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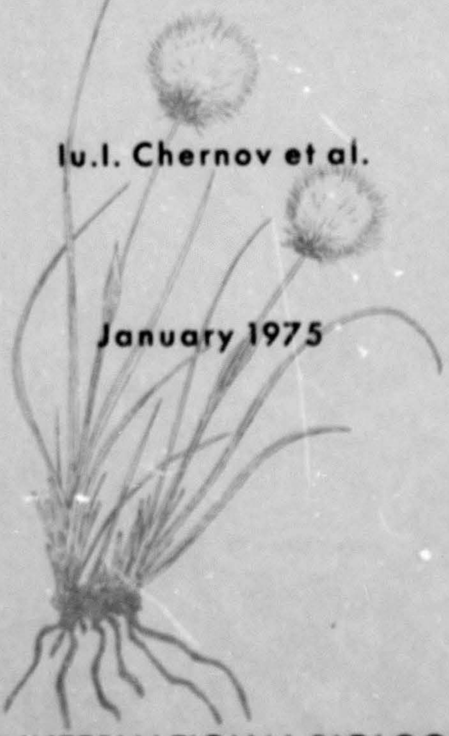

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INTERNATIONAL TUNDRA BIOME TRANSLATION 12, Part 1

Title: Complex of the Soil Invertebrates in the Spot-Medallion Tundra of Western Taimyr

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COMPLEX OF THE SOIL INVERTEBRATES IN THE SPOT-MEDALLION TUNDRAS OF WESTERN TAIMYR

In this article, we present the results of quantitative inventory of invertebrates in the spot-medallion tundra in the area surrounding the Taimyr biogeocenological station mainly from June through August 1968, and to a lesser extent in 1967 and 1969. Our goal was to give a characterization of the microbiotopical distribution of invertebrates according to elements of nanorelief of the spot-medallion tundra with, as much as possible, a full-scale inclusion of all the basic groups of animals. Here we limit ourselves to the particulars of distribution and structure of the animal community in total figures only without a detailed faunal analysis, which will be undertaken in the following publications.

We employed common methods of invertebrate calculation: hand counting in samples of different areas (1 dm^2, $\frac{1}{16}$ m^2, $\frac{1}{4}$ m^2), expelling of microarthropods with the help of an eclector (without heating), calculation of nematodes by the funnel method, harvesting with a gauze net, and others.

In the area around the station a dryas-sedge-moss spot-medallion tundra has developed in relation to the flat elevated portion along the Pyasina. N. V. Matveyeva gives a detailed geobotanical characterization of these tundras (1968). The alternation of a continuous moss cover with a different degree turfed cracked bare soil with a thin coat of lichens with isolated beds of higher plants, or with little cushions of moss, creates the set of ecological regimes which are specific of the zonal communities of the "nival" belt (the Arctic in the wider sense). In the spot-medallion tundra appear in their greatest extent, two very important features of the microstructure of the tundra vegetation: mosaicness and complexity. One may consider a spot of bare ground with ridges framing it and with a trough an ideal example of a complex. At the same time, the distribution of mosses and higher plants on turfy spots has a well-defined mosaic character. The formation of single species aggregations -- the "gregation" (Petrovsky, 1962) -- is extremely characteristic of the primary dominants of these tundras.

Through the profile of nanorelief a comparatively sharp change in hydrothermal conditions is observed. For us, temperature is of the greatest interest (Fig. 1). The least favorable temperature conditions are in the trough between the spots. In connection with this only the eurybiontic forms of the "pedobionts" are more or less plentiful here; these are capable of living in the mossy turf (Chernov, 1966). At the same time in the trough, the very upper portion of the mossy turf heats relatively well, which in combination with the high humidity creates favorable conditions for the hemi-edaphic forms. The contrast between the temperature of the uppermost layer of the mossy turf and its lower part and the peaty layer is the greatest. The higher temperature of the upper layer of mossy turf in the trough in comparison with the ridge surrounding the spot evidently explains itself by the dark color, and perhaps, by the greater heat accumulation in connection with the higher humidity. On the ridge rising above all the elements of nanorelief, the upper layer of mossy turf is generally very dried up and has a light color. Of the mosses here, *Hylocomium alaskanum* plays a large role, and in places *Rhacomitrium lanuginosum*, and likewise lichens, particularly *Thamnolia vermicularis, Dactylina arctica*, and *Cetraria cucullata*.

The lichen-moss turf on the ridges is more continuous and of significantly less thickness than in the trough. The vertical distribution of temperature here is more even; within this soil there is warming to a significant depth. One may include the dryness of the mossy turf among the factors which are unfavorable for invertebrate habitation of the ridges, in connection with this the numbers of hemiedaphic forms of microarthropods and other bryophilic groups on the ridges often is the smallest among the comparatively high number of soil forms.

As is shown in our work (Chernov, 1964, 1965, 1966), in the soil of the non-turfy spot conditions are created which are favorable to mesophilic soil forms, which, concentrated in a thin upper layer, evidently play a substantial role in the further evolution of the spot. Due to the lack of a mossy turf the spot of bare soil heats through in summer to a significant depth; however, sharp daily and seasonal fluctuations in temperature are characteristic for these. One may add the uneveness of the surface of the spot (on account of "frost boils" and cracking) to the factors which are favorable for invertebrates. The high humidity serves as the main obstacle to the invertebrate's inhabitance of the mineral soil of spots. Saturation here often begins even at the depth of 5 cm. At the same time, several forms, for example the euedaphic collembola *Anurida*, penetrate the soil to a depth of 20 cm in spots of relatively low humidity. This contrasts sharply with the peculiarities of the vertical distribution of pedobionts in other tundra zone soils. It is natural to expect great specificity of the microaggregations of the spot-medallions, especially in regard to life-form composition. Evidently, the surface of the spot-medallion is most favorable for the epiedaphic and several of the herpetobiontic species. Due to good warming even soil forms are found at the very surface layer. It is fitting to emphasize the fact that the ecological conditions on the spot-medallions are similar to those on mountain and high-arctic gravelly tundras with an interrupted plant cover. The evolution of a spot-medallion is a long, complicated process, and it would hardly be fitting to consider it as a unidirectional one. Probably it is drawn out for a long period of time, it can go back, slow down, and separate stages can maintain themselves for a long time. The extraordinary diversity of the plant aggregations of the spots within the limits of a single community serves as indirect evidence of this proposition. Evidently, the vegetation of each spot distinguishes itself with substantial individual peculiarities, and several more or less typical paths of succession take place. Thus, the very first stage of succession on

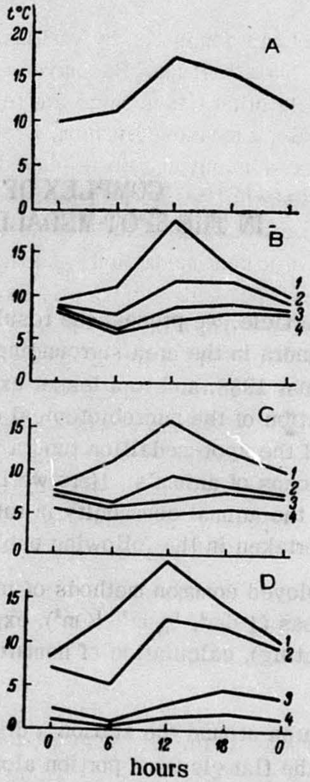

Figure 1. Diurnal temperature fluctuation within various types of nanorelief, July 25, 1966.

A - Air temperature at the height of 1 m; B - spot of bare soil; C - ridge; D - trough; 1 - surface of the soil or of the mossy covering; 2 - depth of 5 cm; 3 - 10 cm, 4 - 15 cm.

different spots is dominated by various species of crustose lichens, most often *Toninia syncomista*, but sometimes *Baeomyces carneus* and species of the genus *Ochrolechia* and *Pertusaria*. In other cases there are few lichens, and the bare ground is colonized right away by moisture-seeking mosses *(Hypnum, Drepanocladus)*; sometimes in the very earliest stages of succession a substantial role is played by flowering plants, for example *Dryas punctata* and the sedge *Carex ensifolia* ssp. *arctisibirica*. Not having the opportunity to investigate all of these variants, we distinguished three conditional "stages", which to some extent reflect the stages of succession of a spot-medallion. To the first stage of spot-medallion succession we assigned the relatively dry spot with a distinctly expressed bare ground frost boil and with a thin coating of crustose lichens *(Toninia, Baeomyces, Ochrolechia)* without a substantial admixture of mosses, fruticose lichens and flowering plants. Spots of stage II are those on which there are still no continuous mossy turfs but a clearly defined thin fragmentary vegetative plant cover of fruticose lichens *(Thamnolia vermicularis, Cetraria cucullata, C. crispa, Cladonia amaurocraea)*, mosses *(Aulacomnium turgidum, Orthothecium chryseum, Ditrichium flexicaule)* and of flowering plants *(Dryas punctata, Carex ensifolia, Luzula nivalis, Cerastium bialynickii, Minuartia arctica)*. The algae *Stratonostoc* sp. are found in abundance in places on such spots. The main feature of this stage is fragmentation, lack of a closed plant cover which, however, distinguishes itself by significant floristic richness (Matveyeva, 1968). To the spots of the third stage of succession we assigned the spots on which a continuous, but still thin (to 2-3,cm) mossy turf was formed. Usually on the surface it is condensed ("Crust-like"). Many lichens *(Thamnolia vermicularis, Dactylina arctica, Cetraria cucullata, C. crispa)* and mosses *(Hylocomium alaskanum, Aulacomnium turgidum, Rhacomitrium lanuginosum)* play the greatest part in this formation. Possibly, each of the stages distinguished by us relates to a certain type of succession and between them there is n o connection as there would be between stages which succeed each other.

A sharply defined and distinctive gradient of microclimatic conditions in the spot-medallion tundra is conducive to the formation of a variegated mosaic of microaggregations of animal population (Chernov, 1965). On account of the extreme var iegation of the mossy cover, particularly in the spot-medallion tundra, one may expect the greatest richness of the bryophilic hemiedaphic complex of invertebrates. Besides this, on spots of bare soil, especially in the middle stages of their succession, conditions are created which are favorable for herpetobiontic forms: a fragmentary plant cover, compact, with an uneven, cracked soil surface, good heating. For typical soil forms, evidently, the most favorable conditions on the spot-medallions are in the early stages of succession and on some parts of the ridges. Least suitable for invertebrate colonization is the peaty soil in the trough between the spots.

It is natural that the phyllobiontic complex must experience strong inhibition in the spot.medallion tundra. *Betula nana, Salix arctica* and *S. Pulchra*, which are sufficiently abundant in these tundras, do not form any amount of close layer and do not rise very high above the moss cover. Highest rise the flowering stalks of the grasses (*Arctagrostis latifolia, Festuca brachyphylla*), the sedges (*Carex ensifolia*), and woodrushes (*Luzula nivalis*), but they are scattered quite thin and do not form a continuous layer.

The data of our calculations of the numbers of various groups of invertebrates in the spot-medallion tundra (Table 1) demonstrate the distinct complexity of the topical structure of the animal community correlated with the microclimatic particulars noted above. A picture of the distribution of the microaggregations of invertebrates is complicated by successional processes, as a result of which one observes alongside their comparatively monotonous stable composition

Table 1. Invertebrate number (specimens/m^2) among various types of nanorelief in the spot-medallion tundra.
(Extrapolations from data obtained by various methods of calculation from soil samples of different area and volume.)

	Spot in stages of succession				
	I	*II*	*III*	*Ridge*	*Trough*
Nematodes	1250000	4500000	1500000	1800000	1100000
Enchytraeidae	1090	1080	570	770	1050
Earthworms	19	14	12	5	10
Gamasid mites	1320	2720	2480	3160	2520
Oribatei	1320	2780	2240	4440	1200
Collembola	19240	34040	32840	44140	24960
Beetle larva	15	30	3	5	--
Beetle imago	3	3	--	1	--
Imago & larva of Staphylinids	3	4	8	16	2
Weevil larva	1	1	--	--	--
Larva of mosquitoes & craneflies	7	20	3	2	--
Fly larva	12	19	17	30	2

on the ridges and in the troughs, an extreme variety of microaggregations on the spot-medallions depending upon the degree and character of overgrowth.

Side by side with the substantial changes in correlations of abundance of the various groups, the tendency towards increase of total numerical indices--zoomass and metabolism--is quite clear in the early stages of succession (Figs. 2, 3). On the other hand, the minimal values of these indices correspond to the elements of the complex with the maximally developed mossy turf (the troughs). The high level of total zoomass in the first stages of succession is mainly determined by the abundance of earthworms and Enchytraeidae. The highest indices of total oxygen consumption[1] are determined by the abundance of small forms -- nematodes; enchytraeids, collembola. Inverse changes in the indices of total biomass of collembola and annelids take place (Figs. 2, 4). The total biomass of the latter, especially enchytraeids, is maximum in the first stages of spot succession. The minimum number of annelids are on the ridge and in the trough, where the soil is less favorable for pedobionts and they are concentrated in the lower part of the mossy turf and in the peat layer. Earthworms living in the spot-medallion tundras have significantly smaller dimensions (on the average 2 times as small) than on the slopes occupied by herb-meadow mosephillic aggregations (their maximum weights respectively 0.8 and 1.6). The weights of *Eisenia nordenskioldii* from the spot-medallion and hummocky tundra are very close. Evidently, the ecological regimes in the spot-medallion tundra are somewhat more favorable than in tundras with continuous mossy cover, all the same they are far from optimal for the given species.

[1]The intensity of respiration of Collembola is calculated according to Dunger's table (Dunger, 1968) of worms, according to Byzovaya (1965) and Zinkler (1966), with calculations of temperature regimes for corresponding elements of nanorelief.

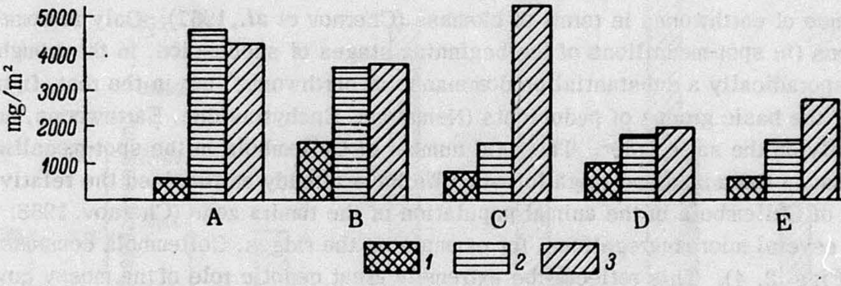

Figure 2. Biomass of nematodes and annelids in spots in various stages of succession and according to nanorelief elements, July 1968.

A-C - spots in stages I-III of succession, respectively, D - ridge; E - trough; 1 - Nematodes, 2 - Enchytraeidae, 3 - Lumbricidae (Eisenia nordenskioldi Eis.)

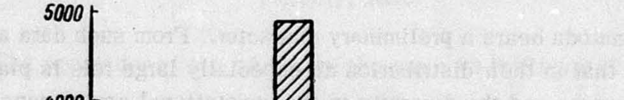

Figure 3. Total magnitudes of oxygen consumption by invertebrates calculated from the numerical data in July 1968.

1 - Nematodes; 2 - Enchytraedae; 3 - Eisenia nordenskioldi Eis; 4 - Collembola; 5 - Tipulidae (larvae). The remainder of marks are the same as in Fig. 2·

Especially important is the circumstance that, in contrast to the large part of the humid belt (forest region, forest-steppe) in the mentioned zonal formation one does not observe any sharp predominance of earthworms in terms of biomass (Chernov *et al.*,1967). Only in some micro-aggregations (in spot-medallions of the beginning stages of succession, in the troughs) one observes sporadically a substantial predominance of earthworms, but in the rest, figures for total biomass of the basic groups of pedobionts (Nematoda, Enchytraeidae, Earthworms, and Collembola) are basically on the same order. The total number of Collembola in the spot-medallion tundra exceeds that in the mixed and taiga forests. We have already emphasized the relatively large proportion of Collembola in the animal population of the tundra zone (Chernov, 1968; Ananjeva, 1970). In several microaggregations, for example on the ridges, Collembola compose ⅓ total biomass (Figs. 2, 4). This reflects the extremely great cenotic role of the mossy cover in the tundras, which on one hand limits the colonization of the mineral soil, but on the other makes possible the formation of a specific bryobiontic complex, the most important component of which is the Collembola (Chernov, 1966).

Oribatei and gamasid mites reveal in the tundra clear signs of adverse conditions (Table 2, Fig. 5). Tyroglyphid mites in these tundras are not noted. The number of Oribatei is on the average ten times lower than the number of Collembola. The sharp decrease of the proportion of saprophilic groups of mites is a characteristic zonal feature of the tundra animal community. In the forest belt the correlation of the abundance of the microarthropod groups is different: the Oribatei exceed the Collembola five to eight times, the number of Tyroglyphids is variable, but in places very high.

Our material on Nematoda bears a preliminary character. From such data as we succeeded in obtaining, it is evident, that in their distribution an especially large role is played by the combination of sufficient warming and the diversity in the vegetational cover, especially of flowering plants. The maximum figures of Nematoda abundance were obtained for the ridges and spot-medallions of stage II of succession.

The general number of Collembola does not change substantially within the limits of the series of microaggregations of the spot-medallion tundra. More significant are the changes of their total biomass, which increases progressively in a series of spot-medallions of the I-III stages, and is maximal on the ridges. The lack of correlation of the changes of total numbers and biomass is explained by the substantial difference in the size composition of the Collembola microaggregations. In particular, on the spots of the first stage of succession the number of Collembola is comparatively higher, however they are represented here mainly by small forms (*Tetracanthella, Proisotoma*). With an increase in thickness of the mossy turf the number of relatively large onychiurids sharply rises. The indices of oxygen consumption, calculated with respect to the temperature regime in the inhabited layer, give another picture of distribution through the microbiotope. They do not correspond either to the numbers nor to the biomass (Fig. 4). Their greatest magnitude appeared for spots of the third stage of succession. On the ridges, despite the greater total biomass, the intensity of metabolism of Collembola is not large, which is explained, firstly, by the less favorable temperature conditions, and secondly, by comparatively larger dimensions of the Collembola. Thus, Collembola as well as Annelida display a substantial dependence upon the degree of development of moss cover and vicariate in the successional series of the spot-medallion tundra.

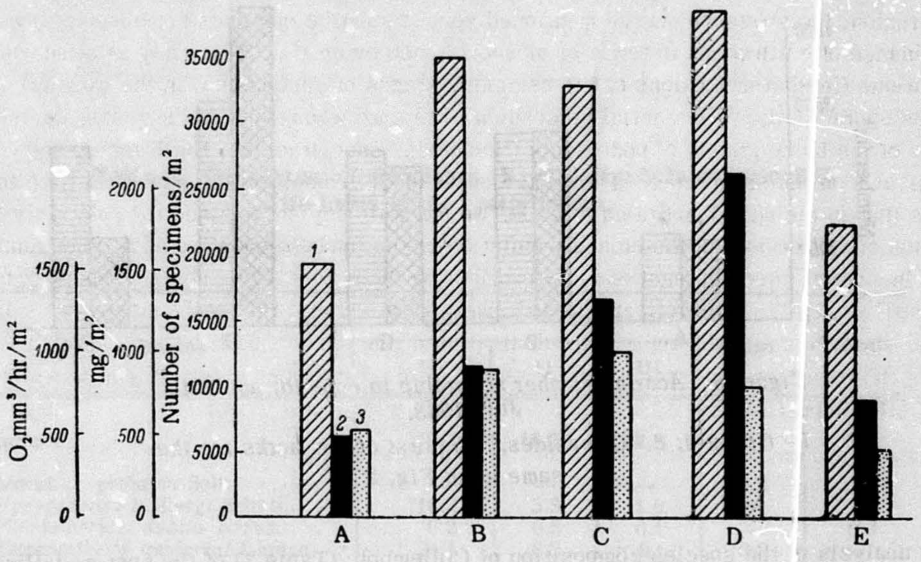

Figure 4. Total quantitative characteristics of the microaggregations Collembola - correlation of population size (1), biomass (2), and intensity of oxygen consumption (3), July, 1968.

The remainder of the marks are the same as in Figure 2.

Table 2. Oribatei number (number of specimens/dm²) in the spotty tundra.

Species	Spot in stages of succession			Ridge	Trough
	I	II	III		
Liochthonius sellnicki S. Thor. . .	12.4	24.4	7.6	14.0	6.0
Trhypochthonius nigricans Willm.	0.4	1.6	1.6	0.4	0.4
Camisia horrida Herm.	—	—	—	4.0	0.8
Hermannia scabra Koch.	0.4	—	4.0	2.4	0.8
Oppia unicaririnata Paoli	—	—	—	3.2	—
O. translamellata Willm.	—	—	—	4.8	—
Ceratoppia quadridentata Haller	—	0.8	4.4	8.4	4.0
C. sphaerica L. Koch.	—	—	1.2	1.2	—
Scutozetes sp.	—	0.8	0.4	—	—
Lepidozetes sp.	—	0.8	—	0.4	—
Mycobates parmelidae Mich. . .	—	—	3.2	4.4	—
Scheloribates latipes Koch. . . .	—	—	—	1.2	—
Zygoribatula exilis Nic.	—	0.4	—	—	—

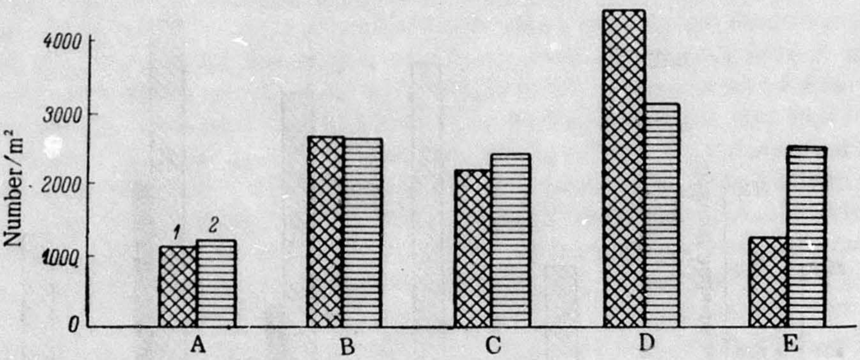

Figure 5. Acarina number according to eclector analysis. July 1968.

1 - Oribatei; 2 - Gamasides. The rest of the marks are the same as in Fig. 2

An analysis of the species composition of Collembola (Table 3) of the spot-medallion tundra shows, that of 5 variant microaggregations the composition of Collembola is most specific on the spot-medallions of the early stages of development, which correlates also with the greater specificity in composition of vegetation cover (Matveyeva, 1968). A calculation of paired coefficients of "biocenotic similarity" according to Vainshtein (1967) gives an especially distinct picture (Table 4). The sums of the coefficients reflect well, in our opinion, the specificity of the different aggregations. The greatest similarity is displayed, on one hand, between spot-medallions of the first and second stages, but on the other hand between spots of the III stage and the ridge. At the same time the spot-medallions of the third stage and the ridges appear less specific in comparison with the other aggregations within the landscape's profile. The sums of their coefficients are highest (149.4 and 145.1). In these microaggregations the most important features of these particular zonal communities are most fully displayed. The spots of Stage I show the greatest specificity (65.3). There dominant species, ***Tetracanthella wahlgreni, Proisotoma*** sp., ***Hypogastrura tullbergi***, which are practically absent from the portions with a continuous moss cover, give a distinctiveness to the aggregations of collembola peculiar to the beginning stages of bare ground succession. ***Tetracanthella wahlgreni*** is an alpine series, widely distributed in the mountainous regions of Europe (Cassagnau, 1967). In the Taimyr we have noticed it in the mountain "gravel" tundras, among them on the height nearest the station, Daksatas, in the foothills of Byrrang. This is one of the examples of the entry of a species in to the "zonal arena," primarily connected with conditions of a clearly defined intrazonal character (Chernov, 1968). In terms of ecological regime the denuded soil of the spot-medallion tundra is undoubtedly close to the "gravelly" mountain tundra.

On spot-medallions of the beginning stages of succession there is a low number of soil collembola--the onychiurids. It is appropriate, however, to mention that in expelling of collembola from the heavy, highly saturated soil of the spot-medallions many are not taken into account. The species composition of collembola naturally is poorest on the barest spots, on which a total of 3-4 species gives a comparatively high figure on the order of 10 specimens per dm^2 and higher. With respect to several sub-litter bryobiontic forms and surface forms one may suppose that there is a migration into the spots from the mossy turf of the ridges.

Table 3. Correlation of abundance (%) of Collembola of various life-forms in the spotty tundra.

Species	Spots in stages of succession			Ridge	Trough
	I	II	III		
Surface	**40.7**	**16.7**	**8.8**	**2.8**	**3.6**
Morulina ghilarovi Soln.	—	—	—	0.8	—
Hypogastrura tullbergi Schäff. . .	16.3	5.8	1.0	—	—
Pseudachorutes dubius Kraus. . .	0.2	0.5	0.1	—	0.3
Tetracanthella wahlgreni Linnan. .	21.1	6.2	4.1	0.2	—
Entomobrya lanuginosa Nic. . . .	—	—	0.7	0.4	—
Corynothrix borealis Tullb. . . .	0.2	0.9	1.0	0.2	—
Sminthurides sp.	0.4	0.3	0.4	—	—
Sminthurus variegatus Tullb. . . .	2.5	2.7	0.4	0.2	2.7
S. viridis L.	—	0.3	1.1	1.0	0.6
Living under the litter and bryobionta	**12.6**	**36.7**	**38.4**	**17.3**	**51.4**
Ceratophysella armata Nic. . . .	—	0.3	0.1	—	8.5
Pseudisotoma sensibilis Tullb. . .	2.8	7.3	23.7	6.1	10.2
Vertagopus sp. n.	4.9	17.6	3.9	1.4	3.8
Isotoma multisetis Carp. u. Phil.	—	0.7	0.6	0.3	0.3
I. viridis Bour.	0.6	3.8	4.1	1.6	1.4
I. sp. n.	—	—	—	0.1	—
I. olivacea Tullb.	0.2	0.2	1.1	3.0	8.8
I. albella Pack.	3.3	5.4	2.3	2.3	10.2
I. violacea Tullb.	0.6	1.4	2.6	2.5	8.2
Isotomurus palustris Müll.	0.2	—	—	—	—
Partial soil	**45.1**	**37.0**	**7.1**	**18.1**	**22.7**
Folsomia diplophtalma Axels. . .	1.6	7.8	5.2	18.0	16.3
Proisotoma sp. n.	43.3	27.6	—	—	—
Isotomina sphagnoticola Linnan. .	—	—	—	0.1	0.8
Isotoma notabilis Schäff.	0.2	1.6	1.9	0.8	5.6
Soil	**1.6**	**9.6**	**45.7**	**61.8**	**22.3**
Onychiurus bicampatus Gisin . . . ; *O. fimatus* Gisin ; *O. sibiricus* Tullb.	1.6	9.6	44.2	61.4	21.7
Anurida sp. n.	—	—	1.5	0.4	0.6

Table 4. Paired coefficients of "biocenotic similarity" (according to Vainshtein, 1967) for Collembola aggregations.

	Spot in stages of succession			Ridge	Trough	*Dryas* cover in upper part of river bank slope	Herb aggregation on river bank slope
	I	II	III				
Spot							
1. stage	100	37.5	11.1	5.0	7.1	1.4	3.2
2. stage		100	31.5	17.4	24.5	4.8	9.1
3. stage			100	38.7	29.1	14.7	24.3
Ridge				100	34.3	22.5	27.2
Trough					100	7.5	12.9
Dryas cover in the upper part of a river bank slope						100	26.7
Herb aggregation on river bank slope							100
Sums of the coefficients	65.3	124.8	149.4	145.1	115.4	77.6	103.4

In the course of succession substantial changes in the life-form composition of Collembola are observed (Table 3). For stage I of succession two groups are most characteristic--the surface and the semi-edaphic groups. On the spot-medallions of Stage II of succession *Tetracanthella wahlgreni, Proisotoma* sp., *Hypogastrura tullbergi,* which are typical for bare soil, still maintain high numbers; at the same time, the abundance of several species increases further, such as the litter-bryobiontic (*Isotoma viridis, Pseudisotoma sensibilis, Vertagopus* sp.), likewise the soil inhabitants (*Onychiurus, Folsomia diplophtalma*). As a result of this, the dominance by a few species of the microaggregation of the bare spots changes to a clearly pronounced poly-dominance with a great species and ecological differentiation of the total abundance. The microaggregations of the spot-medallions of the second stage of succession are characterized by a maximally mixed life form composition. Here there is no substantial predominance of any one of them. This undoubtedly reflects the maximal variation of ecological conditions (interchange of bare ground with small turfs of mosses, lichen cushions, beds of flowering plants). The complex of stage III of succession is significantly closer to the typical tundra bryophilic aggregations, the most characteristic features of which are embodied in the animal population of the ridges. In this stage the number of *Onychiurus* rises sharply, but the species characteristic for the bare ground disappear or are found rarely.

Thus, proportional to the amount of overgrowth of the spot-medallion the number of euedaphic Collembola increases; this does not correlate with the distribution of primary pedobionts--Annelida--and, it would seem, contradicts the thesis of the tendency towards reduction of the soil layer of tundra animal population (Stebayev, 1964; Chernov, 1966). However, this increase shows only a change in the composition of adaptive types of Collembola, which reflects the potential capacity for colonization of one horizon or another. On spot-medallions of stage III of succession and on the ridges the onychiurids dominate, which, despite the features of typical soil forms, are also capable of inhabiting the mossy cover, which has been noted for the tundra several times.

The number of major insect-pedobionts, calculated by hand in plots of $^1/_{16}$ m^2 (see Table 1), emphasizes even more strongly the features of the spots of bare ground as a biotope with relatively favorable microclimatic conditions for soil forms. Their maximum is likewise observed in the first two stages. It is particularly fitting to note the relatively high number of larvae of mosquito-craneflies of the genus *Tipula*, and of Carabidae (mainly the species of the subgenus *Cryobius*, genus *Pterostichus*, and likewise *Amara alpina* F. and *Notiophilus aquaticus* L.). To a large extent the peculiarity of ecological conditions in the spots of bare ground is emphasized by the larvae of the weevil *Lepyrus*, which we noticed occasionally in the soils of such spot-medallions and in other regions (Chernov, 1965), but not once did we meet them in the parts of the tundra with a continuous moss turf. These typical pedobiont-phytophages are characteristic for the herb-dwarf-shrub aggregations as far as the northern limits of the tundra zone. The number of Staphylinids, on the other hand, increases proportionally with the thickness of the mossy turf, which, probably, is connected with the rise in abundance of little-moving onychiurids, which can be their prey. The data set forth emphasize the fragmentary character and the low specificity of the microaggregation of the troughs (the impoverished condition, and the lack of characteristic mass forms).

One of the most characteristic components of the animal population of various mossy tundras are the spiders, of which in the investigated spot-medallion tundra we found mainly two genera of the family Lycosidae: in greatest numbers, *Alopecosa*, and somewhat less commonly, *Pardosa*. These comparatively large, active predators use the spots of bare ground as a peculiar hunting biotope. Under conditions of sufficiently high temperature, it is possible to catch a significant quantity of them on the spots, then, while when their activity is lowered they concentrate mainly in the mossy turf on the ridges.

We calculated the inhabitants of the grassy layer with the help of a harvesting net (Table 5), in connection with which we did not arrange data according to numbers per unit area. In all, the density of the inhabitance of the grassy layer in all variations of mossy tundra, including the spot-medallion tundra, is extremely low. We note that in the harvest on neighboring herb-grass neighboring portions of slopes of the local riverbank the total biomass of invertebrates in 25 sweeps of the net at the end of July consists of an average of 2000 mg, while in the spot-medallion tundra, not more than 200 mg. All the same, in the spot-medallion tundra it is approximately twice as high as in tundras with a compact moss cover, which, evidently, is conditioned by the great variegation of the vegetational cover and nanorelief. Approximately ⅓ of the biomass consists of the sawfly larvae. Likewise, the collembola *Sminthurus* and *Entomobrya* are extremely characteristic, connected with the portion of the vegetational cover above the moss. Sometimes in the harvest various hemiedaphic species of isotomids are captured in a significant quantity; these on warm nights in dry weather migrate actively upwards from the mossy cover. Occasionally one encounters the largest of tundra collembola, *Morulina ghilarovi* Soln., which is likewise characteristic of the mossy tundra (it is found in great quantity on the fruiting bodies of the brown boletus). From the Acarina, the predatory Tideidae and Bdellidae are collected in a great quantity. The first is generally characteristic for the spot-medallion tundra and is rarely encountered in other habitats, the second is abundant in willow thickets as well. In periods of prolonged dry weather, at night, especially when there is dew, the Oribatei rise up to the grassy vegetation in a significant quantity. As a whole the diurnal vertical migration of invertebrates in the spot-medallion tundra is as fully displayed although not as regularly so, as in herb aggregations on the slopes of the local river bank and in more southerly regions (Chernov and Rudenskaya, 1970).

Table 5. Amount of insects (indiv./25 passes) harvested by a handnet in medallion tundra on 18 July 1968.

Animal groups	*1 AM Cloudy, mild dew 19°*	*1 PM Clear, dry 26°*	*Animal groups*	*1 AM Cloudy, mild dew 19°*	*1 PM Clear, dry 26°*
Acarinae	165	26	Butterflv (cater pillar)	1	2
Tideidae	100	18	Sawfly (larvae)	21	7
Bdellidae	29	8	Ichneumon fly	5	13
Oribatei	36	—	Diptera	113	36
Collembolae	94	23	*Tipulidae*	—	1
Entomobryidae	24	—	*Chironomidae*	100	20
Isotomidae	20	—	*Itoniidae*	8	6
Sminturidae	50	23	*Empididae*	2	3
Tripsae	116	19	*Syrphidae*	—	3
Leafminer (larvae)	8	—	*Muscidae*	3	3

Thus, the main feature of the aggregations of invertebrates of bare ground spots is the relatively high abundance of typical soil forms, which is inhibited by greater overgrowth of the spot and by worsening of the temperature conditions in the mineral soil as a consequence of the insulating effect of the mossy cover. The usual concentration of animals (according to indices of biomass, total metabolism) is greatest in spots of bare soil due to the abundance of primary pedobionts Annelida and Nematoda. The largest magnitude of the biomass of Enchytraeidae appears in Stage I of succession, of Nematoda in Stage II, of Earthworms in Stage III. The total zoomass is maximal in the beginning stages. The number of individuals and the biomass of Collembola are maximal on the ridge; however, the calculation of the possible magnitude of oxygen-consumption gives the highest figures for the spots of Stages II and III of succession. In this is displayed one of the contradictory successional relationships, which, by the way, is characteristic not only for tundra communities. Materials which we have at our disposition lead us to calculate that in various communities, especially under hydrothermal regimes which are far from the optimal ones, the intermediate links of the successional series appear to be the most varied, dynamic, and productive, while the final stages (including the ones corresponding to the climax state) are characterized by a more stable and less varied composition, and are less productive. The reasons for such relationships are summed up by the fact that as the bare ground is overgrown and as the fragmentary and variegated vegetational cover is replaced with a continuous moss cover, the microclimatic conditions and the composition of the plant and animal populations become more stabilized, the community acquires more of the features of autonomy, closeness, and stability. The dynamic processes slow down, as is made apparent also by the conservation of permafrost as a consequence of the high insulation properties of the mossy turf, by more stable, but clearly less favorable temperature conditions, by the lessening of the thickness of the active layer (Tikhomirov, 1957; Chernov, 1965, 1966; Matveyeva, 1968; and others). As a result the development of the live cover slows down and for a number of components of the community (specialized soil-dwellers) the conditions become less favorable. The animal population, being immeasurably more labile than the vegetational cover, reacts much more quickly and sharply to changes in the environment, as a result of which also appear inverse correlations between the abundance of vegetational components and the animal population, to which we devoted our attention earlier (Chernov, 1965). The animal population, especially the complex of typical pedobionts, which is most abundant on the middle stages of spot-medallion succession (Earthworms, enchytraeids, nematodes, tipulid larvae), undoubtedly plays a substantial role in spot-medallion evolution in the soil-forming process. As the spot becomes overgrown the role of animals lessens. The change in total metabolism reflects this in particular.

The materials set forth show that the structure of the microaggregations of the animal populations of the spot-medallion tundra (including the spots in the successive stages, the ridges, the troughs, which develop in the place of frost cracks clearly corresponds to the features of the vegetational cover. Taking this into consideration, it is fitting to notice the substantial similarity of the structure of the plant cover and of the animal population of the corresponding microaggregations. Thus, the greatest specificity of composition and of quantitative relations of species is observed in spot-medallions of the first stage of succession: the most varied ecological composition of the invertebrate aggregations is on the spots of the second stage of succession, which also corresponds with the greatest variegation of the plant cover. On the last stages of succession, with the development of a continuous mossy turf, the microaggregation acquires the typical features of the tundra zonal communities, which is expressed in the greatest similarity of the species composition and numerical relations of the aggregations of the spots of Stage III and the ridges.

Evidently, a single direction is common to the different paths and tempos of succession of the separate fragments of the spot-medallion tundra, and one may consider the formation of a continuous mossy cover as the common goal. In this region another type of watershed tundra appears as the concluding stage; the hummocky sedge-moss tundra (Matveyeva, 1968). One may project analogues of comparison between the intermediary and final stages of microsuccession in the spot-medallion tundra and the stages of formation of the climax type of tundra in the place of a predecessor. On the whole, one may consider the spot-medallion tundra as a phase of a single successional process, preceding a final climax stage. According to the data of N.V. Matveyeva (1968) the latter is almost twice as poor as the spot-medallion in a floristic sense; the animal population of this tundra, according to our material, which will be published in one of the following collections, is likewise poorer in species composition and less ecologically varied.

Above we looked at the type of tundra under investigation from the point of view of the dynamics of successional relations. Another aspect is the typology of the aggregations, composing a given type of community. When analyzing the structure of the vegetational cover and the animal population one must take into account the complex of indices. In so doing, one can scarcely be correct in attributing a decisive significance to the species relations (degree of species similarity, the set of species dominants, and so forth). As structural characteristics these indices, especially the degree of floristic and faunal similarity, at times appear extremely nominal. In terms of quantitative characteristics of the leading groups of animals, the series of microaggregations of the spot-medallion tundra and of other types of mossy tundra are quite close (with the exception of several characteristic forms), however, in our opinion, this can scarcely be a basis for the negation of the principal differences in their structure (character of layering, horizontal grouping, total indices of abundance, variation, relations of life forms, and others). In this connection, the hypothesis of N. V. Matveyeva (1968) that one may consider the spot-medallion and the hummocky tundra of this region as variants of a single association on the basis of the similarity of the species dominants appears formal to us. The complex character of the microbiotopical structure of the animal population of the spot-medallion tundra appears as the result of a single successional process; however, on a solely typological scheme (though the association is a typological concept) the community under study presents a motley collection of groups of various types of aggregations, exhibiting features of similarity with formations which are on the opposite ends of a single tundra zone successional series. Thus one may view spot-medallions in the early stages of succession as analogues of fragmentary communities of the subzone of the arctic tundras, polar wastes and high mountains, which can be combined into a single community cycle. The microaggregations on the tops of the ridges are similar to the dwarf shrub communities on the tops of slopes. For example, the degree of similarity of the *Dryas* aggregation with the ridge appeared almost the same, as that with the dwarf shrub-herb aggregation. One must note, that to a greater extent this similarity is expressed in some other spot-medallion tundras we have studied, for example in the Agapa basin. Other fragments of spot-medallion tundra, among them spots in the last stages of succession, the outer slopes of the ridges, and the troughs have the typical features of the zonal mossy tundra. This approach, undoubtedly, does not contradict the analysis of the spot-medallion tundra as a single community of a defined type, but only supplements it. In our opinion, one may hardly adopt a single line of classification of tundra communities; the genetic and the typological lines one may view as supplementary to each other in some way (to a lesser extent), as complementary, but not analogous on the whole.

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INTERNATIONAL TUNDRA BIOME TRANSLATION 12, Part 2

Title: A Review of the Trophic Groups of Invertebrates in Typical Tundra Subzone of Western Taimyr

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A REVIEW OF THE TROPHIC GROUPS OF INVERTEBRATES IN TYPICAL TUNDRA SUBZONE OF WESTERN TAIMYR

Along with special research on the quantitative structure of the animal population and of separate systematic groups and cenotic links in the area of the station, we continually made collections of various invertebrates, carried on ecological observations and performed some laboratory experiments, in particular on food chains, and likewise on the breeding of the preimago phases up to the adult insect. All these materials give us some idea of the composition and cenotic role of the main trophic groups of invertebrates (see Table).

For systematic analysis of the material specialists in various invertebrate groups extended their cooperation to us: E.M. Antonova (diurnal butterflies), A.F. Emel'janov (Cicadas), A.N. Zhelokhovtsev (sawflies), I.M. Kerzhner (water bugs), D.A. Krivolutskyi (Oribatei), V.I. Kuznetsov (butterfly moths), N.N. Kuznetsov (various groups of Acarina), M.M. Loginova (Psyllidae), B.M. Mamaev (Cecidomyiidae), L.N. Medvedev (Chrysomelidae), E.N. Savchenko (Tipulidae), M.E. Ter-Minasyan (beetles-weevils), V.P. Tyshchenko (spiders), and E.V. Tsvetaev (various groups of Lepidoptera), to whom we express our sincere gratitude.

As in the whole territory of the humid belt, the invertebrates connected with dead plant remains (the saprophilic complex in a wide sense) are most important in terms of general energetic potential in the animal population of tundra communities. The main body of this complex is the saprophages, that is the indirect consumers of the dead organic substance. It follows, however, to take it into account that the concept of a "saprophage" is extremely inexact. In particular, it is demonstrated that a significant or a main portion of the digested food of many saprophages consists of live bacteria, fungi and other microorganisms. All the groups of surface Oligochaeta may be enumerated among the saprophages in one way or another – Lumbricidae (in Siberian tundras only *Eisenia nordenskjöldi* Eis.), and also Enchytraeidae, which are represented in the subarctic by a great number of species and considered to be among the most important dominants of soil fauna. The systematics of the polar enchytraeid forms is poorly investigated, and an exact determination of the species of this group at the present time is practically impossible. The faunal diversity of this family in the tundra zone, and in particular in the Taimyr, is quite large (Cejka, 1910, 1912, 1914). They represent a rich series from the typical mesophyllic colorless forms living in the heavy silts and drier sandy soils on heated slopes, to the large heavily pigmented hydrophilic forms. Moreover, the large and dark-colored *Lumbriculus variegatus* Müller (*Lumbriculidae*), distributed through the whole Palearctic, are numerous in places in the polygon swamps in the Taimyr. The nutrition of surface oligochaetes at high latitudes is practically uninvestigated. *E. nordenskjöldi*, evidently, may be classed among the typical saprophages. The consumption of dead plant remains, probably, plays a basic role in the nutrition of soil enchytraeids. Concerning the hydrophilic oligochaetes, they may be considered saprophages only very conditionally.

The larvae of the *Tipulidae* appear as a major component of the saprophilic complex of invertebrates of the tundra zone. Their cenotic role in the subarctic, perhaps, is greater than in all other zones. The significance of tipulid larvae as activators of microfloral activity in polar conditions was demonstrated by I.V. Stebaev (1958). In the area of the station are found more than 10 species of tipulids. Of them the most numerous are *Tipula carinifrons* Holm., *T. arctica* Curt., *T. middendorfii* Lack. Their larvae are particularly numerous on herb and dwarf shrub slopes in places where

Systematic composition of the trophic groups of invertebrates in the typical tundra subzone of Taimyr

	Saprophages	*Caprophages*	*Necrophages*	*Microphytophages*	*Rhizophages*	*Phyllophages*	*Antophiles and Antophages*	*Caprophages*	*Carnivores*	*Animal parasites*
Nematoda	+++*	?	?	+++	+++	–	–	–	++	++
Annelida	+++	–	–	–	–	–	–	–	–	–
Araneida	–	–	–	–	–	+	–	–	+++	–
Acarina	++	+	–	++	–	–	–	–	++	++
Myriopoda	–	–	–	–	–	–	–	–	+	–
Collembola	+++*	+?	–	+++	?	++	+	–	–	–
Jugatae	–	–	–	–	+	++	+	–	–	–
Hemiptera	–	–	–	–	–	+	–	–	++	–
Coleoptera	++	+	++	–	++	++	++	+	+++	–
Lepidoptera	–	–	–	–	++	++	++	++	–	–
Hymenoptera	–	–	–	–	–	+++	+++	++	–	+++
Diptera	+++	++	+++	?	++	+	+++	+++	++	++

Note: +++ - great species diversity and great abundance in the various biotopes.
++ - relatively small number of species with a noticeable cenotic role.
+ - isolated species with an insubstantial cenotic role.
Asterisks indicate the animal groups which are related to a given complex conditionally.

there is an accumulation of willow leaf-fall in the hollows between permafrost mounds. In some places their excrement covers the ground in a rich layer. These species, probably, may be considerd typical saprophages. Several Tipulid species of the arctic fauna eat plant roots.

A characteristic feature of the animal population of the tundra zone in comparison with the more southern zones is the low abundance of saprophilic groups of *Acarina*. Thus, the *Tyroglyphoidea*, which attain particularly high numbers in the broad-leaved forests, are found in the area around Tareya only in small quantities in the turfy-meadow soils on slopes. The numbers of *Oribatei* in the mossy tundras are ten times lower than in forests. Only on the warmest slopes with sandy soils do they attain a hundred individuals per 1 dm^2. (For details see the article S.I. Anan'eva, D.A. Krivolutskii, IU.I. Chernov in this collection.) The reason for the low numbers and poor species diversity of *Oribatei* in the tundras is their thermophily and the long duration of their life cycle. One must take it into consideration that the nutritional links of the *Oribatei* are extremely varied. Besides saprophages, among them are many myco- and algotrophic forms. Animals with this type of nutrition belong to the combined group of microphytophages (sometimes they are isolated as a separate group of mycophages).

Many *Collembola*, which predominate in the tundra complex of microarthropods, belong to the microphytophage group. Moreover they, without doubt, play a definite role in the process of decomposition of senescent plant remains by mechanical and fermentative activity and by means of activation of the microflora. Their role is particularly important in the initial stages of bare-ground succession, in various zoogenic aggregations. A saprophilic characteristic is peculiar to the majority of *Collembola* found in the investigated region. Evidence for this is found in the concentration of many species, both soil and hemiedaphic, in the accumulations of plant litter, in the damaged roots, in the "lemmings' hay" and so forth (for details see the article of S.I. Anan'eva in this collection).

The nematodes, of which L.L. Kuzmin found 162 species in the station's territory, are extremely diverse in their trophic relationships. The saprophilic nature of the nematodes is widely known, however the level of the saprophages within this group is not clear at this time. Thus, in one of the recent ecological classifications (Banage, 1963) the nematodes were subdivided into the phytophages, microbophages, polytrophic, and predatory. The concept "saprophage" is lacking in this classification. Probably, saprophagia is most characteristic of microbophages, the majority of which gravitate toward conditions where there are intensive processes of decomposition.

Extremely significant is the peculiarity of the tundra saprophilic complexes that there is little development of groups of coprophages, which, evidently, is connected with the features of the dung of tundra mammals, which is little appropriate for colonization by coprobionts. Specialized coprophages are practically lacking in the arctic fauna proper. Several widespread coprophages enter only into the southern tundras. Thus, in the forest tundra in the Taimyr the beetle *Sphodias* and the flies *Mesembrina* are found. In the area around Agapa *Paregle cinerella* Fll., which is not found in Tareya, is numerous. *Diptera* are relatively diverse and widespread; by the intermediate type of food of the larvae, they are copronecrophages, and likewise copro- and necrobionts.[1] To the former belongs *Neoleria prominens* Beck (*Helomyzidae*), one of the largest synantrophic species of flies in the whole tundra region. In places several species of *Sepsidae* and *Piophilidae* are also abundant (Chernov, 1965). Many species of *Scatophagidae* are connected with various rotting materials of animal origin. In the area around Tareya *Scatophaga cordylurina* Holm. is common, which swarms on reindeer carcasses, and likewise *S. multisetosa* Holm., *S. apicalis* Curtis, *S. varipes* Holmgr., *S. obscurinervis* Beck., and *S. suilla* F. Into the southern tundra also enter a series of widespread synantrophic copro-necrophages: *Calliphora uralensis* Vill., *Piophila vulgaris* Fll., and others (Chernov, 1965). In the Taimyr they are extremely common in settlements up to the southern part of the subzone of typical tundra (for example, in Agapa), however in Tareya they are found in a small number.

The typical necrophages reach a high abundance and relative systematic diversity in the tundra zone; of these especially characteristic are the typical arctic, arctic-alpine or boreal-arctic species of blue meat flies (*Calliphoridae*): *Boreellus atriceps* Zett., *Acrophaga alpina* Zett., *Lucilia fuscipalpis* Sett., *Abonesia genarum* Zett. *Boreellus atriceps* is particularly interesting; its numbers are subject to fluctuations which are synchronous with cycles of mass reproduction and subsequent decline of lemmings. In the years of their decline, all the carcasses are totally inhabited by the larvae of these flies. In the investigated region this is the most common necrophage. The widely distributed (trans-holarctic) necrobionts *Protophormia terraenovae* R-D. and *Cynomya mortuorum* L., common in the southern tundras, are not numerous in the territory of the station. They most frequently colonize the carcasses of large animals and accumulations of meat refuse. Of the necrobiont beetles in the whole tundra zone only one species of carrion beetle is found, *Thanatophilus lapponicus* F. In our region it is very closely connected with settlements and is rarely found away from them in the tundras.

In biocenological research the analysis of the ties of phytophagous animals with higher plants occupies the central place. Among the insects which eat plants the complex of rhizophages has a particular niche; a rise in their numbers serves as an indicator of aridization (Gilyarov, 1964; Chernov et al., 1967). In the tundra zone this complex is quite impoverished. Larvae of *Coleoptera-Elateridae* are found only up to the southern borders of the subzone of typical tundras. In the Taimyr in the region around Agapa *Hypnoidus* is still common on the herb-dwarf shrub slopes, but in the territory of the Taimyr station they are absent. Likewise sawfly larvae are not encountered in the investigated region. Of the root-eating *Coleoptera* the weevils reach farthest into the north, of these *Lepyrus* is particularly characteristic (Fig. 1). On herb-willow portions of the Pyasina riverbank the numbers of their larvae reaches 30 specimens/m^2. Probably, they eat basically willow roots. Several Taimyr specimens of *Lepyrus* are close to *Lepyrus arcticus* Payk., others do not have characteristics of described species. Evidently, the arctic fauna of this genus needs a special revision. Larvae of *Lepyrus* are the only large rhizophages found in zonal tundras (Chernov et al., 1971).

In mossy tundras rhizophages are very scarce. Here one may find on plant roots mainly small representatives of *Nematocera* —— *Sciaridae (Lycoriidae)* and *Cecidomyiidae*. The larvae of several *Tipulidae* are also inclined to the rhizophagy; for example, according to our observations, one of

[1] A copro- or necrophage, is a species nourishing itself on dung or carcasses; copro- or necrobiont, a species living in dung or on carcasses.

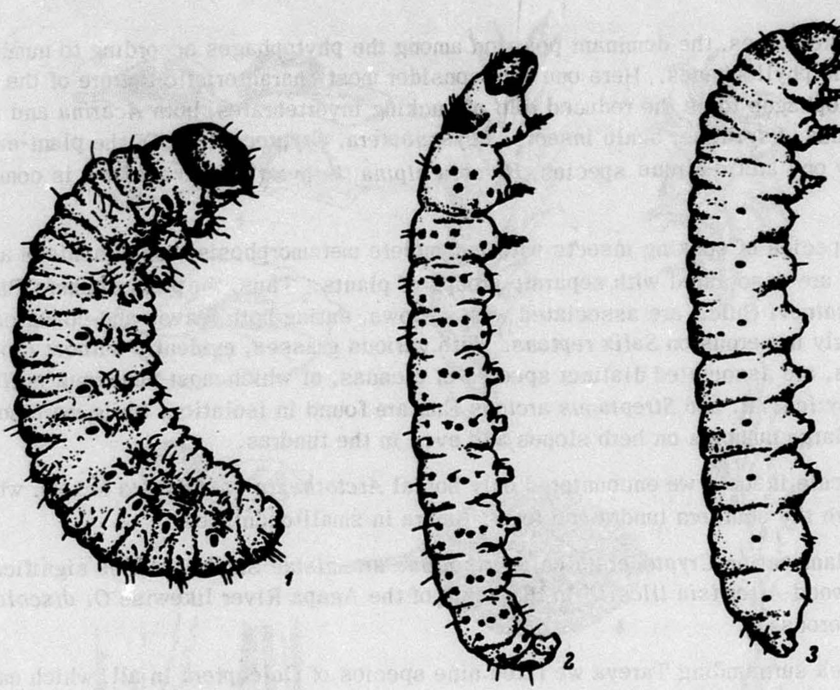

Figure 1. Several representatives of rhizophages of Western Taimyr. 1 – larvae of the weevil Lepyrus sp.; *2 – caterpillar of moth* Olethreutes inquetana; *3 – caterpillar of moth* Epiblema guentheri *Fgstr.*

the smallest species of arctic *Tipulidae*, *Tipula lionota* Holm. The richest fauna of rhizophages is on the well-warmed herb slopes. In these conditions the rhizophages affect the plants with large fleshy roots most intensively, in particular *Pedicularis*, *Compositae*, some *Ranunculaeae* (particularly *Delphinium middendorffi*). However, on the series of plants having large fleshy rhizomes (*Rumex*), rhizophages are not noted. The roots of legumes are little harmed; on these we only rarely noticed *Sitona* larvae. Evidently, the given region is one of the extreme northern points of distribution of this genus.

On the roots of the lousewort *Pedicularis verticillata* and *P. dasyantha*, connected with relatively dry and well warmed portions, the common orange larvae *Bradysia* sp. (*Sciaridae*). To this genus belongs a series of active phytophages, for example the cucumber midge, but all the same it is difficult to say how much the given species is the foremost root injurer, since these larvae are mainly found on roots affected with caterpillars of moths. We separated from the roots of the wormwood *Artemisia tilesii* the midges of the genus *Rhopalomyia*, species of which are generally closely linked with *Compositae*, but mainly with the aboveground parts.

The relatively large larvae of *Tortricidae* appeared to be characteristic and quite common rhizophages in the subzone of typical tundras of the Taimyr; we noted two species of these. On the roots of *Artemisia tilesii*, forming a growth on eroded slopes, caterpillars *Epiblema guentheri* Fgstr. (Fig. 1) are found in great numbers. They reach a size of 23 mm, are whitish-pink, they pupate in a loose gossamer cocoon. In places they affect all the *A. tilesii* plants.

The caterpillars *Olethreutes inquetana* Wilkr., representatives of an arctic-alpine genus (Fig. 1), are found everywhere on the roots of the lousewort *Pedicularis oederi*. These same caterpillars are also found on the roots of *P. dasyantha*, but we could not raise their imago. The development of the caterpillars of *O. inquetana* is interrupted by a long diapause, therefore, laboratory raising is extremely difficult. Out of several tens of collected caterpillars we were able to obtain only two butterflies. These are less specialized rhizophages than *Epiblema guentheri*. They are more mobile and pigmented.

As in other zones, the dominant position among the phytophages according to number of forms belongs to the phyllophages. Here one may consider most characteristic feature of the tundra complex of phyllophages to be the reduced role of sucking invertebrates, both *Acarina* and insects -- aphids, cicadas, *Psyllidae*, scale insects, *Thysanoptera*, *Cryptocerata*. Of the plant-eating *Acarina* only one arctic-alpine species, *Bryobia alpina* Mathys (*Tetranychidae*), is common everywhere.

Single species of sucking insects with incomplete metamorphosis, which achieve a relatively high number, are associated with separate groups of plants. Thus, the plant suckers *Psylla palmeni* Löw and *P. zaicevi* Culc., are associated with willows, eating both leaves and young catkins. They are particularly numerous on *Salix reptans*. With various grasses, evidently without close species relationships, are associated distinct species of cicadas, of which most numerous is *Hardya jongi* Bair; *H. taimyrica* Vil. and *Streptanus arctous* Em. are found in isolation, while more southerly they are found in large numbers on herb slopes and even in the tundras.

Of the scale insects we encountered only boreal *Arctothezia cataphrasta* Schaw. which is widespread through the southern tundra and forest tundra in small quantities.

Of the plant-eating *Cryptocerata* only *Orthotylus artemisiae* Sahlb. reaches significant numbers on the wormwood *Artemisia tilesii*. In the basin of the Agapa River likewise *O. discolor* Sahlb. becomes numerous.

In the area surrounding Tareya we fixed nine species of *Coleoptera* in all, which may be classified as phyllophages. There are six species of *Chrysomelidae*: *Chrysomela (Melasoma) taimyrensis* L. Medv., *Chrysolina (Chrysomela) septentrionalis* Men., *Ch. tolli* Jac., *Ch. marginata* L., *Phrathara (Phyllodecta) polaris* Schneid., *Hydrothassa hannoverana* F., one species of beetle (imago) -- *Amara alpina* F., weevils *Sitona* sp. and *Phytonomus ornatus* Cap., *Ph. ornatus* and *Hydrothassa hannoverana* may be considered phyllophages highly indirectly, since they are closely linked with flowers and fruits of *Leguminosae* and *Ranunculaceae* respectively. Of the leaf beetles the most common is *C. septentrionalis*. Its numbers are particularly high on herb-grass portions. This is the typical polyphage, however in laboratory culture the larvae consumed the leaves of only a small number of species of herbs growing in their typical habitat. They developed best on the composite *Arnica iljinii* and *Ranunculaceae Delphinium middendorffii*, and *Ranunculus* sp. In natural conditions we found larvae mainly on *Arnica* and *Delphinium*, but the imago, on *Myosotis asiatica*, *Pedicularis verticillata*, *Delphinium middendorffii*. The life cycle of this species, probably, is many-yeared, the larvae grew very slowly, and over-winter at various growth stages.

Chrysomela taimyrensis (Medvedev, Chernov, 1969), recently described from the Taimyr, presents a case of great interest; it is connected mainly with *Salix arctica*. In the cited work we called it a typical monophage, which has turned out to be not completely correct. Subsequently, we found the larvae likewise on *S. reptans*. In laboratory culture the larvae *Ch. taimyrensis* ate all the species of local willows. Only on one of them (*S. nummularia*) with the coarsest and smallest leaves the development was not complete and the larvae died. On the rest (*S. reptans*, *S. pulchra*, *S. polaris*, *S. lanata*), the larvae completed their development and became phenotypically normal beetles. Thus, this is not an obligatory, but a facultative monophage, which, evidently, is connected with some biochemical or anatomical features of the leaves of *S. arctica*. The population of this leaf beetle is so high, that in places they ate up 30-50% of the leaves. When agitated the larvae are distinguished by drops of whitish fluid with a specific sharp odor on the sides of the body.

The larvae of the *Tenthredinidae* is the most important component of the phyllophages of the tundra zone. In mossy tundras they represent about 50% of the usual mass of the grassy inhabitants, in herb portions about 25%. By number of species and individuals the sawfly subfamily *Nematinae*, associated with willows, dominates in the tundra zone. Of the open-living larvae the most numerous in the tundras are species of the genus *Amauronematus* Knw. Almost all species

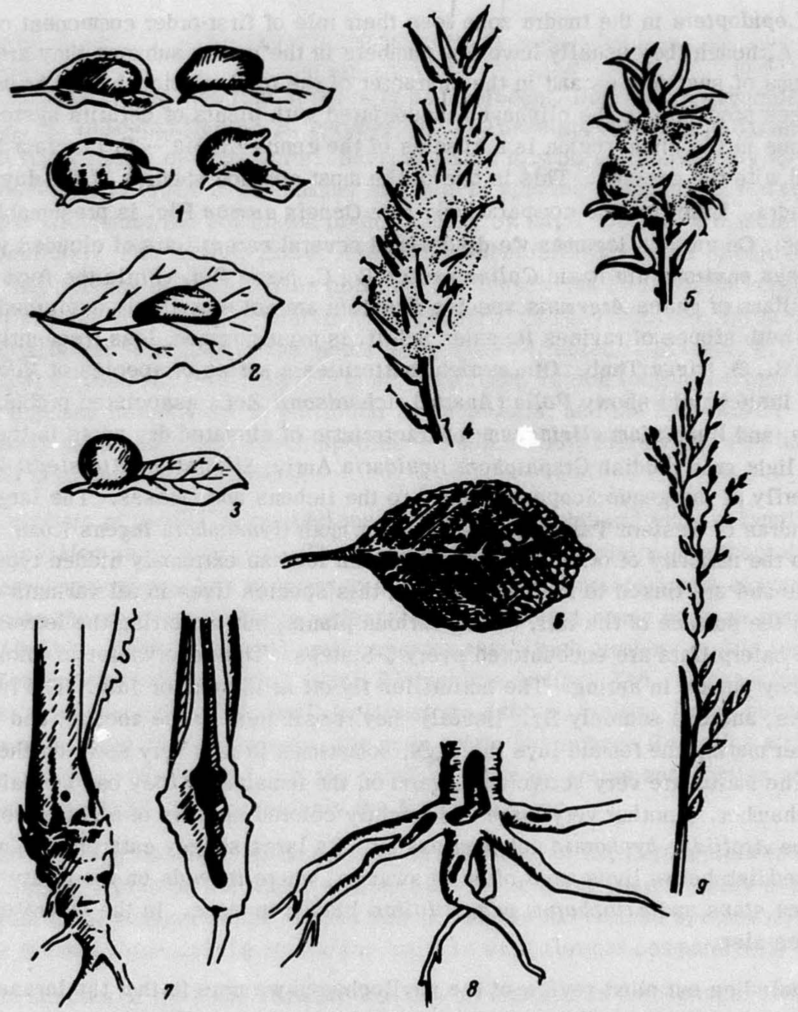

Figure 2. Several examples of characteristic plant damage by insects.

1-3 *Galls of the sawfly* Pontania crassipes *Thomson on willows (1 –* Salix reptans*; 2 –* S. arctica*; 3 –* S. pulchra*)*

4 S. arctica *catkin injured by the larvae of the sawfly* Pontopristia borealpina*; from the bases of ovaries, which are gnawed through, emerges fuzz, forming a dense tampon.*

5 Salix reptans *catkin damaged by the sawfly* Pontopristia sp.

6 Salix arctica *leaf, eaten by the larva* Chrysomela taimyrensis.

7 *Damage of the root collar of* Pedicularis oederi *by larvae of the flies of the family Muscidae.*

8 Pedicularis dasyantha *root damaged by the caterpillars* Olethreutes inquetana.

9 Poa arctica *panicle, damaged by the ground beetle* Amara alpina.

of tundra willows, both shrubs and dwarf shrubs, are greatly damaged by the gall-forming sawflies (Fig. 2). In the area around Tareya and on the shore of the Taimyr Lake we separated sawflies from galls on *Salix reptans*, *S. polaris*, *S. arctica*, and *S. lanata*. All the sawflies removed belonged to one species, according to the determination of A.N. Zhelokhovtseva -- *Nematus (Pontania) crassipes* (Thomson). This is a holarctic species, connected to a large number of species of willows. In Finland it was noticed on *S. herbacea*, *S. polaris* (Vikberg, 1970), in Northern Slovakia on *S. herbacea* (Venev, 1967). In the Taimyr they colonize *S. reptans* particularly intensively.

The *Lepidoptera* in the tundra zone lose their role of first-order component of the phyllophage complex. Although they usually have low numbers in the tundra subzone they are extremely varied both in terms of systematics and in the character of the food relationships. Among the caterpillar-phyllophages predominate the oliphages, associated with plants of definite systematic groups. Thus, unique in the given region is a species of the genus *Erebia* -- *E. fasciata* Butl., evidently associated with the grasses. This is one of the most common species of the day butterflies in the Taimyr tundra. Likewise the comparatively rare *Oeneis ammon* Elv. is presumably connected with the grasses. On various legumes we discovered several caterpillars of clouded yellows, of which in the Tareya environs are found *Colias nastes* B., *C. hecla* Zef. While the food relationships of the caterpillars of genus *Argymnis* species *Brenthis* are not completely explained, on the river-banks and herb slopes of ravines *B. pales* Schiff. is most common, less frequently encountered are *B. polaris* B., B. *frigga* Thnb. Of the night butterflies a series of species of *Noctuidae* are common -- the large bright showy *Polia (Anarta) richardsonii* Zef., associated probably with *vaccinium vitis idaea*, and *Vaccinium uliginosum*; characteristic of elevated dry spots is the thickly covered with hair, light gray reddish *Graphiphora liquidaria* Auriv; *Simpistis zetterstedti* Zef. and others; the large butterfly of the genus *Scoparia*, linked to the lichens and mosses. The largest butterfly in typical tundras of Western Taimyr is the vapourer moth *Gynaephora lugens* Kozh. (*Orgyidae*). In contrast to the majority of other caterpillars, which lead an extremely hidden type of life in the tundra zone and are linked to local conditions, this species lives in all variants of mossy tundras, directly on the surface of the turf, eating various plants, but preferring the leaves of birch. In places the caterpillars are encountered every 5-8 steps. They overwinter in thick wooly cocoons, in which they pupate in spring. The butterflies fly off at the end of July. The females are large and massive, and can scarcely fly. Usually they remain next to the cocoon, and the males fly there. After mating the female lays the eggs, sometimes in this very spot, on the surface of the cocoon. The males are very active and swarm on the females, if they can be maintained in the breeding chamber. Another very large and brightly colored species of night butterfly in the local fauna is the *Arctiidae hyphoraia subnebulosa* Dr. Its large shaggy caterpillar, dark-brown above and light reddish below lives most often in swamps, where it feeds on the meaty portions of the sedge *Carex stans* and *Eriophorum angustifolium* hidden in moss. In the laboratory it readily ate birch leaves also.

In concluding our short review of the phyllophages we note further the larvae of the fly *Omphalophora grandis* Frey (*Rhagionidae*) which feed on the thallus *Marchantia polymorpha*, covering the rubbish in settlements. The larvae are of a very characteristic bright green color.

On the whole the complex of phyllophages of the given region of the subzone of typical tundras is very impoverished, even in comparison with the nearby, more southerly regions of the same subzone (Agapa Basin). It is significant that the most common phyllophages are connected with shrubs and dwarf shrubs, in particular with willows and birch. Only in distinct local conditions, in particular on the herb slopes, the cenotic role of the herbivores may be substantial. Moreover, the qualitative variation of the phyllophages is quite great, and their study may give much interesting material for the understanding of the peculiarities of biocenotic relations in extreme subarctic conditions.

The subarctic complex of anthophiles and anthophages is extremely varied. Under the former are classed the forms tied symbiotically to the flowers (potential pollinators, attracted by the abundance of pollen and nectar). The latter are comprised of the species which feed directly on the flowers (flower buds, petals, stamens, and so forth), and do not play a role in pollenization. With the exception of several intermediate forms these groups differ very sharply. Among them one may distinguish conditionally a group of anthobionts -- species which stay in the flower for a prolonged time, using it as a microhabitat. At the station we carried out detailed research over the course of many years on the pollinating activity of the anthophiles. The results will be reported in a separate article; here we touch only briefly upon several features of the composition of the anthophilic complex.

In the investigated region live four species of bumble-bees: *Bombus hyperboreus* Schon., *B. lapponicus* P., *B. balteatus* Dahlb., *B. pyropygus* Fr. These are the main pollinators of all the legumes and the majority of louseworts. Several plants may be pollinated only by bumble-bees. Among these is one of the most common and largest species of legume in the region of the station, *Oxytropis middendorffii*, pollinated predominantly by large species of bumble-bees (except for *B. lapponicus*). The smaller flower *Astragalus subpolaris* is visited intensively by *B. lapponicus*. All species of bumble-bees pollinate the louseworts *Pedicularis verticillata*, *P. oederi*, *P. sudetica*, and likewise *Delphinium middendorffii*. Of the flies only few are linked with these plants: The larger *Surphidae* of the genus *Helophilus (H. borealis* Staeger, *H. groenlandicus* O. Fabr.) and *Conosyrphus (C. tolli* Frey). These large flies, having long and strong beaks, visit the short-tubed legumes intensively, in particular *A. subpolaris*, and the louseworts. *C. tolli* is particularly closely associated with marsh species -- *Pedicularis sudetica* and *P. hirsuta*. The larvae of *C. tolli* also develop in marshes.

Among the visitors of nearby entomophilous herb areas predominate four fly families: *Syrphidae*, *Muscidae*, *Anthomyiidae* and *Empididae*. The fauna of the most specialized anthophilic fly, the *Syrphidae*, is very impoverished. In contrast to somewhat more southern bands of tundra, in the investigated region the species which are widespread in the forest zones have an insignificant role (Chernov, 1966b). Only the typical arctic species reach high numbers in this region: *Syrphys tarsatus* Zett., *Melanostoma dubium* Zett., *Platychirus hirtipes* Kan. Of them for the zonal tundras the most characteristic is the small *Melanostoma dubium*, visiting *Dryas punctata* flowers. In years of general decline of the lemmings, the main arctic necrophage *Boreellus atriceps* appears in great numbers on the flowers. Of the sawflies the most active anthophiles are the large *Tenthredo*, which especially visit intensively the *Ranunculaceae*.

We have earlier noted the low trophic activity of the imago of the *Lepidoptera* in the tundra zone (Chernov, 1966b). This on the whole applies also to the given region. Only in certain years with long constant clear weather in the second half of July do the various species of day butterfly, at least the *Geometriidae* and the *Noctuidae* begin to visit flowers comparatively intensively.

Only unique species of the local entomofauna can be classed as anthophages, which consume all flower parts. The most typical representative of this group is the widespread leafeater *Hydrothassa hannoveranna*, closely linked to the *Ranunculaceae*, in particular to marsh marigold, on which it is encountered in the tundra zone as well. However, in the Taimyr it is more common on *Ranunculus borealis*. Its larvae consume the petals, stamens, and ovaries. The weevil *Phytonemus ornatus* Cap. likewise belongs to the oligotrophic anthophages. Its larvae develop on the flowering stalks of legumes, mainly *Oxytropis adamsiana* and *Astragalus subpolaris*. Caterpillar-like larvae of this species consume the corrollas when they are still in the bud state. In places they damage up to 20% of the flowers of *Oxytropis adamsiana*. The larvae pupate at the end of summer, in the period of fruit maturation, in a durable semi-transparent cocoon. Likewise small orange larvae of *Cecidomyiidae* (probably *Dasyneura*) are associated with legume flowers. They colonize in particularly large quantity the corollae of *Astragalus umbellatus*. In some years almost all the flowers of the plants of this species are harmed.

The rather common polytrophic anthophages in the researched region -- the beetle *Amara alpina* F. -- is a typical euarct (euarctic species), widespread in the whole tundra zone. The larvae of this species probably belong to the facultative predators with a tendency towards being saprophages. The adult beetles show high activity as phytophages. At night, when there is a reduction in the light and sufficiently high temperatures (not lower than 8°C) they rise in mass into various plants and consume the upper flower-bearing shoots, the buds, the young leaves, the flowers, and the young fruit. They feed particularly intensively on the panicles of *Poa arctica*, which are up to 70% damaged in some places. Often on one panicle one may see simultaneously quite a few beetles. They likewise readily eat the stamens of another arctic grass, *Alopecurus alpinus*; they are encountered on the inflorescences of the only umbelliferous plant at these

Figure 3. Several of the most common representatives of the complex of antophiles and antophages in the area around Tareya.

1. *Fly of the family* Muscidae *on a* Dryas punctata *flower.*
2. *Fly of the family* Empididae *on a* Dryas punctata *flower.*
3. *Male* Aedes, *drinking nectar on a* Ranunculus *sp.*
4. *Beetle* Hydrothassa hannoverana, *eating the corolla of* Ranunculus borealis, *the eaten away portions of the petals are evident.*

5, 6. *Beetle* Amara alpina *on* Myosotis asiatica *and* Potentilla *sp. flowers.*

latitudes, *Pachyplurum alpinum*, and on *Myosotis asiatica, Saxifraga punctata, S. cernua, Pedicularis verticillata*, and so forth. In all we have noted more than 20 species of plants whose inflorescences were consumed by the beetle *Amara alpina* (Fig. 2, 3).

Thus, the complex of insects connected with the flowers in the subzone of the typical Taimyr tundras is relatively varied in terms of food specialization and types of relationships with the plants. Evidently, the anthophilic fauna in the tundra zone is impoverished in comparison with the forest zone significantly less than complexes such as the rhizophage and phyllophage.

The complex of carpophages, the users of seeds and fruits, is joined to the anthophages. A series of so-called higher species, such as the beetle *Amara alpina*, the weevil *Phytonomus ornatus*, likewise consume the ovaries and immature seeds. For this reason they may be classed with the groups of carpophages. The *Cecidomyiidae* form the basis of the complex of insect carpophages in the typical tundras; we determined that these used the seeds of more than 20 species of plants. Particularly intensively damaged were the seeds of *Pedicularis sudetica* and *P. hirsuta*, and likewise *Artemisia tilesii*. The fruit of one of the most characteristic arctic legumes, *Oxytropis nigrescens*, was greatly damaged by particular caterpillars of the small night butterflies, close to moths, whose identification requires a special study of this group. The fruits of a series of species of willows, legumes, louseworts and *Compositae* are eaten by *Muscidae* larvae. Particularly badly damaged are the heads of *Saussurea tilesii*. Unfortunately, we did not succeed in raising the imago from the larvae, in spite of repeated attempts.

As is well-known, in the more southerly latitudes the carpophages among the weevils are extremely varied; in the tundra zone they are represented by solitary species. Besides *Phytonomus ornatus*, *Apion tchernovi* recently described in the Tareya area (Ter-Minasjan, 1973), is probably also connected with legume seeds: the latter species is most numerous in regions with all abundance of various legumes. Somewhat more southerly, the catkin weevils *Dorytomus*, which are not in the Tareya region, are common on the willows.

The fruits of tundra willows are severely damaged by sawflies of the genus *Ponthopristia*, which was earlier attributed to *Nematus* as a subgenus. We succeeded in extracting the imago out of the damaged catkins of four species of willows. On each of them was noted a separate species of sawfly (identification of A.N. Zhelokhovtseva): on *Salix lanata*, *P. latiserra* (Mal.); on *S. arctica*, *P. borealpina* (Lqv.); on *S. pulchra*, *P.* sp. n.; on *S. retans*, *P.* sp. no. 2; according to this species links of the sawflies with certain species of willows are maintained in various regions of the Taimyr. Thus, we extracted *P. borealpina* from *S. arctica*, both in the Tareya region, and on the coast of the Taimyr Lake and the lake Ust'-Tareya. These facts underline the relatively great specialization peculiar to the complex of carpophages in comparison, for example, with the phyllophages complex. In this scheme it is extremely appropriate to compare the sawflies of the genus *Ponthopristia* and the above-mentioned gall sawfly *Pontania crassipes*, which develops on all species of willows, exhibiting only some preference for individual species among them.

The upper heterotrophic levels -- the predators and the parasites -- are among the invertebrates in the surface communities of the tundra zone which belong to a series of large systematic groups which are significantly less impoverished, than the complexes of phytophages. In the northern half of the tundra zone (in intrazonal habitats) many basic groups of predators are present: several families of predatory *Acarina*, spiders, *Myriopoda*-lithobids, *Carabidae*, *Staphylinidae*, fly-(tolkynchiki), predatory bugs, and others. Most flourishing in the tundra zone are the families of Coleoptera -- the majority of them are predatory: *Carabidae, Staphylinidae, Dytiscidae.* Of the bugs the predatory *Saldidae* penetrate furthest to the north. On the other hand in the northern region of the subarctic many major groups of predatory insects are lacking; ants, geophiles, wasps (*Vescidae*), *Asilidae*, and others. Of *Coccinellidae*, in the northern half of the Taimyr only one species is rarely found -- *Coccinella transversoguttata* Fald.

In the mossy tundras the spiders play the greatest role among the large predators. In the subarctic they are represented by several families, among which the species of *Lycosidae* dominate markedly. These species are mainly of two genera -- *Pardosa* and *Alopecosa*. In the area around Tareya each of these is represented by one species -- *Pardosa septentrionalis* (Westr.) and *Alopecosa albostriata* (Grube). These are the most common spiders in various zonal tundras. Their numbers are particularly high in the spot-medallion tundra; where the spot of bare ground serves as a hunting ground for these active predators. Less frequently encountered are the species of *Thomisidae* (we noticed the species *Xysticus viduus* Kulcz.) and of *Tetragnathidae*

(*Pachygnata* sp.). Under the mossy turf and particularly under the grassy turf in herb-covered parts live the small dark *Erigone sibirica* Rulcz. (*Micryphantidae*). Probably their main prey are the *Collembola* and *Enchytraeidae*. In the mossy turf and in the upper layer of the soil the gamasid *Acarina* are quite numerous, which evidently feed upon *Enchytraeidae* and *Collembola*--onychiurids. In the investigated region several more groups of predatory *Acarina* are connected with the grassy layer and the bushes. These are the large red *Bdellidae*, which rise in a mass to the willows, where, probably they feed upon the larvae of *Psyllidae*, and likewise small *Ereynitidae*, which are common in mossy tundras.

The *Carabidae* play the largest role in various herb, shrub and dwarf shrub, and shore aggregations. In the watershed tundras of the northern belt of the subarctic they are among the supposed predators mainly in the small species of the subgenus *Cryobius*, genus *Pterostichus*, and likewise *Notiophilus aquaticus* L. Probably, the *Enchytraeidae* serve as their main food. Of the larger species in the swampy tundras, in particular in the polygonal, in the environs of Tareya, *Pterostichus costatus* Men. is common -- in drier ones the shagreen *P. vermisculosus* Men. is peculiar. On coastal pebbly and sandy spits *Elaphrus riparius* L. is very active, feeding on the larvae of flies and grown Diptera, and likewise the small *Bembidion*, eating *Collembola*, which are numerous on the littoral debris. In addition to these *Carabidae* the bug *Chiloxanthus pilosus* (Aurt.) enters into the complex of predators. It sometimes is also encountered near the small tundra lakes on the surface of mossy turf; and likewise on the paths in settlements.

At the present time, data on the food of the tundra staphylinids is practically lacking. One may only suppose that among them there are a significant number of predatory forms. In addition, the synchronization of many of their species to the accumulation of organic remains, near the lemming holes, leads one to suppose them to be sapro- and corpophages. The largest and most common species of the tundra staphylinids is *Tachinus apterus* Maekl.

Among the surface predatory invertebrates of the tundra zone there are very few species sufficiently large as to be capable of eating up animals like the *Tipulidae*, their larvae, the earthworms, the beetles, and others. Only a few birds and parasites serve as their enemies (Chernov, 1967). In the southern belt of the subarctic and in separate regions of the northern tundras are spread such quite large predators as the spider *Lycosa hirta* Kulcz., which makes holes in the mossy turf, and beetles of the genus *Carabus* (Chernov, 1966). In the described region we did not encounter these species. In the northern tundras are representatives of the main groups of entomophages: the round worms *Mermithidae*, the ichneumon-flies, the parasitic flies of the family *Tachinidae*. Here the *Mermithidae* are mainly connected with water insects, particularly with *Chironomidae*. In places in several lakes the contamination of *Cuculidae* larvae reaches 50%. The half-grown forms of these worms are common in the soil and on the banks of the rivers and lakes. We also separated *Mermithidae* from the larvae of the sawfly *Lepyrus*.

The ichneumon-fly is one of the flourishing groups in the composition of arctic fauna. They are represented mainly by the families *Ichneumonidae*, *Braconidae*, and *Chalcidae*. *Encyrtidae* are characteristically absent in the northern tundras. *Ichneumonidae* were separated from butterfly caterpillars, larvae of *Cecidomyiidae*, *Carabidae*. The gall midges, *Pontania crassipes* are severely damaged by the ichneumon flies. Its larvae, probably, are infected by the female parasites, which penetrate the already developed gall, piercing an opening. On several willow bushes all the galls had an opening. However, part of the larvae, evidently, do not develop, or the females do not always lay eggs, since from some of the galls with openings, normal *Cecidomyiidae* fly out. The largest arctic butterfly *Gynaephora lugens* is parasitized by a large ichneumonid fly, whose species relationship has not yet been identified.

The group of parasitic *Diptera* in the tundra zone is very impoverished. *Phasiinae*, *Sarcophagidae*, *Bombyliidae*, the parasitic *Calliphoridae*, are absent in northern tundras. In the investigated region only one species of *Larvaevoridae*--*Spoggosia gelida* Coquelet (identification by C.W. Sabrosky) is common. This is a specific parasite of *Lymantriidae Gynaephora lugens*, whose caterpillars in some years are infected by this Larvaevoridae by 70%. Several fly larvae parasitize in every caterpillar. This species of Larvaevoridae is described from Alaska. We met it in all places where *G. lugens* is common, on the shores of the Anabarsky inlet, in various regions of the Taimyr.

On the whole damage to many of the dominant insect species in northern tundras by the entomophages is so great, that their substantial role in population size regulation is evident. This is undoubtedly true in regard to insects such as the gall sawfly, *Pontania crassipes*, large *Lepidoptera*, with open-living caterpillars, for example *G. lugens*, some *Carabidae*.

Thus, in spite of the considerable qualitative impoverishment of tundra communities, they are still on a rather high level of organization with main features of balanced, and integrated ecosystem with sufficiently complex hierarchial relations and interdependent components manifesting themselves. The qualitative impoverishment of separate links is compensated for to a significant degree by high abundance and a wide ecological spectrum of a series of main dominants, which provides for sufficiently intense flow of biocenotic processes. The quantitative differentiation of the value of the latter is a first order problem of tundra biocenology.

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INTERNATIONAL TUNDRA BIOME TRANSLATION 12, Part 3

Title: The Peculiarities of Vertical Distribution of Invertebrates in Soils of Tundra Zone

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Translator: Melissa Chapin

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THE PECULIARITIES OF VERTICAL DISTRIBUTION OF INVERTEBRATES IN SOILS OF TUNDRA ZONE

A general feature of the morphology of the live cover of the tundra zone is the tendency towards reduction of the layering, towards the concentration of the principal biomass of organisms into a thinner layer, which at the same time acquires a complicated horizontal structure (Tikhomirov, 1956; Stebayev, 1962; Chernov, 1966). The main layer of the tundra communities is the moss cover, the strong development and complicated structure of which influence the main features of the tundra cenoses. The role played by the herb layer above the mosses and by the complex of the invertebrates inhabiting it in typical and arctic tundras is not great in numerical terms. The variation in the herbage complex increases sharply with the development of a sufficiently sizable closed herb-grass cover on zoogenic meadows in the middle of mossy tundras, on fox burrows and drained slopes; however, even here there are few specialized chortobionts. As in more southern zones, in the tundras there are quite distinct vertical migrations between the herbage and the mossy turf (Chernov *et al.*, 1971).

The mossy turf serves as a major factor in the vertical distribution of soil invertebrates (Chernov, 1966, 1968; Chernov *et al.*, 1971). When the mossy cover is significantly sizable, as a consequence of its strong heat-insulation effect, the mineral soil is colonized to an insignificant depth by invertebrates. On the other hand, when a continuous mossy cover is absent, for example on bare ground in the spot-medallion tundra, the colonization of the upper soil layer by invertebrates increases with the formation of a lichen crust and groups of typical pedobionts appear, in particular the larvae of the craneflies (Tipulidae) which are not found under moss. The decrease in the colonization of the mineral soil with the formation of a vigorous mossy turf is by no means always accompanied by a lowering of the general abundance of all pedobiont groups, the soil collembola *Onychiurus*, *Folsomia*, enchytraeids and the earthworm *Eisenia nordenskioldii*, tipulid larvae, are concentrated in the lower portion of the mossy turf, where their abundance per unit area is sometimes higher than in aggregations with a more inhabited soil horizon (Chernov, 1966; Anan'eva, 1971).

The question of the composition of the layer-adapted types of soil-inhabiting invertebrates in the tundra zone is almost uninvestigated. Among the collembola in the tundra zone the primitive or poorly specialized hemi-edaphic and upper-soil groups predominate. Hammer (1953) further wrote that specialized surface groups of collembola such as *Sminthurus*, *Entomobrya*, are generally absent from arctic fauna, and are limited in their northern distribution by the boundaries of the forest vegetation. With more detailed research it appeared that in typical and arctic tundras these groups are very widespread and quite numerous, although also more sporadic, than other life forms (Chernov, 1968; Anan'eva, 1971). In the subzone of typical tundras of the Western Taimyr a whole series of *Sminthurus* and entomobryids species are numerous, but deep-soil forms, such as *Tullbergia*, were not found in the investigated region. At the present time there is already extensive material about the species composition and the ecology of other groups of the subarctic soil fauna; however, a special analysis of the adaptions to the habitat in the various soil horizons as yet has not been carried out.

In 1968-70 in the environs of the Tareya settlement we carried out a series of special calculations according to layer of nematodes, enchytraeids, earthworms and collembola. Nematodes were calculated in samples of 1 gram, which were taken through 2-5 cm of depth up to the frozen soil. Enchytraeids and collembola were calculated by means of hand sorting under a binocular scope with the aid of eclectors in continuous vertical cores (up to permafrost) of area 5x5 and 10x10 cm, which were cut into samples of 2 or 4 cm height. These calculations, in particular, showed that "funnel" electors are of little effectiveness for the calculation of collembola in thick deep layers of soil, especially loamy soil; hand calculations under the binocular scope, as a rule, gave significantly higher figures. Evidently, collembola cannot withstand the drying layer of loamy soil. The soils of herb, herb-grass, and herb-*Dryas* portions on steep drained slopes of riverbanks were investigated in more detail; there the mineral soil is thawed out to a depth of 150 cm, which allows one to follow more carefully the vertical distribution of invertebrates, since within the inhabited soil layer 20 samples may be obtained for counting collembola and oligochaetes. From the soils developed on the steep slopes of the Pyasina River, the dark loams (probably, sea deposits) in the lower portions of steep eroded slopes are of great interest. They are distinguished by the intensity of black coloration and by a peculiar lumpy structure, which makes them superficially similar to the fertile chernozems, however, at a depth around 20 cm they already have a distinct grayish shade, which indicates gleification processes. On the upper portions of the slopes a sandy soil predominates in which the dark turfy horizon is well developed with a depth of 10 cm. In places a layered soil structure is observed; the sandy is alternated with a heavy loamy soil.

As one might expect, in the tundra soils investigated the maximal abundance of invertebrates, as a rule, appears in the very upper horizon, 1-3 cm, and in the zone of contact of the lower dead section of the mossy turf and the soil. The surface distribution of invertebrates is maintained also in better warmed (Fig. 1) spots of the bare ground, where the largest portion of collembola, enchytraeids, and nematodes is concentrated in the layer up to 5 cm, and likewise in local portions of mossy tundra where the abundance of pedobionts increases sharply as a result of zoogenic influences. Thus, on heavily vegetated grass-sedge-moss meadows, forming as a result of intensive burrowing activity and fertilization by lemming droppings, the average number of nematodes reached 7-10 million in 1 m^2, the level of their abundance in turfy-meadow soils. However, if in the latter they were distributed in a layer up to 70 cm, then in the former the main biomass was concentrated in a layer 0-5 cm. Already at the depth of 15 cm nematodes are rarely encountered. At this depth, the soil had a well-marked bluish color, characteristic of the glei horizon. In spot-medallion tundras likewise all the groups of pedobionts practically disappear at the depth of the appearance of strong gleification, in spite of the fact that in summer these layers warm up rather well. At the same time, under conditions of weak gleification in heavy loamy layers of low humidity invertebrates are encountered in relatively high numbers to a significant depth. The very highest position of the glei horizon is observed in the main climax type of tundras of this region--in the *Dryas*-sedge-moss small hummocky-tundra, where it is sometimes located immediately under the mossy turf. Often it is separated from the glei horizon by a peat-humus crumbly layer, the depth of which is quite varied, usually around 2-6 cm, however, in places of former frost cracks wedges of peaty moss are found, going downwards to 30 cm. In this tundra the mineral soil is the least poorly inhabited of all. The main biomass of invertebrates is concentrated in the upper portion of the peaty layer (A_0A_1) at a depth of 5-7 cm from the surface of the mossy turf. Substantial penetration of invertebrates downwards through peaty tongues is not observed as a result of unfavorable temperature conditions (the deeper peaty layer is usually observed under a thick mossy turf, which strongly limits heating of the lower layers).

In spot-medallion tundras soil inhabitance increases somewhat in spots of bare ground and on the ridges, which rise a little above the rest of the elements of nanorelief. Thus, on the ridges, where the mossy cover is comparatively thin, enchytraeids are encountered up to a depth of 15 cm from the surface of the mossy turf (up to 12 cm from the soil surface), nematodes up to 30 cm. On ridges the maximal abundance of enchytraeids and nematodes is sometimes observed

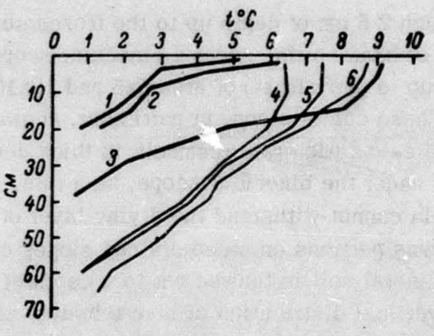

Figure 1. Vertical temperature progression in soil of different elements of relief.

1-3 spot-medallion tundra: 1 - ridge, 0 hrs. Aug. 8, 1966, 2 - spot of bare soil, 0 hrs. Aug. 8, 1966, 3 - spot of bare soil, 12 hrs. July 25, 1966; 4-6 - plots with a grass-herb cover on the southern slope of the Pyasina R. July 28, 1969.

not in the very top layer, but at the depth of 3-5 cm. This, evidently, is linked with some drying of the upper layer. In successional spots the soil collembola *(Onychiurus, Anurida)* are encountered up to a depth of 30 cm.

The invertebrates penetrate significantly deeper in soils of a turfy-meadow type on well drained slopes under herb, herb-grass, and herb-*Dryas* aggregations. Nematodes in loamy soils of these regions are encountered up to a depth of 90 cm, enchytraeids up to 70, earthworms up to 50, collembola *(Onychiurus)* up to 60. As in zonal tundra communities, in soils of herb regions the main portion of the pedobionts is concentrated in the superficial layer. Especially highly colonized is the superficial 2-cm horizon, placed directly under the mossy turf, or, in its absence, under the grassy lawn. The concentration in the surface layer is especially developed in sandy soils, where the upper 10-cm humus horizon sharply differs in structure and concentration of roots from the lower-lying light-colored layers. Thus, in one of the investigated portions of the southern slope, with dense shoots of *Astragalus subpolaris* and an admixture of grasses and herbs on the upper 2 cm layer of the soil 75% of the enchytraeids and 50% of the collembola appeared. The other half of the total collembola numbers was accounted for in the layer 2-60 cm. The nematodes were distributed somewhat more evenly: 70-80% of their quantity came out on the 10-15 cm layer with a maximal abundance at the depth of 4-6 cm (Figs. 2-4). In loamy soils of herb portions the surface maximum in the distribution of all groups of pedobionts was expressed less distinctly.

On the whole, for all the investigated soils of Taimyr station, the surface distribution of pedobionts is characteristic to one extent or another: the main biomass is concentrated in the upper 2-5 cm layer, lower than this their numbers diminish. However, a detailed investigation of the vertical distribution of invertebrates by layer revealed a series of peculiar features. By no means do the numbers of nematodes, collembola, and enchytraeids always diminish proportionally to the depth and have a single maximum in the surface layer. Often when one descends to a certain depth it again increases. Thus, on one of the spots of bare ground with fractional calculation of nematodes at intervals of about 1 cm the maximal number was noted in the superficial layer, at the depth of 2 cm substantially diminished, but then within 2 cm again increased, after which a sharp decrease was observed up to a depth of 15 cm, at which they were practically absent (Fig. 2). Sometimes in the spot-medallion tundra some increase in the abundance of nematodes was observed even at a depth around 15 cm. In deep layers (about 20 cm) under spots of bare ground some heightening of the number of the soil collembola *Onychiurus* and *Anurida* (Fig. 4). A more marked increase in the number of pedobionts in deep soil layers was observed on drained slopes (Figs. 2-4). This concerns all the basic groups of soil fauna--oligochaetes, enchytraeids, soil collembola. In a series of instances a complete or almost complete division in the distribution of collembola and enchytraeids was observed in the soil profile, especially in the portion under the herb cover (Fig. 3, 4). In this portion of the superficial layer of the soil, approximately up to a depth of 25 cm, there is sandy soil, lower, dark loam. In the loamy horizon again appear enchytraeids and nematodes in a relatively high quantity. We further noted three enchytraeid maxima, of which the lower maxima appeared on relatively deep layers in which the temperature conditions were extremely unfavorable. Thus, a high number of enchytraeids and nematodes was noted at a

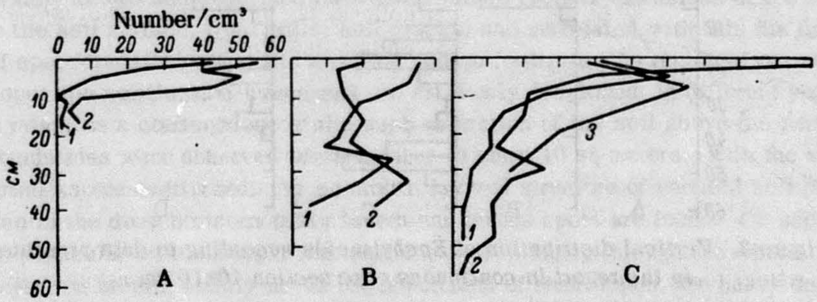

Figure 2. Vertical distribution of nematodes in the soil of different plots.

A - spot-medallion tundra: 1 - ridge, July 22, 1970; 2 - spot of bare soil, July 26, 1968. B - Astragalus subpolaris thicket on the slopes of the Pyasina River, end of July-beginning of August (1968-1969): 1 - up to 26 cm, sand soil with a dark turf layer at 0-10 cm, lower--dark loam, 2 - whole thickness--dark loam; frozen ground in both plots at about 50 cm; C - herbage on the sandy soil on the slopes of the Pyasina River: 1-3 three-fold replication.

depth of about 30-40 cm, with permafrost level at the end of July at 50 cm. This means that soil temperature at this depth was not higher than 1-2℃. Moreover, sometimes at these deep soil layers above permafrost the very absolute maximum number of nematodes and enchytraeids appeared.

The number of terricola under the herb aggregations is on the average on the order of 100 specimens/m². Their maximum appears in the layer at 0-10 cm. They are encountered most frequently up to a depth of 40 cm, isolated specimens are found at depths of 45 and 50 cm. In several samples in the layer of 10-20 cm earthworms were lacking, but at a greater depth were again found in rare instances.

In this same region O. M. Parinkina (1971) investigated the vertical distribution of the soil microflora--bacteria, fungi, and actinomycetes. According to her data, in the spot-medallion tundra the number of bacteria and other groups of microflora decreased sharply with depth. It is necessary, however, to take into account the fact that the sample intervals--not less than 5 cm were very great in comparison with the relatively low magnitude of the active layer in the tundra. Within the limits of these intervals substantial spasmodic changes in abundance of microflora are entirely possible, as was observed in relation to the nematodes, especially in the upper 5-cm layer. On herb portions of the riverbank slopes a distinct increase in abundance of bacteria is displayed in the deep soil layers; the absolute maximum was observed in the lower horizons, directly above permafrost. Comparing these facts with the physical-chemical characteristics of the soil horizons of these same regions according to the data of I. V. Ignatenko (1971), O. M. Parinkina concludes that there is no basis to consider the deep horizons more favorable for microfloral activity than the superficial ones. She sets forth the hypothesis, that the cause of this occurrence might be the yearly washing of microorganisms in spring from the upper layers and accumulation in the cold layer above the permafrost, where the intensity of their activity is extremely low.

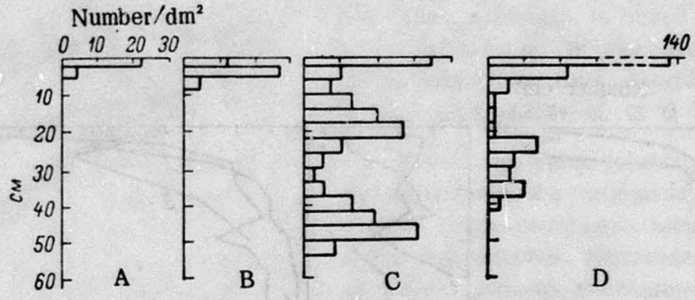

Figure 3. Vertical distribution of Enchytraeids according to data presented in the report in continuous core section 10x10 cm.

A, B - spot-medallion tundra: A - spot of bare soil with a dense lichen crust, Aug. 5, 1969; B - ridge, Aug. 7, 1969. C - herbage on the southern bank of the Pyasina River, whole soil thickness--dark chernozem-like loam at the depth of 25-40 cm humid gleied layer, lower--looser lumpier soil, Aug. 30, 1969; D - herb-Dryas covering on the southern bank of the Pysina River; up to 23 cm--sand, lower--dark loam, 0-10 cm--dense dark-brown turfy layer, 22-28 cm--peaty streaks.

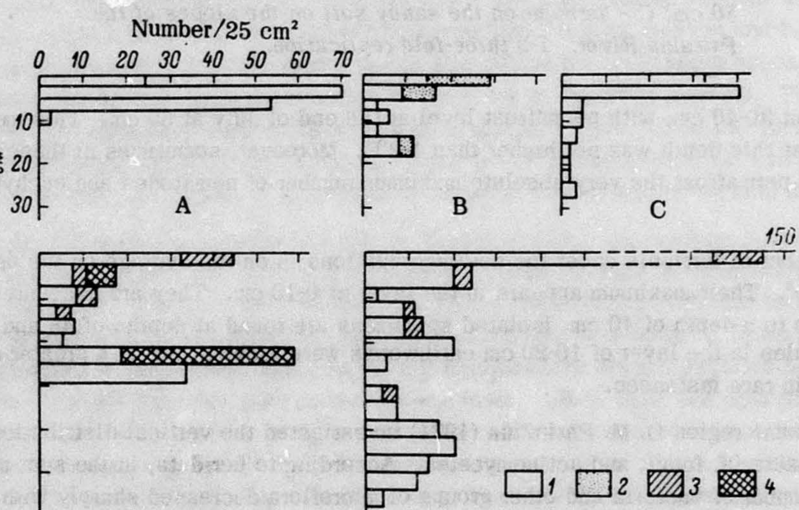

Figure 4. Vertical distribution of soil collembola according to data presented in the article in continuous core section 5x5 cm.

A-B - spot-medallion tundra, Aug. 6, 1969; A - ridge; B - spot of bare ground. C - successional spot; D, E - herbage on the slopes of the Pyasina River, July 28, 1969. 1) Onychiurus; 2) Anurida sp.; 3) Isotoma notabilis; 4) Folsomia bisetosa.

The continuous processes disturbing the regularly vertical distribution of the genetic horizons of soil appear as one of the characteristic features of the soils of the tundra zone. To such belong the widely known and described for various tundra regions extrusions of the saturated horizon onto the soil surface, frost boils, soil cracks, and correlated with this the further processes of spot formation, cryogenic swelling and so forth. In the region of our research on the steep slopes the solifluction processes are extremely developed; in different years after strong warm rains, as a consequence of the supersaturation of the soil above the permafrost, continuous landslides were observed on an area up to some 10 sq meters. With the slipping down, separate hummocks are overturned. As a result a layered structure of vertical soil profile is formed. Often in the deep horizons peaty layers and humus spots are found. On separate portions of slopes, in particular on their upper portions, the soil is sandy through the whole thickness of the active layer, on others, mainly in the lower portions of riverslopes, are heavy dark loams. Along with this often the sandy and loamy layers either alternate in thick separate layers, or among the sandy layers are found thin loamy layers.

The greatest number of nematodes and annelids in the deep layers of sandy soil coincide with the loamy and peaty layers. Under these conditions, it is as if there were laid down two profiles of different types of soil. In the sandy soil the main biomass of nematodes, enchytraeids and collembola is concentrated in the superficial 2-3 centimeter layer, lower it sharply diminishes. If lower one finds a peaty layer or loam, then their number again increases. In loamy chernozem-like soils the surface maximum sometimes is not expressed at all. The abundance of pedobionts stays at the same level up to a significant depth with fluctuations which coincide with moist glei layers .

All these examples evidence the fact that the described features of the vertical distribution of primary pedobionts in the soils of the tundra zone, probably, is linked to the mixing of soil horizons, the features of the hydrothermal regime, and physical-chemical processes. The penetration of invertebrates into deep horizons of loamy soils, evidently is facilitated by a well-defined lumpy structure, caused by cryogenic processes. One must take into consideration the fact that in deep soil layers the temperature conditions are extremely unfavorable. It is possible, that this favors a more prolonged life of the invertebrates, in its own way it promotes their conservation and as a result of this, the accumulation of deep populations is unavoidable.

Not excluded is the replenishment of nematodes and, partly, of collembola not only by reproduction, which, for some of the deepest layers, probably is not possible every year, but also by washing from the upper horizons by thawed water.

An increase in the abundance of pedobionts in the deep layers was also noted in more southern regions, in particular the arid ones, where this phenomenon is connected with moisture distribution features. According to our observation, a double-peaked vertical distribution curve is characteristic of terricola, enchytraeids and some insect larvae for the chernozem soil of the meadow steppe. This is connected with strong drying of the middle soil horizon. The constant supersaturation of tundra soils impels one to search for other reasons for these occurrences in subarctic conditions.

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INTERNATIONAL TUNDRA BIOME TRANSLATION 12, Part 4

Title: **Geozoological Characteristics of the Region of Taimyr Biogeocenological Station**

Author: **Iu.I. Chernov**

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Technical Editor: **Vera Komarkova, University of Colorado**

GEOZOOLOGICAL CHARACTERISTICS OF THE REGION OF TAIMYR BIOGEOCENOLOGICAL STATION

The Taimyr Peninsula is a unique area of the globe, where all three types of tundra subzone are well expressed over a significant area of mainland territory: the shrubby, the typical (lichen-moss), and the arctic tundras, changing in the north of the peninsula into arctic wastes. The vegetative cover, soils and animal population of the subzone of typical tundra in which the station is placed reveal the most characteristic structural features and chorology of tundra communities.

In this article are put forth several items (Chernov, 1971a) of geozoological research performed in 1966-1971 at the Taimyr biogeocenological station of the Academy of Sciences of the USSR. S.I. Anan'eva, E.P. Chayurova, L.L. Kuz'min and L.D. Admiralova took part in the work at various stages. The numerical calculations of the main groups of invertebrates (except for the simplest) were carried out through the whole landscape profile: in watershed spot-medallion tundras and hummocky *Dryas*-sedge-moss tundras, polygon bogs, herb-*Dryas* xeromorphic aggregations on the heights of the local river Pyasina, mesophytic herb-grass meadow-like communities on the lower portion of slopes with sufficient snow accumulation, on sandy-puddingstone spits, in various zoogenic and anthropogenic substrates.

Materials on several groups of animals and separate communities have been published previously (Anan'eva, 1969, 1971; Demchenko, 1969; Chernov et al., 1971; Kuz'min, 1972) or appear in this selection (articles by S.I. Anan'eva, L.L. Kuz'min and IU.I. Chernov).

Invertebrates were calculated by various, primarily absolute, methods in samples taken by area, depth, or weight: nematodes by the funnel method with lactic filters, enchytraeids and small insects by hand sorting in samples 10×10 cm, larger insects and terricola in samples 25×25 cm as deep as they were found, Collembola and Acarina in samples 5×5 cm with the help of a funnel eclector without heating in a special polyethylene film apparatus of the type of a vegetational chamber. The mobile inhabitants of the soil surface and the mossy cover were taken out with soil traps – half-liter jars embedded in the ground level with the soil surface. For the calculation of the herbage inhabitants the method of round-the-clock harvesting with a net of kapron (Miller's gauge no. 56). For the counting of enchytraeids and small arthropods the replication was at least tenfold, with hand counting of samples of $^1/_{16}$ m^2 collected in each sampling period with 16 samplings, that is a totality of 1 m^2. Statistical variation analysis of the material showed that for the most abundant species the standard deviation was within the limits of 10 to 30 percent from the mean, which one may consider admissible for the whole of general total numerical characteristics of the animal population. Special attention was given to complete removal of invertebrates from the samples, which determines the possibility of showing the partial representation of different groups in the total values for animal population abundance.

The abundance of different groups was expressed in indices in number of individuals and biomass, which was estimated both by means of direct weighing of live or anesthetized organisms on apothecary's and torsion balances, and by calculations on the basis of dimensions according to special tables and nomograms (Dunger, 1968; Chislenko, 1968). Likewise, we used magnitudes of total oxygen consumption which were calculated for the temperature regime on the basis of evidence of dependence of the respiration intensity on the animal dimensions of the various systematic

Table 1. Population (no./m²) of the basic groups of soil invertebrates in July 1967-1971.
(Extrapolation of results by various methods.)

	Dryas-sedge moss, hilly tundra	*Spot-medallion tundra*		*Polygon bog*				*Eriophorum-Dryas groups*	*Eriophorum-grass groups*
		Spot with lichen crust	*Spot being overgrown*	*Mossy ridges*	*Trough*	*Wet ditches*	*Dry mossy brows*		
Nematoda	1,300,000*	1,000,000**	4,500,000	1,700,000	3,000,000	800,000	?	7,000,000	10,000,000
Enchytraeidae	550	1,090	1,080	800	1,050	200	1,000	12,600	20,500
Lumbricidae	7	19	14	5	10	–	10	30	150
Lumbriculidae	–	–	–	–	–	90	–	–	–
Lithobiidae	–	–	–	–	–	–	–	32	120
Gamasoidea	3,000	1,320	2,720	3,160	2,520	500	3,200	4,000	8,000
Oribatei	4,500	1,320	2,780	4,440	1,200	100	4,000	20,000	5,000
Collembola	21,930	19,240	35,140	44,140	24,960	8,710	32,700	143,100	31,800
Staphylinidae, l., im.	3	3	4	16	2	?	10	9	32
Carabidae, l.	4	18	39	6	–	2	40	70	64
Curculionidae	–	–	2	–	–	–	–	6	11
Tipulidae	2	7	20	2	1	29	5	50	29
Diptera, l. ( )	6	20	19	30	4	80	37	29	70

* In averaged figures -- recalculation was made for the two types of relief – tops of hills and canals – with respect to area; on hills the population about 3,500,000, in canals about 400,000.

** On spots without a lichen crust, about 100,000.

Table 2. Mass (g/m^2) of dominant groups of soil invertebrates, 1968.

	Dryas-sedge mossy hilly watershed tundra	Spot-medallion tundra			Eriophorum-Dryas groups	Eriophorum grass associations
		Spot of bare ground with lichen cover	Over-grown spot	Wet ridges		
Nematoda	1.2 *	0.78**	2.70	1.02	4.20	7.70
Enchytraeidae	1.00	4.93	3.49	1.66	13.90	25.69
Lumbricidae	2.00	4.18	3.28	1.99	26.00	60.00
Lithobiidae	—	—	—	—	0.11	0.42
Gamasoidea	0.09	0.08	0.14	0.08	0.24	0.40
Oribatei	0.10	0.06	0.08	0.13	0.20	0.10
Collembola	1.53	0.35	0.86	1.86	2.36	2.22
Tipulidae, l.	0.30	0.52	1.20	0.40	4.60	3.83

* Averaged data (on hills – 2.6, on canals, about 0.5).

** On spots without lichen cover about 0.03.

groups (Nielsen, 1961; Byzova, 1965, 1972; Zinkler, 1966; Edwards, 1967; Byzova, Prokop'eva, 1967; Dunger, 1968; Chernov et al., 1970).

On the basis of comparison of the abundances of the main groups of invertebrates (Tables 1 and 2, Figures 1 and 2) with the account of material published previously (Anan'eva, 1971; Chernov et al., 1971; Kuz'min, 1972) in the region investigated (excluding the coastal inundated region) one may distinguish five types of animal colonization:

1. Strictly zonal climax type – associations of watershed portions with a compact mossy cover, including the hummocky tundra, elements of the spot-medallion and polygonal tundra with intermediate moisture content. The average zoomass is about 7000 mg/m^2 when potential intensity of oxygen consumption in July is around 2000 $mm^3/hr/m^2$. The proportion of the bryobiontic complex, especially of the hemiedaphic Collembola of the family Isotomidae, is comparatively very high (up to 2 g/m^2 and 800 O_2 $mm^3/hr/m^2$). The abundance of primary pedobionts – nematodes and annelids – is lower. Oligochaetes (enchytraeids and Terricola) give a biomass around 3 g/m^2 when potential oxygen consumption in July is around 410 $mm^3/hr/m^2$. This is significantly lower than in all other zonal communities of the humid region. In comparison with forest and herb communities the abundance of Oribatei is very low. The number of typical herpetobionts is minimal; of these, only minute species of *Pterostichus* are common. The species composition of the herb inhabitants is extremely poor; of these the specialized chortobiontic forms are very scarce. The latter are represented by a small number of saw-fly larvae and butterfly caterpillars. Sporadically one finds cicadas *Hardya jongi* Beirs, and the jumping plant-suckers, *Psylla*, connected with the willows. The anthophilic complex is represented basically by poorly specialized flies (Diptera): Muscidae, Anthomyiidae, Empididae, small Syrphidae, connected mainly with *Dryas punctata*. The trophic composition is uniform, the saprophages and microphytophages (users of microscopic fungi, algae, bacteria) predominate – as do nematodes (Table 3), enchytraeids, Collembola, and fly larvae.

In the microbiotopical distribution of the majority of soil and bryophillic species mosaicness and aggregation are clearly expressed, delimited both by the structure of the moss cover and by the features of the ecological range of the separate animal species (Fig. 3).

2. Primarily applicative aggregation of invertebrates, colonizing the bare soil of watershed spot-medallion and mountain tundras. There is characteristically some increase in abundance (in comparison with tundra moss communities) and in variety of semi-soil and some specialized surface forms, including the mobile herpetobionts (beetles of the genus *Pterostichus* and spiders *Pardosa septentrionalis* Westr. and *Alopecosa albostriata* Grube). The Collembola may serve as

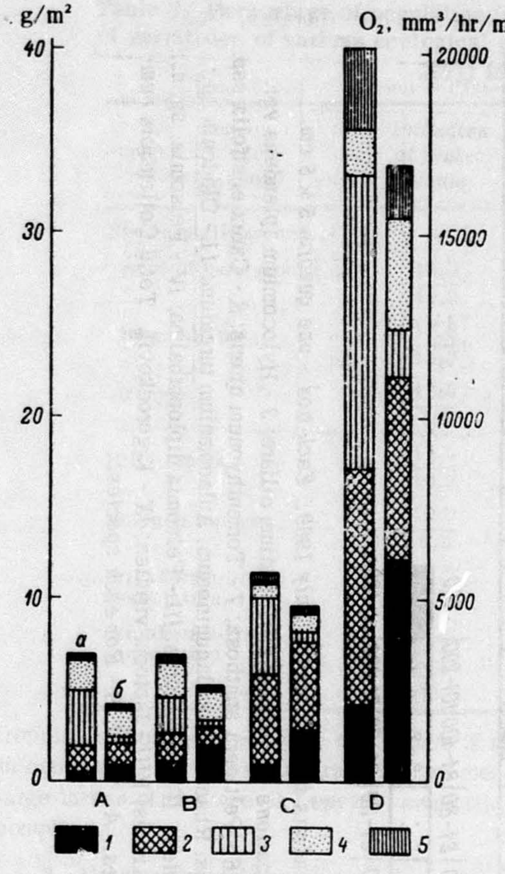

Figure 1. Correlation of mass (a) with the calculated intensity of respiration (b) of the basic groups of soil invertebrates, July 1968. A - hilly tundra; B, C - spot-medallion tundra. B - wet ridges, surrounding a spot of bare ground in the spot-medallion tundra; C - spot with lichen and flowering plants; D - Eriophorum-Dryas *groups in higher portions of riverbanks. 1 - nematodes; 2 -* Enchytraeidae, *3 - earthworms; 4 -* Collembola, *5 - tipulid larvae.*

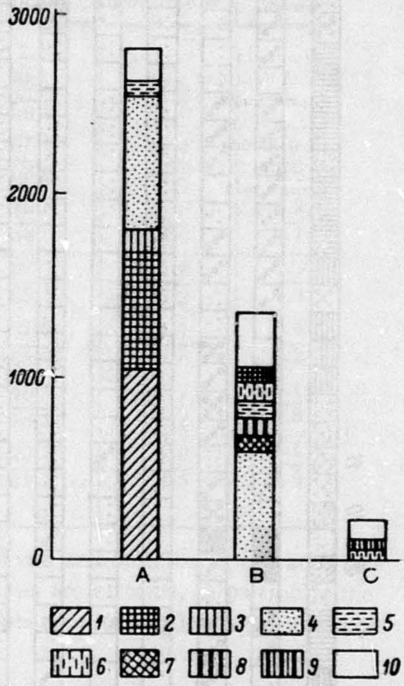

Figure 2. Biomass correlations of the herbage inhabitants (mg collected in 25 sweeps with the net), July 1968. A - Eriophorum-*grass group; B -* Eriophorum-Dryas *groups; C - spot-medallion tundra. 1 -* Amara alpina *- 2 - larva* Chrysolina septentrionalis; *3 - imago* C. septentrionalis; *4 -* Diptera; *5 - larvae* Tenthredinidae; *6 - imago* Tenthredinidae; *7 -* Cicidellidae; *8 -* Oribatei; *9 -* Collembola (Sminthurus viridis); *10 - Others.*

an example of forms specific for bare soil: the arctic-alpine *Tetracanthella wahlgreni* Linnan. and *Proisitoma* sp. nov., inhabiting in great numbers the bare soils of spot-medallion and mountain tundras. In connection with the successional vegetational cover a marked oscillation is observed in invertebrate numbers on bare soil. The extremely impoverished aggregations of young spots with a colonization of lichens and flowering plants give place to the maximal variety of the zonal tundra. The usual principle of animal population succession on the spot-medallions comes to an increase of the faunal variation and numerical differentiation in the intermediate stages (Chernov et al., 1971). In connection with the relatively good heating of mineral soil with a well developed lichen crust and with beds of flowering plants, the number of nematodes, annelids (enchytraeids and terricola) and tipulid larvae is higher than in tundra groups with a dense moss cover. The pedobiont colonization of the upper 2-cm layer of soil is higher than in all other tundra habitats. The average zoomass reaches 12 g/m^2 with a calculated magnitude of oxygen consumption around 4000 $mm^3/hr/m^2$. In

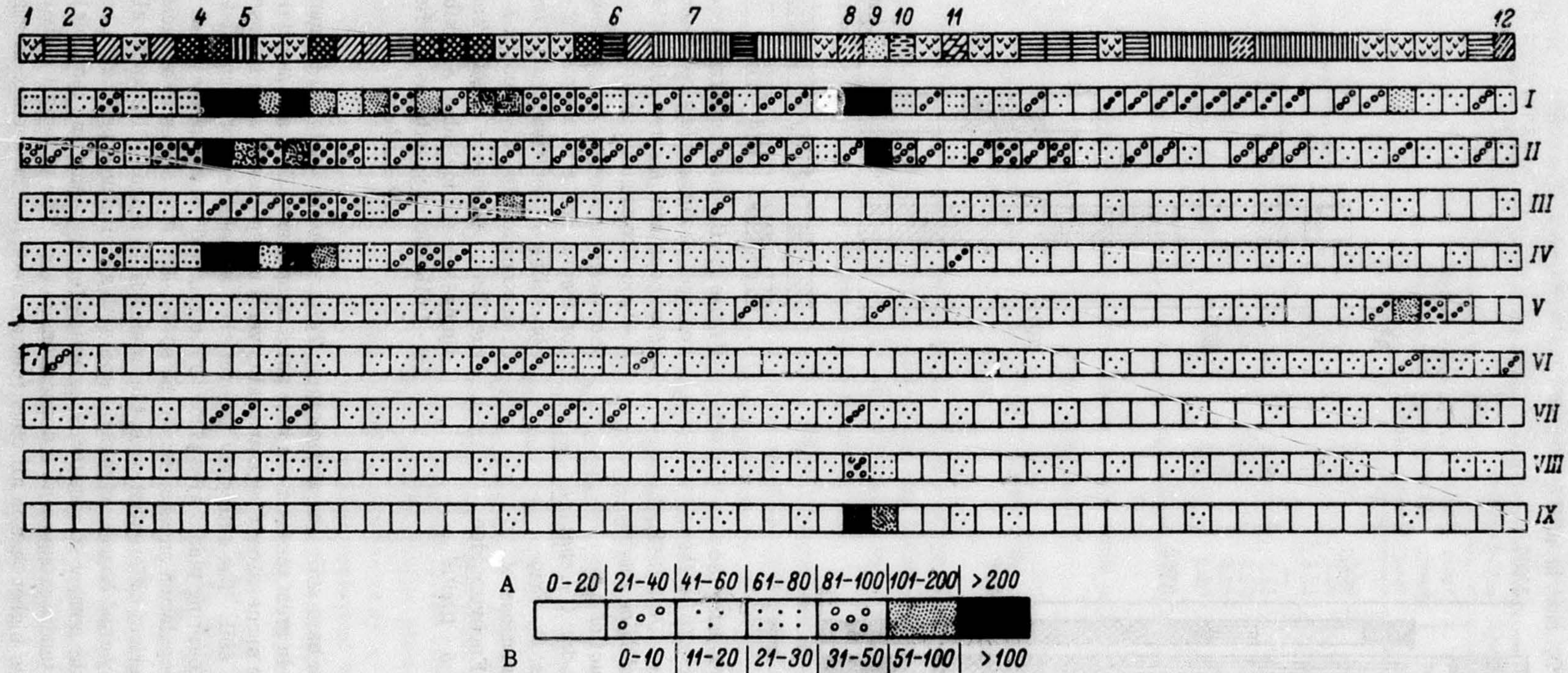

Figure 3. Distribution of Collembola *in a linear series of quadrats in hilly tundra, July 1969. Each box = one quadrat 5 × 5 cm. Top row – species of plants dominating on each quadrat: 1 - aggregations of mosses; 2 -* Ptilidium ciliare*; 3 -* Hylocomium splendens var. alaskanum*; 4 -* Aulacomnium turgidum*; 5 - mosses,* Dryas punctata*; 6 -* Peltigera aphthosa*; 7 -* Tomenthypnum nitens*; 8 -* Carex ensifolia ssp. arctisibirica*; 9 -* Rhacomitrium lanuginosum*; 10 -* Cassiope tetragona, Rhacomitrium lanuginosum, Aulacomnium turgidum*; 11 -* Cladonia sp.*; 12 -* Dicranum sp. *Row I - Total* Collembola*; II-VIII - separate species. II -* Onychiurus*; III -* Felsomia diplophthalma*; IV -* Felsomia, sp. *n.; V -* Isotoma sp. *n.; VI -* Vertagopus sp *n.; VII -* Pseudoisotoma sensibilis*; VIII -* Isotoma viridiss*; IX -* I. gorodkovii. *Total* Collembola *numbers (no./25 cm²) given on two scales. A - Total, B - For each species.*

Table 3. Percentage of population (numerator) and number of species (denominator) of nematodes of various ecological groups (according to Banage, 1963; Wasilewska, 1971) in July 1970-1971.

Habitat	*Parasites of higher plants*	*Mycophage*	*Microbo-phages*	*Polytrophs*	*Carni-vores*
Spot-medallion tundra:					
spot of bare ground	18.3/19.0	4.2/6.0	55.0/50.0	22.5/25.0	
invaded spot	18.8/15.0	0.3/2.2	57.9/58.0	19.1/13.3	3.9/11.0
trough	12.6/7.5	0.4/3.8	70.8/68.0	14.9/15.0	1.3/5.7
Hilly tundra	13.5/10.9	2.1/4.3	69.7/65.3	14.4/15.2	0.3/4.3
Polygon swamp	10.0/6.2	10.6/3.1	57.9/65.7	14.1/18.8	7.4/6.2
Eriophorum-Dryas association	19.5/23.0	1.3/1.9	40.4/48.1	37.7/21.2	1.1/5.8
Eriophorum-grass association	48.5/23.5	1.1/4.4	20.3/41.2	24.0/23.5	6.1/7.4

trophic composition, absolute dominance of microphytophages and saprophages is characteristic; in contrast to the mossy tundras, in spot-medallions rhizophages are common, in particular the large larvae of the weevil *Lepyrus*, some flies (Diptera); the absence of phyllophages is almost complete.

3. Marshy-hydrophilic series of aggregations of the animal population – the aggregations of the polygon swamps, isolated pools in the hummocky and polygonal tundras, and likewise mossy banks of tundra ponds. There is characteristically a relatively high faunal variety of the mesofauna on account of the number of species of fly larvae (Diptera), but along with this, a low total biomass level (about 6000 with 1500 O_2 mm^3/hr/m^2). Most characteristic are the hydrophilic pigmented oligochaetes – Enchytraeidae and Lumbriculidae (*Lumbriculus variegatus* Müller), and likewise Tipulidae larvae (*Prionocera*) and Lamoniidae. In comparison with the dry mossy tundra there is higher ecological, in particular trophic variety; there is greater colonization of the herb layer above the moss. The complex of anthophiles is relatively rich, among which there are specialized forms, in particular, connected with the bog development the larvae *Helophilus groenlandicus* O. Fabr., *Conosyrphys tolli* Frey, which feed on marsh lousewort flowers (*Pedicularis sudetica, P. hirsuta*). There is a relatively high abundance and wide scale of phytophage activity – lemmings, gali midges (Cecidomyiidae), sawflies, and leaf suckers (Psyllidae). In the series of marshy-hydrophilic aggregations a very marked oscillation of total abundance and ecological-systematic composition is observed.

4. Aggregations of invertebrate xeromorphic herb-*Dryas* communities on the tops of high slopes with sandy soil are characterized by great general faunal variety and a fragmentary distribution. The abundance of pedobionts is relatively high: of these, the nematodes, with biomass at 5 g/m^2 reach numbers on the order of 5-7 million/m^2; the annelids, with biomass at 25 g/m^2; the earthworms reach tens per m^2; but the enchytraeids are up to 10,000/m^2. The total zoomass is up to 40 g/m^2 with substantial fluctuation through the micro- and nanorelief. The noted maximum numbers of Oribatei for the region is about 20,000/m^2, which clearly distinguishes this type of community from the strictly zonal tundra. This is connected with the good heating of the mineral soil: the maximal depth of thawing of the soil is 150 cm. A high population size is characteristic for the separate

species of this community. For example, the absolute dominant among the Collembola, *Xenollydes armatus* Axels., is not encountered in any other habitat. On account of the high numbers of this species and of onychiurids, the total abundance of Collembola in these aggregations is higher than in all others (Tables 1 and 2). Along with this the species richness of Collembola is comparatively small (in all, 18 species, while even on bare spot-medallions 20 species are found). Of the nematodes here 43 species are found, as many as are encountered on the separate elements of the spot-medallion tundra. Correlated with the richness of the flora of flowering plants the species composition of the phytophages is quite varied. Particularly characteristic is a high abundance of rhizophages; among the nematodes there is a high percentage of parasites of higher plants (Table 3); the weevil larvae attain high numbers, particularly characteristic are the large *Lepyrus* larvae, connected, evidently, with willows, on the roots of the louseworts, particularly *Pedicularis oederi, P. dasyantha,* are numerous caterpillars of *Olethreutes inquetana* Wlkr. Some large, free-living phyllophages reach high numbers – *Chrysomela taimyrensis* L. Medr., connected with the willows, the polytrophic phytophage beetle *Amara alpina* F., connected with leguminous crane-flies *Phytonomus ornatus* Cap. Anthophilic insects are represented by the bumble bees (Bombidae), hover flies (Syrphidae), real flies, and so forth. The complex of predatory herpetobionts reaches the maximal variety (mainly Carabidae of the genus *Pterostichus*, the spiders *Erigone sibirica* Kulcz., *Alopecosa albostriata* Grube, and *Pardosa septentrionalis* Westr.).

For the invertebrates, a spotty, sporadic distribution is characteristic, which is correlated with the features of the plant cover, in which are combined the relatively homogeneous *Dryas* cover and numerous flowerbed forms scattered on this background, of which *Oxytropis middendorffii, O. nigrescens, Pedicularis oederi,* and *P. dasyantha* are particularly characteristic. Large leguminous beds serve as the focus of concentration of the maximum pedobiont abundance:

	No. of enchytraeids (per 25 cm^2)	
	Rhizosphere	Outside of the root system
Oxytropis middendorffii	92.1 ± 17.6	18.5 ± 4.1
Pedicularis oederi (5 yr)	22.2 ± 3.0	20.5 ± 3.4
(9-12 yr)	33.4 ± 4.0	20.2 ± 4.4

5. A mesophyllic-meadow type of animal population is peculiar to the local herb-grass aggregations, which form on the lower portions of the riverbank slopes when there is sufficient snow accumulation on loamy chernozem soils. The maximal abundance and variety of the typical pedobionts (nematodes – up to 15 million on 1 m^2; enchytraeids – up to 20,000; terricola – up to 150; lithobyids (?) – up to 120). The thickness of the inhabited soil layer was maximal (about 60 cm). There is maximal variety and abundance of herb inhabitants, the greatest variety of trophic groups and morpho-ecological types. The average zoomass is 100 g/m^2 (with 30,000 O_2 $mm^3/hr/m^2$ in July) – approximately the same level as in mesophytic meadow communities of the forest belt. There is a high abundance of phyllophages (leaf eaters *Chrysolina septentrionalis* Men., the beetle *Amara alpina*, various Lepidoptera, sawflies, cicadas). The complex of anthophiles is maximally varied, among them are many specialized forms. With the meadows are connected the population of bumble bees. On the whole this type of animal population contrasts maximally with the zonal tundra community.

To each of the named types is peculiar a definite level of total abundance – of zoomass and potential intensity of metabolism, and likewise specific relations of the components. The given categories have an especially typological character and unite the fragments which enter into heterogeneous communities, where they can be territorially accompanied by other types. Central among them is the peculiarly zonal climax type, which can in fragments be formed in very varied communities (hummocky mossy tundras, elements of polygon and spot-medallion tundras, mossy

Table 4. Faunal similarities of groups of nematodes (Zhakar' coefficients).

Troughs of spot-medallion tundra	*Ridges of spot medallion tundra*	*Spot of baren ground*	*Wet ditches of polygon bog*	*Eriophorum-Dryas association*	*Eriophorum-grass association*	
48	39	28	23	23	16	Hilly tundra
	37	24	17	25	16	Troughs of spot-medallion tundra
		19	16	22	22	Ridges of spot-medallion tundra
			8	24	6	Spot of bare ground
				11	15	Wet ditches of polygon bog
					15	Eriophorum-Dryas association

Table 5. Index of similarity of groups of Collembola according to species populations.

Invaded spot	*Overgrown spots*	*Ridge of spot-medallion tundra*	*Troughs of spot-medallion tundra*	*Hilly tundra*	*Ridges of polygon bog*	*Eriophorum-Dryas groups*	*Erio-phorum-grass groups*	*Elevated tundra*	
43	11	5	7	10	3	1	4	6	Spot of bare ground
	26	18	26	21	12	4	12	5	Invaded spot
		44	31	21	14	13	39	4	Overgrown spot
			32	26	21	23	36	4	Ridges of spot-medallion tundra
				36	17	8	21	3	Troughs of spot-medallion tundra
					33	7	21	2	Hilly tundra
						13	33	2	Troughs of polygon bog
							22	6	*Eriophorum-Dryas* groups
								10	*Eriophorum*-grass groups

ridges, separating polygons and spots, spot-medallions in successional stages and so forth). The closeness of the composition and numerical relations of the invertebrate aggregations can be illustrated by the paired indices of similarity of fauna and species abundance (Chernov, 1971a). As we see in the example of nematodes and Collembola (Tables 4 and 5, Figure 4), the fragments of the various types of tundra with a dense moss cover are not only close to each other, but also give the highest indices of similarity in comparison with all other pairs. Thus, the maximal index of similarity of the nematode fauna is between the hummocky tundra, and the troughs and ridges of the spot-medallion tundra. In abundance of Collembola the highest indices of similarity are between the troughs, the ridges of the spotty tundra and the polygonal swamp, vegetated spot-medallions and the hummocky tundra. It is significant that the aggregations of the herb-*Dryas* portions on the

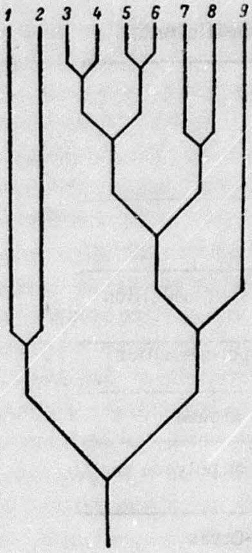

Figure 4. Classification of groups of Collembola according to Mounthford (1962), upon an index of similarity (see Table 5). Length of the vertical line joining the pairs is proportional to the difference. 1-5: spot-medallion tundra; 1-3: spot in the first three (I-III) stages of succession respectively; 4: troughs; 5: ridges; 6: hilly tundra; 7: troughs of the polygon swamp; 8: Eriophorum-Dryas *groups; 9:* Eriophorum-*grass groups.*

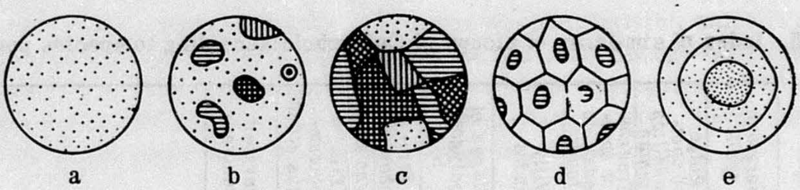

Figure 5. Types of trophic structure of the animal community in the area researched. a - homogeny; b - sporadic--spotty; c - mosaic; d - regularly cyclic; e - nodal.

tops of high slopes give comparatively low magnitudes of indices in comparison with those of meadow communities.

Depending on the combination of types of aggregations and correlating with the character of the vegetational and type of cover (Fridlyand, 1972), the chorological structure of the animal population may be homogeneous, nodal, sporadically-spotty, regularly-cyclic or mosaic (Fig. 5). A typical example of the regularly-cyclic structure are the spot-medallion tundras and the polygon swamps. The pools of the polygon swamps have a comparatively homogeneous structure. The aggregations of herb-*Dryas* portions on the hillsides have a mixed structure: the sporadically-spotty elements are alternated with the nodal. The elements of such combinations may contrast with each other, reflecting the high similarity with elements of other communities. For example, the composition of Collembola living on the ridges with dry mossy turf around a spot of bare ground are closer to the aggregations of the hummocky tundra and even the *Dryas* communities portion of the riverbank heights than to the aggregations of the bare spots (Chernov et al., 1971). The nodal character of the distribution of soil invertebrates is observed around the large solitary and bed-forming plants (*Betula nana, Oxytropis middendorffii, Delphinium middendorffii*, and others). In this the numbers of the majority of groups of soil animals decrease with distance from the plant center.

The extremity of the subarctic regime leads to a substantial lowering of the majority of the basic total numerical indices (zoomass, systematic richness, vertical breakdown, and so forth). However, this is related to the community as a whole. The separate systematic and ecological groups give extremely varied and specific curves of zonal shifts in abundance and in species diversity. Thus the maximal number of Collembola and of tipulid larvae is noted in the tundras, of Oribatei, in the taiga, of earthworms in wide-leaf forests and so forth (Perell, 1964; Chernov, 1966, 1968; Krivolutskyi, 1964). In connection with this in each zone there are specific relations of numbers of the various groups of soil fauna. This is particularly well observed in the example of the complex of small arthropods (Fig. 6). In the tundras, among the microarthropods the Collembola markedly dominate; they are regarded here as the main component of the community as a whole. About ¼ of the total zoomass end of the magnitude of oxygen consumption is attributed to them. In the taiga forests the oribateids dominate, but when there is a very strong development of the mossy cover the Collembola do. Further south, in mixed and wide-leafed forests, and likewise in the steppes, the oribatids predominate, but the general variation of the complex increases. On the whole one may consider that in the subarctic and boreal plant formations, where the basic edificators are the mosses, the complex of microarthropods has a "collembolan" aspect, in forests and herb communities with a significantly deep litter, an "oribateid" aspect. On the basis of these principles lies the individual character of the ecological ranges of the various species and groups of organisms, reflected in the zonal landscape aspect. In other words, one may call the situation a zonal continuum. This again emphasizes the necessity of a differential analysis of the various components of the soil animal population, each of which occupies a specific place in the sum total of the biogeocenotic processes.

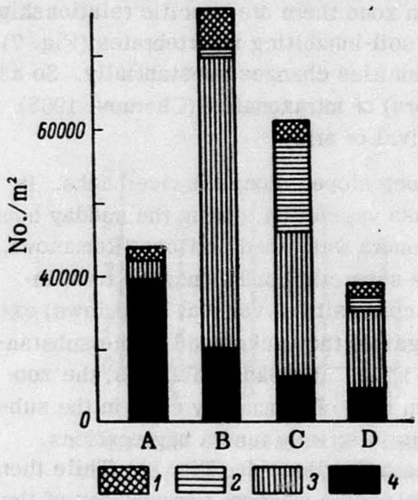

Figure 6. Correlation of abundance of main groups of microarthropods with different zonal associations. A - tundra; E - taiga; C - broad-leaf forest; D - meadow steppe. 1 - Gamasoidea; 2 - Tyroglyphoidea; 3 - Oribatei; 4 - Collembola.

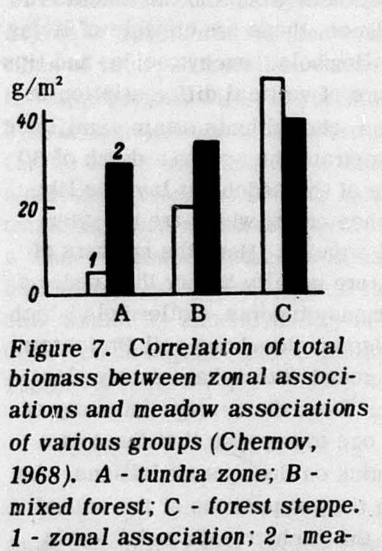

Figure 7. Correlation of total biomass between zonal associations and meadow associations of various groups (Chernov, 1968). A - tundra zone; B - mixed forest; C - forest steppe. 1 - zonal association; 2 - meadow groups on slopes.

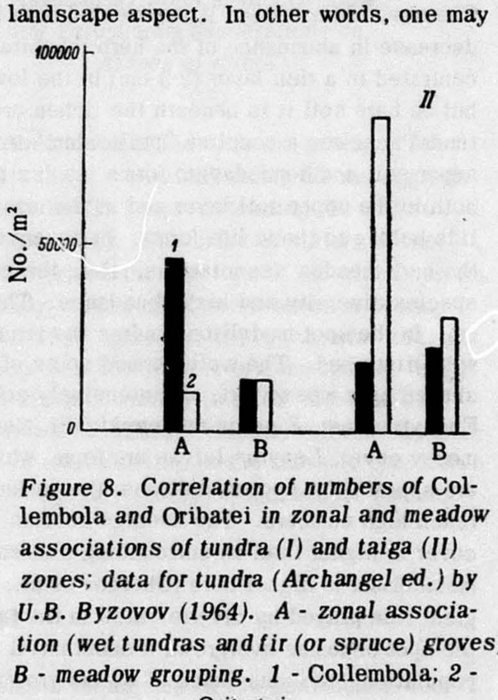

Figure 8. Correlation of numbers of Collembola *and* Oribatei *in zonal and meadow associations of tundra (I) and taiga (II) zones; data for tundra (Archangel ed.) by U.B. Byzovov (1964). A - zonal association (wet tundras and fir (or spruce) groves); B - meadow grouping.* 1 - Collembola; 2 - Oribatei.

The particulars of the structure of the zonal communities reflect only one aspect of the differentiation of the animal cover. The landscape profile of each concrete region along with its typical zonal communities includes varied intrazonal aggregations, connected with the depressions of the relief, the slopes, the floodlands, and so forth. In each zone there are specific relationships between the strictly zonal and the intrazonal aggregations of soil-inhabiting invertebrates (Fig. 7). In particular, the contrast between zonal and intrazonal communities changes substantially. So as a result of the smoothing influence (in terms of climatic factors) of intrazonality (Chernov, 1968), the contrast is maximal in zones with the worst conditions (nival or arid).

In the tundra zone this occurs to a large extent on the steep slopes along the riverbanks. In the Tareia environs the riverbank slopes, covered by herb-grass vegetation, during the midday hours receive on the average 1.5 times more direct radiation than tundra watershed portions (Romanova, 1969). Here are formed the richest animal aggregations of the subarctic conditions; the total indices (average zoomass, ecological diversity, general faunal composition, vertical breakdown) exceed the figures for the zonal tundra community ten times. Against the background of the substantial differences in zoomass of the communities of the various zones, in meadow habitats, the zoomass reaches almost the upper limit of magnitude for the given type of community even in the subzone of the typical tundras. This is ten times higher than it is in strictly tundra aggregations. Another example is the zonal shift in abundance of Collembola and oribateids (Fig. 8). While there are substantial differences in their numbers in zonal communities, the meadow aggregations of these arthropods in the various zones are characterized by almost identical numbers.

The major general feature of the structure of the animal population of the tundra zone is a tendency towards reduction of the layering, of the vertical distribution pattern (Stebayev, 1962; Chernov, 1964, 1966). It is revealed both in the decrease in depth of soil colonization and in the decrease in abundance of the herb inhabitants. The main biomass of animals in the tundras is concentrated in a thin layer (2-3 cm) in the lower portion of the mossy turf and in the peaty-humus layer, but on bare soil it is beneath the lichen crust. In connection with this the animal population of the tundra acquires a peculiar "pellicular" structure. Among the pedobiont groups in the tundras the super-soil and hemiedaphic forms reach a particularly high abundance; these are capable of living both in the upper soil layer and in the mossy turf. Many large Collembola, enchytraeids, and tipulids belong to these life forms. In essence there is another feature of vertical differentiation in the herb-meadow associations. Here the complexes of anthophiles, chortobionts attain significant species diversity and high abundance. The soil invertebrates penetrate the soil to a depth of 60 cm. In the spot-medallion tundras the tendency towards reduction of the pedobiont layer is likewise disturbed. The well-warmed spots of bare ground with a lichen crust, which are not overshaded by a mossy turf, are intensively colonized by typical soil animals. Here the numbers of Enchytraeidae, *Eisenia nordenskioldii*, Nematoda, tipulid larvae, are usually higher than under a mossy cover; *Lepyrus* larvae are found which are lacking in the mossy tundras, Collembola which are specific for spot-medallions, the surface *Tetracanthella wahlgreni*, the above-soil *Proisotoma* – reach high numbers. The average zoomass on the spots of bare ground with a fragmentary plant cover is higher than on surrounding elements with a mossy cover. Even the average intensity of metabolism is higher here (Chernov et al., 1971). All this leads one to suppose that there is a great role played by invertebrates in the further vegetation dynamics on the spot-medallions. As the spot becomes overgrown a substantial change comes about in the composition of the animal population: the abundance of worms grows smaller, in particular the enchytraeids and *Eisenia nordenskioldii*, but the number of Collembola increases, among which the larger *Onychiurus* begins to dominate. However, the total Collembola metabolism under the mossy turf is lower than on bare ground on account of the larger dimensions and lower temperatures. Thus, in the final successional stages the proportion of the invertebrates grows smaller in the biogeocenotic processes, revealing inversely correlated relations of the community components in the successional processes. One of the common tendencies of animal population succession on the spots is the increase in their general variety in the middle successional stages with the presence of a fragmentary vegetational cover.

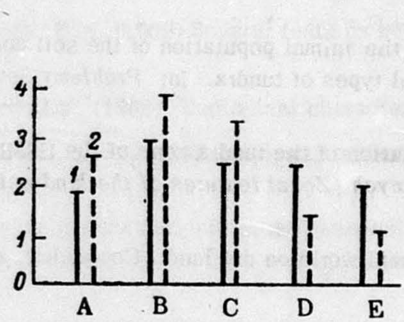

Figure 9. Informational index of diversity (Gulyarov, 1969; Chernov, 1971) of the whole complex of invertebrates calculated on the basis of soil tests (1) and on the associations of Collembola *(2). A-B - spot-medallion; A - spot of bare soil; B - invaded spot; C - hilly tundra; D -* Eriophorum-Dryas *groups; E - meadow groups.*

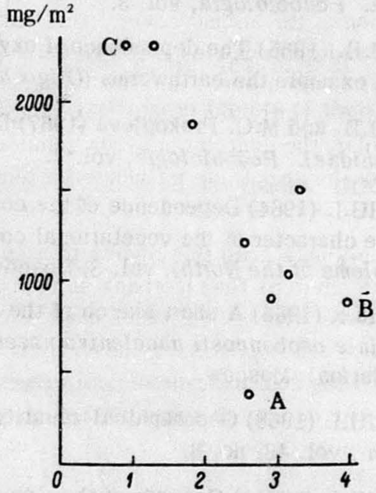

Figure 10. Correlation of the indexes of diversity with the total mass of Collembola*. Each spot = type of association. A-B - spot medallion tundra; A - spot of bare ground; B - invaded spot, with fragmentary plant cover; C - meadow* Eriophorum *associations on slopes of rivers.*

This concerns both the systematic composition and the abundance of the different groups. The degree of differentiation (according to the informational index of variation) among all the aggregations of the spot-medallion tundra investigated is greatest in the stages preceding the climax – the aggregations with the continuous mossy cover (Fig. 9 and 10). The index of variety of the climax aggregations is likewise high enough that it characterizes the stability of the given system. On the whole one observed a tendency towards an inversely dependent relation between average abundance (biomass) and the index of variation (Gilyarov, 1969; Chernov, 1971b), insofar as the maximally high zoomass is achieved most often on account of a low number of components, that is, a tendency towards single dominance. Thus, the lowest index of variety is in the meadow-like herb-grass associations, where the average zoomass is maximal. This evidently reflects the general instability and variability of this community, which is contradictory to the climatic conditions of the given region. These principles agree with the contemporary theory of succession (Odum, 1969).

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