagęszczenie osiągnęło ponad 4-krotny wzrost w stosunku do zagęszczenia teoretycznego.

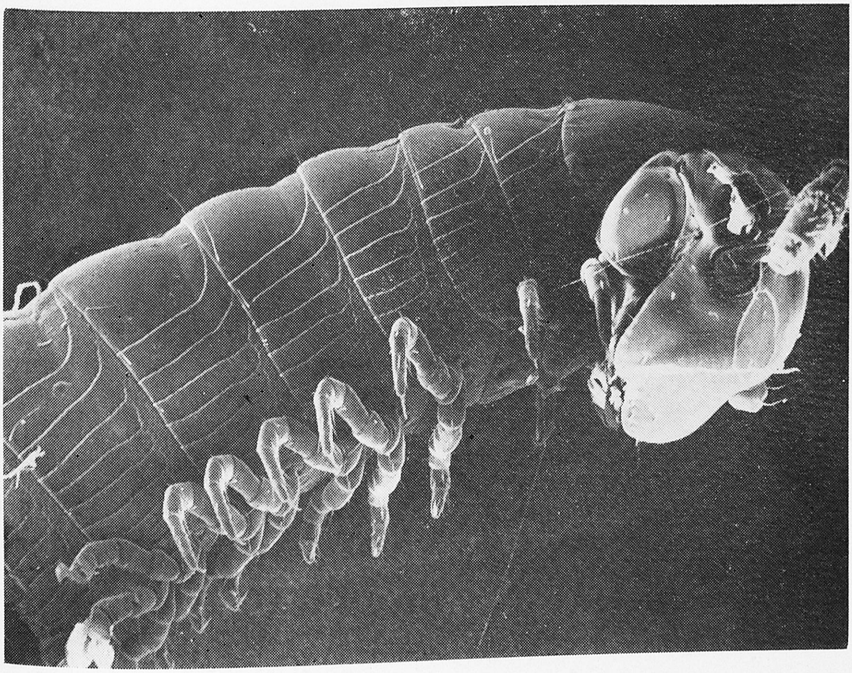
Właściwości *P. fuscus* jak: stosunkowo długi okres trwania rozwoju, długa aktywność życiowa w ciągu roku (III—XI), duże miejscami zagęszczenie populacji osobników, partenogenetyczny sposób rozmnażania, szeroka skala tolerancji wobec zasiedlanych środowisk a także czynników abiotycznych, dość szerokie spektrum troficzne oraz wypływająca z jego działalności pożyteczna rola w środowisku ściółkowo-glebowym, pozwalają w pełni na jego introdukcję do nowych środowisk, jakimi są gleby porolne przeznaczone do zalesień.

Zasilenie zdegradowanych gleb piaszczystych przeznaczonych do zalesienia w ramach rehabilitacji środowisk przyrodniczych szczątkami organicznymi wolno rozkładającymi się, jak kora i trociny, może stanowić dodatkowy korzystny aspekt utylizacji uciążliwych odpadków przemysłu drzewnego, stanowiących problem gospodarczy.

Redaktor pracy: doc. dr A. Szeptycki

Plate XVIII

1. Female — anterior part of body; vulvae, behind 2nd pair of legs, not visible
2. Lateral view of middle and posterior parts of body; anal plates visible



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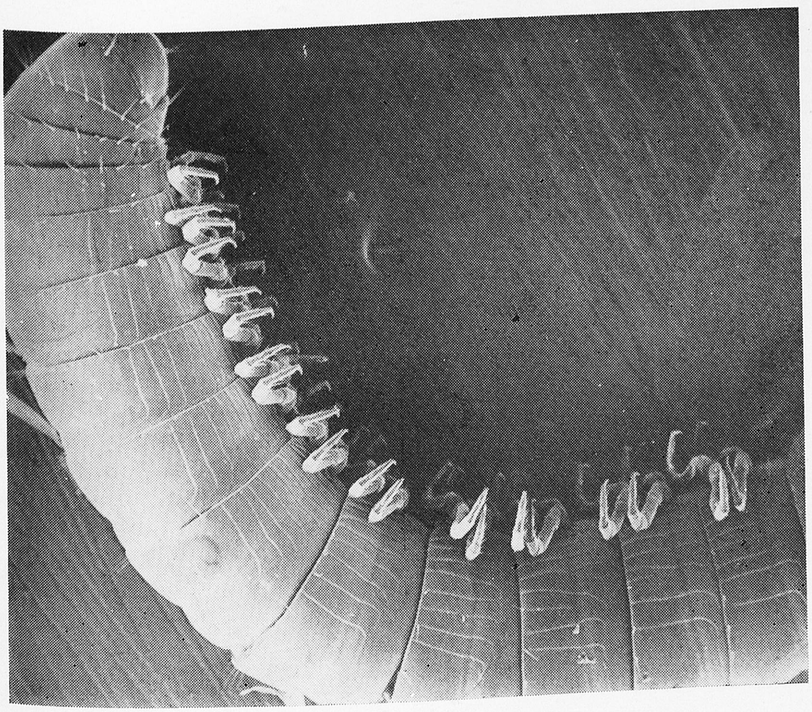
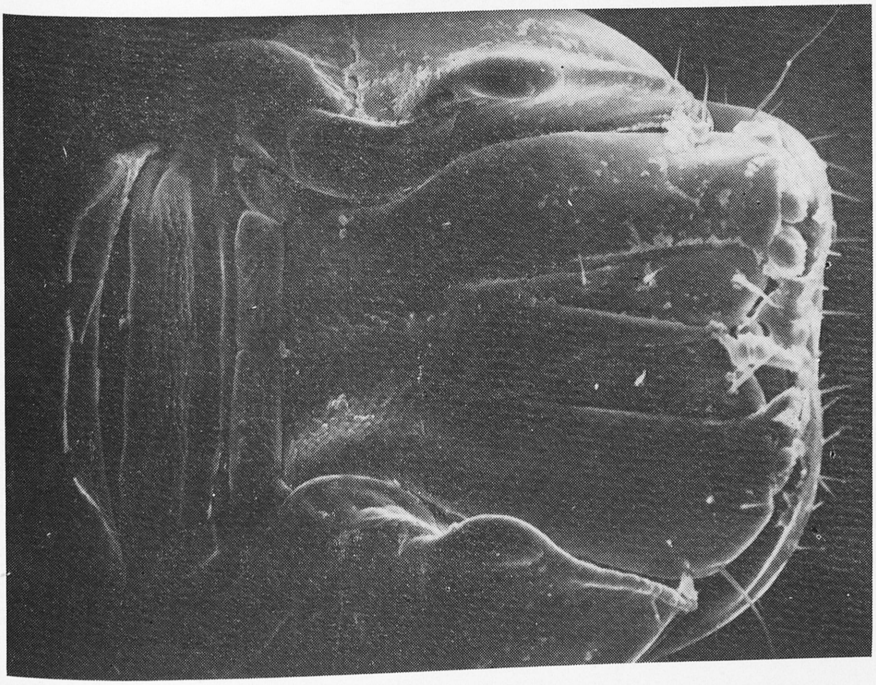


Phot. 2

H. Tracz

Plate XIX

1. Head seen from below — structural details of oral plate
2. Sculpture of lower parts of body segments; double walking legs growing on one segment end ending in claws



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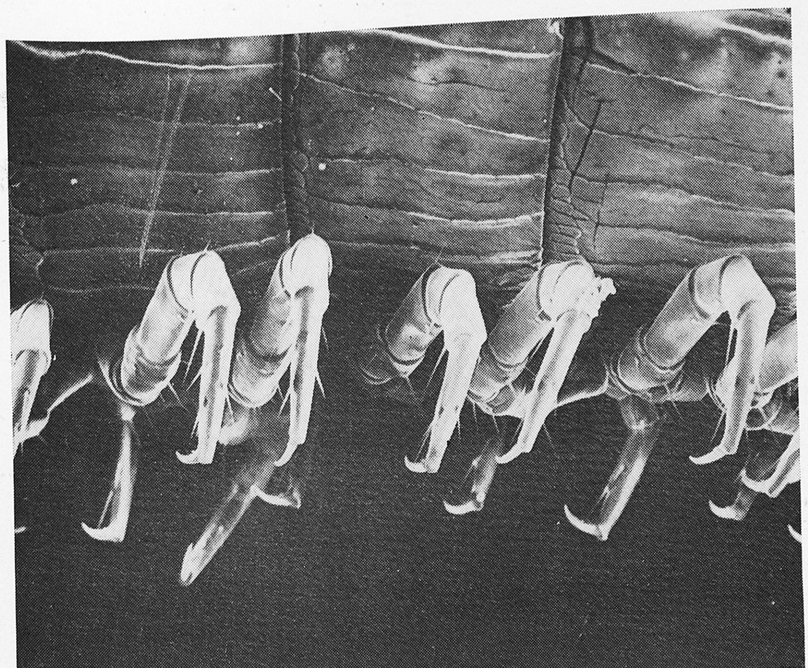
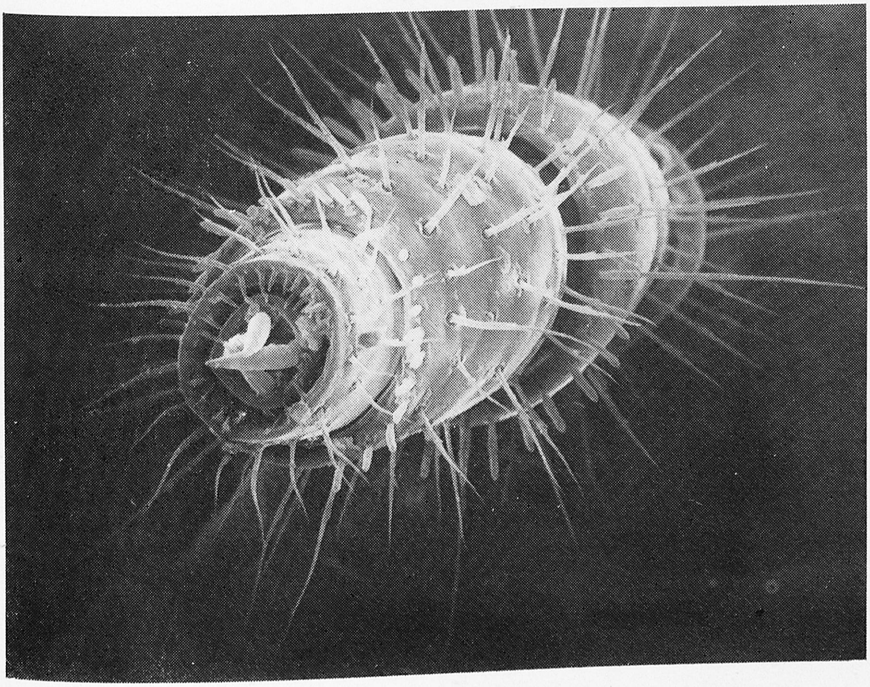


Phot. 2

H. Tracz

Plate XX

1. Antenna; four conical sense bodies on terminal joint
2. Male — stage "C". Anterior part of body seen from below, roundedness of cheek lobe visible, first pair of legs falciform, penis behind second pair of legs



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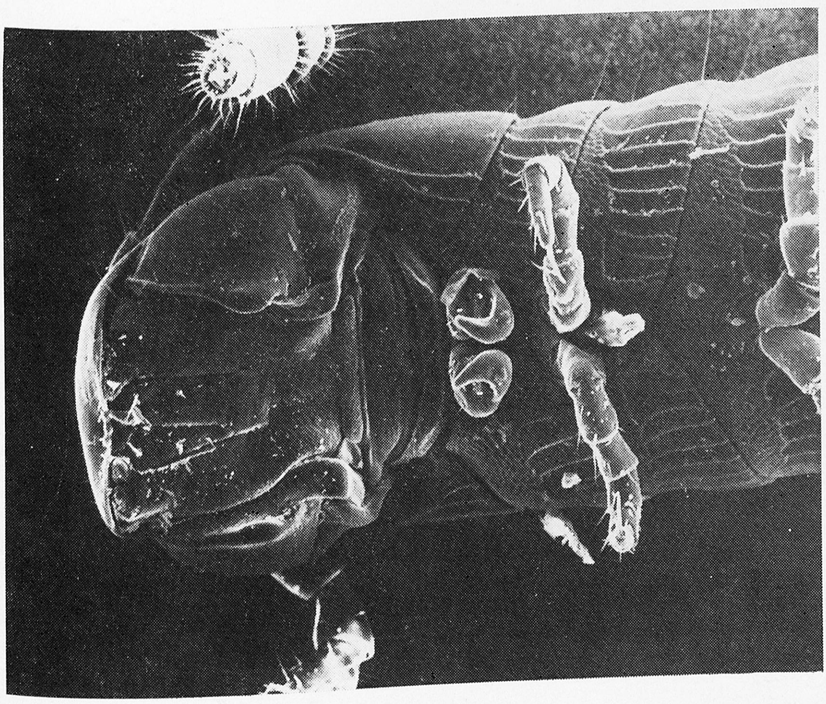
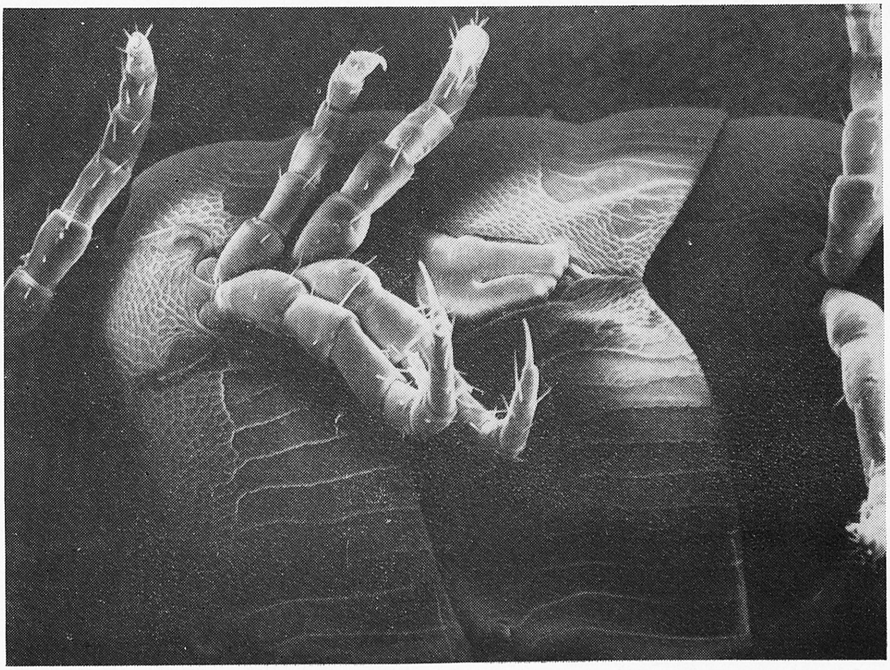


Phot. 2

H. Tracz

Plate XXI

1. Male — stage "S". Only processes visible in place of copulatory legs
2. Male — stage "C" Ventral view of body with copulatory legs on 7th segment, 1st pair of legs falciform, cheek lobe rounded



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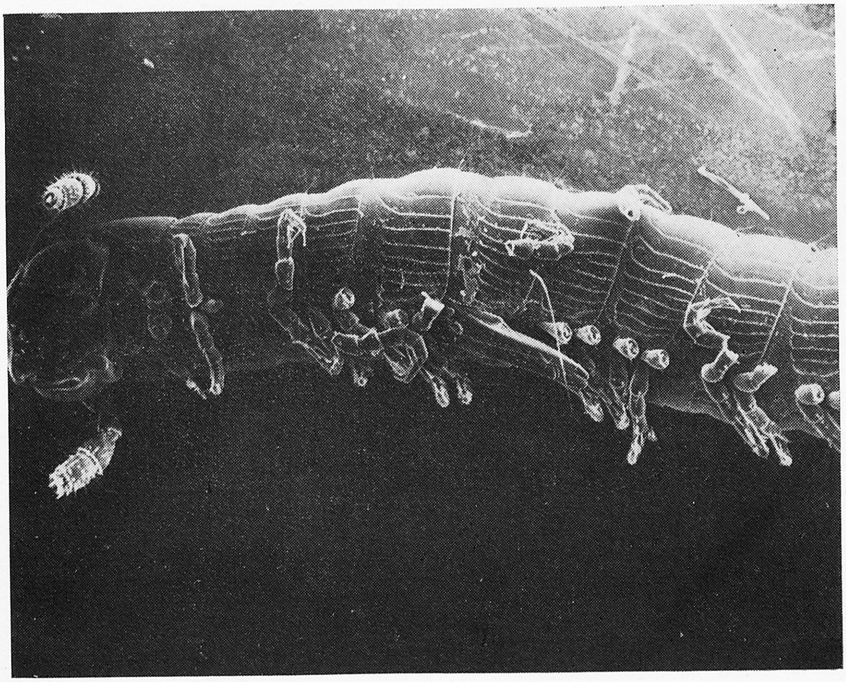
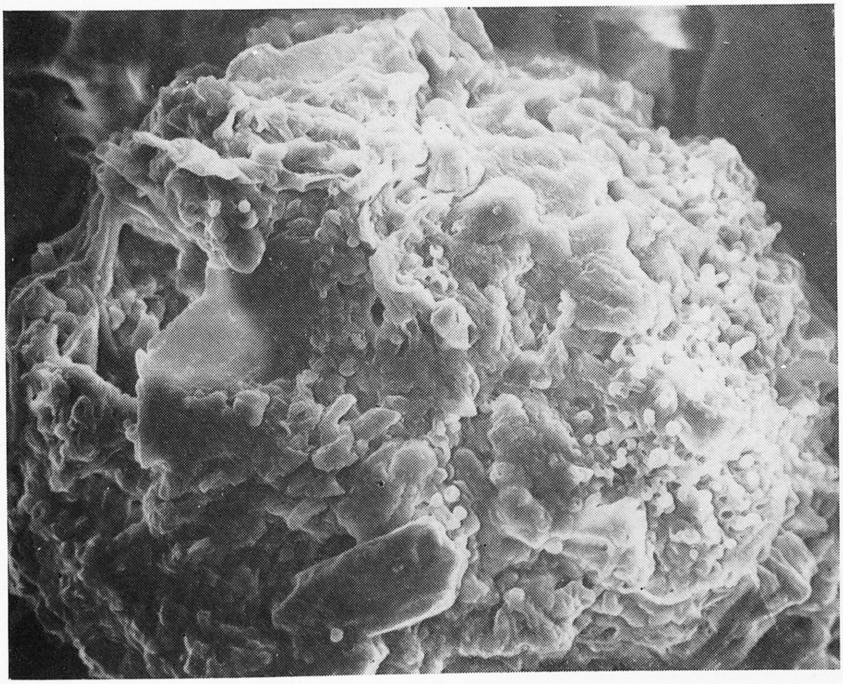


Phot. 2

H. Tracz

Plate XXII

1. Excrement from bark; its breaking up and the cells of co-operating micro-organisms are visible
2. Piece of rotten wood with mycelial hyphae



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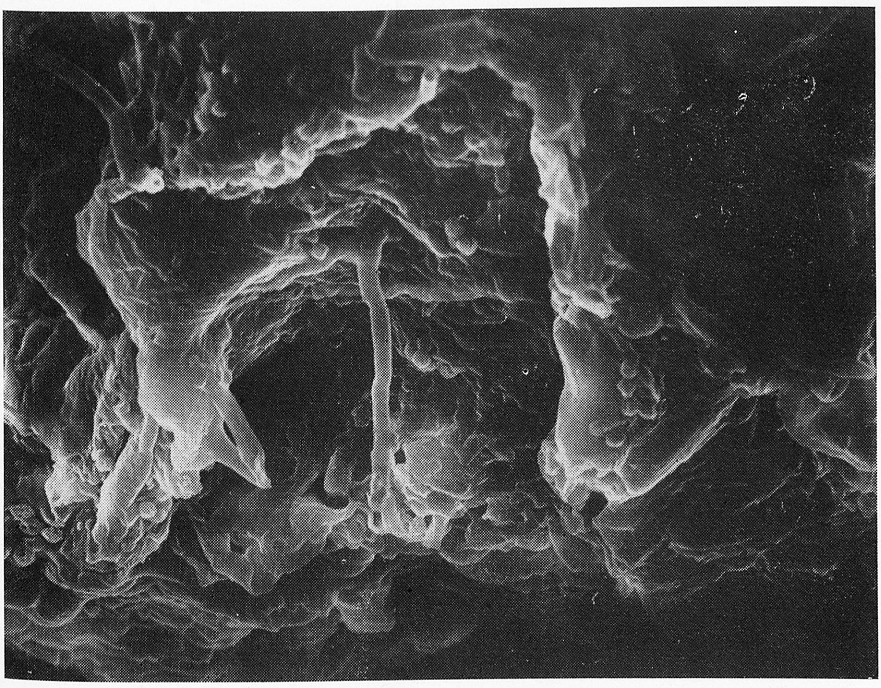
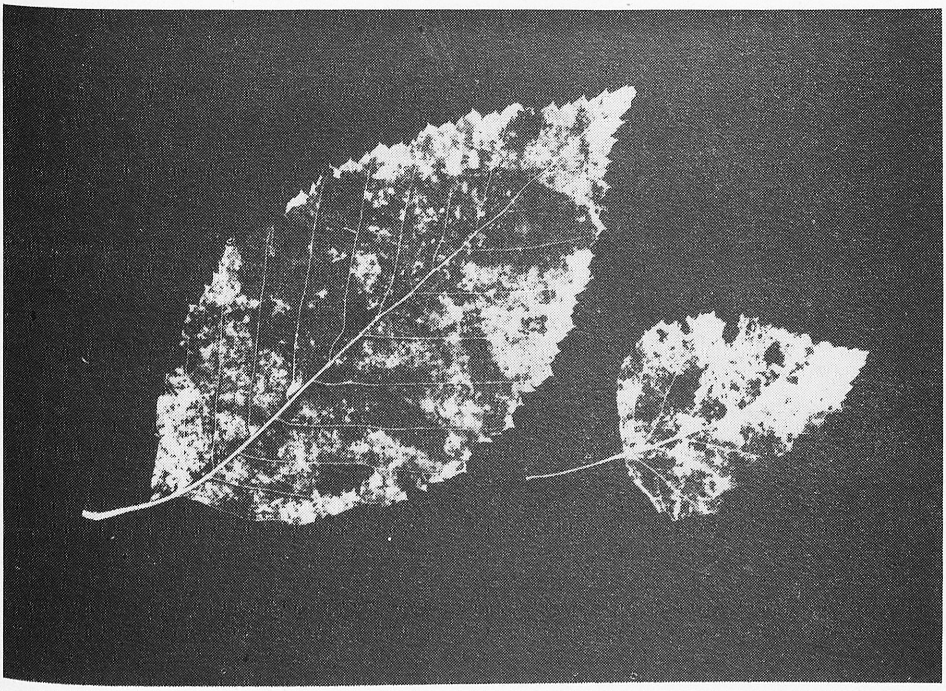


Phot. 2

H. Tracz

Plate XXIII

1. Traces of activity of *Proteroiulus fuscus* in dead leaves of birch and beech — sceletonization
2. Piece of rotten wood with mycelial hyphae — before consumption



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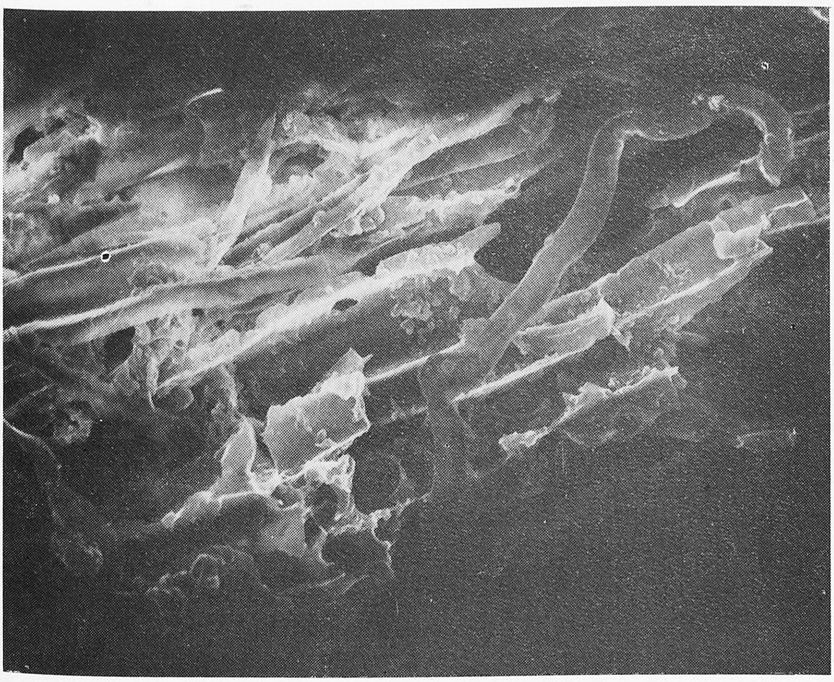
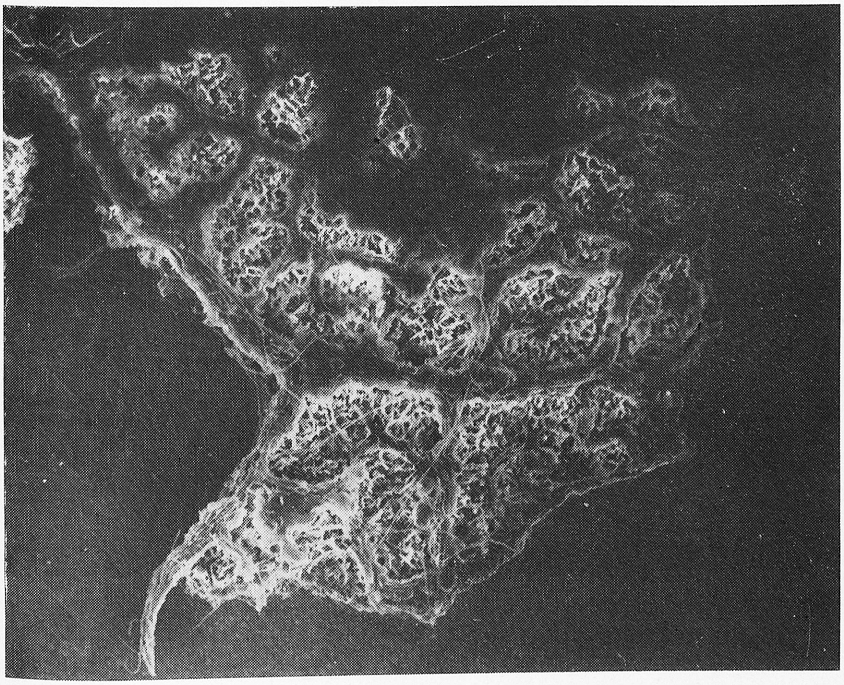


Phot. 2

H. Tracz

Plate XXIV

1. Fragment of dead leaf before consumption — traces of activity of micro-organisms
2. Excrement from leaf; breaking up of substratum; pits visible in cribriform fields



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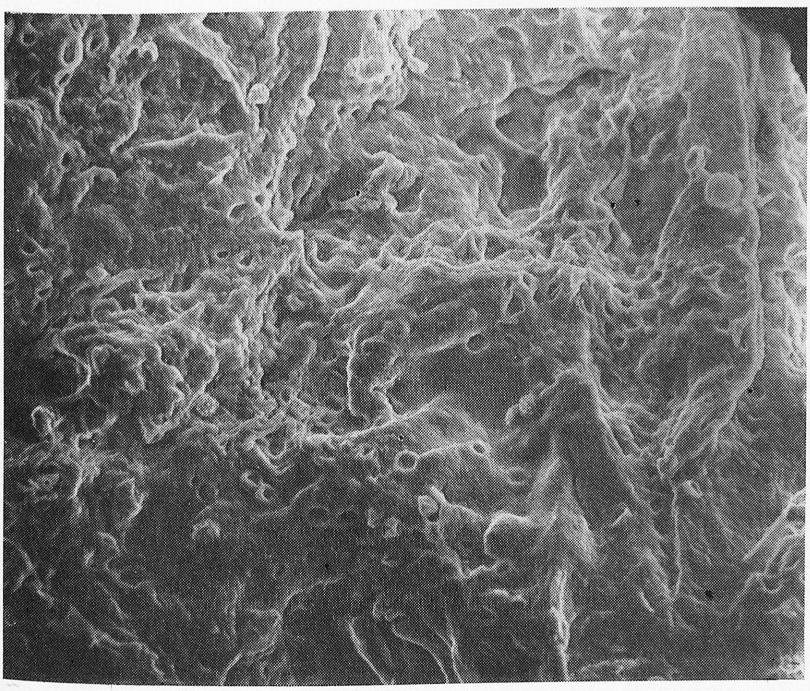
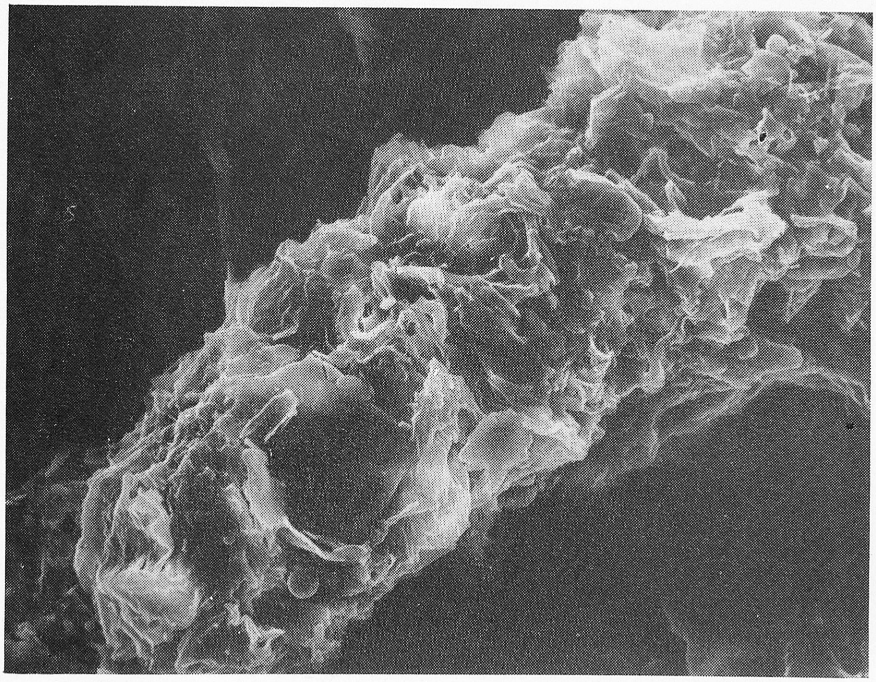


Phot. 2

H. Tracz

Plate XXV

1. Excrement from bark; breaking up is visible
2. Excrement from rotten wood



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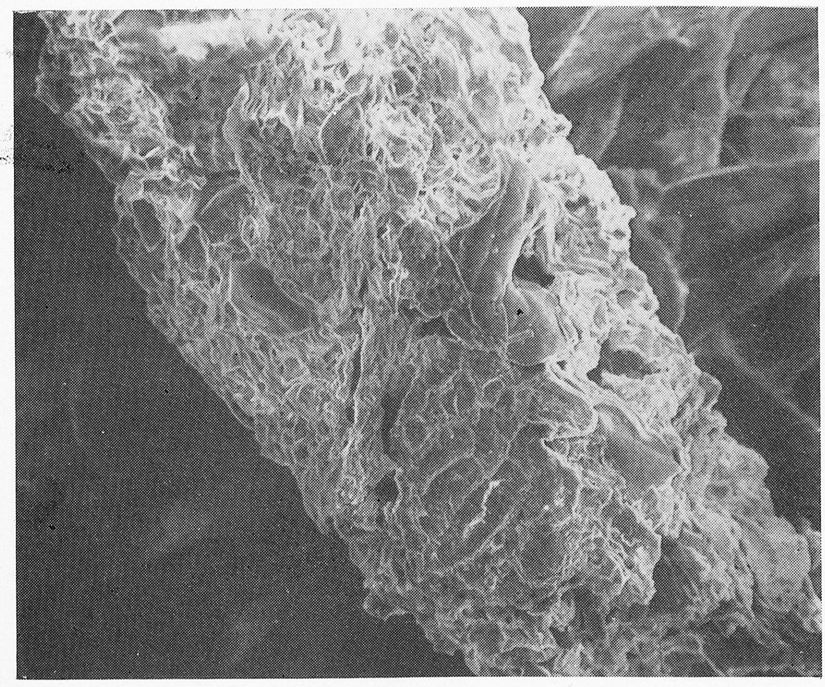

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