A COMPARISON OF THE PHYSIOLOGY, ECOLOGY AND DISTRIBUTION OF SOME NEW ENGLAND WOODLICE

by

John Langworthy Fuller

B. S., Bates College

1931

Submitted in Partial Fulfillment of the Requirements
for the degree of
DOCTOR OF PHILOSOPHY
from the
Massachusetts Institute of Technology
1935

Signature of Author.......Signature redacted.......
Department of Biology and Public Health, May 9, 1935

Signature of Professor in Charge of Research.......Signature redacted.......

Signature of Chairman of Departmental
Committee on Graduate Students.......Signature redacted.......

ACKNOWLEDGEMENTS

Professor Charles H. Blake has aided this thesis through his guidance and helpful criticism. He has also kindly allowed me to use many of his unpublished records. My wife, Ruth Parsons Fuller, assisted in many of the collecting trips, and has aided the preparation of the manuscript in innumerable ways. Miss Mary Fuller prepared certain of the climate maps. I wish to express my appreciation of their help, which made this research possible.

I wish also to acknowledge the assistance of the Department of Biology and Public Health in providing a refrigerating unit and other equipment necessary for the experimental work.

TABLE OF CONTENTS

PART III. SURVEY OF KNOWN DISTRIBUTION

PART IV. CLIMATOLOGICAL ANALYSIS

PART V. TOLERANCE OF WOODLICE FOR EXTREMES OF TEMPERATURE AND MOISTURE

Description of Experiments

Series A

Series B

PART VI. REACTION OF WOODLICE TO CHLORIDES

PART VII. PHYSIOLOGY, ECOLOGY AND DISTRIBUTION COMPARED. DISCUSSION AND CONCLUSIONS

PART VIII. SOME RELATED LITERATURE AND AN APPRAISAL OF METHOD

FIGURES AND MAPS

The climate and distribution maps are bound together at the end of Part III, preceding page 51.

PART I.

INTRODUCTION

The fact that animals do not range unrestricted over the earth has been recognized from the time man first began to wander afield. It was also noticed that a particular animal was usually to be found in the same sort of place from day to day, or that its migrations were associated with seasonal or other changes. In this sense ecology probably ranks second to taxonomy in the development of biological knowledge. During the many years that so-called learned men disdained the study of nature as trivial, farmers, hunters, foresters and the like were obliged to be practical ecologists in their endeavor to earn a livelihood. When interest in nature once more became intellectually respectable, the earlier biologists found a host of animals and plants whose existence had not been previously realized. The cataloging of this assemblage required all their energy, and for a time no one tried to find out just why animals were found in the places that they were. Observations of the habits and ways of animals were often left to unskilled and uncritical observers, while scientifically trained men were busy in their laboratories and museums. Praiseworthy as these researches have been, the neglect of the scientific study of animals as they exist in nature means that many of the important problems of biology have never been seriously attacked.

For example, the effect of climate on the distribution of animals is an obvious fact that requires no proof, but the mechanism through which it works has had very little attention. We do not know a great deal about the adaptations which make some animals hardy to cold while others are killed by slight chilling. It was thought, therefore, that a study of the geographical distribution of several related animals, compared with some of their physiological characters might throw light upon this general question. Such a project would involve a field study of the animals, the determination of the extremes of climate in the range of each species, and an experimental study of the tolerance of each species for high and low temperatures, high and low moistures, and for other factors which might seem important.

It was decided that the Oniscoida, or land isopods, furnished good material for such a study. The distribution of all the New England species was well known due to the work of Blake, and those species which also occur in Europe have been extensively studied there. Most of the species were available in sufficient numbers to be used in a long series of experiments. Although there are distinct differences between the habitats of the different forms, the life requirements are in general very similar. The chief requirements are proper temperature and moisture, food and air. This not only makes the maintenance of cultures for experimental purposes easy, but also cuts down the number of variable factors to be studied. For example, the effects of light and rate of air movement are important in the distribution of many animals but not among the Oniscoida. Since the type of soil might have some effect on animals which live in close contact with it, this factor would require some consideration. Finally, the land isopods migrate only slowly, and presumably have rather stable limits, since they cannot rapidly recolonize an area in which they have been destroyed by particularly severe conditions in any one year. This is not true of strong flying animals such as birds and some butterflies.

It was hoped that some answers could be obtained for the four following questions.

1. Is climatic control of the distribution of woodlice due chiefly to the direct lethal action of low and high temperature, and of dryness upon the animals? If so, we would, for example, expect to find a direct correlation between the low temperature tolerance of a species in the laboratory and the winter isotherm apparently limiting its distribution in nature.

2. Is a wide spreading species more or less tolerant of extreme conditions than a more restricted one? The species with a restricted distribution may be so because it is specialized for extreme conditions, or because it is specialized for a narrow range of moderate conditions.

3. Does the same species in different parts of the world show different climatic limits to its distribution?

4. Does a wide ranging species necessarily inhabit regions with somewhat varying climatic characteristics; and does a more restricted species occur only in regions with rather sharply defined climatic characteristics? If climate

is the factor of chief importance in distribution, the answer to both parts should be, "Yes." If other specifications are more important the answer to the second part will probably be, "No."

In the following pages an attempt is made to answer these questions in accordance with the information available. The plan of attack on the problem has been this: first, a survey of the biology of the group and of the known distribution of the species which are to be especially considered; second, an analysis of climates of the regions occupied by the various species with particular attention to conditions near the limits of distribution; third, experimental determination of the resistance of each species to high and low temperatures, low moisture, and a study of the simultaneous effect of temperature and moisture; finally, a comparison of the climatic factors involved with the laboratory findings, and the bearing of the results on the general problem. In addition, a few other experiments have been carried out testing the reaction of the woodlice to certain chemical characteristics of the soil, a feature of the environment which has been suggested as a factor in the distribution of these animals.

The Animals Used

The woodlice are not considered to be of much economic importance. Nevertheless, their abundance shows that they must play a considerable part in the economy of nature. New England, though poor in number of species, is densely populated in parts by a few dominant species.

Classification of the New England Forms

According to Blake (1931b) fifteen species of land isopods have been described from New England. These may be classified as follows.

Family LIGYDIDAE

Ligyda oceanica (Linne)

Family Trichoniscidae

Trichoniscus (Trichoniscus) demivirgo Blake

Miktoniscus halophilus Blake

Cordioniscus stebbingi (Patience)

Family SCYPHACIDAE

Scyphacella arenicola S.I. Smith

Armadilloniscus ellipticus (Harger)

Family ONISCIDAE

Oniscus asellus Linne

Philoscia (Philoscia) muscorum (Scopoli) var. sylvestris (Fabricius)

Family PORCELLIONIDAE

Cylisticus convexus (DeGeer)

Porcellio (Porcellio) pictus Brandt

Porcellio (Porcellio) scaber Latreille

Porcellionides (Porcellionides) pruinosus (Brandt)

Trachelipus (Trachelipus) rathkei (Brandt)

Family ARMADILLIDIIDAE

Armadillidium (Armadillidium) vulgare (Latreille)

Armadillidium (Armadillidium) nasatum Budde-Lund

PART II.

THE ANATOMY AND BIOLOGY OF THE ONISCOIDA

A certain amount of information concerning the anatomy and habits of the land isopods is necessary for the understanding of the factors influencing distribution. This is especially true of the respiratory apparatus and the reproductive cycle. Chapman (1931) has called attention to the need for correlating climatic studies with the mode of life of an animal, and with the occurence of critical periods in the life cycle.

General Anatomy

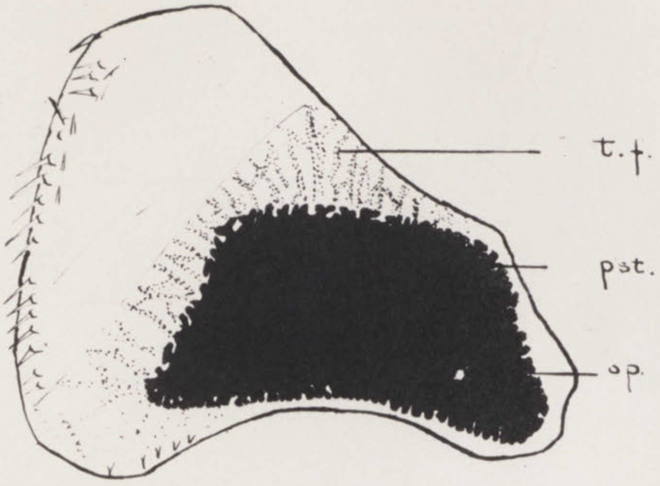
The land isopods are dorso-ventrally flattened animals divided into a head, a thorax of seven segments, and an abdomen of six segments. There are two pairs of antennae, a pair of mandibles, two pairs of maxillae and a pair of maxillipeds. All the thoracic appendages, or pereiopods, are ambulatory. The abdominal appendages include five pairs of pleopods and, on the terminal segment, a pair of uropods. The pleopods are biramous, the exopodite being generally foliaceous, the endopodites usually smaller and more or less differentiated. The second and often the first pairs of endopodites in the male are modified as copulatory organs. The remaining endopodites are of a delicate, spongy structure, and are protected by the overlying, more heavily chitinized exopodites. In some species the exopodites have a thickened region containing structures known from their appearance in life as the "Weisskörper" or from their function as pseudo-tracheae. The uropods are also biramous, and project more or less behind. In all our families except the Ligydidae and the Trichoniscidae, the inner rami can be approximated to form part of the water conducting system described by Verhoeff (1917c).

Respiration

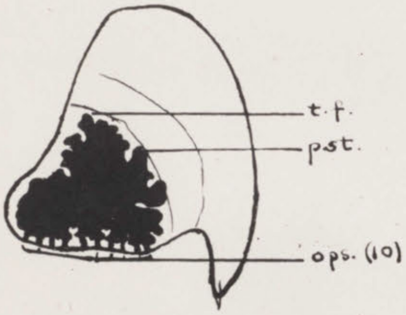
Several investigators have studied the respiration of the Oniscoida and their conclusions have not always agreed. This has been especially true in regard to the function of the pseudo-tracheae. Bepler (1909) stated that they had very little function in breathing, thus contradicting the classical belief. The further studies of Herold (1913) and of Verhoeff (1917c and 1920b)seem to show that Bepler was in error, and I have followed them in my description of the respiration of the land isopods.

For our present purposes the Oniscoida may be divided into two groups, the amphibious forms, and the strictly land forms. The former, represented in New England by Ligyda, can withstand a week or more in water, while the latter can live in water only three days at the most. The following discussion considers particularly the respiration of the true land forms.

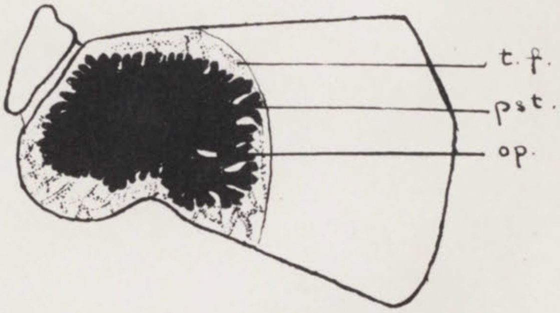
In the presence of an abundance of water the endopodites serve as gills, taking up dissolved oxygen from the water spread out over them in a thin layer. If moisture is scarce they behave only as spongy blood sacs, and there is only a feeble exchange of air between them and the atmosphere. A secretion is produced which acts as a protection against the



Armadillidium vulgare
Exopodite of first pleopod - dorsal
x 40



Trachelipus rathkei
Exopodite of first pleopod - dorsal
x 40



Porcellio scaber
Exopodite of second pleopod - dorsal

t.f.	tracheal field
pst.	pseudotrachea
op.	opening of pseudotrachea

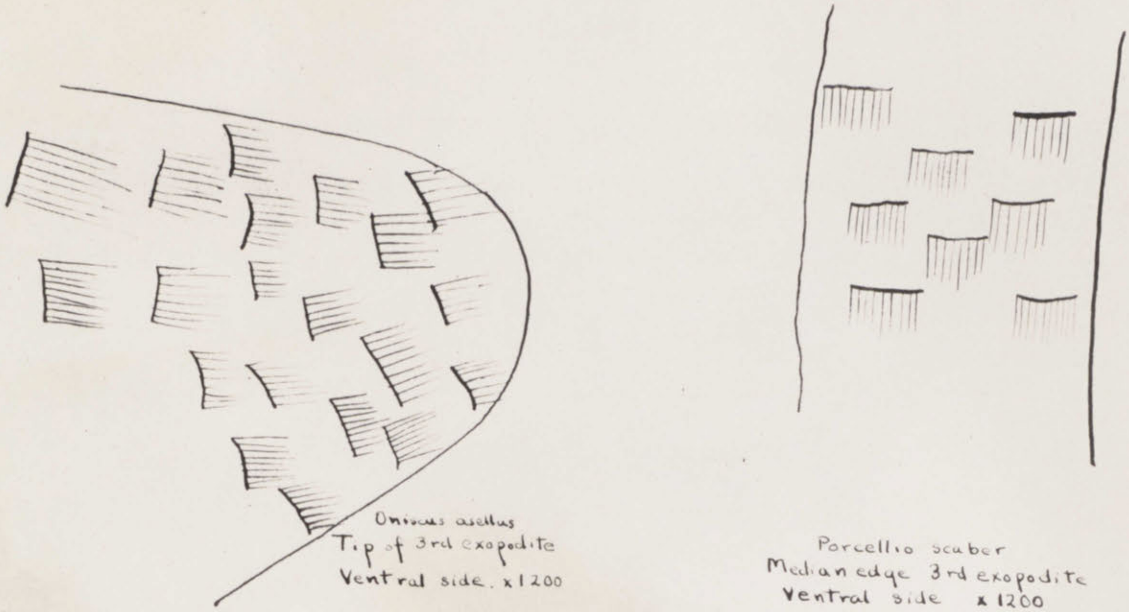
Figure 1.

JLF

drying out of the pleopods. Even among those forms in which water never normally comes in contact with the endopodites, these organs are still well developed (i.e. Cubaris or Pentheus).

The pseudo-tracheae are also respiratory organs, but function differently from the branchial endopodites. Essentially they consist of an air chamber opening to the exterior on the dorsal surface of the exopodite, and surrounded by a blood sinus. (Fig. 1) There is only a very thin layer of tissue between the blood and the air; thus gaseous interchange goes on rapidly. The importance of these pseudo-tracheae is shown by some of Verhoeff's experiments in which he amputated the first two exopodites of Porcellio scaber and Armadillium vulgare which in these species are the only pleopods bearing pseudo-tracheae. The animals died. They would, however, survive the amputation of the third to fifth exopodites, since they could continue to breath by means of their tracheal systems. Oniscus and Trachelipus survived the amputation of all five exopodites, since their branchial endopodites could still provide sufficient oxygen.

Most true land isopods possess a water conducting system, the purpose of which is to convey water to and from the endopodites and thus to carry on branchial breathing. The two endopodites of the uropods can be placed together to act as a capillary tube and suck up water from the soil. The water is carried farther, still by capillary attraction, to the pleopods or to the rectum where it is stored as a reserve

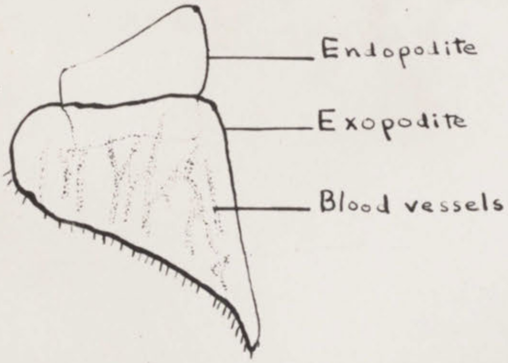


Oniscus asellus
Tip of 3rd exopodite
Ventral side. x1200

Porcellio scaber
Median edge 3rd exopodite
Ventral side x1200

FIGURE 2. COMB BRISTLES

JLF



Oniscus asellus
4th pleopod - right side
Camera lucida. x22

FIGURE 3.

JLF

supply. An abundance of water is spread out on the surface of the pleopods, and the interchange of air facilitated. This conducting system may be observed by placing a drop of colored fluid on the uropods. In many forms with a water conducting system, rows of bristles are present on the inner margin of the exopodites which filter the water as it flows through. (Fig. 2) Strongly developed bristles have been considered as indicating that water was very important to the animal possessing them, as they are weaker in species living in dry situations. (Verhoeff 1923)

There is a definite relationship between the predominant type of respiration of a species, and its choice of habitat. Those species which possess well developed pseudo-tracheae live in dry places, and do not long survive immersion in water. Those which depend upon branchial breathing are limited to moist environments. The following table modified from Herold (1913) shows this connection.

TABLE I

Species	Moisture of Habitat	Pairs of pseudo-tracheae	Development of endopodites				
			1	2	3	4	5
P.pictus	Variable dry tendency	2	*	*	**	**	**
P.scaber	Variable dry tendency	2	*	*	**	**	**
A. vulgare	Variable dry tendency	2	*	*	**	**	**
C.convexus	Intermediate	5	*	*	**	**	**
T.rathkei	Intermediate	5	*	*	**	**	**
O.asellus	Moist	0	*	*	**	**	**
P.muscorum	Moist	0	*	*	**	**	**
T.demivirgo	Very moist	0	*	*	**	**	**
L.oceanica	Amphibious	0	***	***	**	**	**

* Not modified for respiration
** About one-half size of exopodite, modified for respiration
*** Large - modified for respiration

The tracheal systems of T. rathkei and of C. convexus are not as capacious as those of Porcellio or Armadillidium. (Fig. 1 and 2) Hence they are less able to live in a dry place. Oniscus has a simple respiratory system, but on the outer part of the exopodite are radial furrows which bring the blood into excellent contact with the air. (Fig. 3)

Reproduction

The reproductive cycle of a species is important in any consideration of its ecological relationships. The resistance to any given factor, and the requirements of food and protection may vary enormously between different stages of the life cycle. This is strikingly shown among insects. In the land isopods the course of development is more simple, and is similar in each of the species under consideration here.

However, a region where unusually severe conditions prevailed at the breeding season might fail to support a species, even though the adults survived, because so many young perished. A species with similar physiological tolerance,in which the breeding season coincided with more suitable conditions,might be able to establish itself firmly in the same region.

I have followed the summaries of Vandel (1925) and of Verhoeff (1920a)in my discussion of reproduction among the Oniscoida.

Organs of Reproduction

The male organs consist on each side of three testicles lying near the digestive tract, and attached to the body wall by suspensory ligaments. Each set opens into a large seminal vesicle which is connected to the penis by a vas deferens. The vas has muscular walls which contract and expel the sperm at the time of copulation. The penis is situated on the ventral side of the body at the posterior margin of the seventh thoracic segment, and is a single organ in our forms, except in Ligyda where it is paired. The endopodites of the second pair of pleopods act as an intromittent organ during copulation, while those of the first pair conduct the sperm from the penis to the second endopodites.

The ovaries consist of two tubes extending the length of the thorax above the digestive tract. The size of these tubes varies according to the stage of the reproductive cycle. The eggs are released into the cavity of the ovary surrounded by a vitellin membrane and a chorionic membrane. Each ovary has a separate oviducal opening on the ventral surface of the fifth thoracic segment near the attachment of the pereiopod. The internal part of the oviduct has a chitinous lining which constitutes a seminal receptacle and is continuous with the cuticle of the body. At the time of the molt which coincides with the first egg-laying, this lining is replaced by a chitinous plug which completely obstructs the oviduct and the genital opening. After the last reproduction of the year, the plug is in turn replaced by the original thin-walled sac. Thus it is possible for copulation to take place only once a year, in the spring. Correlatively, the sperms for all the broods of one season must be supplied at one act of copulation.

Development

Copulation is difficult to observe, and apparently always takes place in the dark. Fecundation takes place in the ovary. The eggs then pass down the oviduct and are held in the marsupial pouch formed by four pairs of broad lamellae issuing from the bases of the second to fifth pair of legs. Here they undergo their embryonic development. The young break through the egg membranes while still in the brood sac, and remain there as larvae for a further period. In the marsupium the developing young are kept moist by a fluid secreted by outgrowths from the ventral body wall, the cotyledons. Vandel believes this fluid has nutritive value, while Verhoeff believes that the cotyledons are primarily respiratory organs. When the young finally emerge they lack the seventh pereiopod and the first pleopod, and are still larvae.

There are three larval stages which may be distinguished by Verhoeff's key (1920, p. 170). All first stage larvae lack pseudo-tracheae even though the adult forms may possess them. Thus the larvae of the tracheate species are not as well adapted for air breathing as are the mature animals. Verhoeff (ibid) describes the development of the tracheal system in six species, four of which are of present interest. In *Porcellio scaber* and *Armadillidium opacum* (close to *vulgare*) the second stage larvae and third stage larvae have pseudo-tracheae only on the second exopodites. The first exopodites lack them until the first immature stage which follows the larval stages directly. On the other hand, the second stage larvae of *Cylisticus convexus* have pseudo-tracheae on the second to fifth exopodites. Larvae of *Trachelipus rathkei* develop a tracheal system more slowly. There are no pseudo-tracheae present in any of its larval stages or in the first immature stage. Young animals from 5-7 millimeters long acquire first four and then five pairs of pseudo-tracheae.

The duration of the various larval stages varies according to many conditions. Verhoeff gives the following data for one brood of *P. scaber*.

TABLE II

Habit	Stage	Duration
In marsupium	Embryonic	35 days
	1st stage larva	16 "
Free-living	1st stage larva	5 "
	2nd stage larva	23 "
	3rd stage larva	23 "
Total		102 "

Development is usually more rapid, the time from the first appearance of the marsupium to the first immature stage being commonly from 50-70 days. About half of this time is spent in the brood pouch. A second brood follows very closely upon the first.

Time of Breeding

In general, there are three broods a year, though young individuals may have only two, and as many as four have been observed. T. rathkei and C. convexus are said to have only two broods annually. Each brood is separated by a molt and there are two extra molts in those animals having three sets of young annually. The order of events is: 1st molt, copulation, 1st brood, 2nd molt, 2nd brood, 3rd molt, 3rd brood, 4th molt, growth, 5th molt. Females are not able to breed in the same year that they leave the marsupium.

The season of year in which the young are released varies in different regions. Development is slower at lower temperatures, and probably also varies with humidity and other factors. Blake and the writer have found that in the laboratory P. scaber, O. asellus, T. rathkei and other forms will produce young as early as February. There are, unfortunately, no data concerning the dates of the various broods in New England under natural conditions. The observations of Blake and the writer in this area would place the time of the first brood about the first of June, and the second early in July. All females of Porcellio scaber collected at Acton, Me., July 2, 1933, were found to be bearing young almost ready to hatch. This was probably the second brood of the year. The third brood would then come late in July or early in August. Several female specimens of P. pictus were collected at Acton, Me., August 16, 1933, all of which bore young in the marsupium. We might presume that the broods in the north of New England come a little later than in the south of the region, but as to differences between the species, we know little.

Nutrition

Climatic conditions might indirectly influence distribution, by favoring or by inhibiting necessary or preferred food plants or food animals. This does not appear to be the case among the land isopods as these animals apparently live on decaying wood, leaves, and the like which are available all the year. It is possible that symbiotic microorganisms assist in extracting nutriment from this material, but no one has yet proved this point. Oniscoida are also carnivorous, and are definitely cannibalistic when crowded. Cannibalism is practiced both within and without the species, though small species are apt to be preyed upon by larger ones. Individuals in the process of molting are often attacked by their fellows.

Natural Enemies

Very little is known concerning the function of woodlice as food for other animals. Presumably any insectivorous carnivore would overlook the taxonomic difficulties involved in eating a land crustacean. A large Lycosid spider (probably *Lycosa carolinensis*) kept in captivity was observed to kill a *Porcellio scaber* and suck juices from its body. In the National Geographic magazine (Vol. 64, p. 199, 1933) there is a photograph of a trapdoor spider attacking a sow-bug which appears to be Porcellionides.

Woodlice are parasitized by Tachinid flies, one of which, *Melanophora roralis*, is sometimes very abundant in New England. This fly was found in some of the animals collected for experimental purposes. Thompson (1934) reviews the Tachnid parasites of woodlice and discusses the role which they play in controlling the numbers of the woodlice. Thompson has long been a student of the effect of parasites in controlling animal populations. He concludes that in England, the parasites are of little importance in controlling numbers of land isopods as the percent of infection is so low, and the reproductive capacity of the host so high. He believes that the important factor controlling numbers is the cannibalistic tendency of the group which is especially dominant when space is at a premium.

If Thompson's conclusions hold in other parts of the world, climate may well be expected to play a more important part in limiting the distribution of woodlice, and in controlling their numbers than does any other factor.

Wintering of Woodlice

Woodlice winter as adults, though the young of the previous summer do not function sexually until the following spring. It is generally stated that they bury themselves in the ground, but the exact distance that they penetrate is not well known. Observations in the Blue Hill Reservation in November and December have shown that Porcellio scaber and Oniscus asellus concentrate under rocks which extend six inches or more below the surface of the soil. O. asellus is found under rocks in damper places than is P. scaber, though the two species often commingle. Six inches must be as deep as many ever go, for at the time these observations were made, the animals were inactive due to the low temperature of the soil.

In Lincoln, observations on Trachelipus rathkei in late October showed that the animals were about two inches below the surface of the soil, and that they were often associated with the roots of the trees.

Porcellio pictus was found in a fairly exposed situation November 25th on the under side of shingles. This was at Lime Rock, R. I. Other individuals were located deep in a pile of debris where they were presumably well protected from the weather.

We shall have occasion to consider the protection against low and high temperatures afforded by soil, snow, trees and other features of the environment. Thus the habits of a species with respect to the choice of a place for wintering over are of great importance in determining its ability to survive.

Habitat Relationships of the New England Oniscoida

Many of the workers on the land isopods have made some mention of the habitats occupied by the various species. The following three investigators should be noted here, because of the extensive nature of their studies. Blake (1931a,b,c) has reported the habits of certain New England species, although he has been chiefly interested in the question of geographical distribution. Dahl (1916 and seq.) has devoted a large section of his monograph on the isopods of Germany to a consideration of habitat, and has composed an unique type of key to the species based largely upon the types of localities frequented. His later papers on the ecological and zoogeographical features of the Oniscoida contain much of interest. Herold (1929 et seq.) has made extensive studies in Pomerania, the East Baltic region, and the islands of the Baltic Sea. Both of the last two investigators have made quantitative collections from various biotopes, and have used this information to determine the dominant species in each type of environment. Conversely they have been able to compare the individual species with respect to habitat preferences. I shall refer to the work of these men more extensively in relation to the factors limiting distribution.

There are three main habitat groups of Oniscoida in New

England. First is the synanthropic group, which in our climate is restricted to environments such as hothouses. In this group fall Armadillidium nasatum, Porcellionides pruinosus, and Cordioniscus stebbingi. Second, we distinguish the halophilous group limited to the sea shore or to salt marshes. Four species are here included: Armadillioniscus ellipticus, Scyphacella arenicola, Ligyda oceanica, and Miktoniscus halophilus. The third group has a less restricted distribution, is not limited to the immediate neighborhood of the ocean, and its members are able to overwinter outdoors in parts of New England.

Since the distribution of the first group in New England depends upon accidental transportation by man, followed by establishment in a warm place, I propose to treat it only incidentally in the following pages.

The second group comes under the influence of climatic conditions, and the distribution of its members along the coast is undoubtedly limited by temperature and by other factors. It is difficult, however, to reduce seashore and inland conditions to a common basis in experimental procedures. There are also practical difficulties involved in collecting and maintaining mass cultures of these forms. Thus I shall also treat the halophilous group only incidentally.

The third group has been the object of special experimental study. I have, therefore, compiled notes on the occurence of its members in the field. Except where acknowledgement is made, all observations are from the writer's field book.

Oniscus asellus

This is a common woodland form in eastern Massachusetts where it is found in many places. Although it lives under logs and leaves, it seems to prefer the underside of stones. On the drier side of its range it is an associate of P. scaber, though it has a tendency to crowd out the latter under moist rocks, and is itself crowded out from favorable drier places. On the moist side of its range its chief associate is Ph. muscorum; in the middle portion, T. rathkei. If collecting is restricted to the under side of rocks, Oniscus generally outnumbers the other two. Deciduous forest is its usual habitat though it occurs in the Blue Hills Reservation in Milton under a beech-oak association in which a young growth of white pine is prospering. Northward, according to Blake, Oniscus becomes synanthropic.

Philoscia muscorum

This is a small active form found peregrinating about moist woods in leaf and twig litter, or sometimes in grass. It may be very abundant. Its habitat overlaps that of Oniscus, though Philoscia is less petrophilous. In swampy places it is found in company with Trichoniscus, while near the ocean it may be taken with Porcellio scaber.

Porcellio scaber

This species is often found in enormous numbers under the bark of old logs which are in contact with the ground. Where such habitats are not available it lives under leaves and stones. It may be found on the seashore where masses of seaweed offer protection. As mentioned above, it is commonly found in company with Oniscus, though it tends to prefer drier places. In the southern part of its range, P. scaber is often associated with Armadillidium vulgare. Towards the north it becomes somewhat synanthropic as is the case at North Conway, N. H. P. scaber may be found in both deciduous and coniferous forest. In New England, very few land isopods are found under conifers, for reasons which are somewhat obscure.

Porcellio pictus

The habitat relationships of this species are quite distinct from those of scaber, and the two species do not occur together. European authors stress the xerophilous characteristics of pictus, but this does not seem to be a constant feature. Certainly pictus cannot withstand extreme dryness, and it does not expose itself during the day, but retires into places where evaporation is not great. It is found under stones, and in stone walls; occasionally in various sorts of litter. The distribution of this species is peculiar in that while it occurs only sporadically, wherever found it is usually abundant. The outstanding feature of its locals is the presence of large quantities of lime, either as a natural outcrop, or as part of a human project. Thus the prediction was made that pictus should be common at the limestone quarry at Lime Rock, R. I. This proved to be true. At Orange, Mass., the species is evidently restricted to the brickwork of a ruined farmhouse, in which there is considerable lime mortar. In general pictus is not found in close association with other species of land isopods, as it has a tendency to climb upward away from the ground. It does not, however, seek out especially xeric situations. Oniscus, Cylisticus, and Trachelipus are often found near colonies of P. pictus.

Trachelipus rathkei

This form frequents moderately moist woodland, and is also common in gardens and under boards. I have found it under rocks on the shore of Lake Champlain, though it usually prefers logs and leaf mould. Inland this is our most common species, and under favorable conditions it may attain great concentration. Near the coast it is less common. Dahl and Herold (ibid.) have considered this species as a sort of biological stopgap, not very aggressive, and multiplying only in less desirable environments where it is less subject to competition from other land isopods. It would seem equally reasonable to consider Trachelipus as a species adapted to conditions for which no other species was suited. In New England Trachelipus is not crowded out by other species, and is often found abundantly in colonies which include such forms as Oniscus and Cylisticus.

Cylisticus convexus

Although Cylisticus has a wide distribution in New England, it is a rather rare species. Its associations among the land isopods have been described above. There is a possibility that this species, like Porcellio pictus, has a high lime requirement, but the evidence in New England is not clear cut. Dahl lists it as a species found in rich calcium soils in Germany. In Maine, according to Blake, this species appears to be always synanthropic. I have found it most abundantly in an abandoned cellar hole at Orange, Mass.

Armadillidium vulgare

In my own collecting I have been unable to acquire many specimens of this species, possibly because most of my searches followed the severe winter of 1933-1934. It is found under logs, boards and stones, and under beach debris on the sea shore.

Trichoniscus demivirgo

This small animal is found in swampy places under leaves and in moss. It is the most definitely hygrophilous of our land isopods, though Philoscia and Oniscus are occasionally found in places just as wet.

PART III

SURVEY OF KNOWN DISTRIBUTION

General Considerations

There exist no modern comprehensive accounts of the distribution of the land isopod species under consideration here. Dollfus (1897b) reviews the records of five species, two of which, Porcellio scaber and Armadillidium vulgare, are of present interest. Except for this contribution the statements in the literature are at best incomplete, and are often misleading. For example, Miss Richardson (1905, p. 622 and p. 666) speaks of both Porcellio scaber and Armadillidium vulgare as being "world-wide" in distribution. It is probable that no species is ubiquitous to this extent. As a matter of fact the two species mentioned have very definitely circumscribed distributions within so small an area as New England, and the same is true in other regions where they occur. A similar inaccuracy is the recording of an animal's habitat as North America, Sweden and the like. Large geographical and political divisions are usually divided into more or less distinct zoogeographical areas, but this fact has not always been recognized. It was necessary, then, to review the literature with special attention to those records which would assist in setting boundaries for the distribution of each species. The difficulties in this task are due to four defects in our present knowledge of zoogeography.

In the first place detailed investigation of the fauna of many parts of the world has never been undertaken. This is especially true of the less showy groups such as the land isopods. On the entire North American continent, New England is perhaps the one place where the distribution of the woodlice is at all well known. In Europe the situation is better due to the work of such students as Budde-Lund, Dollfus, Hellen and Ehrstrom, Sars, Herold, Carl, Verhoeff and others.

The second defect is that of positive errors. These may be the result of wrong identifications, or of incorrect locality references. Such mistakes are very troublesome, as there is no way of definitely disproving them, unless the specimens are at hand for examination. Records which place a species far outside its usual range must be carefully scrutinized.

Undetected synonomy is the third cause of difficulty. When adequate descriptions of the animals are provided, synonomy may be detected. In the case of many early records, however, there will always be doubt as to the actual species given a certain name.

Finally, certain records do not give a correct idea of the mode of occurence of a given species. The mere recording of an animal from a given locality does not necessarily mean that the species can live there under natural conditions. A tropical animal may be found far to the north in a hothouse, but its occurence in an unnatural habitat should always be noted in the record. This is an important factor in the case of the land isopods as certain species are commonly associated with human habitations, while others seem to be restricted to natural habitats.

Method of Reporting Distribution

In the following pages the known distribution of eight species of terrestrial isopods is reported. The records have been carefully studied, and interpreted conservatively in accordance with the principles outlined above. When any record has appeared doubtful, the reasons for questioning it have been fully explained.

Maps have been drawn with the range of each species shown as completely as possible. Two maps are presented for each species except Trichoniscus demivirgo, one showing the world distribution, the other covering only New England. Because of the small scale of the world maps only points close to the limits of distribution are shown. Areas where a species apparently occurs generally,as shown by several records, are evenly shaded. Other areas which appear to be climatically suitable, according to the analysis of Part IV, are stippled. Positive climatic stations of Part IV are indicated by squares and negative stations by crosses. The stippled areas may be considered as the major regions of predicted future distribution, though no rigorous search has been conducted for small local areas which might prove suitable.

The known distribution of the eight species treated here is reported by grand divisions, countries, and cities. Where there are many places recorded only characteristic ones are given. No attempt has been made, therefore, to track down the large number of early records made at the very beginning of zoological science, when later papers have adequately and more completely treated the subject. Likewise, no effort is made to duplicate the extensive synonomy which may be found in Budde-Lund (1885), and Richardson (1905). Credit is given in each case to the original author. If the original paper has not been seen, the name of the author from whom the citation is taken follows within parentheses.

Distribution of Individual Species

Trichoniscus demivirgo Blake

This species which was described by Blake in 1931 has been reported only from New England, but may have been identified in other localities as Trichoniscus pusillus which it closely resembles.

Maine: Bar Harbor (Biol. Surv. Mt. Desert Reg. 1933), Woolwich (Blake, unpublished).

Massachusetts: Middlesex Fells (type locality), Boston, Sharon, Woods Hole, Nantucket (Blake, 1931). Duxbury, Milton (new records).

Rhode Island: Lime Rock (around upper rim of lime quarry) (new record).

Oniscus asellus Linne

Europe

Norway: Oslo, Langesund, Kragerö, Grimstad, Trondhjem (Sars, 1896).

Sweden: (Johnsson, 1858: Budde-Lund, 1885).

Finland: Castelholm (Cajander; Hellen and Ehrstrom, 1919).

Several other localities in hothouses.

East Baltic Region: Synanthropic over entire range (Herold, 1930).

Germany: Spreads over entire country, but is most common in the west. It becomes synanthropic in the east. (Dahl, 1916).

North Alps up to 1000 meters. (Verhoeff, 1917a).

Denmark: Over all Denmark where there is sufficient moisture. Often about dwellings. (Meinertz, 1934).

Netherlands: (Hoek, 1888).

France: Normandy (Maury, 1931). All north and central France. In the mountains (Col de Cucheron) up to 1300 meters. (Dollfus, 1899).

Great Britain: Generally in England, Wales, Scotland and Ireland (Webb and Sillem, 1906). Orkney and Shetland Islands, Isle of Wight, Isle of Man (Collinge, 1917).

Spain: Madrid (de Buen; Dollfus, 1892b). Villa Rutis, Guetaria, Fuentarrabia (Dollfus, 1892b). Alsasua (Simon; Budde-Lund, 1885). Absent from Mediterranean region according to Dollfus.

Switzerland: Malans, St. Anthony's Valley (Am Stein; Carl, 1908). Visp, Montreux, (Verhoeff; Carl, 1908). Abundant in central valley. Vertical limit at about 1200 meters (Carl, 1908).

Oniscus asellus

Italy: Sicily (Mus. Petrograd; Budde-Lund, 1885). There is some doubt as to this record as O. asellus has never been reported from any other Mediterranean locality.

Hungary: Rare in this country (Dollfus, 1901).

Austria: Plank (Verhoeff, 1917b).

Russia: Kamienitz-Podolski (Belke; Budd-Lund, 1885). The most easterly occurence known to Budde-Lund.

North America

Canada: Ontario: Niagara (Stuxberg, 1876; Johansen, 1922). Toronto (synanthropic) (Walker, 1927). London (Ross, 1914; Walker, 1927). New Brunswick: Shediac (Johansen, 1928). Nova Scotia: Pictou, St. Mary's Bay (Johansen, 1928). Quebec: Quebec (Johansen, 1922), Hemmingford (synanthropic) (Walker, 1927). Newfoundland: Quidi Vidi Village (Stuxberg, 1873; Johansen, 1922).

United States: Illinois: Rock Island; New York: New York, Syracuse, Schenectady; Pennsylvania; New Jersey; Richardson, 1905).

Atlantic Islands

Azores: San Miquel (Budde-Lund, 1885).

Faroes[1]: Transgjisvaag (small size). (Dollfus, 1893a).

---

[1] Dollfus reported this locality as Iceland, but there is no Transgjisuaag in that country. In the same paper he records P. scaber from Thorshaon, Iceland, although no such town is listed in Ritter's Lexicon. Both Transgjisvaag and Thorshaon are in the Faroe Island group, and it is probable that Dollfus made a mistake in the location of these two cities.

New England

Maine: Freeport (Rathbun, 1905), Mt. Desert Island, Jonesport, (Biol. Surv. Mt. Desert Reg., 1933), Blue Hill, Farmington (Blake, 1931). According to Blake this species is definitely synanthropic north of Boston.

New Hampshire: Center Harbor (Blake, 1931), Sanbornville (synanthropic) (new record).

Vermont: North Ferrisburg (new record).

Massachusetts: Very common over all eastern part of state. The most westerly localities recorded from this state are Princeton (over 1200 ft.) and Sudbury (Blake, unpublished). Oniscus is somewhat rare in these places.

Ipswich, Lincoln, Braintree, Weymouth, Duxbury (new records).

Rhode Island: Providence (Rathbun, 1905). Glocester (rare), North Rock (extremely abundant in fields under logs) (new record).

Connecticut: New Haven (Kunkel, 1918). Manchester, Danielson (Blake, unpublished).

Philoscia muscorum Scopoli

Three varieties of this species have been described.

Var. muscorum Verhoeff - Distributed throughout Italy, Switzerland, and in Wurttemberg.

Var. sylvestris (Fabricius) - Northern Germany, North America.

Var. algirica Dollfus - Algeria and other north African localities.

It is, of course, very likely that each of these varieties is distinct physiologically as well as morphologically. For that matter physiological races may exist within any one morphological variety. For this reason due conservatism must be exercised in applying experimental data obtained with a particular stock to the distribution of the whole species.

Africa

Var. algirica

Algeria: Abundant (Meinert; Budde-Lund, 1885). Algiers, Fort l'Empereur (Dollfus, 1896). Edough (E. Simon; Dollfus, 1896).

Europe

Var. sylvestris

Norway: Extremely rare in Norway. Taken at Brevik and Langesund (Sars, 1896).

Sweden: Not on mainland. (Budde-Lund, 1885).

East Baltic Region: Extremely rare. Dubenalken (Herold, 1930).

Germany: Pomerania, Hiddensee, Lübeck (Herold,1929,1932,1933) West Germany as far east as Danzig. Most common near the coast but not limited to it. (Dahl, 1916a). Var. muscorum in the north Alps to an altitude of 700 meters. (Verhoeff, 1917a).

Denmark: Very abundant, especially on the islands and in East Jutland. Uncommon in West Jutland (Meinertz, 1934).

Netherlands: (Hoek, 1888).

Philoscia muscorum

France: Normandy (Maury, 1931). Common in all France, especially in the north. Southern localities, Nice, Isle St. Honnorat, Beziers, Mastia, Hendage, Biarritz, Fountaine de Mouraie, Cimiez (Dollfus, 1899).

Great Britain: England, Scotland, Ireland (Webb and Sillem, 1906). Wales, Channel Islands, Isle of Wight, Orkney Islands (Collinge, 1917).

Spain: Montserrat, Gualba, Lloret, Hostalet de Bas, Les Font, St. Pere de Vilamajor, Font de Cay Surell, Riera Vallestrins, Montseny (up to 800 meters), Lagarra (Arcangeli, 1924). Guetaria (Dollfus, 1892b).

Switzerland: Limited to regions with a mild climate which are accessible to southern and western immigrants. In the south Tessins, the lower Leman basin, and the lower Puschlavs (Carl, 1908).

Italy: Sardinia (Dauny; Dollfus, 1897a), Naples (probably all the Apennines), Istria, Carniola (Dollfus, 1897a). Castelmarte-Lombardy, Valsalice-Turin, Rapallo, Capaccio-Salerno, Nizza, Collina di Spezia, Isola Tino, Usseglio (Tua, 1900). Island of Sicily (Dollfus, 1896). Verhoeff (1933) considers this species to be limited to northern and middle Italy. On the Apennine peninsula it is found between 250 and 1300 meters.

Jugoslavia: Hercegovina: Draceo (Dollfus, 1896a).

Russia: Kamienitz-Podolski (Belke; Dollfus, 1901).

Philoscia muscorum

North America

United States

New Jersey; New York (Richardson, 1905).

New England

Maine: Mt. Desert Island (Biol. Surv. Mt. Desert Reg., 1933), Blue Hill (Blake, 1931), Nobleboro (Blake, unpublished).

Massachusetts: All along the coast extending inland about ten miles. Cape Cod (various localities), Nantucket, Martha'a Vineyard (Blake, 1931). Ipswich, Lincoln, Blue Hill Reservation (new records.

Rhode Island: Riverview, Newport (Blake, 1931).

Connecticut: Stony Creek (Harger, 1880).

Cylisticus convexus (DeGeer)

Europe

Norway: Oslo, Drobak, Skien, Kragerö (Sars, 1896).

Sweden: (Johnsson, 1858; Budde-Lund, 1885).

Finland: Kastelholm, Dalsbruck (Cajander; Hellen and Ehrstrom, 1918), Ekstensholm, Helsingfors, Sveaborg, associated with human habitations, (Hellen and Ehrstrom, 1918).

East Baltic Region: Spreads over entire region (Herold, 1930).

Germany: Pomerania (Herold, 1929). All Germany, but rare towards the north (Dahl, 1916a).

Denmark: Entire country,especially near the coast. (Meinertz, 1934).

Netherlands: (Hoek, 1888).

Cylisticus convexus

France: Havre (Maury, 1931). Common near houses and in gardens over nearly all France, especially in the east and southeast. Ault, Naours, Lyons-la-Foret, Paris, Marlotte, Saoultzbad, Vialle, Marseilles, Goulon (Dollfus, 1899).

Great Britain: England, Scotland and Ireland (Webb and Sillem, 1906).

Switzerland: Rare in the central region and in the foothills of the Alps. Found in the large broad river valleys with alluvial deposits such as the Rhone valley and the Rhine valley. Altitude limit about 1250 meters. Often synanthropic (Carl, 1908).

Italy: Valtravaglia-Lombardy (Tua, 1900). Mt. Titano-San Marino (most southerly record in Italy). On the Apennine peninsula C. convexus occurs between the altitudes of 280 meters and 500 meters (Verhoeff, 1933). Bergamese Alps (Verhoeff, 1931b).

Hungary: Budapest, Monor, Papa, Velejte, Dicso-Szent-Marton (Dollfus, 1901). Very abundant according to Dollfus.

Austria: Plank (Verhoeff, 1917b).

Rumania: Divitaschka Cave near Lowetch, Belowo, Drenowski-Kloster, Suchata Cave near Tirnowo (Verhoeff, 1929).

Albania: (Arcangeli, 1931).

Russia: Chersonesus (in the Crimea) (Budde-Lund, 1885).

Turkey: (Budde-Lund, 1885).

Cylisticus convexus

North America

Canada: New Brunswick: St. Andrews, Fredericton, (Wallace, 1919; Johansen, 1922). Shediac (Johansen, 1929). Nova Scotia: Pictou (Johansen, 1929). Quebec: Hemmingford (Walker, 1927). Ontario: Niagara (Stuxberg, 1876; Johansen, 1922). Brockville, Belleville, Humber Valley, Lake Simcoe, Long Point on Lake Erie. Next to T. rathkei the commonest woodlouse in eastern Canada (Walker, 1927).

United States: District of Columbia; Illinois: Rock Island; Michigan: Saginaw; New Mexico: Las Vegas Hot Springs; New York: New York, Syracuse, Norwich, Piseco; Ohio: Westwood, Devils Backbone in Hamilton Co., Cincinnati, Miami Grove, Springfield. (Richardson, 1905).

New England

Maine: Mt. Desert Island, Jonesport (Biol. Surv. Mt. Desert Reg., 1933), Blue Hill, Strong, Gilead (Blake, 1931), Bluff Island (Norton, 1909), Greene(Blake, unpublished). According to Blake this species is synanthropic in Maine.

Vermont: No. Ferrisburg (new record).

Massachusetts: Warwick (Richardson, 1905), Prides Crossing, Roxbury, Needham, Dennis, Woods Hole (Blake, 1931). Annisquam (Blake, unpublished). Orange (new record)

Connecticut: New Haven (Kunkel, 1918), Mansfield, Pomfret (Blake, unpublished).

Porcellio pictus Brandt

Europe

Norway: Oslo, Trondhjem (Sars, 1896).

Sweden: As far as Upsala (Johnsson; Budde-Lund, 1885).

Finland: Lojo, Hango, Helsingfors, Kirjola, Kokkola (Hellen and Ehrstrom, 1919).

East Baltic Region: All over this area (Herold, 1930).

Germany: Throughout Germany (Dahl, 1916). Limiting altitude in the German Alps is 1000 meters. (Verhoeff, 1917a).

Denmark: All over country. Seldom free living in the neather region of Jutland. (Meinertz, 1934).

France: Nancy, Paris, Havre, Lyons-la-Foret, Sologne, Pont du Gard, Orange (Dollfus, 1899).

Great Britain: Generally in England, Scotland, Ireland (Webb and Sillem, 1906). Also Wales, Channel Islands, Isle of Man, Isle of Wight (Collinge, 1917).

Switzerland: Over entire country to an altitude of 1500 meters. Less common in lower parts of country. (Carl, 1908).

Italy: Cevasco, Colle di S. Giovanni-Turin (Tua, 1900). Limited to Piedmont and Liguria (Verhoeff, 1933).

Austria: Plank (Verhoeff, 1917b).

Hungary: Pest (Budde-Lund, 1885).

Russia: Leningrad, Kieff, Saraisk (Budde-Lund, 1885).

North America

Canada: Ontario: Rockcliffe, Ottawa (Johansen, 1922), Niagara (Stuxberg, 1876; Johansen, 1922), Belleville, Toronto (Walker, 1927). Quebec: Hemmingford (Walker, 1927).

Porcellio pictus

United States: New York: Niagara, New York City (Richardson, 1905).

New England

Maine: Hampden (Blake, 1931), Acton (new record).

New Hampshire: North Conway (new record).

Vermont: Larrabees Point (Blake, 1931), No. Ferrisburg (new Record).

Massachusetts: Dover, Sudbury (Blake, 1931). Groton, Attleboro Falls, Princeton (Blake, unpublished), Orange (new record).

Rhode Island: Wickerford (Blake, 1931). Glocester, Tiverton Four Corners (Blake, unpublished), Lime Rock (new record).

Connecticut: Goshen (Rathbun, 1905), New Haven (Kunkel, 1918).

Porcellio scaber Latreille

Africa

South Africa: Cape of Good Hope (Budde-Lund, 1885).

Asia

Siberia: Kamschatka (Budde-Lund, 1885).

Ceylon: Nuwara Eliya (E. Simon; Dollfus, 1897b). The Altitude of this place is 6,188 feet.

Japan: Sapporo (coll. R. Takasashi; Arcangeli, 1927).

Australasia

Australia: Melbourne (Dollfus, 1897b), Sydney (Webb and Sillem, 1906).

Tasmania: (Webb and Sillem, 1906).

Porcellio scaber

New Zealand: Port Chalmers (Chilton; Dolfuss, 1897b).

Europe

Norway: Oslo, Trondhjem, Sausund, Lofoten Islands, Finmark (commonest species in Norway), (Sars, 1896).

Sweden: (Johnsson; Budde-Lund, 1885).

Finland: Eckero, Jomala, Helsingfors, Bjorneborg, Vasa, Muonio, Oevertornea, Kola, extends up to 69° N. L. (Hellen and Ehrstrom, 1919).

East Baltic Region: Islands of Dago, Oesel, Moon and Worms. Absent from the mainland except from favored locations near the coast (herold, 1930).

Germany: All Germany, but more common in the western portion (Dahl, 1916b). Limiting altitude in the German Alps at 1000 meters. (Verhoeff, 1917a).

Denmark: All over Denmark. Free living in the heather region. (Meinertz, 1934).

Netherlands: (Hoek, 1888).

France: Normandy (Maury, 1931). Extremely common in all France except in the Mediterranean region. Not found above 1300 meters in France. (Dollfus, 1899).

Great Britain: Very common in England, Ireland and Scotland (Webb and Sillem, 1906). Wales, Channel Islands, Isle of Man, Isle of Wight, Outer Hebrides, Orkney and Shetland Islands (Collinge, 1917).

Spain: Gijon, Vigo, Villa Rutis (Coruna), Potes, Fuenfria, limited to northern provinces (Dollfus, 1892). San

Sebastian, Terruel (mountainous region) (Dollfus, 1893b). Esterri and surroundings (1000-13000 meters), other localities in Province of Lerida (Arcangeli, 1926).

Portugal: Porto (Dollfus, 1897b).

Switzerland: Found all over Switzerland where it is limited to altitudes below 1200 meters. (Carl, 1908).

Italy: Valtraglia (Tua, 1900). Limited to Piedmont and Liguria (Verhoeff, 1933). Bergamese Alps (Verhoeff, 1931b).

Hungary: Uj-Pest, Papa, Uj-Banya, Bodajk (Dollfus, 1901). Transylvania (Dollfus, 1897b).

Austria: Plank (Verhoeff, 1917b), Vienna, Salzburg (Dollfus, 1897b).

North America

Canada: Prince Edward Island: Tyne Valley; Nova Scotia: Truro, St. Mary's Bay, Scott Bay (Johansen, 1929); Bew Brunswick: St. Andrews (Walker, 1927), Grand Menan (Richardson, 1905); Anticosti Island (Johansen, 1924); Magdalen Island (Richardson, 1905); Ontario: Belleville, Toronto (rare), Long Point on Lake Erie (Walker, 1927); British Columbia: Vancouver Island, Victoria (common) (Walker, 1927), Comax, Gabriola Island (Richardson, 1905).

United States: Florida: Key West (doubtful); Indiana; Lake Maxinkuckee; Maryland: Woodside; Michigan: Saginaw; New Jersey: Ocean Grove; New York: New York, Westfield; Ohio: Norwood, Anderson's Ferry, Cincinnati; Pennsylvania; Virginia;

Porcellio scaber

California: San Diego, Oakland, Colfax, Crescent City, Lagonistas Creek, San Pedro (doubtful), San Francisco (Richardson, 1905); Oregon: Dalles (Dollfus, 1897b).

Var. americanus[1]: California: San Mateo (Arcangeli, 1932).

Mexico: Tusitlan (near Perote), Cordoba (Saussure; Budde-Lund, 1885).

Atlantic Islands

Greenland: Frederikshaab (Fabricius, 1780; Budde-Lund, 1885)[2].

Iceland: Oefjord, various localities (Moeller and Halgrimson; Budde-Lund, 1885).

Faroes[3]: Thorshaun, (Dollfus, 1893a).

St. Pierre and Miquelon: (Dollfus, 1897b), St. Croix (Budde-Lund, 1885).

Canary Islands: (Dollfus, 1897b).

---

[1] Ordinary specimens of Porcellio scaber were found by Blake to vary among themselves in much the same way as Arcangeli's variety americanus. He concludes that the variety, even if distinct, has no geographical significance. The same is true of the many color varieties of P. scaber which have been described.

[2] Concerning this record we may note the remarks of Stephenson (1917). (Author's translation). "O. Fabricius reported Oniscus asellus from Greenland. What species this actually was cannot now be determined with certainty, for never since have land isopods been found in Greenland. H. J. Hansen (1887, p. 224), mindful of this, states that Fabricius' specimens were surely introduced. Budde-Lund was of the opinion that they actually must have been Porcellio scaber."

It is quite possible that some species was introduced but was never able to establish itself.

[3] See footnote, page 29.

Porcellio scaber

Ascension Island: (Budde-Lund, 1885), Inaccessible Island, Triston d'Acunha (Challenger Expd., Dollfus, 1897b). The Bermudas (Richardson, 1905). St. Helena (Mus. Comp. Zool., Harvard).

South America

French Guiana: Cayenne (Miers, 1877; Budde-Lund, 1885)[1].

Chile: (Dollfus, 1897b).

Pacific Islands

Juan Fernandez (Challenger Expedition; Dollfus, 1897b).

Hawaii: (British Museum; Webb and Sillem, 1906).

Indian Ocean Islands

St. Paul[2]: (Novara Exped., Budde-Lund, 1885).

New England

Maine: Freeport (Rathbun, 1905), Mt. Desert Island, Jonesport, Beals Island (Biol. Surv. Mt. Desert Reg., 1933), Portland, Saco Bay, Muscongus Bay, Matinicius (Norton, 1909). Acton (new record).

New Hampshire: Rye Beach (Blake, unpublished), North Conway, (new record) (synanthropic).

---

[1] This record concerns a species described by Miers as Porcellio cayennensis of which he says: "As the external antennae are wanting, it must be a matter of uncertainty whether this species is to be referred to this genus or to Oniscus". According to Budde-Lund, the specimens are not distinct from P. scaber. The climate in this part of South America is so different from that normal for P. scaber, that we may very well doubt a record which is none too good anyway.

[2] Erroneously considered St. Paul Island, Alaska, by Johansen (1922).

Porcellio scaber

Massachusetts: Very abundant in all eastern parts of state, on Cape Cod, Nantucket Island, etc. Inland records are: Lawrence (Rathbun, 1905), Sudbury (Blake, 1931). Apparently absent from central and western portion of state.

Rhode Island: Wickford (Blake, 1931), North Tiverton, Tiverton Four Corners, Sakonnet (Blake, unpublished), Ashton (new record).

Connecticut: West Haven (Rathbun, 1905), New Haven (Kunkel, 1918), Mansfield, Manchester, Putnam (Blake, unpublished).

Trachelipus rathkei (Brandt)

Asia

Transcaucasus: Daratschy-Tschack (Budde-Lund, 1885).

Europe

Norway: Oslo, Drøbak, Skien, Frederikstad, Kragerø (Sars, 1896).

Sweden: (Johnsson; Budde-Lund, 1885).

Finland: Dagero, Hango, Westerlund, Helsingfors, Viborg, Jaakimvaara, Ladoga, Slumgu and other localities (Hellen and Ehrstrom, 1919).

East Baltic Region: Extends over entire region and to the east. (Herold, 1930).

Germany: Over all Germany, but more abundant in the eastern part than in the western part (Dahl, 1916a). Limiting altitude in the German Alps, 850 meters. (Verhoeff, 1917).

Trachelipus rathkei

Denmark: Abundant in East Jutland and the Danish islands (Meinertz, 1934).

Netherlands: Moderately common (Hoek, 1888).

France: Common in middle France, Paris, Chaville, Ableiges, Compeigne, Beaumont-sur-Oise, Chaumont-en-Vexin, Rouen, Blois, Cadillac, Alsace (Dollfus, 1899).

Great Britain: England (Webb and Sillem, 1906), Isle of Wight, (Collinge, 1917a); Scotland (rare) (Collinge, 1917b).

Switzerland: Found in the Swiss Hugelland and in the lower regions of the Jura. Does not go up into the high valleys. Highest point is Airolo-Val Piora, 1179 meters. Replaced in the southern cantons of Tessin and Bergell by the variety transalpina Carl.

Italy: Montcalieri-Turin (Tua, 1900). Limited to Piedmont and Liguria (Verhoeff, 1933).

Jugoslavia: Sarjevo, Dervent, Pozareyac (Dollfus, 1896a).

Austria: Plank (Verhoeff, 1917b).

Hungary: Budapest, Uj-Pest, Papa, Mezo-Zah, Dicso-Szent-Marton, Brasso (Dollfus, 1901).

North America

Canada: New Brunswick: Chatham, Shediac (Johansen, 1922), St. Andrews, Fredericton (Wallace, 1919; Johansen, 1922); Nova Scotia: Pugwash, Pictou, Truro, Halifax, Little Lake, Avenport, Scott Bay (Johansen, 1928: Prince Edward Island: Tyne Valley (Johansen, 1928); Quebec: Quebec, Montreal, East-man, Hemmingford, Covey Hill (Walker, 1927); Ontario: Ottawa, St. Josephs Island in Lake Huron (Johansen, 1922), Toronto, Camperdown, Brockville and other points (Walker, 1927). Commonest woodlouse of eastern Canada, but limited to settled districts. Absent, although carefully searched for from Lake Nipigon district, Lake Abitibi, and Godbout on the northern side of the lower St. Lawrence River. (Walker, loc. cit.)

United States: Georgia: St. Mary's; Michigan: Saginaw; New York: Chaumont, Syracuse, New York; Ohio: Springfield, Lockland, Columbus, Clifton, Cincinnati; Texas: Victoria; (Richardson, 1905).

New England

Maine: Freeport (Rathbun, 1905), Portland, Westport, Washington Junction (Norton, 1909), Mt. Desert Island, Jonesport, Beals Island, (Biol. Surv. Mt. Desert Reg., 1933), Blue Hill, Newport, Farmington, Strong, Silver Ridge Plantation, Greenville, Dover-Foxcroft, Alton, Harmony, Holden, Green and others (Blake, 1931 and unpublished), Acton (new record).

New Hampshire: Lancaster, Glen, North Woodstock, Center Harbor, (Blake, 1931), Fitzwilliam, Auburn, (Blake, unpublished), North Conway (new record).

Vermont: Guildhall, Wolcott, Charlotte (Blake, 1931), Brattleboro (Blake, unpublished), North Ferrisburg (new record).

Massachusetts: Lawrence, Lanesboro (Rathbun, 1905), Salem, Beverly (Richardson, 1905), Boston, Sudbury, Sharon,

Trachelipus rathkei

Williamstown (Blake, 1931), Groton, Annisquam, Ipswich, Greenfield, Northampton, Sturbridge, East Holliston, Canton, Norton, Attleboro Falls, West Bridgewater, Norfolk, Dighton, Taunton, Pittsfield and others (Blake, unpublished), Orange, Lincoln (new records).

Rhode Island: Providence (Rathbun, 1905), Riverview, Smithfield (Blake, 1931), Lime Rock (new record).

Connecticut: New Haven (Kunkel, 1918), Kent (Blake, 1931), Pomfret, Mansfield (few), Manchester, Washington, Bantam (Blake, unpublished).

Armadillidium vulgare (Latreille)

Africa

Algeria: Algiers (E. Simon; Dollfus, 1896), Oran (Dollfus, 1896).

Morocco: Rabat (abundant) (Schlumberger; Dollfus, 1896).

Egypt: (Budde-Lund, 1908; Verhoeff, 1931).

Asia

Syria: Damascus (Barrois; Dollfus, 1897b).

Palestine: (Verhoeff, 1923).

China: Wu-Chang, Wu-hu, Hankow (Arcangeli, 1927).

Japan: Kobe, Tokio, Kamakura (Arcangeli, 1927).

Australasia

Australia: Melbourne (Shaufuss; Budde-Lund, 1885).

Europe

Norway: Near Frederikshald (Sars, 1896).

Sweden: (Johnsson; Budde-Lund, 1885).

Armadillidium vulgare

Finland: Abo (Cajander; Hellen and Ehrstrom, 1919), Lojo (Hellen and Ehrstrom, 1919).

Germany: Extends over the entire country though less common in the north. Abundant in the vineyards of the Rhine and in Wurttemberg (Dahl, 1916a). Limiting altitude in the German Alps at 1000 meters (Verhoeff, 1917a).

Denmark: On most of Danish islands. Replaced on Bornholm by A. opacum. Rare in Jutland. (Meinertz, 1934).

Netherlands: (Hoek, 1888).

France: Common in all France except in the high mountains (Dollfus, 1899).

Great Britain: Many localities in England, Scotland and Ireland (Webb and Sillem, 1906), Wales, Channel Islands, Isle of Wight (Collinge, 1917a).

Spain: Abundant in all Spain (Dollfus, 1892), Montserrat, Gualba, S. Pere de Vilamajor, various other localities near Barcelona, Montseny up to 600 meters. (Arcangeli, 1924).

Portugal: Cap Sagres (Dollfus, 1897b).

Switzerland: Locally distributed in protected valleys. Vertically it extends up the south slope of Wallis to 1200 meters, but in general it reaches its limit as 1000 meters. (Carl, 1908).

Italy: Randazzo-Etna, Cosena, S. Cataldo-Lecca, Capaccio, Salerno, Asinara, Sassari, Spezia, Rivarassa-Piedmont, Sagra di S. Michele, Turin, Nizza, Otrento (Tua, 1900), all Italy (Verhoeff, 1933). Sicily (Dollfus, 1896).

Armadillidium vulgare

Jugoslavia: Sarajevo, Ivan, Gacho, Stolac (Dollfus, 1896), Dalmatia (Dollfus, 1897b).

Hungary: Budapest, Bodajk, Papa and others. Probably common in all Hungary (Dollfus, 1901).

Austria: Vienna (Dollfus, 1897b), Plank (Verhoeff, 1917b).

Bulgaria: Berendo-Izwor (West Bulgaria), Euxinograd near Achtopol, south of Burgas on the Black Sea (Verhoeff, 1929).

Greece: Athens, Isle of Corfu, Le Korak, Nicaria, Island of Samos (Dollfus, 1897b).

Albania: (Dollfus, 1897b).

North America

United States: California: San Mateo, Los Angeles; Kentucky: Lexington; Louisiana: New Orleans; Maryland: Woodside; Mississippi: Canton; New Jersey; New York: Bay Shore, Syracuse; Ohio: Many localities; Pennsylvania: South Carolina: Aiken, Charleston; Virginia: Berkley; District of Columbia; (Richardson, 1905), Tennessee (Mus. Comp. Zool., Harvard).

Atlantic Islands

Madeira (Bronniche; Budde-Lund, 1885); Bermudas (Challenger Exped.; Dollfus, 1897b); Azores; Canaries; (Dollfus, 1897b).

South America

French Guiana: [1]Cayenne (Miers; Budde-Lund, 1885).

Chile: Valparaiso (Dollfus, 1897b)

---

[1] Miers considered this record very doubtful. In the vial with these specimens of A. vulgare purporting to come from Cayenne was a European millipede Glomeris marginata Oliver. As the consignment of material which he studied included some European material, it is quite possible that the wrong locality was assigned to these specimens.

Armadillium vulgare

Uruguay: Montevideo (Sörensen; Budde-Lund, 1885).

Argentine: Buenos Aires (Borelli; Dollfus, 1897b).

New England

Massachusetts: Salem (Richardson, 1905), Nahant, Cambridge, Wellfleet, Boston, Brookline, Mattapoisett, Mashpee, Woods Hole, Edgartown (Blake, 1931), Nantucket, Marion (Blake, unpublished), Duxbury, Milton, Weymouth (new records).

Rhode Island: Providence (Rathbun, 1905), Riverview, Wickford, (Blake, 1931).

Connecticut: New Haven (Kunkel, 1918).

Summary of Geographic Survey

It will be noted at once that all the species treated except Trichoniscus demivirgo occupy two centers: middle Europe and Eastern United States. Since there is a great variety of closely related species in Europe, it is probable that the seven other species under consideration originated there. Out of the hundreds of species native to Europe, these seven and a few others such as Porcellio laevis and Porcellionides pruinosus have been able to spread over a large part of the northern hemisphere. Just why certain species have remained endemic while others have been able to colonize new regions is not entirely determined. Trichoniscus demivirgo has close relatives in Europe and in western North America, but it is apparently endemic in the eastern United States and possibly in eastern Canada.

Some species have been able to establish themselves outside of the two centers mentioned above. Most noteworthy in this respect are Porcellio scaber and Armadillidium vulgare. Both are found on the Pacific Coast of North America, In Australia, and on various islands all over the world. Dollfus (1897b) considered the distribution of Porcellio scaber to be one of the most difficult of zoogeographical puzzles. His statement that P. scaber could not have been transported to such islands as Tristan d'Acunha by means of ships seems to have been made without adequate basis. Nevertheless, the possibility of transportation on floating logs, while improbable, is not impossible, especially for P. scaber which is frequently found on the sea shore. Certainly most of the records of A. vulgare and P. scaber in distant corners of the world have resulted from transportation by man.

Since we are not primarily concerned with means of dispersal of these animals, but rather with the effect of climate on their establishment, we shall pass on to a study of the climatic indices of the various species. It will be noted from the maps that the reported distribution of no two species is precisely similar, and that there are great differences between certain pairs. Allowing for inaccuracies in the maps, the northern boundaries of most species are known in both North America and Europe. The southern boundaries are only poorly known in North America, but are shown fairly well in Europe. Neither the eastern boundary in Europe, nor the western limit in the United States and Canada is at all well known. The data available make it possible to study the effects of temperature on limiting distribution, but the effect of rainfall cannot be determined as accurately since critical data near the boundaries of low rainfall areas are lacking. This will be evident from Map 3 which shows the mean annual rainfall over the earth.

Additional Records

Since compiling the above list, the following records have come to attention.

Oniscus asellus - Garberville, Calif. (Blake, unpublished).

Philoscia muscorum - Hilton Road and Mid-Illovo, Natal (Collinge, Barnard 1930).

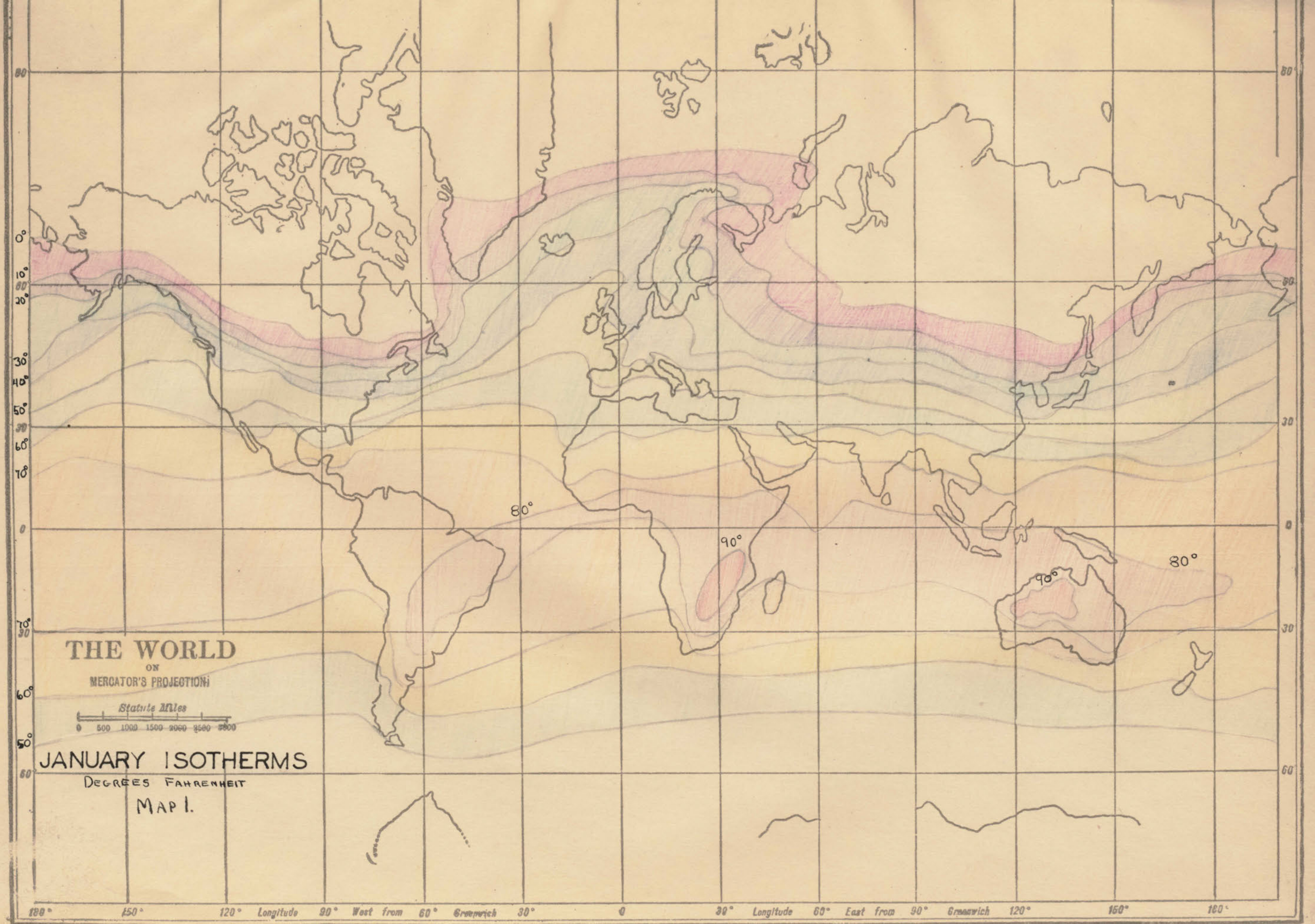
Porcellio scaber - Denver, Colorado. (Specimens from General Biological Supply Co. det. C. H. Blake.)

Armadillidium vulgare - Cape Town (Barnard, 1930).

These interesting records do not in any way change the previously determined climatic indices. In fact, they confirm the probable distributions predicted from previous observations.

Explanation of Symbols Used on Maps 5-19

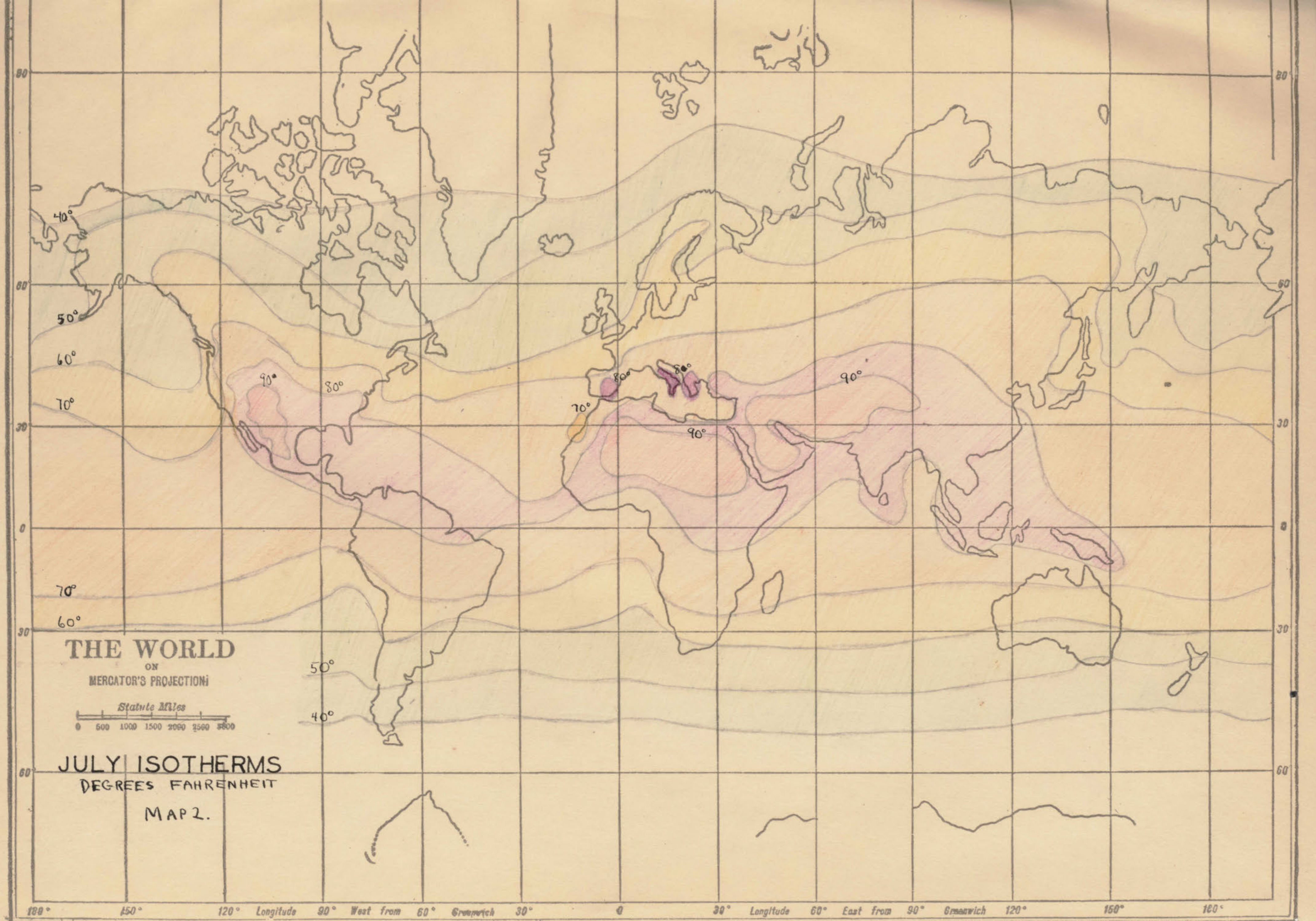
▓	Area of known distribution
•	Locality records
□	Climatic Stations in area of known distribution
×	Climatic Stations where species is probably absent based upon negative results of collectors.
░	Area of predicted distribution based upon climatic factors.



JANUARY ISOTHERMS

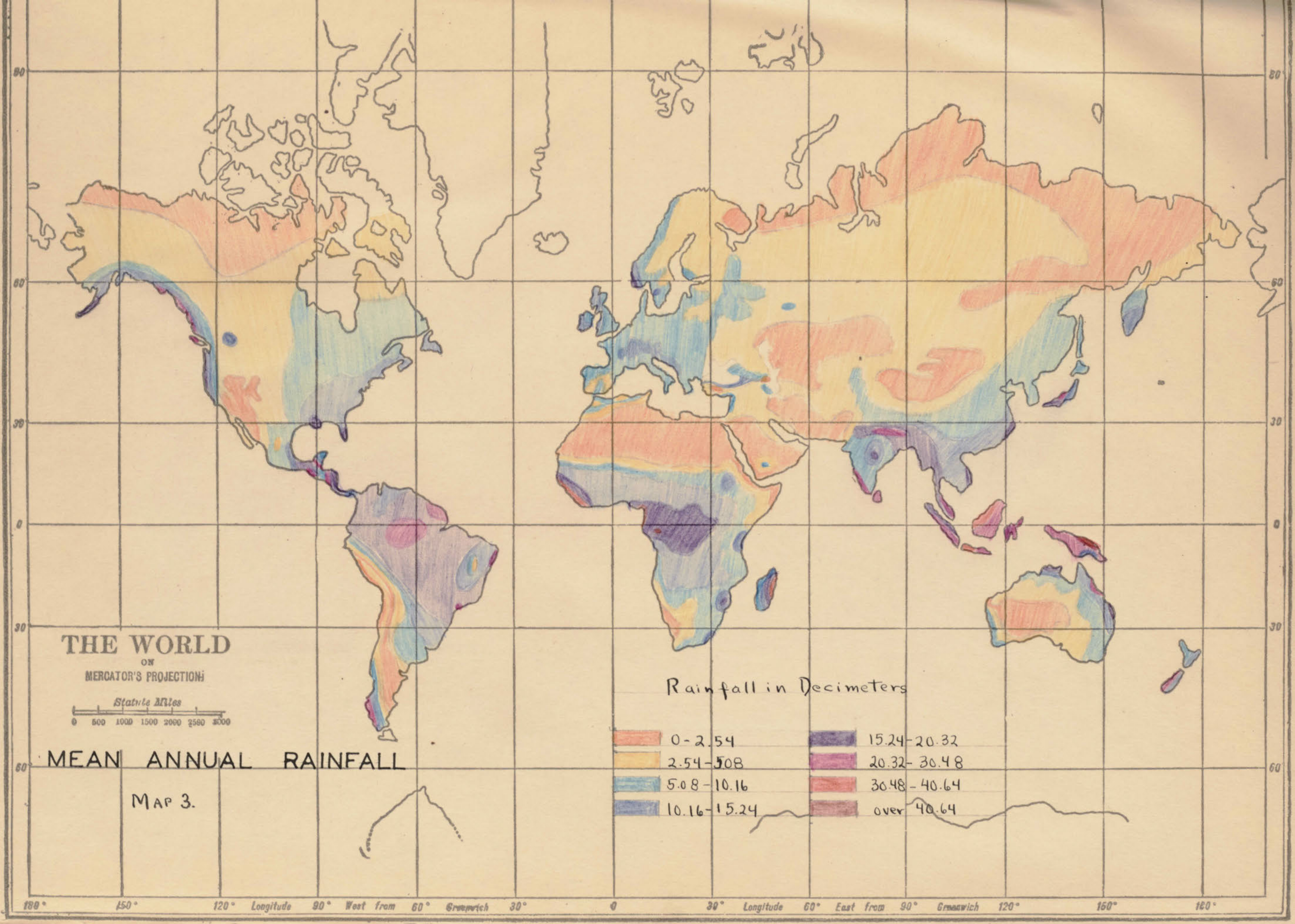
DEGREES FAHRENHEIT

MAP I.



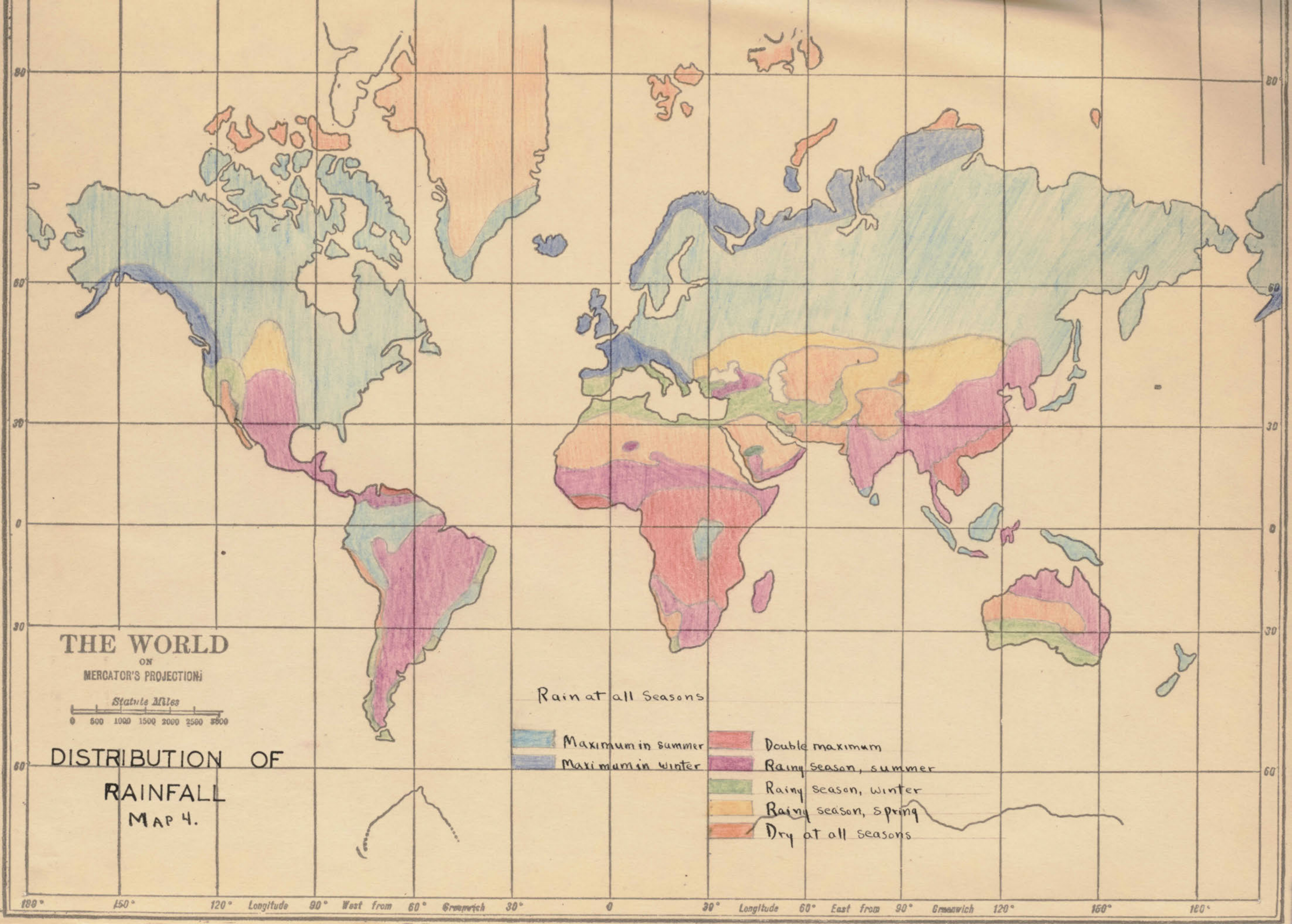
THE WORLD
ON
MERCATOR'S PROJECTION

JULY ISOTHERMS
DEGREES FAHRENHEIT
MAP 2.



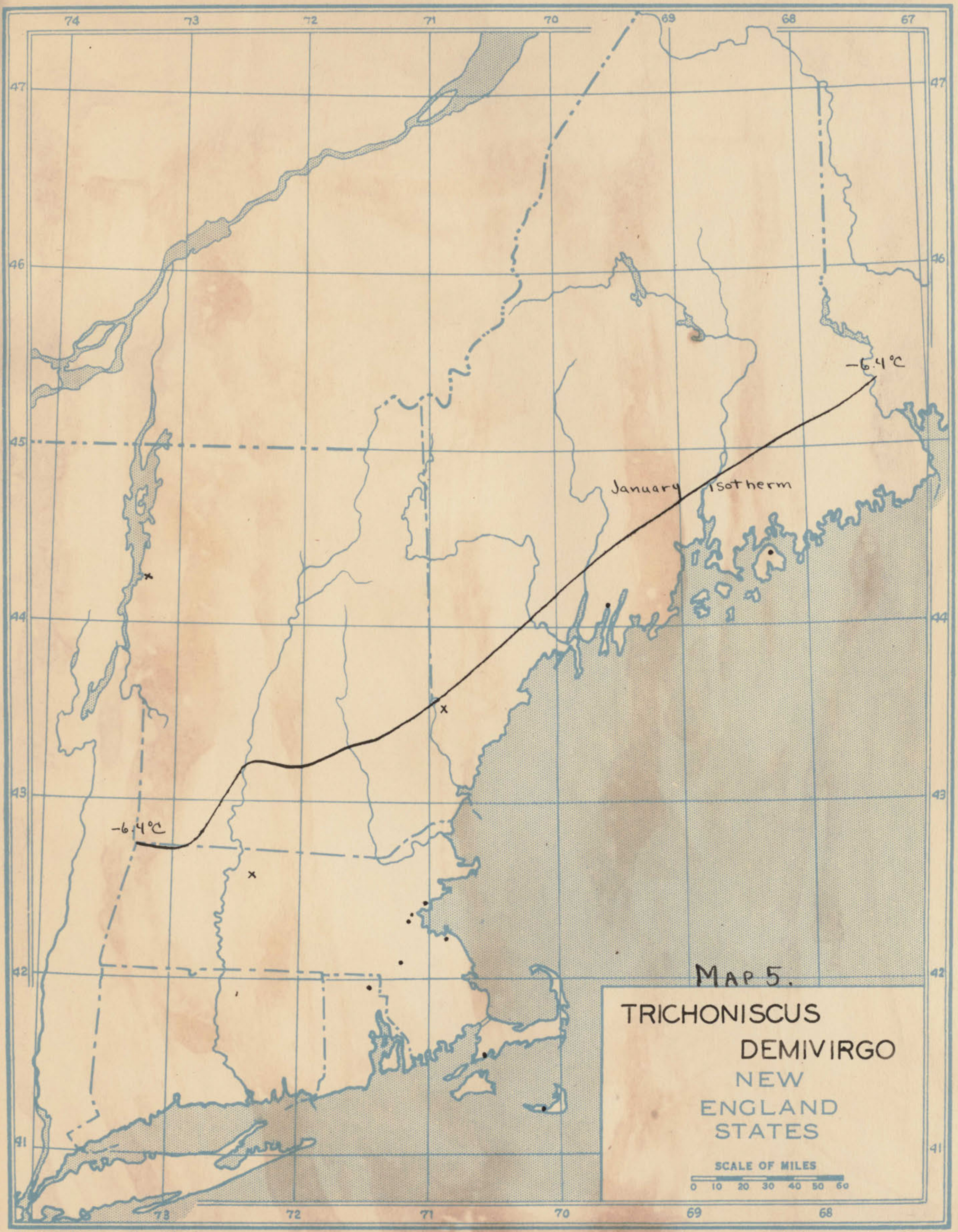
MEAN ANNUAL RAINFALL

MAP 3.



DISTRIBUTION OF RAINFALL

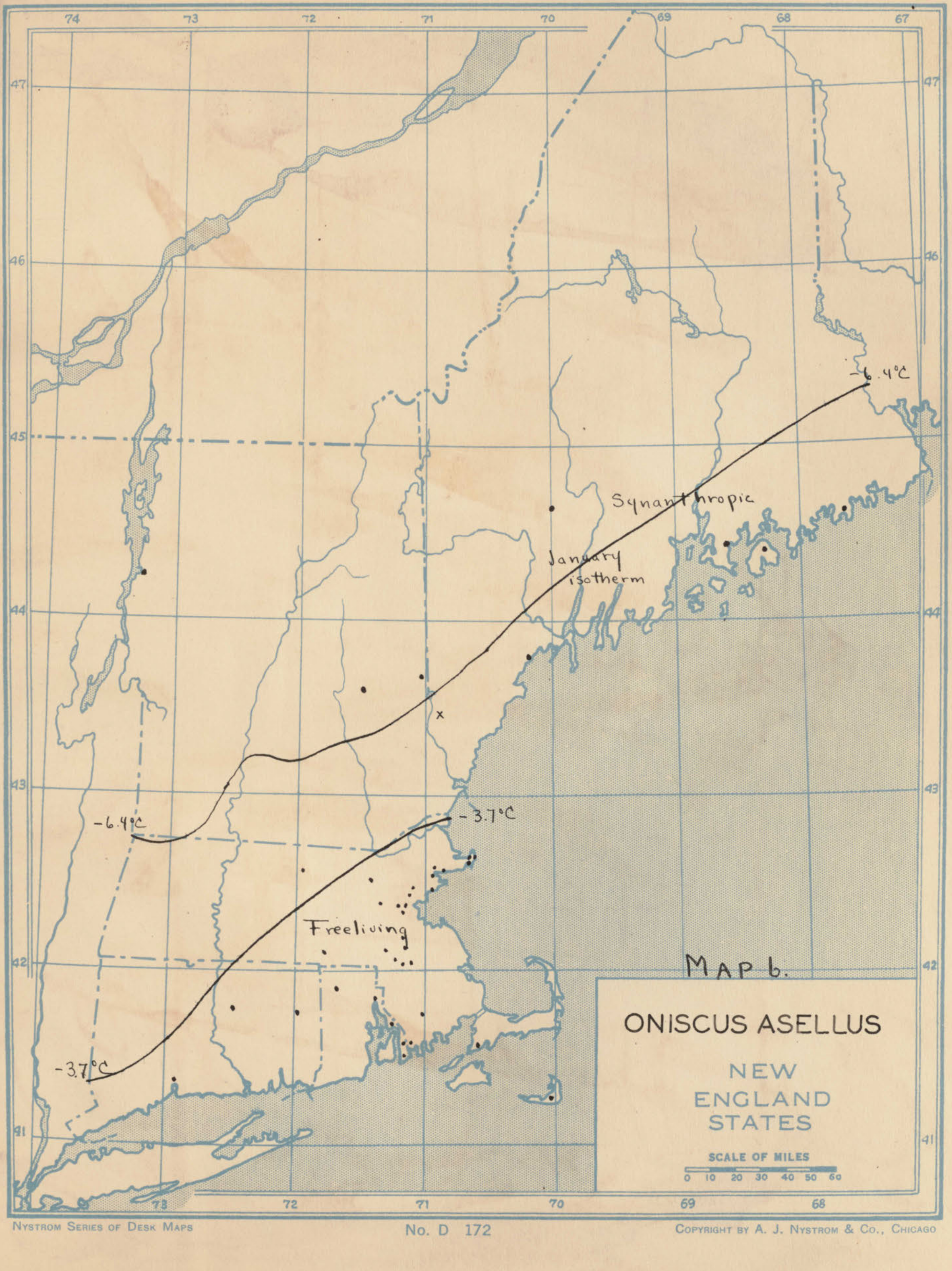
Map 4.



Map 5.

TRICHONISCUS
DEMIVIRGO
NEW
ENGLAND
STATES

Nystrom Series of Desk Maps
No. D 172

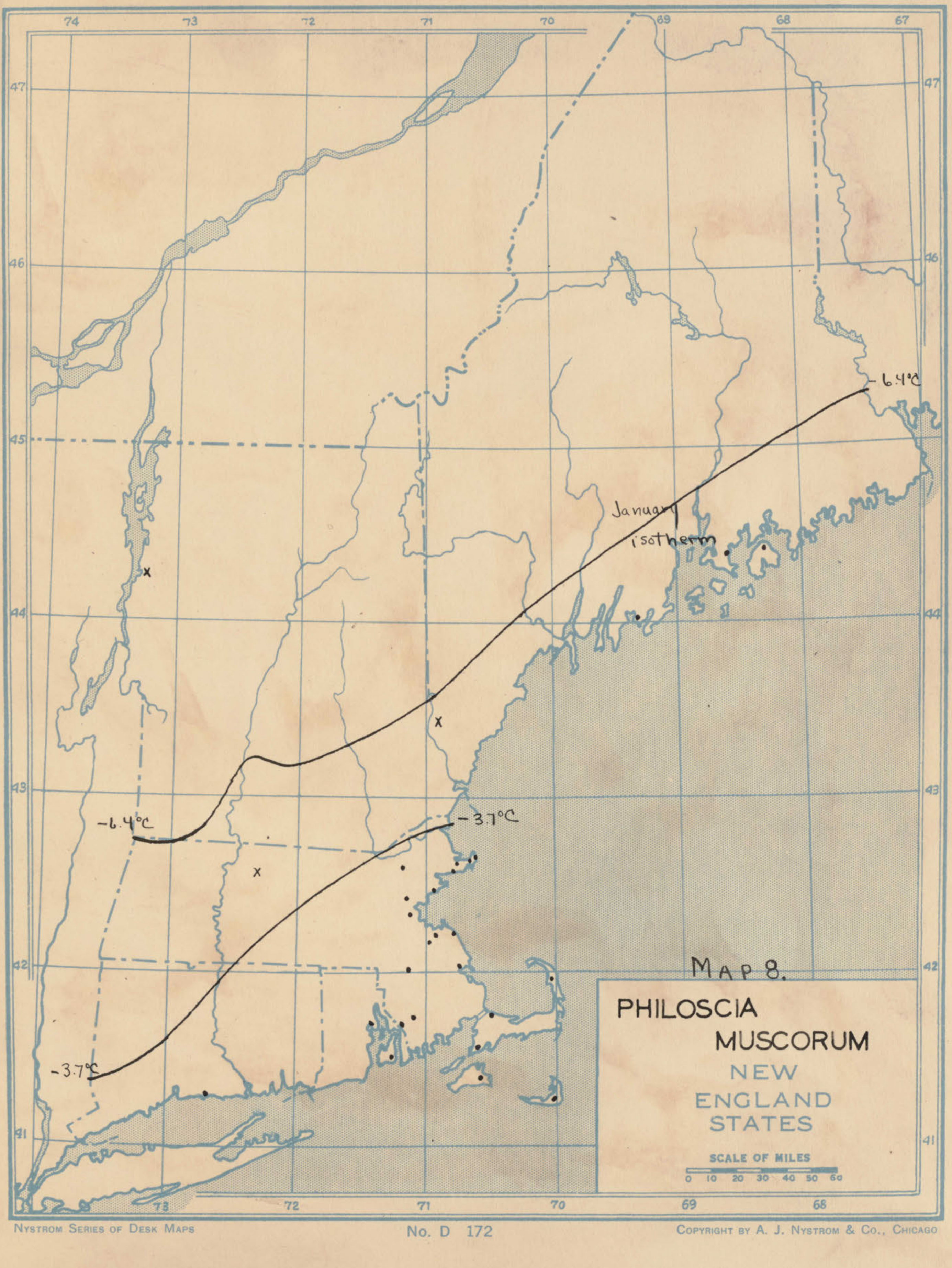


Nystrom Series of Desk Maps

No. D 172

ONISCUS ASELLUS

MAP 7.



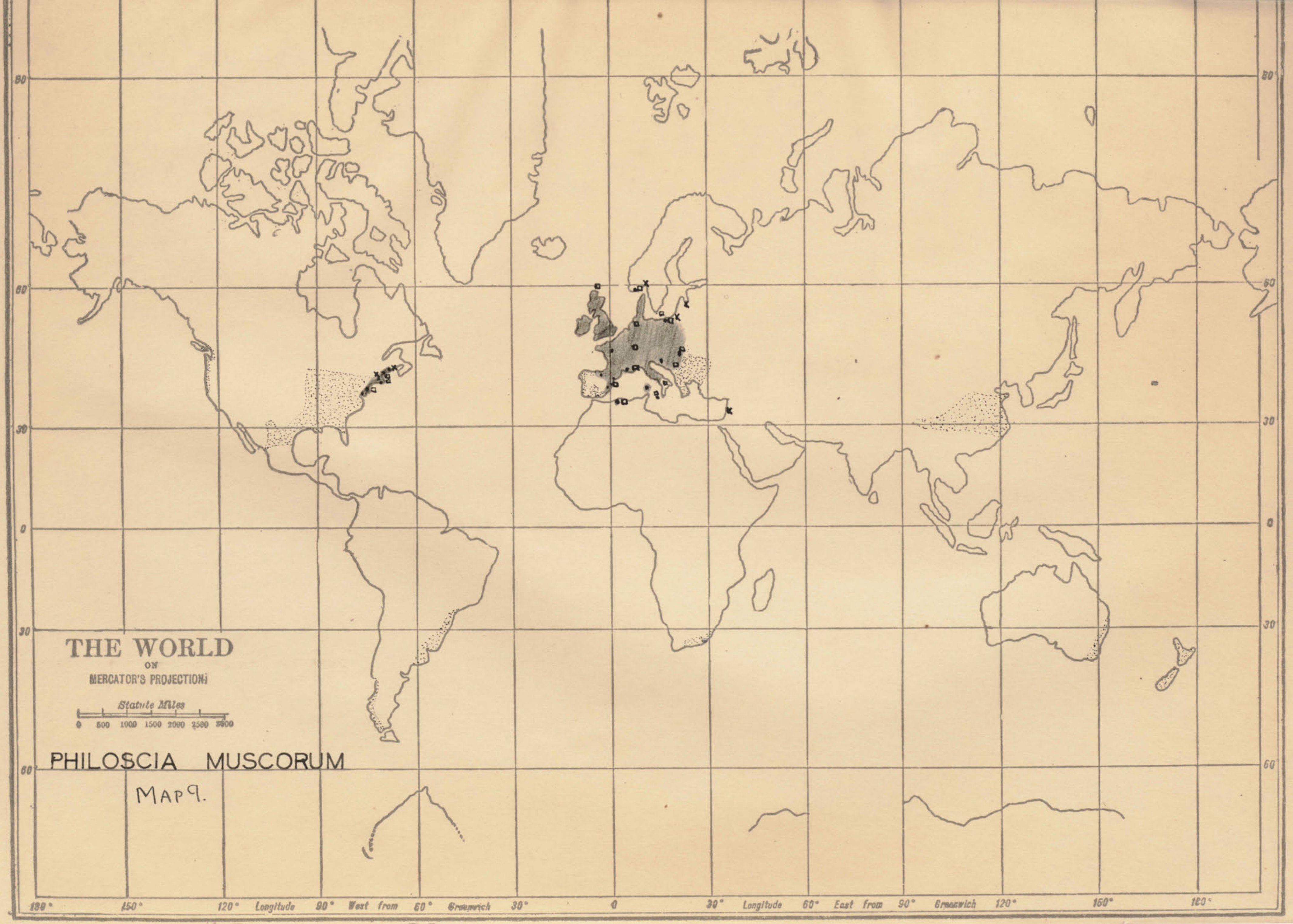
MAP 8.

PHILOSCIA MUSCORUM

NEW ENGLAND STATES

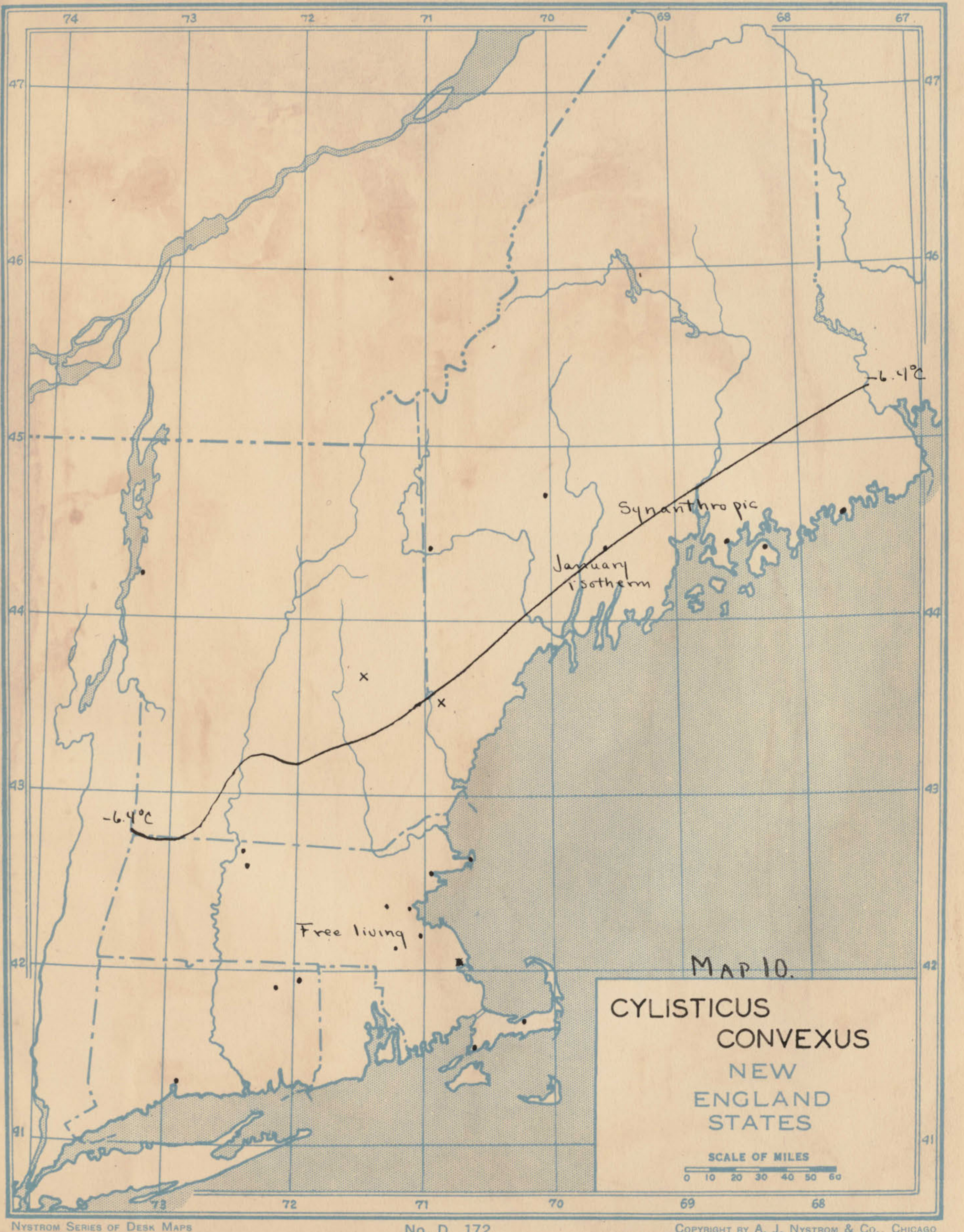
NYSTROM SERIES OF DESK MAPS

No. D 172



PHILOSCIA MUSCORUM

MAP 9.



MAP 10.

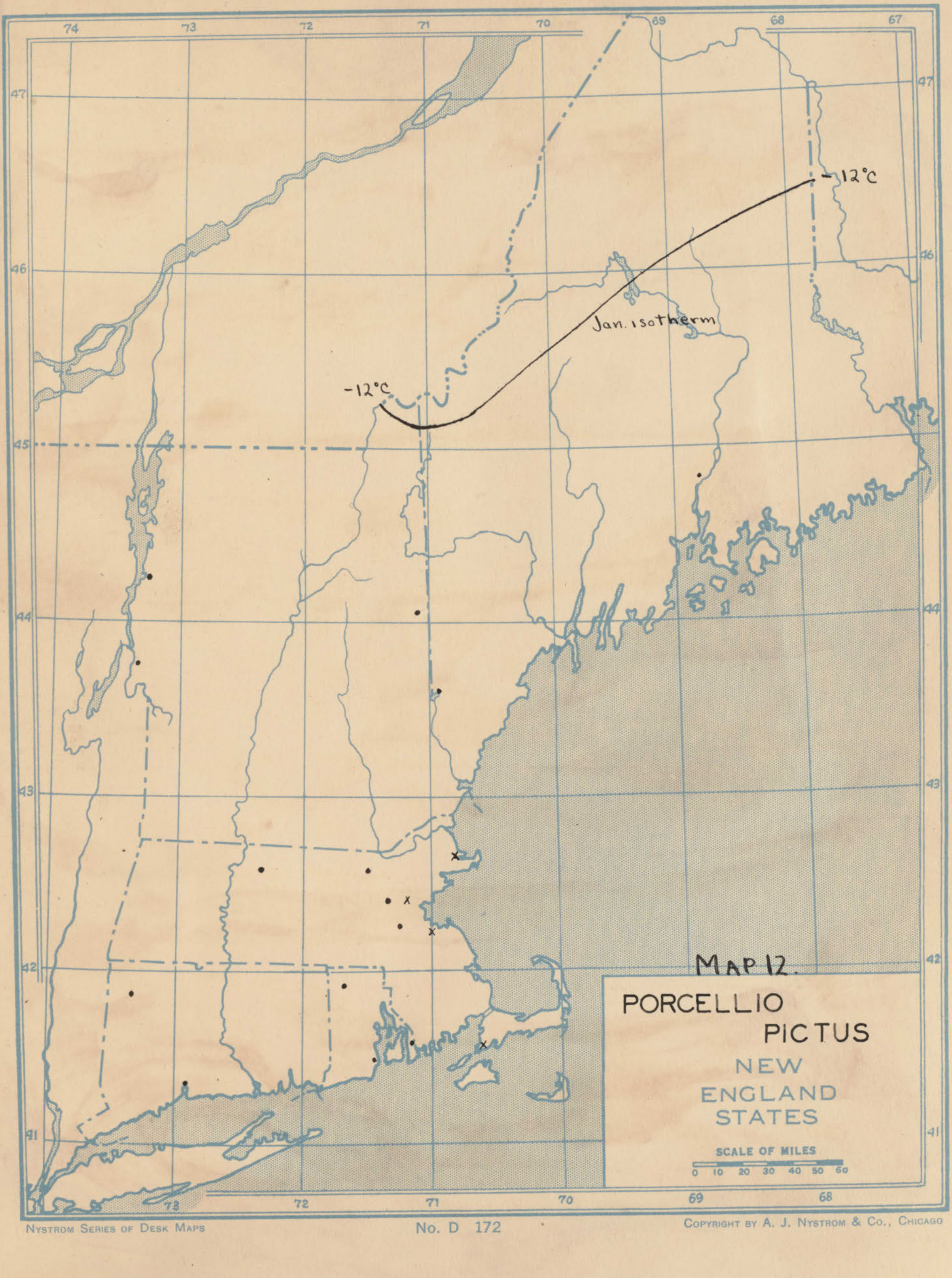
CYLISTICUS CONVEXUS
NEW ENGLAND STATES

NYSTROM SERIES OF DESK MAPS

No. D 172

CYLISTICUS CONVEXUS

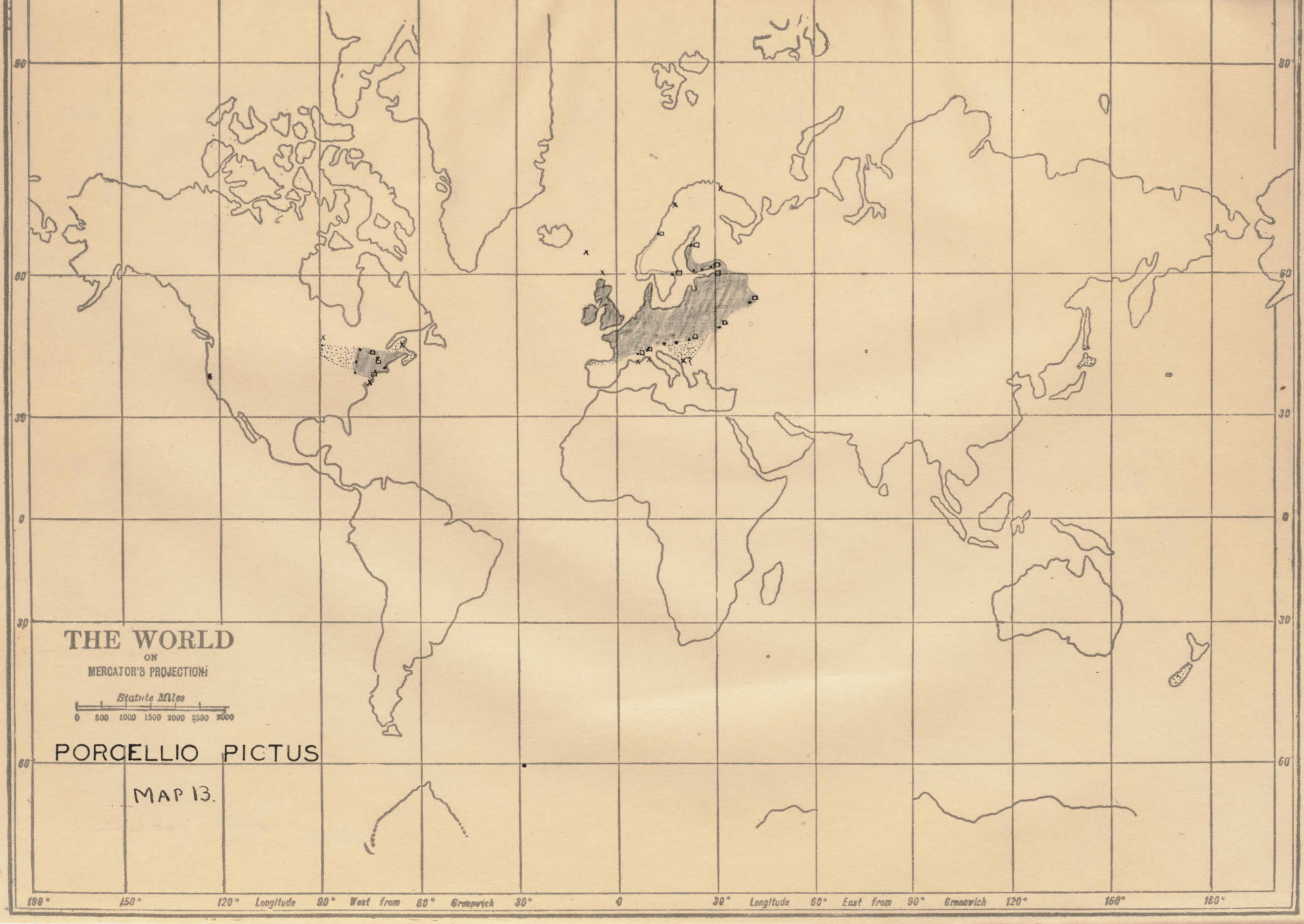
MAP II.



MAP 12.

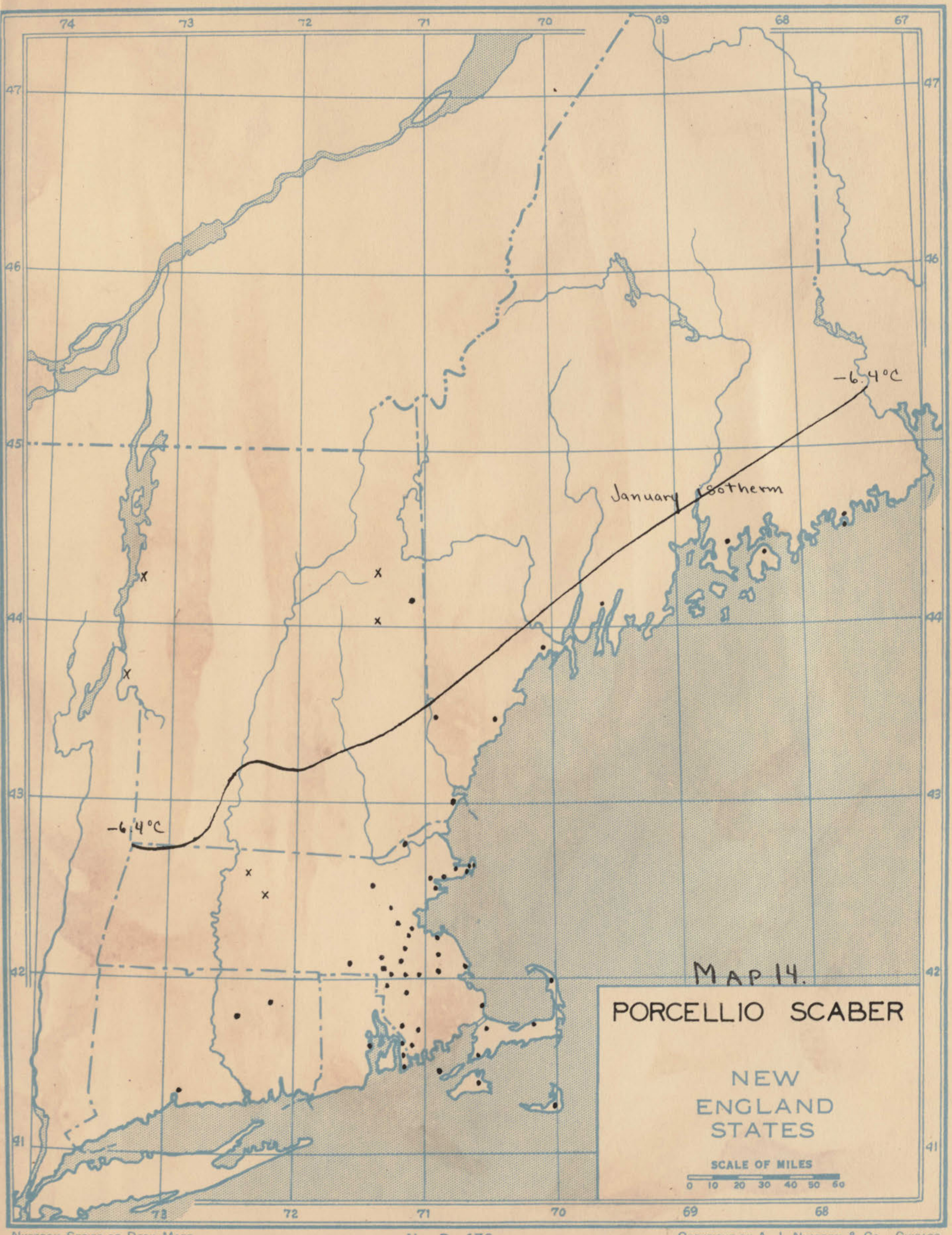
PORCELLIO PICTUS

NEW ENGLAND STATES



PORCELLIO PICTUS

MAP 13.



MAP 14.

PORCELLIO SCABER

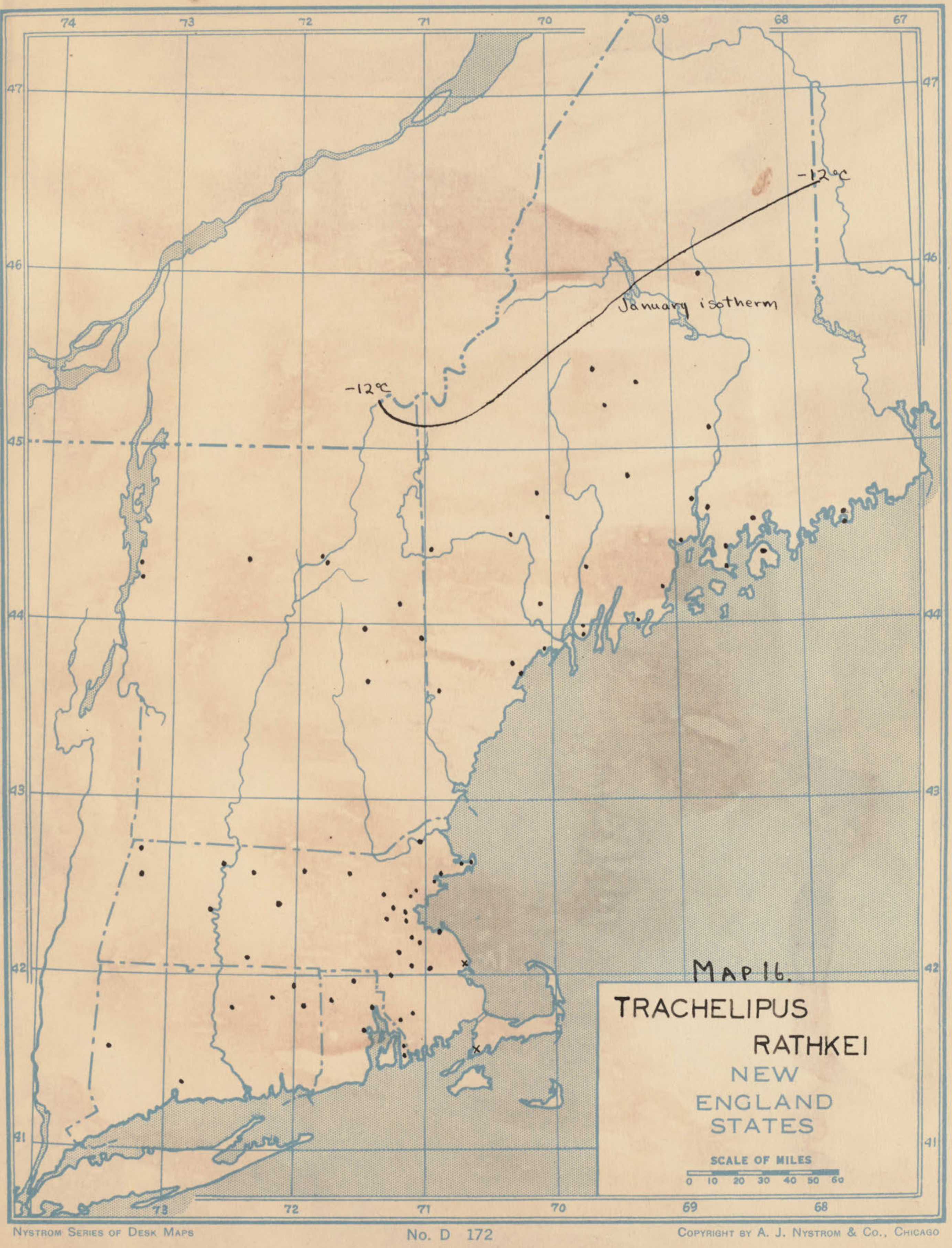
NEW ENGLAND STATES

NYSTROM SERIES OF DESK MAPS

No. D 172

PORCELLIO SCABER

MAP 15.



Map 16.

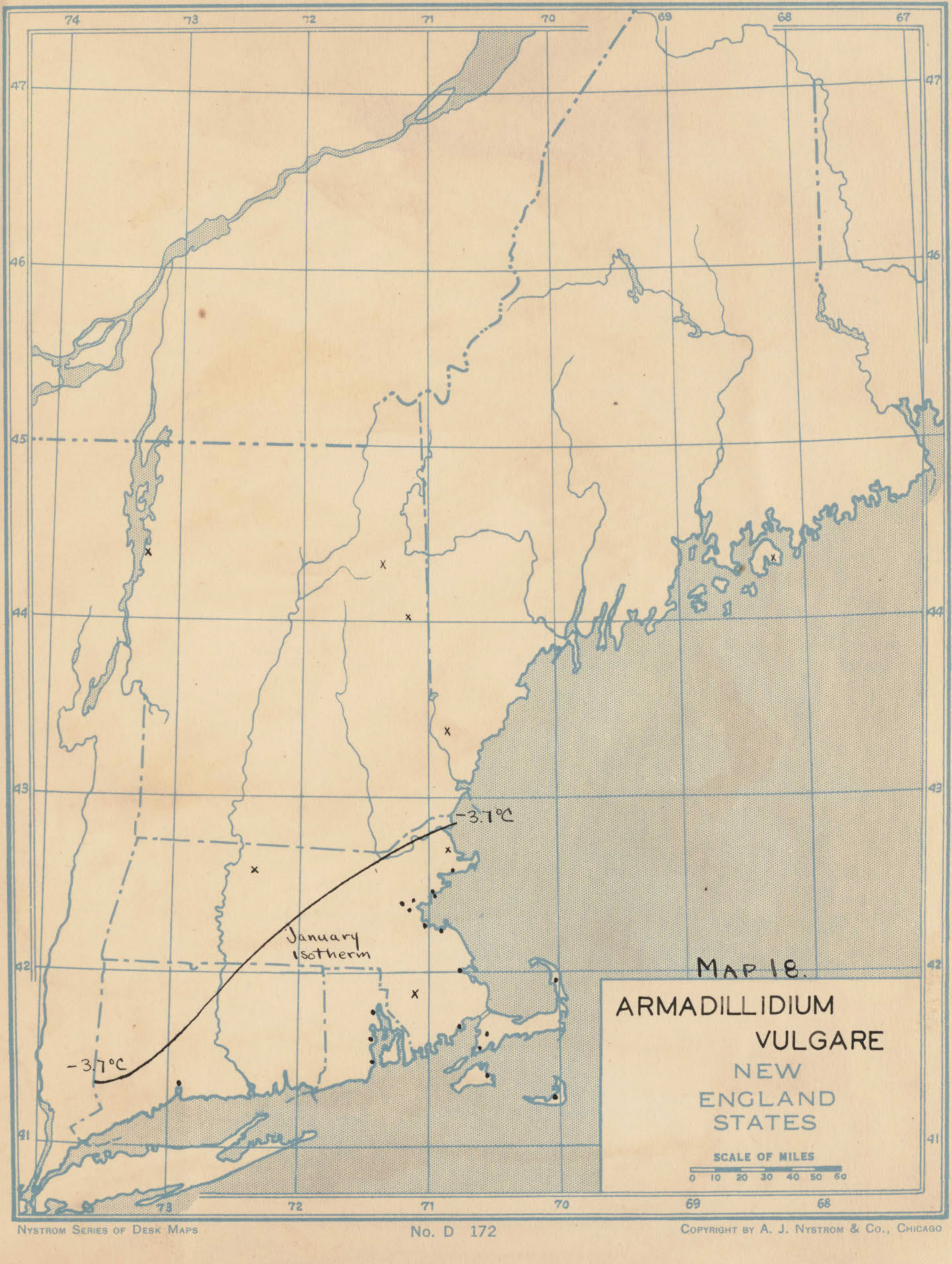
TRACHELIPUS
RATHKEI
NEW
ENGLAND
STATES

NYSTROM SERIES OF DESK MAPS

No. D 172

TRACHELIPUS RATHKEI

MAP 17.



Map 18.

ARMADILLIDIUM
VULGARE
NEW
ENGLAND
STATES

Nystrom Series of Desk Maps

No. D 172

ARMADILLIDIUM VULGARE

MAP 19.

PART IV

CLIMATOLOGICAL ANALYSIS

Climate as a Limiting Factor in Distribution

The factors determining the presence or absence of an animal at a particular spot at a particular time may be considered as intrinsic and extrinsic. Intrinsic factors are the characteristics of the animal itself. Extrinsic factors may be divided into two classes, ecological and chorological. Ecological features determine the precise location chosen by an animal; chorological features determine its general range and operate over a wide area. The presence of logs with loose bark, the drainage of the soil, and an abundance of lime are examples of ecological factors of importance for land isopods. Climate and physiographic barriers are the chief chorological factors. The absence of a given species from any locality may be because there are no suitable habitats, because the species has never been able to reach the place in sufficient numbers to establish itself. or because severe environmental conditions cause the death rate to be higher than the birth rate.

In the case of the woodlice, there are few originally forested areas where suitable habitats are lacking for the relatively cosmopolitan species considered here. Verhoeff (1931a)has pointed out that the land isopods are to some degree opportunists in their choice of habitat, and that they will live in whatever sheltered places are available. Dahl (1916a) in his key for the separation of species by habitat was often obliged to place a single species under several rubrics because of the variations in its choice of habitat. Porcellio scaber, for example, has been found under stones, under logs, in cellars, in greenhouses, in ant's nests, under seaweed, and in deciduous and coniferous forests. In Part II of this paper the overlapping of habitats on the part of various species has been brought out, yet the geographical range of no two species is exactly alike. The lack of suitable habitats, except where severe climate creates tundra or desert conditions, cannot be an important factor in the geographical distribution of woodlice.

Physiographic barriers might be expected to have significance, but they do not explain the limits of distribution as recorded in Part III. Even though the woodlice travel slowly and possess no special mechanisms for their dissemination over the world, certain species have managed to cross oceans, and to cross or circumnavigate mountain ranges. Through the agency of man long distances may be covered rapidly. The obvious fact that seven of the species treated here have spread so widely indicates that physiographic features are in general of secondary importance. Of course, the failure of a species to occur on a linely mid-oceanic island, or in Australia, may be because it has never been introduced. Offshore islands, however, have an isopod fauna almost like that of the mainland (Herold, 1929). All of the European species considered here are found on both sides of the Alps.

A comparison of the distribution maps with the maps of climate will show that there is an apparent limitation of the northward spread of all species by certain January isotherms. The southern boundaries are similarly related to various July isotherms. The agreement is not perfect, however, and the present study is an attempt to determine more accurately the climatic conditions under which each species thrives, and the extremes which it will tolerate. There are advantages in making this study on widely distributed species. The effects of local features on distribution are smoothed over. For example, the absence of Porcellio pictus from a given locality may be due either to an unfavorable climate, or to the absence of lime in the soil. Only by studying the distribution of the species over a wide area can the true controlling factor be determined.

The example cited in the preceding paragraph brings up a question about which very little is known. It may be called the problem of ecological isolation. This problem does not arise for species whose preferred habitat is of rather general occurence. Neither does it occur in the case of species with peculiar requirements which are able to explore and to locate suitable places. It may, however, be a very real thing in the case of species with specialized requirements and poor means of locomotion. Often suitable places, though numerous, occur only sporadically and are of such limited extent that the chances of a male and female reaching one at the same time must be very slight. Ecological isolation may explain the scattered occurences of Porcellio pictus and Cylisticus convexus, and their absence from places which seem eminently suitable. At the same time it must be remembered that these two species have been able to spread over an extensive area, and that they do occur abundantly in locations far from any other colonies.

The facts brought forward above show that climate is an important factor in regulating the distribution of woodlice, and the remainder of this section is concerned with a detailed study of its influence.

Previously Suggested Climatic Indices

In working out the climatic indices for each species, the choice of controls is dictated by the climatological information available, and the relation of each category of information to the life of woodlice. Dahl (1919) attributed the difference in distribution between Porcellio scaber(coastal) and Trachelipus rathkei (inland) chiefly to the difference between the relative humidities of the air in the two regions. Actually there is no ground for this assumption. The records of relative humidity taken at weather stations are practically useless for biological purposes, especially when they are applied to animals which live under logs, in the soil, or in other protected places. In such situations the humidity depends upon the amount of water in the soil, and the water absorbing power of the soil colloids (Lebedeef, 1928). In the habitats occupied by most woodlice the relative humidity must be close to 100%. (This point is discussed in Part V.) Precipitation and soil drainage are of more ecological significance in the case of land isopods than is relative humidity as measured at weather stations.

Herold (1925 and 1930) has discussed the limitation of certain species by the isotherms for January, generally the coldest month of the year in the north temperate regions. In the area studied, east Germany and the east Baltic countries, these isotherms do seem to be the most important limiting factors.

Blake (unpublished) suggested that the distribution of the woodlice in New England is also largely controlled by the January isotherms, though he found evidence for further control by the July isotherms and the annual isohyets. The actual indices assigned to each species by Blake and by Herold are presented later for comparison with those found by the writer.

Because of the small scale (in a geographic sense) of these studies, there are many facts which remain unexplained. The influence of climate in limiting distribution to the south is not considered. In both New England and the east Baltic region precipitation is distributed evenly throughout the year, so that the effects of seasonal fluctuation cannot be determined. Certain points are not explained by considering the isotherms for only one or two months. For example, <u>Porcellio scaber</u> in both Europe and North America is restricted to synanthropic environments where the mean January temperature is lower than -6.0 C. <u>Trachelipus rathkei</u> is free living in regions where the mean January temperature is as low as -11.5C.

Nevertheless, P. scaber extends farther north in coastal regions than does T. rathkei. A detailed study of the climates of the regions involved is necessary to ascertain whether these differences in distribution have a climatic basis.

Basic Climatic Requirements

Every species of land isopod requires certain conditions of climate. All of these conditions must be satisfied at the same time, or the climate will be unsuitable. Special conditions which render climatic control inoperable are discussed below. The specifications which must be met are these:

1. The summers must not be so hot as to kill the adults or the young.
2. The summers must be warm enough for the species to reproduce in numbers sufficient to maintain itself.
3. The winters must not be so cold as to kill the animals which will reproduce in the summer.
4. The annual precipitation must be high enough to maintain areas of sufficient soil moisture.
5. Precipitation must be so distributed that the minimum moisture requirements are always satisfied.

Regulation of distribution by climate is not to be considered as an arbitrary affair in which certain isotherms and isohyets are absolute barriers. A species may secure exemption from the ordinary controls imposed upon it through certain ecological adaptations. Protection from high temperatures is afforded by caves and by other recesses, and by high altitudes. Forests and bodies of water are other modifying

FIGURE 4. (After McDougall, 1925)

agencies. The effect of cold winters may be moderated by synanthropism and by heavy snows which protect the soil from the very low temperatures attained in the air. Cool summers, however, cannot be overcome by a cold blooded animal except under very artificial conditions such as are found in hothouses. Actual precipitation is not a measure of available moisture in irrigated areas, along the course of permanent rivers, or near other bodies of water. All these facts must be considered in evaluating the influence of climate upon the distribution of a particular species.

Choice of Controls

The mean monthly temperatures of the coldest month and of the warmest month have been taken as measures of the extremes of temperature to which the woodlice are subjected. These are not, of course, the actual temperatures of the microclimate about the animals, but in the absence of such records they must be used. These temperatures do give a comparative measure of the average thermal characteristics of the climates at various places. The winter temperatures at any one place vary more from year to year than do the summer temperatures.

The sum of the mean temperatures of the four warmest months of the year has been taken as a measure of the heat available for reproduction and growth. This is in accord with the principle of Merriam (1898). Actually the temperature sum obtained is only an approximation of one term in the equation giving the velocity of development. Without entering into a theoretical discussion of this equation, it may be stated that, over a certain range of temperature, velocity of development is proportional to the difference between the temperature of the animal and the so-called developmental zero, the lowest temperature at which development is possible.

In considering the adequacy of the moisture supply, it must be recalled that the amount of moisture available to a strictly terrestrial animal depends upon the amount of precipitation, the amount of runoff and the amount of evaporation. The latter is in turn dependent largely upon temperature. McDougall (1925) has calculated the combinations of mean annual temperature and mean annual precipitation at which evaporation equals rainfall. Regions with less than the critical amount of precipitation are considered semi-arid; those with less than half this amount as arid. For the present purpose, months which normally have less than one twenty-fourth the critical amount of annual rainfall are considered as deficient. The deficiency must be made up by a surplus from the preceding months, so that the relationship between the number of deficient months and total precipitation is of importance. Figure 4 gives the critical combinations of temperature and moisture according to McDougall. Annual rainfall and number of deficient months are taken as indices of the moisture characteristics of each climatic station.

Interaction of Controls

A given species in different parts of its range is not always limited to the north by the same winter isotherm.

This difference might be due to intraspecific variation in cold hardiness. It might also be due to the modifying effect of other climatic conditions on the action of cold as a limiting factor. It was thought that the sum of the summer temperatures might be important in this respect. It has been shown experimentally that there is considerable variation in cold hardiness between individuals of the same species (Part V). Thus moderately severe conditions might be expected to destroy only a part of the population, not to annihilate it completely. In this case summer temperature, because of its effect on reproductive rate and growth rate of the young, would be important in determining whether the species would be able to recoup its losses and successfully maintain itself. Thus a given species would withstand a lower winter temperature in regions with warm summers than in regions with cool summers. This reasoning applies only to the species as a whole, not to its individual members. It is argued here that a certain percentage of individuals will manage to protect themselves against severe conditions by selecting favorable places to winter over. Enough must survive to reproduce in numbers sufficient to overcome the ordinary hazards of existence. A warm summer will be favorable to reproduction, although it might conceivably render the species less cold hardy. There are both experimental and geographical reasons for doubting the latter suggestion.

When this hypothesis was tested by plotting the combinations of the coldest month control and the "four summer months" control for stations within and without the range of a single species, it was found that the two sets of points were grouped separately, and that a smooth curve could be drawn separating them. It was apparent that the limiting winter isotherm is profoundly affected by the amount of heat available in the summer. For each species this relationship appears to be the same over its entire range. This fact explains the difference between the limiting winter isotherms of certain species in Europe and in North America. North American and central European summers are warm so that the limiting winter isotherms are lower than in northern Europe and the Atlantic islands.

In North America each land isopod species extends into regions with warmer summers than does the same species in Europe. Southern Europe has drier summers than the southeastern United States, and it seems likely that this fact explains the difference in the limits. It has been shown experimentally that within limits high moisture increases heat resistance (Part V). It has also been found that moist soil is cooler in summer than is dry soil under similar conditions (Shelford, 1912, p. 159). For these reasons the minimum moisture requirements of a species vary with summer temperature, and the limiting summer isotherm must be considered in relation to moisture conditions.

Selection of Climatological Stations

Stations for climatological investigation were chosen to correspond as closely as possible with the actual localities recorded in Part III. The locations of the stations used for each species are shown on the distribution maps by squares. Care was taken to choose stations in mountainous regions with altitudes similar to those at which the species concerned occurs. Most of the stations are close to the limits of distribution of the species considered, but for each species a few points were selected in regions of maximum abundance.

Northern and Southern Climatic Indices

The stations used in determining the climatic requirements of each species are divided into two sets. In the first group are included stations within the range of the species. In the second list a number of stations just outside the range are named. A list of all stations and the values of the five controls at each is given in Appendix A. The limiting factors for each species are determined by comparing the two sets of stations. Due consideration is given to special conditions of existence. In the lists of weather stations, the letter "s" following a city means that the species is found there only synanthropically. An asterisk after the name of a place indicates that the species is very abundant there.

The controls are numbered as follows:

I. Sum of mean temperatures of four warmest months in degrees Centigrade.

II. Mean temperature of coldest month in degrees Centigrade.

III. Mean annual precipitation in decimeters.

IV. Number of months with deficient rainfall as defined on page 58.

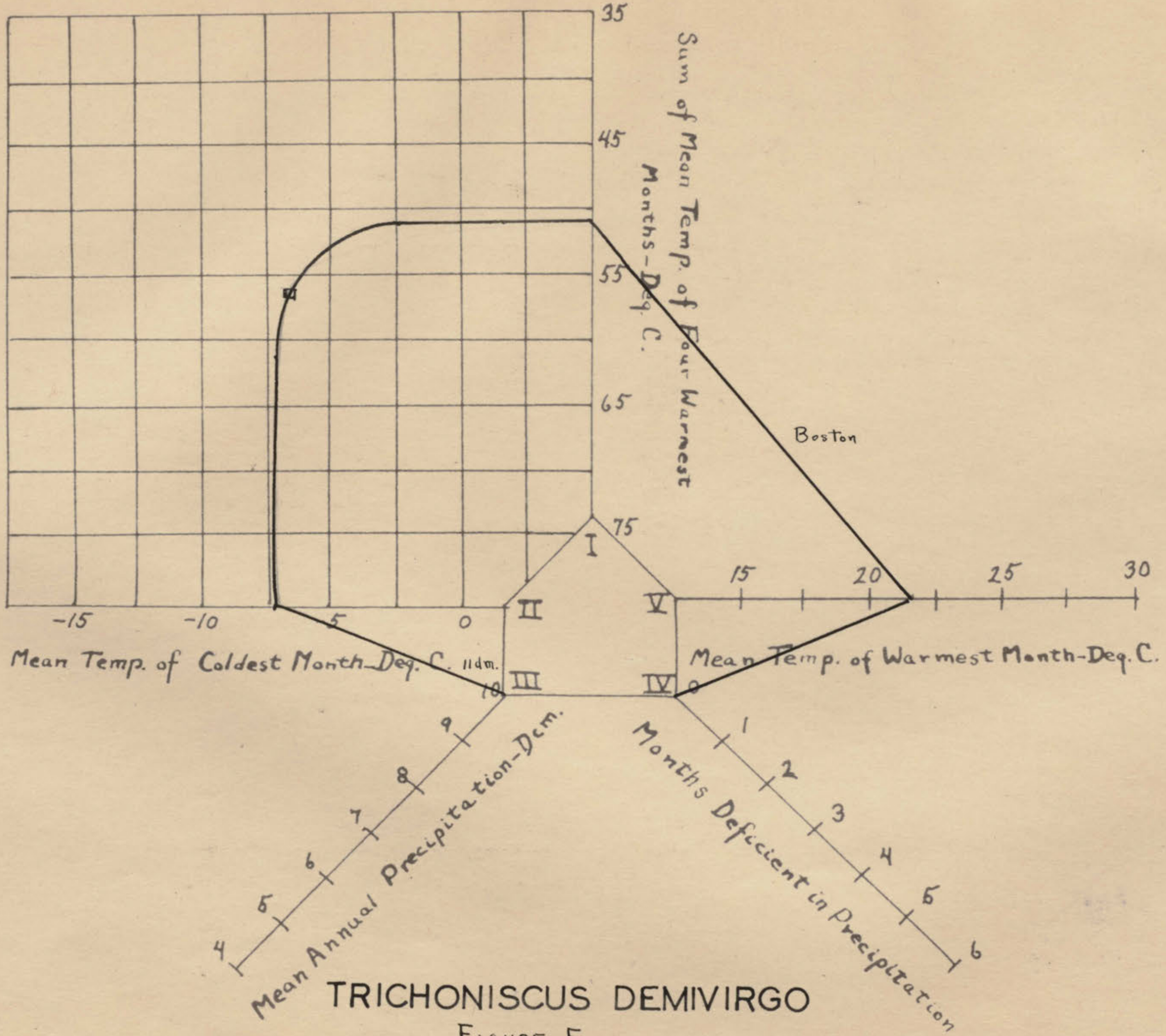
V. Mean temperature of warmest month in degrees Centigrade.

Controls III, IV, and V are interdependent and their limiting values (hottest and dryest) are considered as the southern index. The lower limiting values of controls I and II constitute the northern index. In practically every case more than one combination of controls is found to be an index value.

The indices of Blake in New England and those of Herold in the east Baltic countries are compared with these which are derived from a world-wide survey.

Graphical Representation of Climatic Indices

In order to show the simultaneous action of five controls graphically a system of radial coördinates was devised. Each coördinate represents one of the five indices selected. On each radius the scales are so arranged that more rigorous conditions are represented in the direction out from the center. In the quadrant between coördinates I and II is graphed the relationship between the limiting winter isotherm and the sum of the temperatures of the four warmest months. The points from which this curve is drawn are indicated. A square on the graph indicates that the species is found under the corresponding conditions; a cross indicates its absence; the letter "s" means that the species occurs synanthropically; a "?" indicates doubtful occurence.



TRICHONISCUS DEMIVIRGO

FIGURE 5.

Straight lines are drawn between points on the other coördinates representing the extreme conditions under which the species concerned is found. The area enclosed by these lines and the curve will be spoken of as a "tolerance polygon". A tolerance polygon is a composite diagram, not a representation of the climate at one station. Total precipitation, the number of months with deficient precipitation, and limiting summer isotherms are, however, closely related. Thus joined points on coördinates III (annual rainfall), IV (deficient months) and V (summer isotherm) represent conditions at a single station or several very similar stations. It often happens that several combinations of points on these coördinates will meet the minimum requirements of a species. Each combination is then shown distinctively. In effect the species has more than one tolerance polygon representing different sets of limiting conditions.

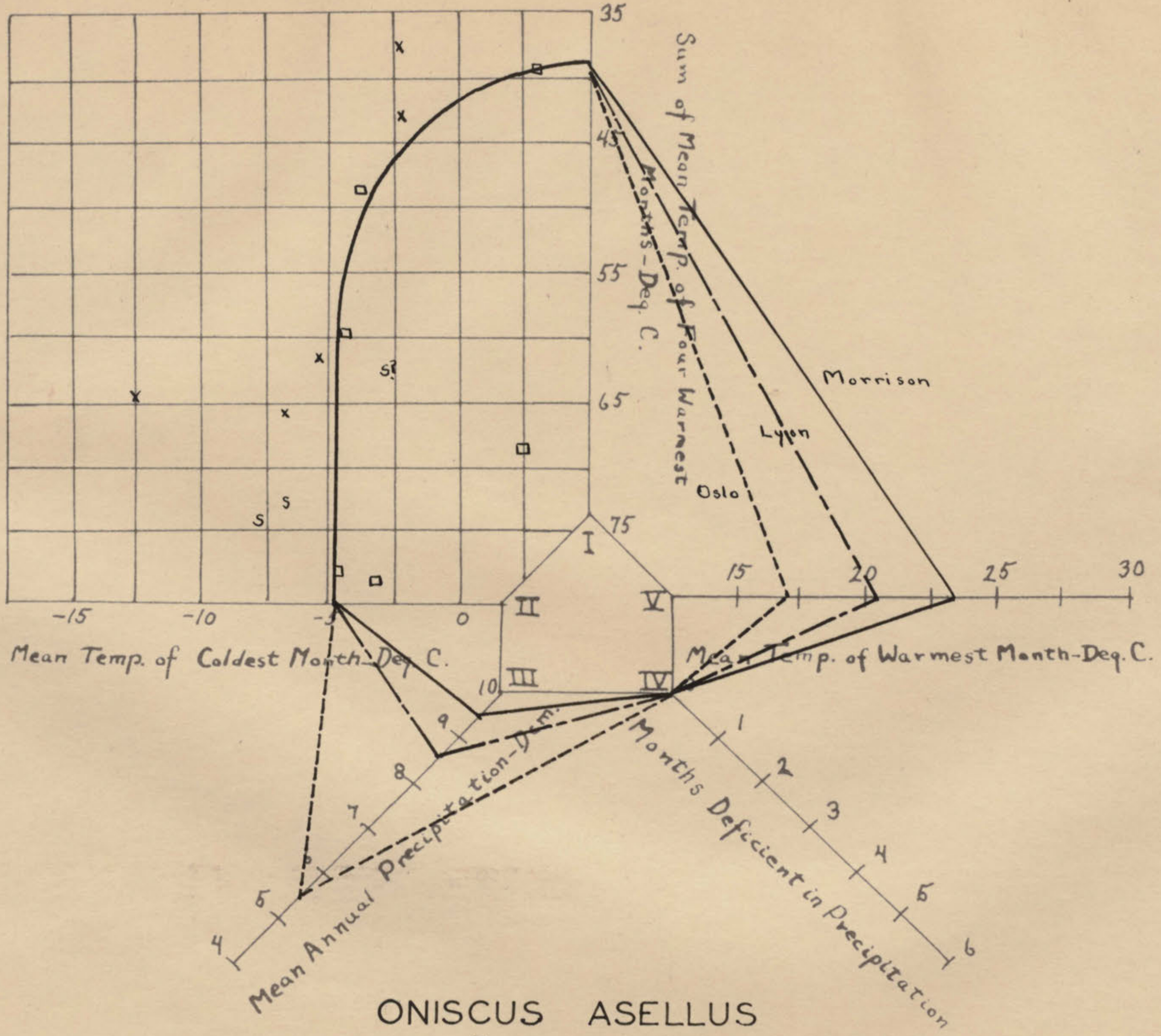
If the climatic conditions at any point can be represented entirely within one of the tolerance polygons for a species, the climate of that place is presumably suitable for the species. If this is not so the climate is presumably unsuitable and the limiting factor is shown by inspection.

Indices for Individual Species

Trichoniscus demivirgo

Positive stations: Eastport, Maine (?); Boston, Mass.; Nantucket, Mass.

Since further investigation of our isopod fauna will



ONISCUS ASELLUS

Figure 6.

probably extend the range of this species outside New England, it is impossible to select negative stations safely.

T. demivirgo is not found inland in New England, possibly due to severe winter conditions. The indices as shown at three stations are:

Northern Index		Southern Index - Precipitation Index		
I	II	III	IV	V
Eastport			Boston	
57°C.	-6.4°C.	11.2 dm.	0	21.8°C.

Blake's indices are: January, -7.2°C. to -6.7°C.; July, 18.3°C.

The rainfall index is certainly too high as ecologically similar species are found in cool regions with about half the rainfall.

Oniscus asellus

Positive stations: Fredericton, N. B. (s); Burlington, Vt. (s); Concord, N. H. (s); Fitchburg, Mass.; Boston, Mass.*; New York, N. Y.; Morrison, Ill.; Thorshavn, Faroes; Oslo, Norway; Trondhjem, Norway; Mariehamn, Finland (s?); Cernauti, Roumania; Lyon, France; Bilbao, Spain; Paris, France; Madrid, Spain (?); Königsberg, Germany (s?).

Negative stations: Greenville, Maine; Baltimore, Md.; Stykkisholm, Iceland; Marseille, France; Barcelona, Spain; Riga, Latvia; Bodo, Norway; Wilno, Poland; San Francisco, Cal.

The determination of the northern boundary of Oniscus is complicated by the fact that this species often occurs synanthropically in the northern part of its range. This is probably true at Mariehamn since Oniscus is found only associated with human habitations over the climatically similar east Baltic region. It is doubtful if Oniscus is free living in Madrid as the summers there are very hot and dry. DeBuen might have found it there in irrigated places.

This species will tolerate low rainfall in the northern portion of its range. It is absent, however, from San Francisco with four months of deficient rainfall during the summer.

Northern Index		Southern Index - Precipitation Index		
I	II	III	IV	V
Thorshavn 39.4°C.	3.0°C.	9.5 dm.	Morrison 0	23.3°C.
Königsberg 62.4°C.	-2.8°C.	8.7 dm.	Lyon 0	21.2°C.
Fitchburg 76.8°C.	-4.7°C.	5.6 dm.	Oslo 0	17.4°C.

Blake's Indices:

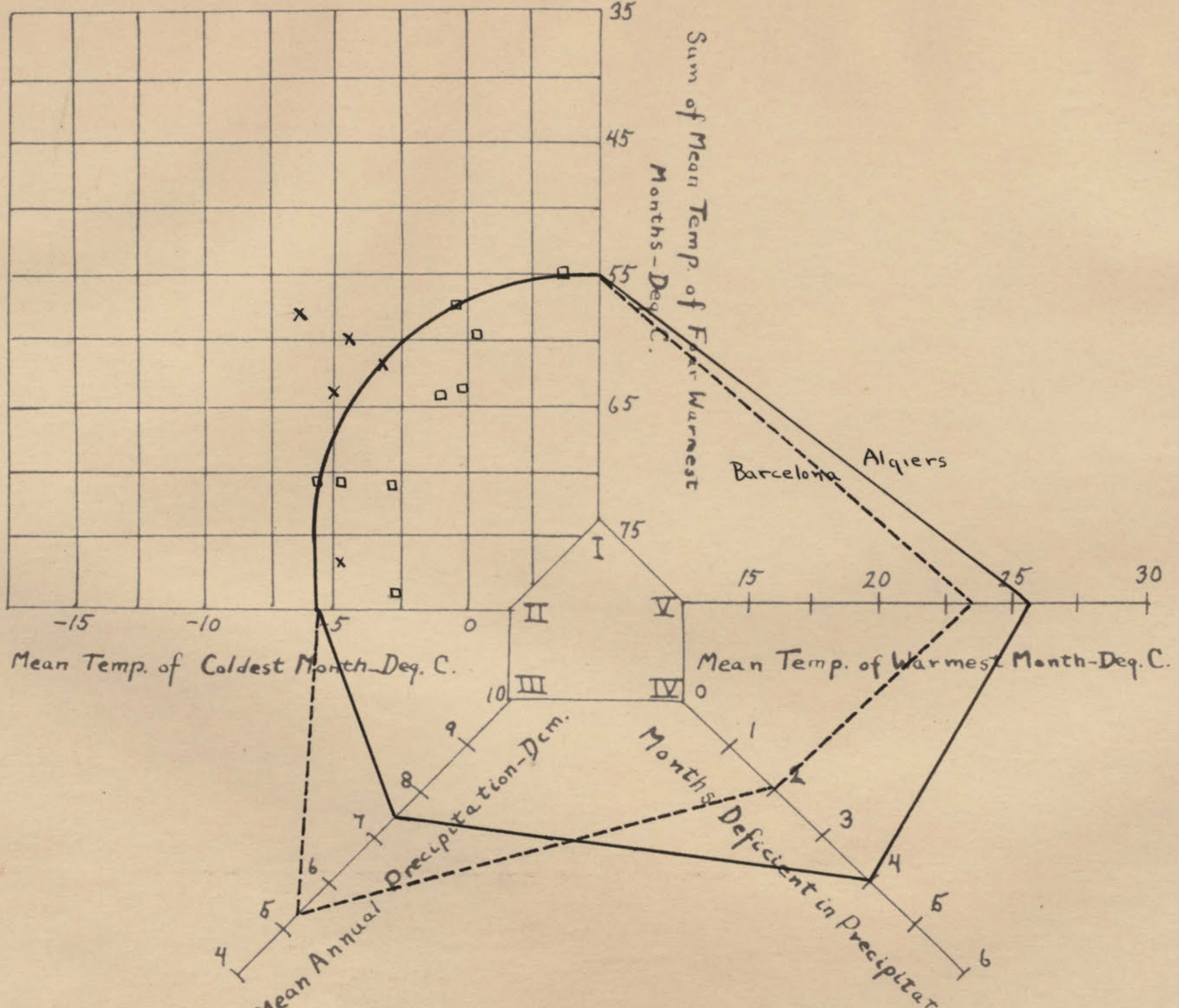
Winter: -3.9°C.
-7.8°C. (s)
Precipitation: 10.2 dm.

Herold's Index: -2.5 °C.

Philoscia muscorum

Positive stations: Portland, Maine; Boston, Mass.*; New York, N. Y.; Orkney Islands; Hammershus, Island of Bornholm, Denmark; Mandal, Norway; Danzig; Hamburg, Germany*; Karlsruhe, Germany (southern limit of Var. sylvestris; northern limit of Var. muscorum); Cernauti, Roumania; Sarajevo, Jugoslavia; Potenza, Italy; Palermo, Italy; Nice, France; Barcelona, Spain; Algiers, Algeria (Var. algirica).

Negative stations: Eastport, Maine; Fitchburg, Mass.;



PHILOSCIA MUSCORUM

FIGURE 7.

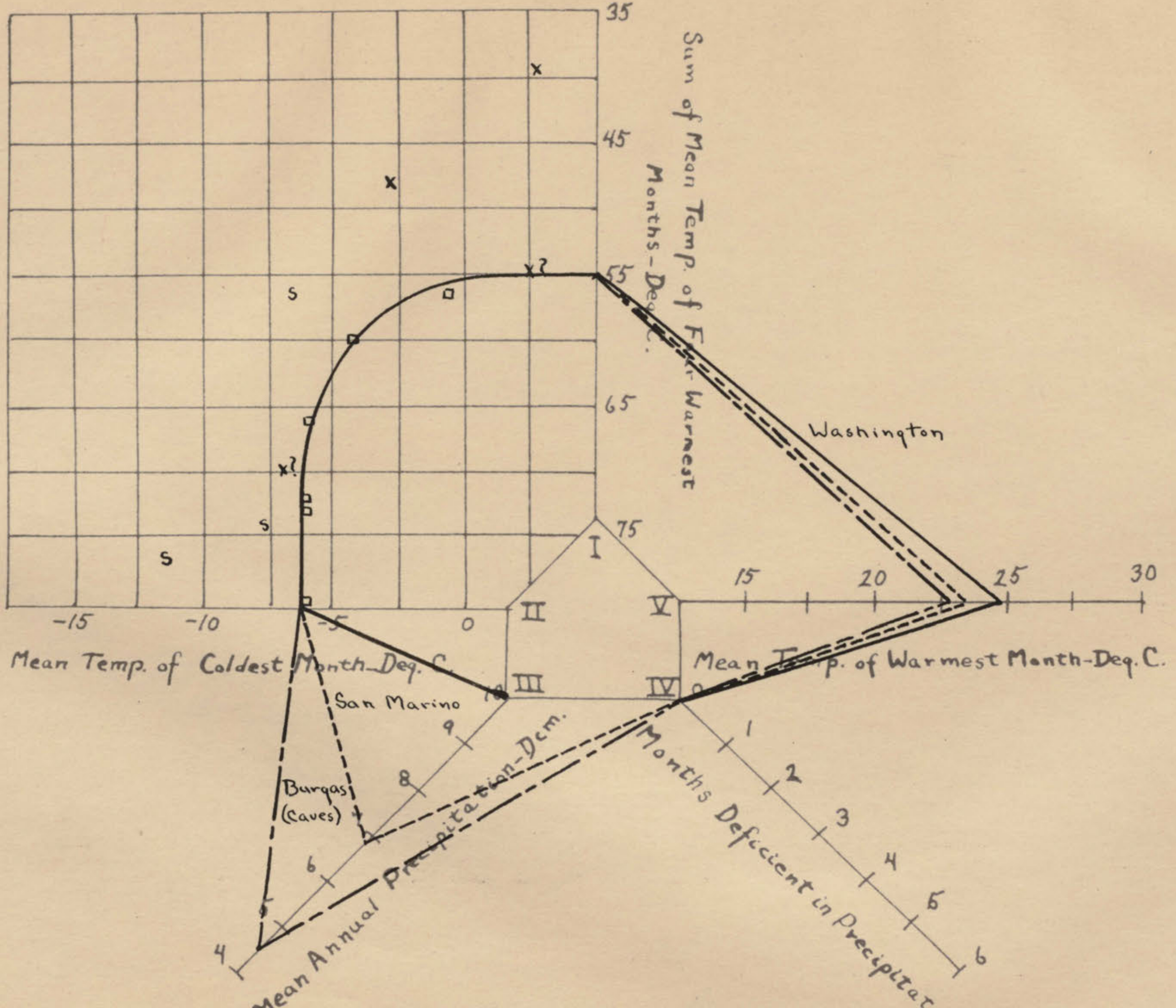
Oslo, Norway; Riga, Latvia; Königsberg, Germany; Beirut, Syria.

It is impossible to select any negative stations in the southern United States as the true distribution of this species is unknown. Several rather poorly defined species of Philoscia are recorded from the south by Richardson, but whether any of these should be *muscorum* is a matter of doubt.

Ph. muscorum is not commonly associated with human habitations so that the determination of its winter index is more simple than in the case of Oniscus. Determination of the southern index is complicated by the fact that we are dealing with three named varieties with fairly distinct geographical ranges. The boundary between *sylvestris* and *muscorum* in Germany is close to the 20°C. July isotherm. *Ph. muscorum sylvestris* is apparently never found in regions with low rainfall, while the other two varieties show a surprising independence of regular rainfall. This appears to be due to its choosing moss beds by the banks of permanent streams as habitats. The indices presented here refer to the species as a whole, and not to *sylvestris* alone.

Northern Index		Southern Index - Precipitation Index		
I	II	III	IV	V
Portland-Eastport			Algiers	
65.0°C.	-6.0°C.	7.5 dm.	4	25.3°C.
Mandal			Barcelona	
55.0°C.	-0.4°C.	5.4 dm.	2	23.3°C.

The only index suggested by Blake is the ground water isochlor of 2.5 parts per million which presumably is some function of soil salinity.



CYLISTICUS CONVEXUS

FIGURE 8.

Cylisticus convexus

Positive stations: Fredericton, N. B. (s); Burlington, Vt. (s); Toronto, Ontario; Turners Falls, Mass.; Cincinnati, Ohio; Washington, D. C.; Las Vegas, N. M.; Copenhagen, Denmark; Oslo, Norway; Helsingfors, Finland (s); Wilno, Poland; Akhiar, Russia; Burgas, Bulgaria (in caves); Cetinge, Jugoslavia; San Marino; Marseille, France.

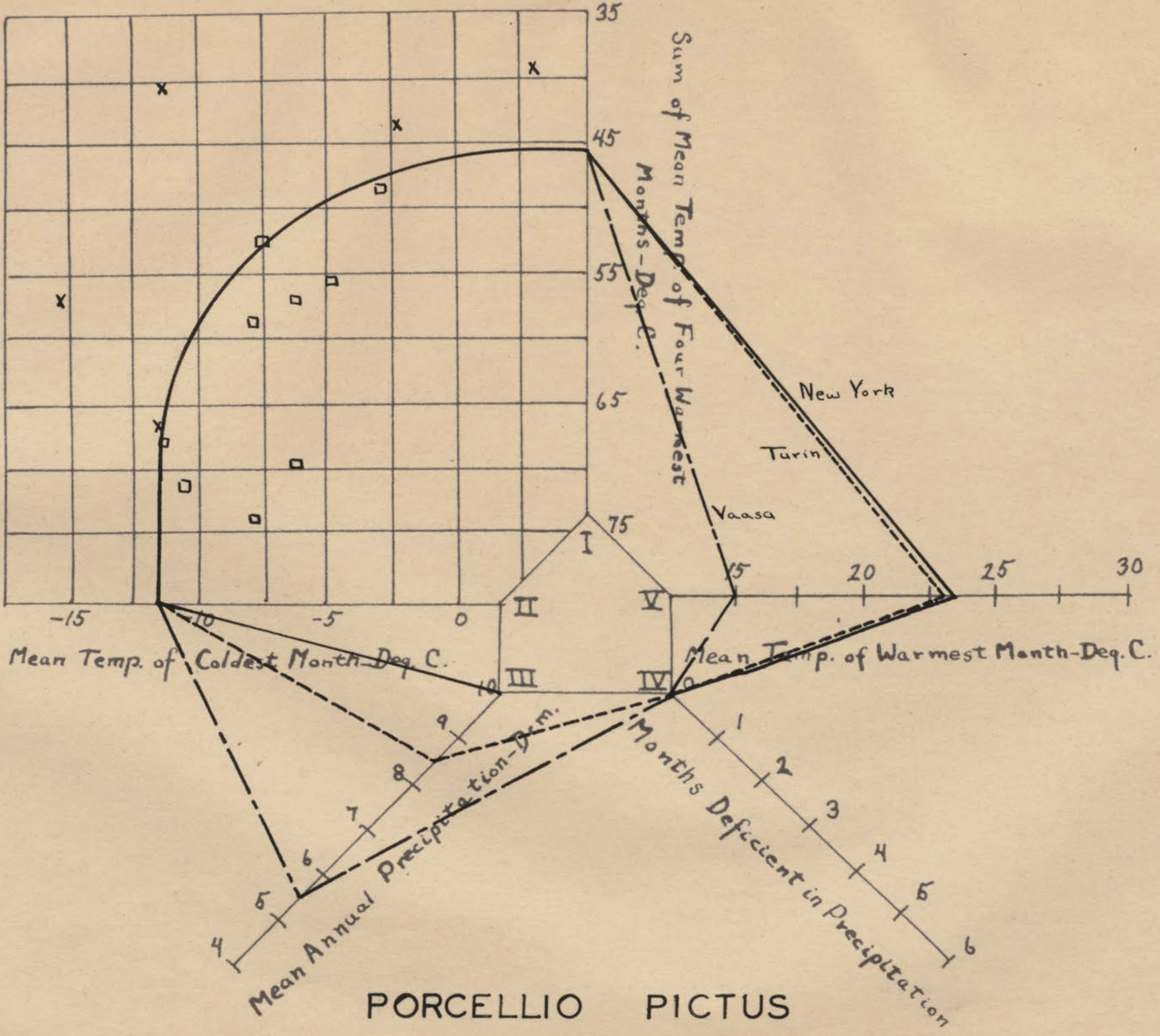
Negative stations: Trondhjem, Norway; Kiev, U.S.S.R.; Orkney Islands (?); Thorshavn, Faroes; Genoa, Italy.

In the northern part of its range C. convexus is found synanthropically, while in the southern part it is an inhabitant of caves or mountains. As a cave species it avoids the effect of very low rainfall. This is shown in the Black Sea area.

Northern Index		Southern Index - Precipitation Index		
I	II	III	IV	V
Copenhagen			Washington	
56°C.	-0.7°C.	10.9 dm.	0	24.9°C.
Wilno			San Marino	
66°C.	-5.7°C.	6.8 dm.	0	23.6°C.
			Burgas	
		4.5 dm.	0	23.0°C.

Blake's indices are: Winter: -3.9°C. to -4.4°C.; rainfall less than 10.2 dm.

Herold states that it occurs up to the -7.5°C. January isotherm.



PORCELLIO PICTUS

FIGURE 9.

Porcellio pictus

Positive stations: Montreal, Que.; Burlington, Vt.*; New York, N. Y.; Trondhjem, Norway; Upsala, Sweden; Vaasa, Finland; Helsingfors, Finland; Leningrad, Saraisk, Kiew, U.S.S.R.; Budapest, Hungary; Turin, Italy; Lyon, France.

Negative stations: Port Arthur, Ontario; Fredericton, N. B.; Thorshavn, Faroes; Orkney Islands; Bodo, Norway; Kola, U.S.S.R.; San Francisco, Cal.; Baltimore, Md.; Marseille, France; Genoa, Italy; Sarajevo,"?", Jugoslavia.

Since this species is found in colder regions than is any other land isopod studied, its absence in northern New Brunswick, Canada, is probably due to other ecological factors. Although sometimes associated with man, <u>P. pictus</u> appears to be found free living over practically all its range.

Northern Index		Southern Index - Precipitation Index		
I	II	III	IV	V
Trondhjem			New York	
48°C.	-2.9°C.	11.4 dm.	0	23.1°C.
Saraisk			Turin	
68°C.	-11.4°C.	8.6 dm.	0	22.9°C.
			Vaasa	
		5.5 dm.	0	15.3°C.

Blake's indices are the winter isotherm -7.2°C., and the July isotherm 18.3°C. which is indefinite. Herold found that <u>P. pictus</u> occurred at least up to the January -7.5°C. isotherm.

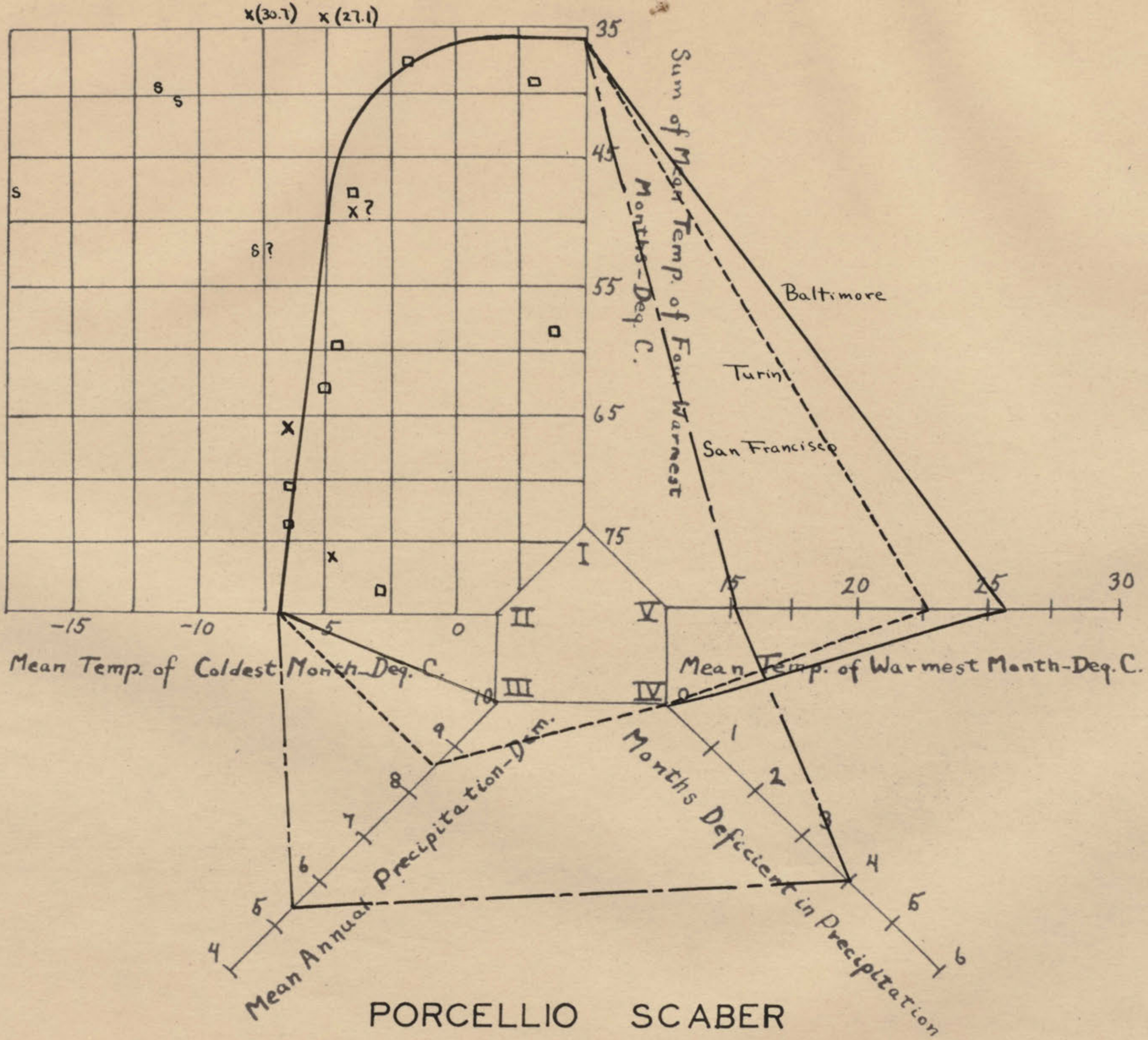
Porcellio scaber

Positive stations: Anticosti Island (s); Toronto, Ontario; Eastport, Maine; Boston, Mass.*; Baltimore, Md.; Cincinnati, Ohio; San Francisco, Cal.; San Diego, Cal. (?); Victoria, B. C.; Key West, Fla. (?); Vestmanno, Stykkisholm, Iceland; Thorshavn, Faroes; Oslo, Norway*; Kola, U.S.S.R. (s); Vaasa, Finland (s); Riga, Latvia (s?); Budapest, Hungary; Turin, Italy; Bilbao, Huesca, Spain; Petropavlosk, Siberia; Sapporo, Japan*; Dunedin, New Zealand; Melbourne, Australia; Nuwara Eliya, Ceylon; Cape Town, South Africa; Honolulu, Hawaii.

Negative stations: Juneau, Alaska (?); St. Paul Island, Alaska; Ivigtut, Greenland; Wilno, Poland; Fitchburg, Mass.; Marseille, France; Barcelona, Spain; Charleston, South Carolina.

P. scaber is not the most cold resistant species studied here, but it is the one land isopod which is best able to withstand cool summers. This explains its predominance in northern maritime regions, and on the north Atlantic islands. The absolute limiting winter temperature is difficult to determine, since _P. scaber_ is often synanthropic to various degrees, and the statements in the literature do not always bring this out. The species is well able to endure prolonged deficient rainfall when the summers are cool.

As for the doubtful records noted above, it is probable that _P. scaber_ does not occur at Key West since it has not been taken there by collectors recently. Blake, from personal observation, doubts if _P. scaber_ is found in southern California. At San Diego lack of rainfall would be more of an unfavorable factor than would high temperature, since July



PORCELLIO SCABER

FIGURE 10.

is a cooler month here than at Cincinnati where P. scaber is found. This species would certainly be restricted to artificially watered places in southern California. The climates of Hawaii and of Nuwara Eliya are similar in showing very small annual and diurnal fluctuation. Conditions of existence in these places would resemble those in a laboratory, and would undoubtedly satisfy the requirements of P. scaber. The same holds true for several other islands from which this woodlouse has been reported. Although P. scaber has not been reliably reported from Alaska, it may very well occur in the southern extension of this territory. Juneau has a climate similar to that of Trondhjem, Norway, where scaber is abundant.

Northern Index		Southern Index - Precipitation Index		
I	II	III	IV	V
Vestmanno			Baltimore	
37°C.	-2.1°C.	11.0 dm.	0	25.3°C.
Eastport			Turin	
57°C.	-6.4°C.	8.6 dm.	0	22.9°C.
			San Francisco	
		5.6 dm.	4	15.5°C.
Synanthropic			Questionable	
Anticosti			San Diego	
46°C.	-17.6°C.	2.4 dm.	8	20.4°C.
			Key West	
		9.7 dm.	0	28.6°C.

Blake's indices are: Winter, -6.1°C.; July, 21.7°C.

Herold's index is: January, -2.5°C. to -5°C.

The distribution of P. scaber is not dependent entirely upon climate, as it is absent from many inland points which are suitable according to the above indices. This will be apparent from Figure 9. No entirely satisfactory explanation of this fact can be given, although the question is discussed later in this paper.

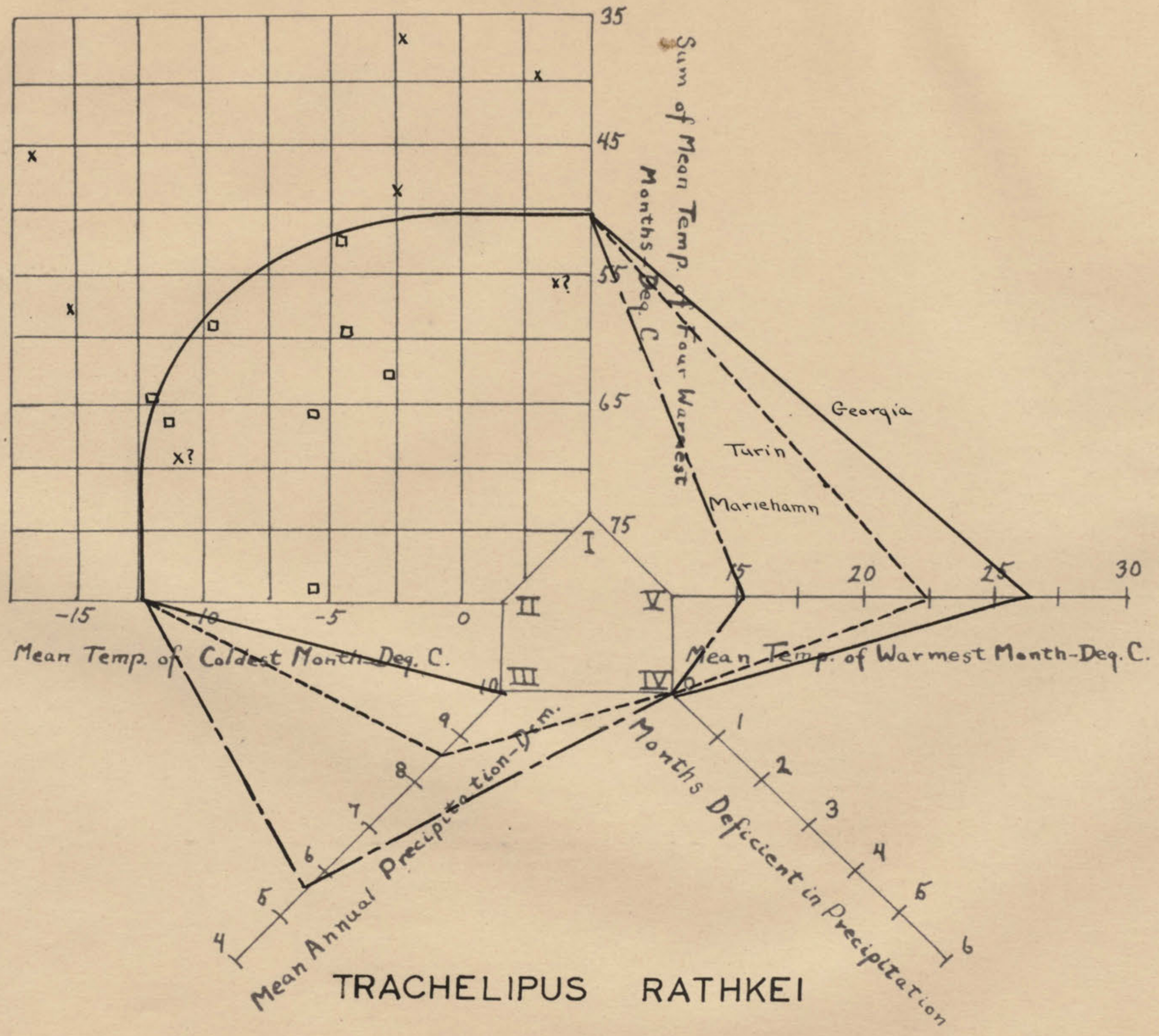
Trachelipus rathkei

Positive stations: Chatham, N. B.; Quebec, Que.; Greenville, Maine; Turners Falls, Mass.*; State of Georgia; Victoria, Texas (?); Mariehamn, Finland; Sortavala, Finland; Oslo, Norway; Konigsberg, Germany*; Belgrade, Jugoslavia; Wilno, Poland; Turin, Italy; Besancon, France.

Negative stations: Port Arthur, Ontario; Anticosti Island; Stykkisholm, Iceland; Thorshavn, Faroes; Trondhjem, Norway; Orkney Islands(?); Saraisk, Russia (?); Athens, Greece; Genoa, Italy; Marseille, France; Port-au-Prince, Haiti; San Francisco, Cal.

This is the common woodlouse of northeastern North America. Though sometimes found around settled places it is not usually synanthropic except possibly in the northernmost part of its range. The absence of T. rathkei from the northern coast of Europe where P. scaber is found is probably due to its slower rate of reproduction during the cool summers. Since T. rathkei is the more cold resistant it occupies regions with a subcontinental type of climate, cold winters and warm summers, which are unsuitable for P. scaber.

Richardson's record of Victoria, Texas, for this species is out of line with all other records. The mean July temperature at this place is 28.9°C. This is about 6°C.



TRACHELIPUS RATHKEI

FIGURE 11.

higher than the limiting temperature in Europe. Pierce (1911) in discussing the importance of sowbugs as cotton pests in Texas mentions only *Armadillidium vulgare*, *Porcellio laevis* and *Porcellionides pruinosus* as being found in the cotton belt. If *T. rathkei* was ever taken at Victoria, it certainly is a rare species there, and it is safer not to use Victoria as a positive station. The other doubtful stations are in incompletely studied regions.

Northern Index		Southern Index - Precipitation Index		
I	II	III	IV	V
Quebec			Georgia	
64.4°C.	-12.4°C.	12.6 dm.	0	26.6°C.
Mariehamn			Turin	
52.4°C.	-4.5°C.	8.6 dm.	0	22.9°C.
			Mariehamn	
		5.6 dm.	0	15.3°C.

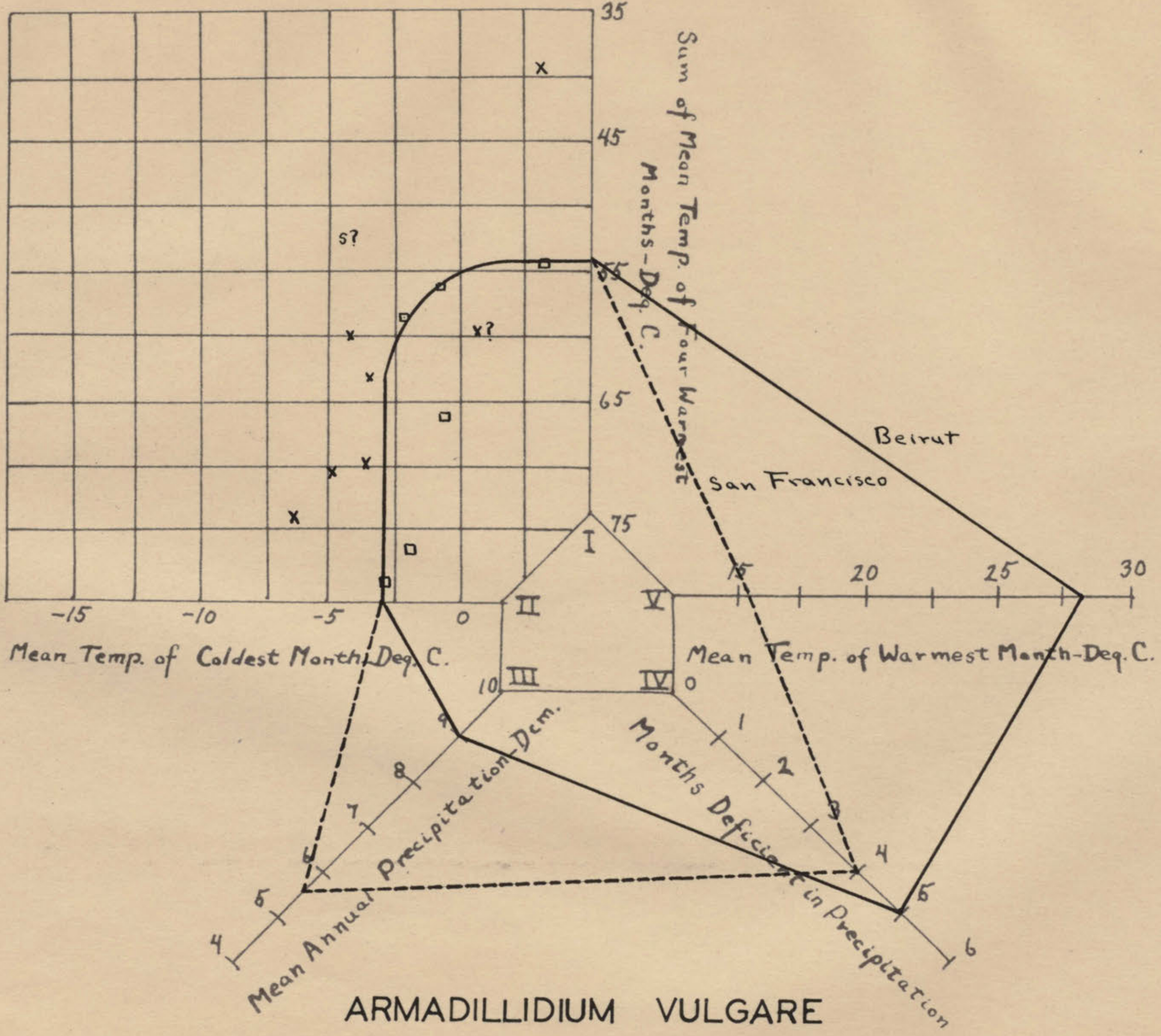
Blake's indices are: Winter, -10.0°C. No other in New England.

Herold's index: Will withstand climate with mean January temperature less than -7.5°C.

Armadillidium vulgare

Positive stations: Sandesund, Norway; Copenhagen, Denmark; Mariehamn, Finland (s?); Stettin, Germany; Edinburgh, Scotland; Budapest, Hungary; Barcelona, Spain*; Casablanca, Morocco; Algiers, Algeria; Beirut, Syria; Burgas, Roumania; Boston, Mass.; New Orleans, La.*; San Francisco, Cal.; Austin, Texas*; Valparaiso, Chile; Hankow, China; Tokio, Japan.

Negative stations: Konigsberg, Germany; Oslo, Norway; Rockport, Mass.; Hammershus, Denmark; Thorshavn, Faroes; Cer-



ARMADILLIDIUM VULGARE

FIGURE 12.

nauti, Roumania; Toronto, Ontario; Port-au-Prince, Haiti.

This is the most southern species to occur free living in New England. It also appears to be the one species least dependent upon regular rainfall, as it occurs around Beirut and Valparaiso, both of which have long dry periods annually.

The northern limit is sharply drawn except for the record from near Mariehamn. As A. vulgare is not found in the southern Baltic islands, it is probable that its presence here is accidental or synanthropic. The southern limit is probably one of moisture rather than one of high temperature. There is no apparent climatic basis for the absence of this cosmopolitan species from the West Indies. Possibly any immigrants would be placed in direct competition with the native cubarids of this region, and would be unable to gain a foothold. We know too little of the mechanism of competition in nature to more than venture a guess at this possibility.

Northern Index		Southern Index - Precipitation Index		
I	II	III	IV	V
Copenhagen			Beirut	
56°C.	-0.7°C.	9.0 dm.	5	28.4°C.
Boston			San Francisco	
78°C.	-2.8°C.	5.6 dm.	4	15.5°C.

Blake's index is: Winter, -1.7°C. to -2.2°C.

Summary of Climatic Study

1. A consideration of the ecology and geographical distribution of the land isopods shows that climate is probably the most important factor in limiting their distribution.

2. By choosing five climatic controls it is possible to explain most of the distributions recorded in the literature. These controls are:

I. The sum of the mean temperatures of the four warmest months.

II. The mean temperature of the coldest month.

III. The mean annual precipitation.

IV. The number of months which, ordinarily, are deficient in rainfall.

V. The mean temperature of the warmest month.

3. Controls I and II interact to determine the northern boundary of each species. Controls III, IV, and V interact to determine the southern boundary, or the boundary in areas of low rainfall.

4. By applying these controls the individual species may be characterized as follows:

Porcellio pictus and Trachelipus rathkei tolerate severe winter conditions, but require warm summers and regular precipitation.

Porcellio scaber and Oniscus asellus tolerate moderately severe winters and cool summers. They differ in their moisture requirements as P. scaber withstands long periods of deficient rainfall, while Oniscus is found only in regions with regular precipitation.

Cylisticus convexus tolerates moderately severe winters, but requires warm summers. Its moisture requirements are intermediate between those of P. scaber and O. asellus.

These five species are found in regions with warm temperate, but not hot summers.

<u>Trichoniscus demivirgo</u> tolerates moderately cold winters, and is found only where the summers are cool and the rainfall heavy.

<u>Philoscia muscorum</u> tolerates moderately cold winters, but requires warm summers. It tolerates a moderate periodic rainfall deficiency and fairly hot summers.

<u>Armadillidium vulgare</u> is found only where the winters are mild and the summers warm. This species is able to tolerate long periods of deficient rainfall during hot summers.

PART V

TOLERANCE OF WOODLICE FOR EXTREMES OF TEMPERATURE AND MOISTURE

Purpose of the Study

In Part IV it has been shown that there is considerable variation between the extremes of climate which different species will tolerate. One should not be too hasty in postulating that therefore the species must vary between themselves in cold hardiness, and in resistance to heat and to dryness in the same order as their climatic limits indicate. Special adaptations such as have been considered may explain the different distributions. A species may be excluded from a certain area, not because physical conditions are definitely unfavorable to it, but because they are much more favorable to its competitors. The action of climate on distribution is certainly too complex to be completely analysed from geographical and climatological data. It is necessary to isolate portions of the complex, and to study the effects of these portions on living organisms. The convenience of the land isopods for such a study has already been pointed out.

Eight species have been compared with respect to their resistance to low temperatures, to high temperatures, and to dryness of soil. These factors correspond to the coldest month, warmest month, and precipitation controls used in comparing the climatic limits of these species. The effect of different conditions of temperature and moisture upon rates of reproduction and of growth has not been studied. The woodlice are not convenient for this sort of work as the eggs are carried by the female. The young are difficult to handle, and a comparison of all eight species would require the full time of several men. It will be necessary to make such a comparison between two contrasting species such as P. scaber and T. rathkei before the controlling action of climate on these animals is fully understood. Much can be learned, however, from the determination of the physiological limitations of the different species.

An objection may be raised to the application of results of experiments performed on animals collected within a limited area to the whole of a wide ranging species. In the absence of pertinent experimental evidence, this objection can neither be confirmed nor refuted. Certain facts tend to show that each species has rather definite characteristics over all its range. It has been shown that the climatic limits in Europe and North America are, insofar as the climates can be matched, about the same. The general habitat relationships of a species are similar over all its range except where it is restricted to synanthropic environments. Finally, it is generally accepted that seven of the land isopod species considered here originated in Europe. The fact that they have spread so widely in America indicates that they were either preadapted to American conditions, or managed to adapt themselves after their arrival. The latter alternative seems unlikely since adaptation would have to take place very rapidly and be of a hereditable type in order to insure survival.

Description of Experiments

Methods of Collection and Maintenance

The animals were collected in the field into glass jars containing moist soil and leaves. In some cases collections were made on a quantitative basis with respect to time and area. These will be reported later. In the laboratory the species were separated and placed in various types of containers. The choice of container is chiefly dictated by the moisture requirements of the species concerned. It is necessary to separare the species in order to facilitate finding the right animal when it is needed, and to prevent the aggressive species from destroying the submissive ones.

T. rathkei, O. asellus, Armadillidium vulgare, and Ph. muscorum were kept in wooden boxes 18" square and 6" deep. (Fig. 13.) Tacked closely to the edge of these boxes were tops 18" or 12" high made of Sun-Ray-Glas* supported upon a wooden frame. On one side of each superstructure was a wooden door. These tops allowed a certain amount of light to enter the cages and cut down evaporation considerably. Provision for light was made, not because it is necessary for woodlice, but to render the cages suitable for a variety of purposes. Each wooden box was filled with soil to within about two inches of the top. In each an effort was made to maintain conditions especially favorable for the particular species kept therein. T. rathkei is fond of cornstalk litter and loose bark. Leaf litter and moss were placed in the cage

---

*Sun-Ray-Glas is the brand name of the Sears Roebuck Co. for iron screening, the interstices of which are filled with cellulose acetate.

with Ph. muscorum. Most of the O. asellus colony congregated under two large stones, while Armadillidium showed a preference for the under side of a board. Water was added as necessary, usually about twice a week. Porcellio scaber and P. pictus were maintained in copper mesh cages supported over water in battery jars. These containers were designed after a type used by Shelford (Shelford, 1929, p.553). It was found necessary even in these cages to add water about once a week. A wad of newspaper was soaked, the excess water squeezed out, and the moist mass placed in the top of the animal compartment. The containers were cooled by running cold water around them in a sink. Soil and small sticks of wood were placed with scaber; soil and lumps of limestone with pictus. In spite of the xerophilic nature of pictus, it is much more susceptible to dryness than to extreme moisture.

Cylisticus and Trichoniscus were kept under definitely moist conditions. The former species was placed in a tin coffee can with holes in the bottom. The closed can was set in a sink with running water, and the water rising through the contained soil by capillarity preserved proper moisture conditions. Trichoniscus was maintained in the same manner in a smaller can.

Feeding was simply managed as the animals subsist on the organic debris in the cages. Slices of potato were also given as food, and are eaten readily by Oniscus and Trachelipus. The woodlice generally eat their own cast skins

FIGURE 13. Maintenance cages

FIGURE 14. Cold Cabinet

after shedding them, and thus appear to conserve nitrogen and calcium.

Breeding takes place readily when male and female individuals are placed together. Regular observations were made for females with a marsupium, and these were found after the middle of January. Such females were removed to glass jars containing moist soil, three or four of the same speeies being alloted to a jar. A daily inspection of the jars was made, and any female which had borne young was removed to prevent her devouring her brood.

Places of Collection

The animals used in the experimental part of the study were, except in one instance, collected by the writer in New England. The places from which each species was taken are listed below.

Species	Places of Collection
Trichoniscus demivirgo	Blue Hills Reservation, Milton, Mass.
Oniscus asellus	Blue Hills Reservation, Milton, Mass. Lime Rock, R. I.
Philoscia muscorum	Blue Hills Reservation, Milton, Mass.
Cylisticus convexus	Orange, Mass., at ruined farm house.
Porcellio pictus	Orange, Mass., at ruined farm house. Lime Rock, R. I.
Porcellio scaber	Blue Hills Reservation, Milton, Mass.
Trachelipus rathkei	Orange, Mass., several places. Lime Rock, R. I.
Armadillidium vulgare	New Orleans, La., Southern Biological Co.

There is a possibility that A. vulgare from New Orleans is less resistant to cold than is A. vulgare in New England, and that it may react differently in other ways. This objection to the use of imported animals cannot be contradicted. Since several collecting trips in southern Massachusetts yielded only a very few specimens of Armadillidium, it was thought better to perform the experiments on imported animals than to omit them altogether.

I have also experimented casually with Ligyda oceanica from the coal wharf at Duxbury, Mass., and with Armadillidium nasatum from a greenhouse at Proctor, Vt.

General Procedure of Experiments

Only active healthy animals were selected as subjects of experimentation. They were placed in pint glass jars with tightly fitting metal tops, or in tin cans of the same capacity with closely fitted covers. In the containers was a weighed quantity of soil of a definite moisture content. Container and soil were weighed together, so that any loss in weight due to evaporation could be made up. Experimental jars were placed in constant temperature chambers before adding the animals, so that they would attain the desired temperature by the time the experiment was commenced. Often several species were placed together in the same container during an experiment. All combinations are safe at low temperatures when the animals are inactive, but species were not mixed in experiments carried on at high temperatures. Even with this precaution many animals were killed by their companions. Moulting individuals were avoided when possible, as they are often attacked by their associates and killed, thus complicating the experiment. Observations were made daily, and the condition of the subjects noted on special forms. Dead animals were removed at once. The degree of activity of the living animals was recorded, as well as any special fact which might be significant. In some cases an animal secreted itself so that it could not be found. In these instances the animal was recorded as missing until a very careful search of the contents of the experimental jar had been made. Any living animal betrayed itself by activity; if none were found alive the missing animal was presumed to be dead.

The number of animals used in a single experiment varied from one to ten. The higher number would have been preferable in all cases from the statistical point of view, but it was necessary to conserve stock. Certain species are difficult to obtain in large numbers at any time, while none can be secured during the winter except from cultures maintained in the laboratory.

The experiments may be divided into two groups, A and B. The first, Series A, tested the validity of the January isotherms as indicating the northerly limits of distribution. The lowest temperature which each species could withstand under given conditions of soil moisture was determined. These experiments were performed on adult animals collected in the fall, and therefore about to go into hibernation under natural conditions.

Series B, the second group of experiments, tested the value of the July isotherms as indicating the southerly limit for various species. The highest temperature tolerated by each species under various given conditions of soil moisture was measured. Since the young are born in summer, these determinations were made on both newly hatched and adult animals. This was to see whether any significant difference existed between the toleration of high temperatures by the relatively soft bodied young, and the more protected adults. The least resistant stage would be the critical one in determining survival under adverse conditions.

Both series A and B also tested the effect of rainfall as a zoogeographical influence, since moisture was considered in relation to temperature in both cases.

Series A

Temperature Control

Low temperatures were obtained in a Frigidaire 4A Ice Cream cabinet (Fig. 14). In one end of this there is a cubical compartment in which the experimental jars were kept. Around this compartment is a jacket containing brine. In the other end of the cabinet are located the compressor and the motor. It was found that the ordinary cold control with which the Frigidaire was equipped was not accurate enough for this work, as the temperature in the experimental chamber fluctuated about 3°C. The original control was, therefore, replaced by a Hiergesell Red-Top thermo-regulator operating a relay to start and stop the refrigerating mechanism as necessary. The thermo-regulator was supported on a wooden stand in the chamber with the experimental jars. Even with this control there was a slight temperature fluctuation due to lag in the conduction of heat between the brine jacket and the regulating device. When the chamber was not disturbed the maximum variation in temperature amounted to about 0.25°C. During observations the temperature usually rose about 0.5°C. above the average for about half an hour, and following this fell about half a degree below the average due to over compensation. From three to four hours were required for the temperature to come back to normal. Temperature records were made on a Bristol recording thermometer and the charts preserved with the other experimental data. This thermometer records on the Fahrenheit scale, and its readings were converted to the Centigrade scale. The accuracy of the recording thermometer was checked against a high grade mercury thermometer, which had in turn been checked against a standard thermometer.

Moisture Control at Low Temperatures

Experiments on the toleration of woodlice to low temperatures were carried on according to the general procedure described above. Soils of two sorts were used, one of a sandy type obtained from a road cut at Orange, Mass., the other a rich loam taken from a woods at Lincoln, Mass. The sandy soil when air dried in the laboratory contained about 1.5% of water. The loam contained 8.5% water after air drying. Soil moisture is calculated as the percentage weight of the contained water as compared with the dry weight of the soil. Desired moistures in the experiments were obtained by weighing out a definite quantity of the air dried soil into the experimental containers, and adding water to make the required moisture. For example, 101.5 grams of air dried sandy soil, representing 100 grams of oven dried soil, and 3.5 grams of water would be mixed in an experimental jar to make a 5% sandy soil. To make a soil of 10% moisture content 8.5 grams of water would be necessary. Because of the greater bulkiness of the loam, only 54.3 grams of the air dried soil corresponding to 50 grams of oven dried soil were used in each container.

There is a great difference in the water absorbing characteristics of the two types of soil; thus the absolute moisture values used in the two kinds of experiments are also different. In the sandy soil moistures ranged from 5% to 25%. In the humus soil they ranged from 12% to almost 300%. An attempt to compare the different values on a common scale is described later in this paper. Moisture contents of 5%, 15% and 25% were arbitrarily chosen for the first experiments in sandy soil. There appeared to be no difference in the first trials between the effects of 15% soils and 25% soils, so that the higher value was little used in subsequent work. Since 5% moisture in the sandy soil represents a moisture percentage increment of 3.5, the same percentage increment was added to air dried humus soil, the resultant moisture being 12%. This soil appeared so dry that larger intervals were taken between the next two higher moistures. These were made up to average values of 20.4% and 39.5% moisture. Other moistures chosen were 100% which produced a typical moist woodland soil, and 200% which produced a boggy soil. Because of the heterogenous nature of the humus soil used, it was difficult to obtain a thorough mixing of soil and water. According to analyses, the moisture values of individual experiments with humus soil varied ± 2% from these averages. Variations in the moisture content of the sandy soil were of the order of ± 1%. For reasons which are discussed under the moisture requirements of the individual species, it is believed that variations of this magnitude have little ecological significance in this particular case. The jars were kept tightly covered except during the observations so that little evaporation could take place. Experiments which ran for over a week were weighed regularly and water was added to make up for any loss.

The Study of Hardening

It was important to learn whether animals exposed for a time to low temperatures just above the lethal range became more resistant to severe cold than animals kept previously at room temperatures. To test this animals were kept for periods of a week or more at some temperature above zero, 4.5°C. and 2.2°C. in two cases. The temperature was then lowered and the results on "hardened" animals compared with those on animals introduced from stock kept at room temperature. Such comparative experiments could not be performed with every species as some failed to survive the hardening period.

Tabulation of Experiments

A complete tabulation of the experiments arranged by species is presented in Appendix B. In the textual tables duplicate experiments are combined. Each experiment is designated by a capital letter, or letters, indicating the series to which it belongs, its number in the series and a small letter following. The significance of the small letter is that each experiment in Series A was usually carried on at successively lower temperatures. Each part at a different temperature is designated by a small letter; e.g. experiment A54b at -1.0°C. and experiment A54c at -1.8°C. All experiments bearing the same number include the same individual animals. The survival times in days at each combination of temperature and soil moisture are given. Minimum, maximum and average values are given when possible. In cases in which some animals are still living at the close of the experiment, average and maximum values for survival time cannot be given and the symbol # is used. The number of survivors and the duration of such experiments are given. The survival time is taken as extending to the day on which the animal was found dead. Thus a survival time of one day means that the animal actually lived less than twenty-four hours. A question mark in the "Hardened" column of the tables means that the period of exposure to low temperatures was less than a week, so that any slow hardening effect might not have had time to develop.

Toleration of Woodlice for Low Temperatures in Loam

The effect of temperature upon a living organism cannot be considered except in its relationship to other factors. Probably the chief modifying agency in most instances is moisture. The importance of this factor will be apparent from the data presented below.

This data summarizes experiments performed at -1.0, -2.0, and -3.0°C. in loam with a moisture content of 39%. In humus soil of lower moisture content some species suffered from dryness. In soil of a higher moisture content resistance to low temperatures is decreased. Thus this series of experiments probably measures cold hardiness under very nearly optimum conditions.

Table 3

Comparison of Species at -1.0°C., 39% moisture, loam.

Species	Expt. No.	No.	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A54b& A105b	5	Yes	#	#	#	7	5
Ph. muscorum	A57b& A104b	4	Yes	1	4	7		0
P. pictus	A73a	2	No	#	#	#	7	2
P. scaber	A48b	3	Yes	5	#	#	7	2
	A110a	3	No	1	#	#	7	1
C. convexus	A60b& A108b	2	Yes	6	#	#	9	1
T. rathkei	A51b	3	Yes	#	#	#	8	3

Tr. demivirgo: Experiment not performed as soil is too dry for this species.

A. vulgare: Experiment not performed. Unhardened animals all died at 0.5°C.

Table 4

Comparison of Species at -2.0°C., 39% moisture, loam.

Species	Expt. No.	No.	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A54c	3	Yes	4	#	#	7	2
"	A105c	2	Yes	#	#	#	2	2
Ph. muscorum	A82a	4	No	#	#	#	5	4
P. pictus	A73B	2	Yes	#	#	#	9	0
P. scaber	A48c	2	Yes	8	#	#	9	1
"	A110b	1	Yes	#	#	#	2	1
"	A76a	3	No	#	#	#	6	3
C. convexus	A60c	1	Yes	8	8	8		0
T. rathkei	A51c	2	Yes	4	6	8		0
"	A79a	4	No	3	#	#	7	2
A. vulgare	AD3b	4	Yes	3	#	#	7	1
"	AD7a	3	No	1	1.3	2		0

Table 5

Comparison of Species at -3.0°C., 39% moisture, loam.

Species	Expt. No.	No.	Hardened	Survival Time			Duration	Survivors
				Min.	Ave.	Max.		
O. asellus	A85a	3	Yes?	4	#	#	7	1
	A95a	3	No	1	1	1		0
Ph. muscorum	A83a	3	Yes?	1	1	1		0
P. pictus	A73c	2	Yes	#	#	#	7	2
	A93a	3	No	1	#	#	2	1
P. scaber	A48d	1	Yes	6	6	6		0
	A84a	3	Yes?	1	2	4		0
	A92a	3	No	1	#	#	2	1
A. vulgare*	AD3c	1	Yes	1	1	1		0
T. rathkei	A79b	2	Yes	5	#	#	7	1
	A94a	3	No	2	2	2		0

* Experiment at -4.°C.

In the experiments at -1.0° and -2.0°C. <u>P. pictus</u> is the only species with no deaths. At the other end of the scale is <u>C. convexus</u>, two specimens of which failed to live out the experimental period. The small number of <u>C. convexus</u> used is explained by the fact that others of this species started at the same time died at temperatures above 0.0°C. The surviving animals, both of which were large females, actually represent the hardiest portion of the species. <u>A. vulgare</u> when unhardened is extremely susceptible to -2.0°, but one individual out of four previously exposed to 2.2°C. for a week lived a week at -2.0°C. The other experiments are inconclusive as to the effect of hardening.

The remaining species are closely matched with the possible exception of Ph. muscorum. The maximum time of survival of four individuals at -1.0°C. was seven days, while four individuals lived five days at -2.0°C. The experiment at -2.0°, No. A82a, was accidentally destroyed, and it was impossible to repeat it later, as the stock of this species was low. The best record attained by a species should, however, be considered at the truest measure of its potentiality.

In the experiments at -3.0°C. the hardening process appears to be beneficial in all cases except that of Ph. muscorum. Either this species hardens much more slowly than the others, or it is less cold resistant. There is evidence that under certain conditions hardening may take place with extreme rapidity, so that the second explanation seems most likely. P. pictus at -3.0°C. is again the most resistant species. T. rathkei, O. asellus and P. scaber are essentially equal. The experiment on A. vulgare is not exactly comparable since it was carried out at a temperature one degree lower. The individual in experiment AD3c was much more cold resistant than any others of its species, since it lived a week at -2.0°C. Judging from its condition at the end of the week, it would probably have died at -3.0°C. as readily as at -4.0°.

It is apparent that there is considerable variation between individuals of the same species. These discrepancies are less when experimental conditions are severe, but under these circumstances we are reducing the precision of analysis so that resistant and unresistant species are killed together. Two factors contribute to the apparent discrepancies exemplified by the results on Ph. muscorum at -1.0 and -2.0°C. One is the fact that large numbers of animals could not be used, so that a sampling error may occur. The other is that under border-line conditions there appear to be two entirely different mechanisms of death. Death by freezing is a quick process; the bodies of the dead animals are hard and their appendages are rigid. An animal may freeze and recover if removed to a warm place within a few minutes. The death which takes place only after a long exposure to low temperatures does not appear to be due to freezing of the body fluids. Since a small poikilothermic animal must take the temperature of its environment very rapidly freezing of the body fluids must take place rapidly or not at all. The freezing point of the body fluids of "normal" land isopods lies between -2.0 and -3.0°C., for it is within this range that death by freezing is first noted. The freezing point is influenced, however, by many environmental and physiological factors. In deaths which take place after several days exposure to low temperatures, the animals are limp and the appendages relaxed. Such deaths are due to a gradual pathological change induced by low temperature, the nature of which is at present unknown. It may be associated with a disruption of the water relationships between the body fluids and the intracellular colloids. The general subject of physiological cold hardiness is discussed later in this paper.

It is interesting to compare the results on loam with 39% soil moisture with those of experiments carried out in the same soil containing 100% moisture.

Table 6

Comparison of Species at -1.0°C., 100% moisture, loam.

Species	Expt. No.	No.	Hardened	Survival Time			Duration	Survivors
				Min.	Ave.	Max.		
O. asellus	A74a	2	No	#	#	#	6	2
Ph. muscorus	A74a	2	No	#	#	#	6	2
Tr. demivirgo	A62b	1	Yes	4	4	4		0
	A106b	2	Yes	1	1	1		0
P. pictus	A74a	2	No	#	#	#	6	2
P. scaber	A74a	3	No	5	#	#	6	2
C. convexus	A74a	1	No	1	1	1		0
T. rathkei	A74a	2	No	6	#	#	6	1
	A109b	3	Yes	1	#	#	7	2

A. vulgare: Unhardened individuals lived less than two days at 0.5°C.

Table 7

Comparison between Species at -2.0°C., 100% moisture, loam.

Species	Expt. No.	No.	Hardened	Survival Time			Duration	Survivors
				Min.	Ave.	Max.		
O. asellus	A74b	2	Yes	1	1.5	2		0
Ph. muscorum	A74b	2	Yes	3	3	3		0
P. pictus	A74b	2	Yes	#	#	#	9	2
P. scaber	A74b	2	Yes	1	1	1		0
T. rathkei	A74b& A109c	2	Yes	1	#	#	9	1
A. vulgare	AD4b	4	Yes	1	1.2	2		0

The one T. rathkei and two P. pictus which survived at -2.0° were able to live seven days at -3.0°C. at which time the experiments were terminated.

Except for the three individual animals mentioned above, the low temperature limit in 100% moisture soil is about a degree higher than in 39% moisture soil. Tr. demivirgo and C. convexus could not live at -1.0°C. A. vulgare was not tested at -1.0°C., but almost certainly could not tolerate this temperature unless previously hardened. Even hardened individuals of A. vulgare do not survive at -2.0°, and the same is true in this experiment of O. asellus, P. scaber and Ph. muscorum. At least some T. rathkei are resistant to -3.0°C., and it is possible that there are also especially resistant individuals in other species. P. pictus is again outstanding in respect to cold hardiness.

One experiment was carried out under very wet conditions, the soil moisture being 200%. This is more water than the soil used can absorb, and water stood on the surface. Movement of the animals was hindered by the surface tension of the water.

Table 8

Comparison between Species at -1.0°C., 200% moisture, loam.

Species	Expt. No.	No.	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A75a	2	No	2	4	6		0
Ph. muscorum	A75a	2	No	2	2.5	3		0
Tr. demivirgo	A75a	2	No	4	#	#	6	1
T. rathkei	A75a	2	No	4	4	4		0
P. pictus	A75a	2	No	#	#	#	6	2
P. scaber	A75a	2	No	1	1	1		0
C. convexus	A75a	1	No	1	1	1		0

One individual of <u>Tr. demivirgo</u> from experiment A75a lived nine days at -1.8°C., but died immediately when the temperature was reduced to -3.0°C. The only other survivors from this experiment were two <u>P. pictus</u> which lived two days and four days, respectively, at -1.8°C.

Two interesting points are brought out by this experiment. <u>Tr. demivirgo</u> differs from the other species studied in being most cold resistant in loam of a high moisture content. This might be expected in view of the fact that it is a species adapted to living in extremely wet soil. The other observation is more surprising. <u>P. pictus</u> has been considered to be especially adapted to dry situations, yet it is much more cold resistant under the conditions of the experiment than is <u>O. asellus</u>, a hygrophilous species. The absence of <u>P. pictus</u> from wet situations is probably not due to its inability to survive there, but is more likely due to tropistic reactions.

It was thought that the harmful effect of extreme moisture at low temperatures might be due to the freezing of water picked up from the soil on the pleopods and bodies of the animals. It will be noticed that survival was fairly good at -1.0°C. in loam containing 100% moisture. This soil was still unfrozen. At -2.0°C. the soil froze, and most of the animals died. This theory was tested by first freezing the soil and then placing the animals in the containers. The results of these experiments are summarized in Table 9.

Table 9

Number of survivors at hours after commencement of experiment. Comparison between species on frozen loam, -3.0°C., 200% moisture.*

Species	All unhardened						Expt. No.
	Hours after commencement						
	0	3	9	24	51	72	
O. asellus	3	3	0	0	0	0	A86a
P. pictus	3	3	3	2	1	0	A90a
P. scaber	3	3	1	0	0	0	A86a
T. rathkei	3	3	0	0	0	0	A88a
Tr. demivirgo	3	1	0	0	0	0	A89a

---

* The exact moisture content varied somewhat, but gravita- or free water was present in all cases after the containers were warmed.

This experiment demonstrates again the remarkable cold hardiness of P. pictus. Since death occurs rapidly under the conditions of the experiment, it is apparent that the freezing of external water is not the cause of death. Excessive moisture, even though present in a frozen state, has some effect on cold hardiness as will be seen by comparing the above experiments with experiments A95a, A93a, A92a and A94a summarized in Table 5.

Toleration of Woodlice for Low Temperatures in Sandy Soil

These experiments were carried on in the same way as those in loam. The experiments at temperatures above zero are not pertinent to the question of cold hardiness as deaths in these experiments were obviously due to lack of moisture.

Table 10

Comparison between Species, -1.0°C., 5% moisture, sandy soil.

Species	Expt. No.	No.	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A28b	3	Yes	6	#	#	14	2
	A38a	5	No	#	#	#	14	5
Ph. muscorum	A40a	3	No	13	#	#	14	2
P. pictus	A44a	3	No	#	#	#	14	3
P. scaber	A22b	2	Yes	8	9	10		0
	A34a	5	No	2	#	#	14	2
T. rathkei	A25b	2	Yes	1	2.3	4		0
	A36a	5	No	8	#	#	14	4
C. convexus	A42a	3	No	1	1	1		0

A. vulgare: Three individuals at 0.5°C. were all dead on second day of experiment.

Hardening for the animals of this group of experiments was at 4.5°C. for 14 days. Ph. muscorum did not survive the hardening period. P. pictus and C. convexus were not available at the time the hardening process was being carried on. In the experiments of this set hardened animals do more poorly than do animals introduced from stock. This is probably due to a gradual lowering of resistance under rather dry conditions.

Table 11

Comparison between species, -2.0°C., 5% moisture, sandy soil.

Species	Expt. No.	No.	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A28c& A38b	7	Yes	1	2.6	5		0
Ph. muscorum	A40b	2	Yes	1	1.5	2		0
P. pictus	A44b	3	Yes	1	#	#	7	1
P. scaber	A34b	2	Yes	2	3	4		0
T. rathkei	A36b	4	Yes	1	4.5	7		0

As in loam, P. pictus is the most cold hardy species. T. rathkei is only slightly better than O. asellus and P. scaber. Ph. muscorus falls between these relatively hardy species and the two cold susceptible species, C. convexus and A. vulgare. The available moisture in sandy soil will be seen later to be about half that in the loam of 39% moisture. It might be expected, considering the effect of moisture on resistance to low temperatures, that lower temperature would be tolerated in sandy soil. The fact is, however, that for all species the low temperature tolerated in this soil is about 1°C. higher than in loam. No definite reason for this pecularity has been discovered.

Experiments with sandy soil containing 15% moisture show that, in this soil also, moisture plays a part in determining cold resistance.

Table 12

Comparison between species, -1.0°C., 15% moisture, sandy soil.

Species	Expt. No.	No.	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A29b	3	Yes	#	#	#	14	3
	A39a	5	No	13	#	#	14	4
Ph. muscorum	A32b	3	Yes	7	#	#	14	2
	A103b	2	Yes	#	#	#	7	2
	A41a	3	No	4	#	#	14	1
P. pictus	A45a	3	No	13	#	#	14	2
P. scaber	A23b	3	Yes	13	#	#	14	2
	A35a	5	No	7	#	#	14	4
T. rathkei	A26b	3	Yes	#	#	#	14	3
	A37a	5	No	#	#	#	14	5
C. convexus	A43a	3	No	1	1.7	2		0
A. vulgare *	A101b	1	Yes	1	1	1		0

* Experiment A101b was in 10% moisture sandy soil. Three specimens of A. vulgare lived two days at 0.5°C. in sandy soil containing 15% moisture.

Table 13

Comparison between species, -2.0°C., 15% moisture, sandy soil.

Species	Expt. No.	No.	Hard-ened	Survival Time Min.	Survival Time Ave.	Survival Time Max.	Dura-tion	Survi-vors
O. asellus	A29c& A39b	7	Yes	1	1	1		0
Ph. muscorum	A32c& A103c	3	Yes	1	1	1		0
P. pictus	A45b	2	Yes	1	1	1		0
P. scaber	A23c& A35b	8	Yes	1	1.6	3		0
T. rathkei	A26c& A37b	8	Yes	1	2.4	5		0

These tables require little discussion as they only confirm facts already brought out. One interesting feature is the displacement of P. pictus as the most cold hardy species by T. rathkei and P. scaber. The smaller number of P. pictus used may explain this.

O. asellus, P. scaber, T. rathkei and Ph. muscorum were subjected to low temperatures in sandy soil containing 25% moisture. These experiments, numbers A30, A24, A27 and A33, respectively, are summarized in Appendix B, but their results would add nothing to the discussion here. Cold resistance is poorer than in 15% moisture sandy soil.

The Effect of Hardening on Cold Resistance

It was found impossible to obtain clear evidence on the effect of the hardening process from the data heretofore presented. In some cases a preliminary exposure to low temperatures seemed actually to diminish cold hardiness. See Table 10. It was decided to carry out a special series of experiments on two species, one reasonably cold hardy, the other only poorly so. Trachelipus rathkei and Armadillidium vulgare were chosen for this purpose. This series of experiments was designated as Series AD. It was carried out in loams of two moisture contents, 40% and 110%. The temperatures used were 2.0°C. for a hardening period of one week, and subsequent temperatures of -2.0°C. and -4.0°C. for seven days each. The results are summarized in Tables 14 and 15.

Table 14

Results at 2.0°C., 40% moisture in loam.

Species	Expt. No.	No.	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
T. rathkei	AD1a	5	No	#	#	#	7	5
A. vulgare	AD3a	7	No	1	#	#	7	4
At -2.0°C., 40% moisture in loam								
T. rathkei	AD1b	5	Yes	1	#	#	7	2
	AD5a	5	No	7*	#	#	7	3
A. vulgare	AD3b	4	Yes	3	#	#	7	1
	AD7a	3	No	1	1.3	2		0
At -4.0°C., 40% moisture in loam								
T. rathkei	AD1c& AD5b	5	Yes	1	2.2	5		0
	AD10a	3	No	1	1	1		0
A. vulgare	AD3c	1	Yes	1	1	1		0

* Temperature rose to 5°C. on previous day due to failure of current. No harmful effects on other experiments noted.

Table 15

Results at 2.0°C., 110% moisture in loam.

Species	Expt. No.	No.	Hard-ened	Survival Time Min.	Ave.	Max.	Dura-tion	Survi-vors
T. rathkei	AD2a	6	No	1	#	#	7	5
A. vulgare	AD4a	6	No	3	#	#	7	4
	At -2.0°C., 110% moisture in loam							
T. rathkei	AD2b	5	Yes	6	#	#	7	3
	AD6a	5	No	3	#	#	7	4
A. vulgare	AD4b	4	Yes	1	1.2	2		0
	AD8a	3	No	1	1.6	2		0
	At -4.0°C., 110% moisture in loam							
T. rathkei	AD2c& AD6b	7	Yes	1	1	1		0

Two conclusions may be drawn from this experiment. Preliminary exposure to low temperatures increases cold hardiness only under relatively dry conditions. The increase in cold hardiness in the case of T. rathkei is a matter of less than two degrees Centigrade. It is probably about three degrees for A. vulgare as this species failed to live at 0.5° without preliminary treatment, while one individual was able to live a week at -2.0° when previously exposed to 2.0°C. for a week.

Experiment AD9a

This experiment merits particular attention since it may explain the mechanism of hardening as it takes place in nature. It is also interesting as a possible starting point for further investigation of the physiology and physical chemistry of cold hardiness. The conditions of this experiment were as follows:

> Experiment AD9a; temperature, -4.0°C.; moisture, 40%; soil, loam. Subjects - 3 <u>T. rathkei</u>, adult, from room temperature.

Date	Time	Observations
3/11/35	10:00 A.M.	5A
"	11:30 A.M.	4 very stiff; 1 moderately so. Removed to warm place. Twitched legs as they thawed out. Placed in jar at room temperature.
"	1:35 P.M.	3 recovered to A-, replaced in cold box; 2 D.
"	2:35 P.M.	3 S+
3/12/35	10:40 A.M.	3 S, limp, placed on top of refrigerator for observation.
"	11:30 A.M.	2 A-, replaced in cold box. 1 S (did not recover).
3/13/35	1:30 P.M.	1 S, recovers slowly in hand; 1 D (?), placed on top of refrigerator, recovered.
3/14/35	1:30 P.M.	1 S (kept in cold); 1 A (kept on top). Both replaced in cold.
3/15/35	2:00 P.M.	2 S, yesterday's A in best condition.
3/16/35	2:00 P.M.	2 D, placed on top of refrigerator.
3/17/35	1:00 P.M.	No recovery.

Symbols used in reporting results: A-active; S-inactive; D-dead.

The significance of this experiment is in the difference in the reaction of the animals to cold after having been frozen and thawed. The second time that they were placed in the experimental chamber, they did not freeze solidly as before, but were as cold hardy as any animals studied. One lived almost continuously at -4.0°C. for from four to five days. The other lived as long, but was at room temperature for one of the days. Experiment AD10a was carried out under the same conditions, but the animals were not removed for twenty-four hours. None recovered. Apparently there is a time during which the harmful effects of freezing are reversible. If an animal is thawed out during this period, it will not only live, but will be cold hardy. Such a mechanism would be of great value to an animal, for it might be exposed to low temperatures for a short time and thereby be able to tolerate more severe and continued cold later. The rapidity of the change is its most striking characteristic.

Physiology of Cold Resistance

In comparing these results with similar studies on the cold hardiness of insects, both similarities and differences are to be noted. Fink (1925) states that, in general, insect hibernation is preceded by a period of intensive feeding followed by a lowering of the metabolic rate. Individual species possess an intrinsic periodicity which controls the hibernation reaction, while the action of temperature on this reaction is secondary. Payne (1926) also found a periodicity in the cold hardiness of certain oak boring larvae, but states that this may be broken up by removing the animals to an artificial environment. She believes that the rhythm observed in nature may be simply a reflection of the temperature cycle of the temperate zone. Bodine (1923) discovered that Chortophaga australior, a grasshopper of tropical climates, when exposed to suitable conditions reacts similarly to C. viridifasciata, which normally hibernates at a definite stage in its life cycle. C. viridifasciata from the vicinity of Philadelphia seems to be adapted to hibernate for a period of time equal to the length of the winter season. Animals brought into the laboratory late in hibernation recover more quickly than do animals brought in at an early stage.

No such hibernation rhythm can be demonstrated in the case of the land isopods. The period of winter inactivity seems to be due only to the effect of low environmental temperature. There is no drastic change in the metabolism of these animals when kept at low temperatures,for they become exceedingly active as soon as their temperature is raised. Mr. James Johnson tells me that he has observed the same phenomenon in the case of Collembola and other primitive insects. To this type of winter inactivity the term pseudo-hibernation is appropriate.

A striking difference is to be noted between the absolute cold tolerance of many insects and that of the wood-lice. The freezing points of oak borers, Synchroa larvae, in Miss Payne's experiments varied with their previous history, but ranged as low as -8.0 to -10.0°C. The under-cooling points which represent supercooling of the body fluids ranged from -13.0 to nearly -15.0°C. Death does not occur until the supercooling point is passed. The temperature of the animal then rises to the freezing point as heat is given off during the freezing process. Such cold tolerances are characteristic of insects which are exposed to extremes of low temperature. There are many non-hardy insects, however, whose toleration of cold as adults or larvae is very slight. Some of these winter as eggs or pupae.

Insects are more resistant to cold when their moisture content is low. Thus Fink found that the water content of the potato beetle, Leptinotarsa decemlineata Say, was reduced from 75% to 55% during the prehibernation period. Miss Payne reports that the larvae of Synchroa, when dehydrated over calcium chloride in the laboratory, became more resistant to low temperatures than were untreated larvae. Thus one effect of all hardening processes and of all preparations for hibernation is a withdrawal of water from the animal. Robinson (1927) has shown that the withdrawal of water in such hardy species as Telea polyphemus and in the moderately hardy Callosamia promethea may consist only of a change in the physical state of the water. Thus in T. polyphemus the total water remains nearly constant during the hardening process, but bound water increases from 10% to 50% of the total while free water falls from 90% to 50%. Robinson does not go deeply into the physical chemistry of the process, but states that bound water is firmly attached to the body colloids, does not conduct electricity, nor react as readily chemically. Bound water is determined by subtractin the moisture content as measured electrically from the total moisture determined by drying in an oven. The effect of binding water is twofold, the body fluids are concentrated and have a lower freezing point, and the volume of the cell contents is decreased so that if freezing of the water does occur the cells may not be ruptured. Robinson also found that in the non-hardy grain weevil, *Sitophilus granarius*, there is no increase in bound water, but rather a gradual decrease which is followed by death. This may be the basis of the slow type of death found in the land isopods.

These studies from the field of entomology harmonize with the results obtained with land isopods. In dry soil the water content of the woodlice is probably lowered, and the animals are more resistant to low temperatures. This process cannot take place in soils with excessive moisture. Whether the hardening process involves a progressive diminution in total moisture or simply a change in the physical state of the water cannot be told until further research is carried out. The rapid change in cold hardiness which occured in experiment AD9a must have involved a physico-chemical change in the cells of the animals involved, as there was scarcely time for the animals to reduce their total water content.

Summary of Experiments on Cold Tolerance

1. The eight species investigated differ characteristically in their tolerance of low temperatures. The range of tolerance is rather small, between 2.0 and -2.0° for unhardened animals, and between -1.0 and -3.0° for hardened animals.

2. The rank of the species arranged according to cold hardiness is as follows: P. pictus, T. rathkei, O. asellus and P. scaber, Ph. muscorum, Tr. demivirgo, C. convexus and A. vulgare. This arrangement has been determined by a consideration of all the experimental evidence. Species connected by "and" are essentially equal in cold hardiness.

3. Preliminary exposure to low temperatures increases the cold tolerance of land isopods. Increased cold tolerance is also conferred by quick freezing and immediate thawing.

4. The hardening process is interfered with by excessive soil moisture. This fact suggests that the process is concerned with the water balance of the animals.

5. Excessive soil moisture reduces the cold tolerance of all species except Tr. demivirgo.

6. The minimum temperature tolerated in sandy soil is about one degree Centigrade higher than it is in loam.

7. Death at low temperatures may be due to freezing, or to progressive pathological changes, by analogy with insects, probably concerned with the hydration of the protoplasmic colloids.

Series B

Temperature Control

A series of chambers originally designed for bacteriological work was used to obtain constant high temperatures. These are fully described by Jennison (1932). A Hiergesell thermo-regulator in each chamber operates a relay which switches the heating element on and off as necessary. Cold water can be run through the chambers to balance the heating element when it is desired to operate near room temperature. A motor driven fan prevents air stratification. The ordinary fluctuations from mean temperature in these chambers were of the order of 0.2°C., although in two instances there was a rise of over one degree when the room temperature rose suddenly. In all cases where deaths might have been attributed to an accidental rise in temperature the experiments were discarded.

In the final experiments of this series a water bath was used to maintain constant high temperatures. In these experiments it was necessary to make frequent observations, each of which would have involved opening the chamber door several times, with a consequent temperature fluctuation. Each container could be removed separately from the water bath without disturbing the temperature of the others. The water bath was heated by an immersed electric heater controlled by a Hiergesell thermo-regulator through a relay mechanism. Thorough distribution of heat was insured by a stirrer. No temperature fluctuations could be detected with a mercury thermometer graduated in tenths of degrees Centigrade.

Moisture Control

Air dried soil was made up to the desired moisture content as described on page 85. Sandy soil alone was used in this series. The experimental containers were all tin cans with tightly fitting tops, so that very little moisture was lost during the seven days that most of the experiments ran. The loss in moisture varied from 0.2 g. to 0.5 g. during this seven day period.

General Considerations

The reasons for including both adult and young animals in this series of experiments have already been presented. Certain technical difficulties are involved in handling the young animals. They are easily killed by over manipulation. If caught in a drop of water they may be drowned. Because of their small size it is often impossible to determine their condition without examination under a lens. In fact, it is sometimes impossible even to find all the young animals without breaking up the experiment. It was impossible to use the loam used in series A for experiments with the young, for they would burrow so deeply into it, that observations were impossible. In order to obtain the best possible comparison between the high temperature tolerations of young and adults, sandy soil alone was used for both groups. Even under the best conditions, however, some animals could not be found after careful search. The missing animals usually must have been dead, and decomposed or eaten, as the final examination of the experiments was very thorough.

No special consideration is given to the question of acclimatization to high temperatures. This is because the stock animals were kept at a temperature which is fairly high compared with that in natural environments. Animals which survive a prolonged exposure to high temperatures generally appear to be in poorer condition than at the start of the procedure. In nature the highest temperatures occur irregularly rather than continuously. The highest soil temperatures are attained under a bright sun, and only occur at the period of maximum insolation. They alternate with temperatures many degrees lower. Two kinds of experiments will yield information of ecological importance. In the first type the effect of prolonged exposure to moderately high temperatures is investigated. The exposure period chosen was one week, as preliminary experiments had indicated that a fair comparison between species could be obtained within this time. The second type of experiment compares the tolerance of each species for short exposures to temperatures which are fatal if long continued. Both types of experiments were carried out, and are reported here.

Factors Influencing Resistance

Within limits moisture plays a role in the determination of resistance to low temperature. The presence of gravitational or free water is, however, probably more harmful at high temperatures than in the median range, for Herold (1925) has shown that land isopods survive a shorter time in water at 20°C. than in water at 4.0°C. In the experiments described here the moisture content of the soil was so regulated that all the water was absorbed on the soil particles, or held in the capillary spaces between the particles.

There are certain critical periods in the life of the woodlice. The time of moulting is one of these Many authors have stated that moulting individuals are attacked and partially eaten by their companions, if they are confined in a small space. In the experiments at low temperatures this habit does not create complications since moulting does not take place under such conditions. In the experiments of Series B there was a fairly high mortality from cannibalism. Often the individual which was killed was not moulting, but was probably attacked when it became weakened. In other cases individuals moulted successfully and were not attacked. It might be argued that this difficulty could be avoided easily by separating the animals. If this is done, conditions are made more artificial since most species occur in aggregations in nature. Allee (1931, p. 182) has shown that the survival and water conservation of aggregated land isopods under conditions of desiccation is better than for isolated individuals. It was decided, therefore, to keep the animals together, and to make allowances for deaths due to cannibalism. In the final group of experiments it was convenient to place individuals separately in test tubes. Because of the high moisture in these experiments, it is probable that water conservation would not be an important factor, and that aggregation would not greatly influence survival.

Quite apart from the danger of cannibalism, individuals are less hardy while moulting than at other times, and many deaths were associated with this process.

Females with a marsupium are another less resistant class. They were not generally used in experiments, but a few were introduced for comparison with the others. This fact is of importance for the maintenance of the species, since the loss of a female and her brood is equivalent to the death of a large number of individuals.

Nutrition might be expected to play an important role in determining tolerance for high temperatures. The metabolic rate of poikilotherms increases as temperature rises. An animal not supplied with food might burn itself out within a short time. To obviate this possibility, thin slices of potato were placed in the experimental containers. In some cases these were used as food, in others they were apparently untouched. There appeared to be no difference, over the period of the experiments, between survival in containers where the food was used, and in those where it was not. The soil, though sandy, was not entirely devoid of organic matter, and probably furnished some nutriment. In experiments prolonged beyond a week, the question of nutrition would require more attention.

Arrangement and Tabulation of Experiments

Four grades of soil moisture were used in this series, 5%, 10%, 15% and 25%. The latter was used for only two species. The 5% moisture soil feels dry and is slightly dusty. With 10% moisture the soil is loose, but does not feel dusty. The 15% moisture soil feels moist and is firm. Water can be squeezed from the 25% soil, and it packs firmly.

The base temperature used was 25°C. Other temperatures used ranged up to 32.5° in 2.5° steps. It was known from a preliminary investigation that 35°C. if prolonged for 24 hours was a fatal temperature for all species, possibly excepting <u>A. vulgare</u> and <u>P. scaber</u>. Experiments at 35°C. and above were continued over a period of about six hours, or until there were no more survivors. The highest temperature used was 44.5°C.

If a species failed to survive at one combination of temperature and moisture, and did survive under more severe conditions, its best record is considered as its potentiality. Once a definite set of limiting conditions was found, further experiments were not carried out under absolutely fatal conditions.

It was planned to compare the physiological tolerances of the young of all species with that of the adults. This was found to be impossible since some species did not produce young in sufficient numbers. No young at all were borne by <u>C. convexus</u>. <u>Porcellio pictus</u> and <u>Trichoniscus</u>

demivirgo each produced a few, but not enough for satisfactory experimentation. In the case of the other species sufficient young were obtained. Young of Armadillidium nasatum were compared with other species in certain experiments.

The experiments are tabulated essentially as in Series A. Entirely new experiments were set up at each temperature, so that small letters are not used following the experiment number. Since deaths occurring as the result of cannibalism are not chargeable directly to unfavorable physical conditions, notes at the end of each table give the number of such deaths. The figures for survivors in the tables are the actual uncorrected values. Other notes record the birth of young, the death of females carrying broods, and deaths coinciding with moults.

Toleration of Woodlice for High Temperatures

The results of experiments at 25°C. are summarized in Tables 17, 18 and 19. From Table 17 it will be apparent that conditions at this temperature and 5% moisture are generally unfavorable. A. vulgare and P. scaber are the only two species to do well. The apparently poorer showing of P. scaber is entirely due to its cannibalistic tendencies. O. asellus is the only other species to show any survivors and the condition of this animal at the close of the experiment indicated that it would have died soon. Since in this experiment dryness is more of an unfavorable factor than high temperature, the results measure resistance to low moisture.

In the experiments at 10% moisture, survival is much better. In only three experiments are there no survivors, and only five deaths in other experiments are not due to cannibalism.

Table 17

Comparison between species at 25°C., 5% moisture, in sandy soil.

Species	Expt. No.	No.	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	B51	5	6	#	#	7	1
" , young	B39	5	1	1	1		0
Ph. muscorum	B46	3	2	2	2		0
" , young	B36	5	2	3	4		0
P. pictus	B55	3	3	4.7	7		0
P. scaber	B59	5	1	#	#	7	2
T. rathkei	B52	3	2	3	5		0
" , young	B43	3	1	1.3	2		0
A. vulgare	B49	3	4	#	#	7	2
" , young	B66	5	5	#	#	7	4

Notes: B51, one brood female dead.

B36, at 20°C.

B55, one newly moulted animal killed.

B59, two animals attacked and killed.

B49, one animal died during moult.

Young Ph. muscorum have a high mortality in all experiments, as may be seen in the appendix. It is possible that 10% moisture in experiment B37 is still low for it. Low moisture is probably also the cause of death in the case of young T. rathkei. The failure of P. pictus cannot be explained as this species lived a week in 10% moisture soil at 27.5°C.

Table 18

Comparison between species at 25°C., 10% moisture in sandy soil.

Species	Expt. No.	No.	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	B48	5	1	#	#	7	3
" , young	B40	5	1	#	#	7	2
Ph. muscorum	B53& B62	6	2	#	#	7	2
" , young	B37	3	3	3	3		0
C. convexus	B64	2	#	#	#	7	2
P. pictus	B56	3	5	5.7	7		0
P. scaber	B60	4	6	#	#	7	3
T. rathkei	B47	5	7	#	#	7	4
" , young	B44	5	4	4.6	6		0
A. vulgare	B50	3	#	#	#	7	3
" , young	B67	Became infected with mold disease.					

Notes: B48, two deaths due to cannibalism.

B62 and B53, one death due to cannibalism, in each experiment.

B37, at 20.0°C.

B56, one death due to cannibalism.

B60, one death due to cannibalism.

B47, one death by cannibalism; 2 young born did not live.

Table 19

Comparison between species at 25°C., 15% moisture in sandy soil.

Species	Expt. No.	No.	Survival Time			Duration	Survivors
			Min.	Ave.	Max.		
Tr. demivirgo	B54& B78	6	1	3.4	6		6
O. asellus, young	B41	5	1	#	#	9	3
Ph. muscorum	B63	3	5	#	#	7	2
" , young	B38	2	4	4.5	5		0
P. pictus	B61	3	1	#	#	7	1
T. rathkei, young	B45	5	#	#	#	7	5
A. vulgare, young	B68	9	1	#	#	7	7

Notes: B63, female with brood died.

Experiments were carried out at 15% moisture and 25°C. only when it was desired to check the results in 10% moisture soil. Tr. demivirgo was not used in the lower moistures because they were obviously too low for it. It appears from the results here either that 15% is too low a moisture, or that 25° is too high a temperature for this species. Two individuals of Tr. demivirgo lived for seven days in 25% moisture soil at room temperature, about 20°C. It did not live even in high moisture soil at 27.5°C. Obviously the species is adapted only to moist cool locations.

Young Philoscia lived a week in 15% moisture soil at 27.5°C., so that this experiment does not measure its maximum resistance. All the other species tested had one or more survivors.

It is shown that given sufficient moisture, 25°C. is tolerated by all the species studied, with the possible exception of <u>Tr. demivirgo</u>. Young <u>Ph. muscorum</u> on the borderline, since although no individuals lived at 25°, slightly older ones were able to tolerate 27.5°.

Table 20

Comparison between species at 27.5°C., 5% moisture in sandy soil.

Species	Expt. No.	No.	Survival Time Min.	Survival Time Ave.	Survival Time Max.	Duration	Survivors
O. asellus	B72	5	1	#	#	7	1
C. convexus	B85	2	5	5.5	6		0
P. pictus	B104	2	2	3	4		0
P. scaber	B87	3	7	#	#	7	2
" , young	B126	5	1	1.6	4		0
A. vulgare	B74	5	2	#	#	7	3

Notes: B104, one death at time of moult.

B74, one female with brood died; another released about 100 young which lived.

Table 21

Comparison between species at 27.5°C., 10% moisture in sandy soil.

Species	Expt. No.	No.	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	B73	5	3	#	#	7	1
" , young	B120	5	2	#	#	7	1
Ph. muscorum	B82	3	1	2.7	4		0
" , young	B133	4	1	2.0	4		0
C. convexus	B86	2	3	#	#	7	1
P. pictus	B80	3	3	#	#	7	2
" , young	B105	3	1	1	1		0
P. scaber	B79	3	4	#	#	7	2
" , young	B127	5	4	#	#	7	3
T. rathkei	B69	5	1	#	#	7	1
A. vulgare	B75	5	#	#	#	7	5
" , young	B76	10	1	#	#	7	4

Notes: B73, one death by cannibalism; 30 young born, 23 of which lived four days to the termination of the experiment.

B82, one death by cannibalism.

B80, one death by cannibalism.

B105, the subjects of this experiment appeared in poor condition at the start.

B79, one death due to cannibalism.

B75, 100 young born; practically all had disappeared within five days. Possibly they did not survive their first moult.

Experiments carried out at 27.5°C. are summarized in Tables 20, 21 and 22. Five species which might be expected to be resistant to dryness were compared at 5% moisture. A. vulgare and P. scaber are the most successful species. One individual of O. asellus also survived, while the survival time of C. convexus is good. P. pictus is the least resistant of the species tested. The species not included here were shown to be non-resistant to this degree of dryness at 25°C. (See Table 17). Young animals of the two most resistant species were also observed. The young of P. scaber lived an average of 1.6 days. The young of A. vulgare were not observed for a full week, but most of the hundred born in Expt. B74 lived the three days to the termination of the experiment.

Table 22

Comparison between species at 27.5°C., 15% moisture in sandy soil.

Species	Expt. No.	No.	Survival Time			Duration	Survivors
			Min.	Ave.	Max.		
Tr. demivirgo	B84	3	4	4.3	5		0
O. asellus, young	B41	3	#	#	#	7	3
Ph. muscorum	B83	3	1	2.7	5		0
" , young	B134	4	3	#	#	7	3
P. pictus	B81	3	#	#	#	7	3
" , young	B106	2	1	2.5	4		0
T. rathkei	B70	5	1	#	#	7	3
" , young	B71	10	4	#	#	7	7
A. vulgare, young	B77	10	?	#	#	7	5

Notes: B41, a continuation of B41 at 25°C.

B106, subjects of this experiment in doubtful condition at the start.

B70, two deaths due to cannibalism.

At 27.5° and 10% moisture most species do well. Only Ph. muscorum has no survivors at all, and it has also low average survival time. Adults of T. rathkei and O. asellus appear to be near their limits since each has only one survivor from five animals at the start. Young animals do just as well as adults under the conditions of these experiments.

The adults of P. scaber, A. vulgare and O. asellus were not tested at 15% and 27.5° moisture since they had already shown an ability to live at 5% and 10% moisture under the same conditions. In only three of the experiments summarized in Table 22, were there no survivors. Tr. demivirgo lived an average of 4.3 days. Two individuals of this species lived six and seven days, respectively, at 27.5° in soil of 25% moisture content. This is near the maximum amount of water which the soil will take up. Increased moisture helps survival, but 27.5° is probably too high for Tr. demivirgo over a prolonged period. The poor showing of Philoscia is peculiar, for the young do better than the adults. In another experiment with young of this species at 27.5° and 25% soil moisture, the average survival time was only 1.8 days, and the maximum 5 days. Overhandling may explain the high mortality. In a later experiment, B118, two out of three Philoscia lived a week at 27.5° and 25% moisture. The temperature is not too high for this species, if adequate moisture be provided. The death of young P. pictus has no significance, as the animals were in poor condition when released from the brood pouch.

Experiments at 30°C. are summarized in Tables 23, 24, and 25. At this temperature only one species, P. scaber, is able to live at 5% moisture. The only animal of this species to die was killed by its companions. The young of P. scaber do not live under these conditions. A. vulgare and O. asellus are also unable to survive, although 5% moisture had sufficed them at lower temperatures.

Table 23

Comparison between species at 30°C., 5% moisture, sandy soil

Species	Expt. No.	No.	Survival Time			Duration	Survivors
			Min.	Ave.	Max.		
O. asellus	B146	5	1	1.8	4		0
P. scaber	B97	3	5	#	#	7	2
" ,young	B144	5	2	3.0	4		0
A. vulgare	B93	5	4	4.6	7		0
" ,young	B95	10	1	3.8	5		0

Notes: B97, one death due to cannibalism.

B93, one death due to cannibalism.

Table 24

Comparison between species at 30°C., 10% moisture, sandy soil

Species	Expt. No.	No.	Survival Time			Duration	Survivors
			Min.	Ave.	Max.		
O. asellus	B132	5	4	5.6	7		0
" ,young	B147	10	1	2.6	4		0
C. convexus	B116	2	7	#	#	7	1
P. pictus	B102	2	1	3	5		0
P. scaber	B98	3	#	#	#	7	3
" ,young	B128	5	6	#	#	7	3
T. rathkei	B88	5	3	#	#	7	3
" ,young	B145	10	1	#	#	7	8
A. vulgare	B94	5	2	#	#	7	4
" ,young	B96	10	1	4.6	7		0

Notes: B116, one death due to cannibalism.

B94, one death due to cannibalism.

Table 25

Comparison between species at 30°C., 15% moisture, sandy soil

Species	Exp. No.	No.	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	B91	5	2	#	#	7	2
" , young	B92	10	1	#	#	7	7
Ph. muscorus	B148	5	1	#	#	7	1
C. convexus	B117	2	#	#	#	7	2
P. pictus	B103	2	3	#	#	7	1
T. rathkei	B89	5	3	#	#	7	3
" , young	B90	10	1	#	#	7	6
A. vulgare, young	B149	10	1	#	#	7	8

Notes: B91, one death due to cannibalism. One death at time of moult.

B89, two deaths due to cannibalism.

Conditions are too severe at 30°C. and 10% moisture for O. asellus, adults and young, adults of P. pictus, and young A. vulgare. All three lived at the same temperature with 15% soil moisture, showing again that high moisture aids in resisting high temperatures. Philoscia was tested only at 15% moisture at 30°, and one out of five animals lived seven days. It has the lowest percentage of survivors of any species.

The experiments thus far indicate that all species except Trichoniscus can live at temperatures of 30°C. and under, providing sufficient moisture be present. At 32.5° three species are no longer able to survive this period, even with abundant moisture.

Table 26

Comparison between species at 32.5°C., 5% moisture, sandy soil

Species	Expt. No.	No.	Survival Time Min.	Survival Time Ave.	Survival Time Max.	Duration	Survivors
P. scaber	B122	3	2	4.3	7		0
" , young	B122y	10	1	1.2	3		0

Table 27

Comparison between species at 32.5°C., 10% moisture, sandy soil

Species	Expt. No.	No.	Survival Time Min.	Survival Time Ave.	Survival Time Max.	Duration	Survivors
C. convexus	B138	1	7	7	7		0
P. pictus	B124	2	2	3.0	4		0
P. scaber	B123	3	4	#	#	7	1
" , young	B140	10	1	1.4	3		0
T. rathkei	B107	3	2	#	#	7	1
A. vulgare	B112	3	4	#	#	7	2
" , young	B114	10	1	1.5	3		0

Notes: B123, two deaths due to cannibalism.

B112, one moulting animal attacked and killed.

Even P. scaber can endure 5% soil moisture for only a short time at 32.5°C. However, since the maximum survival time is seven days, it is probable that some individuals would live a week under these conditions.

When the moisture is increased to 10%, conditions are still too severe for the young of even the two species most resistant to dryness. The adults of these species,

<u>P. scaber</u> and <u>A. vulgare</u>, survive one week in good condition. One individual of T. rathkei also survives this period, but the other species tested fail to do so.

Table 28

Comparison between species at 32.5°C., 15% moisture, sandy soil

Species	Expt. No.	No.	Survival Time			Duration	Survivors
			Min.	Ave.	Max.		
O. asellus	B110	3	1	1	1		0
" , young	B111	10	1	1.2	2		0
Ph. muscorum	B150	5	1	1.0	1		0
C. convexus	B139	2	6	#	#	7	1
P. pictus	B125	2	2	2	2		0
P. scaber	B142	5	1	#	#	7	2
" , young	B143	10	1	#	#	7	5
T. rathkei	B108	3	4	#	#	7	1
" , young	B109	10	1	#	#	7	1
A. vulgare	B113	3	1	#	#	7	1
" , young	B119	10	1	#	#	7	1

Notes: B113, one death due to cannibalism.

B142, two deaths due to cannibalism; one animal died during a moult.

Although increasing the moisture to 15% improves survival, three species, <u>O. asellus</u>, <u>Ph. muscorum</u> and <u>P. pictus</u> can live only a few hours under such conditions. The percentage of survival is low in most of the other species, although <u>P. scaber</u> has no deaths chargeable to high temperature alone.

The experiments at 35°C. and above were carried out for shorter periods as has already been explained. The animals were placed individually in glass test tubes which had already been warmed to the temperature of the experiment. Experiments were carried out in a water bath except in one case, when this was out of order and a Jennison incubator was used. The experiments were run for from five to six hours, observations being made at the times indicated on the accompanying tables. The tubes were set aside to cool after the last observation, and were examined again the next day. The number of animals still living was recorded in the extreme right hand column of the table.

Table 29 gives the results on adult animals at 35°C. and Table 30 the results on young animals. The differences between certain species are striking. In the adult group, Trichoniscus and P. pictus live less than one-half hour. O. asellus and Ph. muscorum are all dead at the end of 5½ hours while the average survival time of each is about 2.9 hours. All representatives of other species were alive at the end of the experiment, although the one specimen of C. convexus used was dead on the following day.

The same relationships hold between the different species of young insofar as it was possible to determine them. Thus, young Ph. muscorum and O. asellus lived less than 4 3/4 hours, while the other species all had survivors after 6 hours.
The results suggest that young T. rathkei are close to their limit, since they alone of the hardy species have any deaths.

Table 29

Experiment: B 1

Temp.: 35.1°C. Moisture: 15% in sandy soil. Water bath

Number of animals living at hours after commencement.
Adult animals

Time-Hours

Species	: 0	$\frac{1}{2}$	$1\frac{1}{2}$	$2\frac{1}{2}$	4	$5\frac{1}{2}$	Next day
Tr. demivirgo	3	0	0	0	0	0	
O. asellus	5	5	5	3	1	0	
Ph. muscorum	5	5	4	3	1	0	
C. convexus	1	1	1	1	1	1	0
P. scaber	5	5	5	5	5	5	5
P. pictus	2	0	0	0	0	0	
T. rathkei	5	5	5	5	5	5	5
A. vulgare	5	5	5	5	5	5	5
A. nasatum	4	4	4	4	4	4	4

Table 30

Temp.: 35°C. Moisture 15% in sandy soil. Incubator

Number of animals living at hours after commencement

Young animals

	Time-Hours						
Species :	0	1	2 1/4	3 1/4	4 3/4	6	Next day
O. asellus	5	5	3	1	0	0	
Ph. muscorum	5	4	4	0	0	0	
P. scaber	5	5	5	5	5	5	5
T. rathkei	5	5	5	5	5	3	3
A. vulgare	5	5	5	5	5	5	5
A. nasatum	4	4	4	4	4	4	4

Table 31

Experiment: B 3

Temp.: 37.6°C. Moisture 15% in sandy soil. Water bath

Number of animals living at hours after commencement

Adult animals

Time-Hours

Species :	0	1	2	3	4 1/4	5 3/4	Next day
P. scaber	4	4	3	2	0	0	
T. rathkei	5	5	0	0	0	0	
A. vulgare	5	5	4	4	3	2	2
A. nasatum	3	3	3	1	1	1	1
C. convexus	1	0	0	0	0	0	

Young animals

Species :	0	1	2	3	4 1/4	5 3/4	Next day
P. scaber	5	5	3	2	1	1	0
T. rathkei	5	3	0	0	0	0	
A. vulgare	5	5	5	5	5	5	5
A. nasatum	3	3	2	2	2	2	2

Table 32

Temp.: 40°C. Moisture 15% in sandy soil. Water bath

Number of animals living at hours after commencement

Time-Hours

Species	: 0	1½	3 1/4	4 1/4	5 1/4	Next day
A. vulgare, adult	5	4	2	1	0	
A. vulgare, young	5	5	4	4	2	1
A. nasatum, adult	3	3	1	1	1	1
A. nasatum, young	5	2	2	0	0	
P. scaber, young	5	2	0	0	0	

The species which survived the experimental period at 35°C. were tested in the same way at 37.5°C. This resulted in a further separation of the species. Results of these experiments are reported in Table 31. The two species of Armadillidium are the only ones to endure this temperature. One young P. scaber was still living at the end of 5 3/4 hours, but it was dead the next day. On the other hand, all five of the young A. vulgare used lived through the experiment. This was the best record made by any group.

The young and adults of two species of Armadillidium were tested at 40°C. for 5 1/4 hours. Results are given in Table 32. The survivors on the following day were 1 young A. vulgare and an adult A. nasatum. Five young of A. vulgare were exposed to 44.5°C. for one hour; none survived.

Summary of Experiments on High Temperature Tolerance

1. Experiments show that the eight species of woodlice tested differ characteristically in their tolerance of high temperatures.

2. The effects of moderately high temperatures for periods of a week, and of higher temperatures for shorter periods were investigated.

3. High soil moisture increases tolerance to high temperature.

4. The young of a species are equal or superior to the adults in resistance to high temperatures, but they are less resistant to low moistures.

5. In sandy soil of 15% moisture content the high tem-

perature tolerances of individual species may be summarized as follows:

Trichoniscus demivirgo: The one species least resistant to high temperatures. Limit for prolonged exposure near 27.5°C.

Oniscus asellus: Limit for prolonged exposure between 30° and 32.5°C. Lives about three hours at 35°C.

Philoscia muscorum: Limit about the same as those of O. asellus, but individuals are more variable.

Cylisticus convexus: Limit for prolonged exposure about 32.5°.

Porcellio pictus: Limit for prolonged exposure between 30° and 32.5°. Lives less than one-half hour at 35°C.

Porcellio scaber: Limit for prolonged exposure above 32.5°C. Time limit at 35° not determined, but over six hours. Lives less than 4 1/4 hours at 37.5°.

Trachelipus rathkei: Limit for prolonged exposure about 32.5°C. Time limit at 35° not determined, but is over six hours. Limit at 37.5° less than two hours.

Armadillidium vulgare: Limit for prolonged exposure about 32.5°C. Time limits at 35° and 37.5° not determined, but over six hours in both cases. Young more resistant to high temperatures than adults. Maximum resistance of young was 40° for 5 1/4 hours.

Moisture Requirements of Woodlice

Even a cursory study of the habits of the land isopods shows that all species are found in moist situations, and that the animals die if left in a dry place for more than a short time. Field observations indicate that the choice of habitat is primarily dependent upon soil moisture. Animals placed in an experimental moisture gradient take up positions where the soil feels definitely moist. In nature such places are often also dark, so that negative phototropism and positive hydrotropism would both lead the animal to the same habitat. If an experiment is carried out in total darkness on a generally dry substrate, the isopods will congregate about a spot of moisture. This demonstrates that the two reactions are independent.

The water content of the soil may influence the well being of woodlice in three ways. Branchial breathing through the endopodites of the pleopods has been described in Part II. Verhoeff's view is that the endopodites are covered with a film of moisture picked up from the substratum. This film facilitates faseous interchange. Thus the moisture content of the soil would be expected to influence respiration, particularly in the cases of those species which do not possess pseudo-tracheae. (See Table 1, p. 10). The moisture content of the soil may also affect the total water content of the animal. It has been shown (Allee, 1926a)that the water content of land isopods is profoundly affected by the moisture conditions of the environment. Finally the water content of the soil modifies its physical properties. Thus in low moisture soils, the animals become covered with particles of dust. These have been observed on the surface of the pleopods, and must have reduced respiration.

Previous Work on the Subject

The moisture requirements of woodlice have received more attention than has their ability to withstand extremes of temperature. This is largely because there has been interest in the structural and functional adaptations necessary to make a crustacean suited for terrestrial existence.

Herold (1913) carried out experiments on the duration of life of several species in dry air and in water. Dry conditions were obtained by placing the animals in a desiccator over sulfuric acid or anhydrous copper sulfate. His results are tabulated here.

Table 33 (Herold, 1913)

Species	Dutation of Life in Dry Air Hours
Oniscus asellus	8-10
Cylisticus convexus	8-10
Porcellio scaber	16-24
Armadillidium nasatum	17-26
Porcellio pictus	30-35

Though it is not stated, these experiments were presumably carried out at ordinary room temperature. The variations in survival time within a single species were related to the size of the animals, small ones dying sooner. This suggests that the differences were due to loss of water, rather than to respiratory failure. In a large animal the area of respiratory surface in proportion to its total volume is less than in a small animal. Thus respiratory difficulties would be expected to occur more quickly in large animals. Loss of water, however, will occur relatively more rapidly in the case of small animals because of the same surface area/volume relationship.

In Herold's experiments, the ability to survive in water was in general correlated negatively with ability to survive in dry air. Herold showed later (1925) that Trachelipus rathkei could live almost indefinitely in water, if the temperature was maintained at 4°C. He attributed this to the higher oxygen content of water at this temperature. From an ecological point of view, we are not particularly interested in the comparative ability of different species to live in water. The habitats of most woodlice are well drained, even though the soil remains moist. In Herold's experiments all species except P. pictus lived two days. We have already seen how P. pictus chooses well drained places for its habitat. Toleration for water for two days would take care of most emergencies.

Allee was primarily interested in the physiological effect of aggregation on water conservation. On a moist substrate (filter paper) three bunches of Oniscus gained an average of 3.8% in weight. Eight similar isolated animals gained an average of 9.7%. The results on a dry substrate are expressed in Table 34.

Table 34 (Allee, 1926)

Arrangement	Wt.mg.	Loss of water in percent original weight			
		76 min.	153 min.	283 min.	447 min.
Bunch of 10	44.7	4.3	6.7	10.0	15.8 all alive
Single	44.05	12.4	16.5	34.2 d	
"	62.4	8.1	15.4	24.6	37.8 d
"	54.0	15.6	22.3	28.8	49.6 d
"	28.2	24.4	30.1	37.5 d	
"	34.6	12.4	13.9	30.9 d	

d : dead animal   Average $\frac{\text{bunch}}{\text{single}}$ ratio: 0.31

It will be noted that a very marked protection was afforded by aggregation. Death follows a moisture loss of over about 30%. As in Herold's experiments, small animals died sooner than larger ones.

Characteristics of Soil Moisture

It has long been known that the absolute moisture content of soil was no measure of its ability to support plant growth. The plant physiologists have employed various methods to determine the "available moisture". Some of these are to a certain degree applicable to animal ecology.

B. E. Livingston (1931) has invented a small porcelain cone with a porous absorbing area of 12 square centimeters. By the use of these soil points it is possible to measure the amount of water absorbed from a soil by a standard surface in a certain period of time. If this is done, one finds that the rate of water absorption is not directly proportional to the total water. Instead, it changes very slowly in certain ranges and rapidly in others. This is because water in the soil exists in three different states.

Adsorbed water is present as a film on the soil particles, chiefly on those of colloidal dimensions. Its maximum value is about equal to the hydroscopic coefficient of a soil, which is the percent moisture of a soil in equilibrium with water saturated air. Capillary water occupies the small spaces between soil particles. It is driven off by evaporation, but does not drain away by gravity. Gravitational water will drain away from the large spaces in the soil which it occupies.

If the water content of a soil exceeds the hydroscopic coefficient, then the relative humidity of the soil atmosphere must be 100%. This would be predicted upon theoretical grounds, and may be shown to be true by measurement. (Lebedeef, 1928). In the range of moisture content between zero and the hydroscopic coefficient, water distributes itself between the soil particles and the soil atmosphere in a definite ratio. Thus the entire range of soil atmosphere humidity may occur within the range of a few percent of total moisture. Obviously it is extremely difficult to control the humidity of soil atmosphere, since it may be greatly affected by a small variation in soil moisture.

Moisture Conditions in Experiments

The hygroscopic coefficients of the two soils used were determined at 20°C. They were: loam, 16.9%; sandy soil, 2.69%. Except for the experiments in loam of 12% moisture, all moistures exceeded these values. Therefore the relative humidities in the other experiments would be expected to be 100%. The relative humidities in the upper part of several experimental containers were measured by the dew point method. The values over sandy soil of various moisture contents were: 5% moisture, 95% relative humidity; 10% moisture, 97% relative humidity; 15% moisture, 99% relative humidity. The relative humidity over loam of 20% moisture content was 98%. These values represent conditions several centimeters above the animals. In the soil itself humidity was probably 100% in all cases. Occasionally an animal would manifest an avoidance reaction, and would remain for a long period on the side of the experimental jar. In these cases, the animal was exposed to the humidities measured.

The amount of absorbable water was measured with Livingston soil points. These were oven dried at 105°C., cooled and inserted into the soil for a period of one hour. The gain in weight per cone divided by twelve gives the amount of water taken up per square centimeter of absorbing surface. Two or four cones were used for each measurement. Livingston states that the results are quantitatively proportional only over a limited range.

Table 35

Grams of water absorbed per sq. cm. per hour by porcelain soil points.

Soil	Moisture Content per cent	Grams of water absorbed
Sandy	5	.0019
Sandy	10	.0142
Sandy	15	.1975
Loam	10.4	.00208
Loam	17.7	.00265
Loam	30.0	.00317
Loam	34.1	.00367
Loam	80.5	.00675
Loam	91.5	.0282
Loam	130	.0561
Loam	139	.0408
Loam	188	.399
Loam	220	.357

The results of these measurements were not as consistent as had been hoped, probably because the heterogenous nature of the loam used made good contact with the points very difficult. However, the differences are so large, that we can at least compare the orders of magnitude of the absorbable water present in the different soils used.

Sandy soil of 5% moisture is about equal in absorbable water to loam of 12% moisture. Sandy soil of 10% moisture is similarly equivalent to loam of slightly under 100% moisture. The 15% moisture sandy soil lies about midway between 100% loam and 200% loam in absorbable water. It is interesting to see whether the biological effects of the different moistures match up in the same way.

Gravitational water was present in loam above about 150% water content. In sandy soil the corresponding point was 30%.

Resistance of Woodlice to Dryness at Low Temperatures

Several species were carried out in loam of low moisture content. The results on the species tested at 12% soil moisture are given by Tables 36 and 37. The moisture content of the soil in these experiments is below the hydroscopic coefficient of the soil, so that the relative humidity in them must be below 100%. The soil feels very dry, and the animals placed in it were soon covered with dust.

The results of these two groups of experiments show that this moisture is too low even for the supposedly xerophilic Porcellio pictus. This species has the longest average and maximum survival times. All species except P. scaber do better at -1.0° than at 2.2°, and this is probably a general tendency.

Table 36

Comparison between species at 12% moisture, loam, 2.2°C.

Species	Expt. No.	No.	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A52a	2	1	1.5	2		0
Ph. muscorum	A55a	2	1	1.5	2		0
C. convexus	A58a	1	1	1	1		0
P. scaber	A46a	2	1	3.5	6		0
T. rathkei	A49a	2	2	2	2		0

Table 37

Comparison between species at 12% moisture, loam, -1.0.

Species	Expt. No.	No.	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A64a	2	2	3.0	4		0
Ph. muscorum	A68a	2	1	2.5	4		0
P. pictus	A65a	2	5	7.0	9		0
P. scaber	A67a	2	1	2.5	4		0
T. rathkei	A66a	3	2	4.3	6		0

Tables 38 and 39 give the results in the next higher moisture of the loam series.

Table 38

Comparison between species at 20% moisture, loam, 2.2°C.

Species	Expt. No.	No.	Survival Time			Duration	Survivors
			Min.	Ave.	Max.		
O. asellus	A53a	2	4	5.0	6		0
Ph. muscorum	A56a	2	5	#	#		1
C. convexus	A59a	1	7	7.0	7		0
P. scaber	A47a	3	#	#	#	6	3
T. rathkei	A50a	2	#	#	#	6	2
A. vulgare*	A97a	3	2	#	#	9	1

* Experiment at 0.5°C.

Table 39

Comparison between species at 20% moisture, loam, -1.0°C.

Species	Expt. No.	No.	Survival Time			Duration	Survivors
			Min.	Ave.	Max.		
O. asellus	A64a	2	4	#	#	6	1
Ph. muscorum	A71a	2	2	#	#	6	1
"	A56b	1	1	1	1		0
P. pictus	A69a	2	#	#	#	7	2
P. scaber	A47b	3	2	#	#	7	1
T. rathkei	A50b	2	3	5	7		0
A. vulgare	A97b	1	2	2	2		0

It will be noted in Table 39 that without exception animals previously exposed ("b" experiments) did more poorly than those brought in from stock. This can be explained by the fact that these are borderline conditions, and the loss in water is gradual. Animals previously exposed are suffering from the effects of continued deprivation of moisture. Therefore the last three species listed in Table 39 should not be compared with the first three, since they were at an initial disadvantage.

Loam of 39% moisture meets the requirements of all species except Trichoniscus at temperatures around zero. Trichoniscus will live in loam of 100% moisture content at this temperature.

The lowest grade of moisture in sandy soil was 5%, and even this is scarcely below the minimum for any species. The results at 4.5°C. are presented in Table 40.

Table 40

Comparison between species at 5% moisture, sandy soil, 4.5°C.

Species	Expt. No.	No.	Survival Time Min.	Ave.	Max.	Duration	Survivors
O. asellus	A28a	3	#	#	#	12	3
Ph. muscorum	A31a	3	4	4.3	5		0
P. scaber	A22a	3	11	#	#	12	2
T. rathkei	A25a	4	8	#	#	12	2
A. vulgare*	A100a	3	2	2	2		0

* Experiment at 0.5°C.

Excepting A. vulgare, whose death is undoubtedly due to cold rather than dryness, the order of resistance is exactly that of size, large species doing better than small ones.

For a comparison between species at 5% moisture and

-1.0°C., see Table 11, page 99. Moisture conditions are apparently satisfactory over the period of the experiment. Fresh animals do better than those previously exposed. The death of C. convexus is due to low temperature rather than to insufficient moisture.

Discussion

It is a little surprising to find all species so nearly even in their moisture requirements at temperatures below zero. Those species equipped with pseudo-tracheae seem to have no definite advantage over those without them. This might be expected, for at low temperatures evaporation and metabolism will be slowed down. Thus there is neither excessive loss of water, nor activity which might bring on a crisis.

Trichoniscus is definitely the most susceptible to dryness. The differences between the other species are mostly due to the action of low temperature. Ph. muscorum does appear to be more susceptible than the other species at 4.5°C. in 5% moisture sandy soil. At -1.0°C. it does as well as the others.

One species only was able to live more than seven days in loam of 12% moisture. This was Porcellio pictus. This soil contains less than the maximum hygroscopic water. Sandy soil of 5% moisture and loam of 20% moisture were about equal in meeting the minimum requirements. According to soil point measurements, the latter soil contains a slightly greater amount of absorbable water. Survival in soil of low moisture content is definitely better at -1.0°C. than at temperatures above zero. In the next section the effect of temperature on optimum soil moisture is discussed further.

Effect of Temperature on Optimum Moisture

Experiments A22 to A45 show a very definite relationship between the effects of moisture and those of low temperature. At temperatures down to -1.0°C., the high moistures are most favorable, while at -2.0°C., it is evident that high moistures are adverse. The tables presented here represent the sum of several experiments using different species. Since every species behaved exactly the same in respect to the moisture-temperature relationship, grouping them together does not conceal any exceptions to the rule. This may be verified by consulting the summarized experiments in Appendix B. The species used in these experiments were P. scaber, P. pictus, C. convexus, Ph. muscorum, O. asellus and T. rathkei.

Table 41

Number of living animals after each three-day period, 4.5°C.
Sandy soil.

Moisture %	Start	Days 3	6	9	12	% survival after 12 days
5	12	12	10	9	7	58
15	12	12	12	12	12	100
25*	9	9	9	9	9	100

* : One experiment excluded because of cannibalism.

Table 42

Number of living animals after each three day period, -1.0°C.
Sandy Soil

Moisture	Start	Days 3	6	9	12	14	% survival
5%	31	21	24	20	20	18	58
15%	36	33	32	30	30	26	72
25%	10	10	10	10	10	9	90

Table 43

Number of living animals each day, -2.0°C., sandy soil

Moisture	Start	Days 1	2	3	4	5	6	% survival
5%	18	11	9	6	6	5	3	17
15%	26	8	6	1	0	0	0	0
25%	9	3	0	0	0	0	0	0

The probable explanation of these results is that at the two higher temperatures, lack of moisture is a more common cause of death than is low temperature. At -2°C. the order of favorable moistures is reversed, since death now is caused by freezing. It has already been shown that high moisture increases the severity of the action of cold.

Resistance of Woodlice to Dryness at High Temperatures

This topic has already been considered in connection with the high temperatures tolerated by the woodlice. It was shown that high soil moisture increased resistance to high temperatures, and that low moistures were tolerated less well at high temperatures. Tables 17 to 28 summarize the experimental work on which this discussion is based.

A soil moisture of 5% was sufficient for only three species, O. asellus, P. scaber and A. vulgare. The first of these suffers most from the effects of dryness as is evidenced by its sluggish behavior and dirty appearance in the experiments. When the temperature is raised to 30°C. only adult P. scaber can withstand 5% moisture soil for a week. Young animals of no species, except A. vulgare, withstood such dry conditions for as long as a week. These young were aboe to do so at 25°C., but not at higher temperatures.

A soil moisture content of 10% at 27.5°C. is sufficient for all species except Philoscia muscorum and Trichoniscus. At 30°, however, this moisture is less favorable. Oniscus asellus, P. pictus, and young A. vulgare are also unable to maintain themselves. The effect of this moisture at 32.5° is more severe than at 30°. Survival times are lowered, and only P. scaber, T. rathkei and A. vulgare have any survivors. No young are able to live at this combination of factors.

Soil moisture of 15% apparently meets the requirements of all species except Trichoniscus, which required about 25% in these experiments. Deaths in soil of this moisture content appeared to be due to high temperatures, or to factors beyond the control of the experimenter. In fact, Trichoniscus did not appear dry in soil of 15% moisture content.

Discussion and Summary of Moisture Requirements

The adults of the eight species studied may be ranked in the order of least dependence upon soil moisture. The arrangement is: P. scaber, A. vulgare, O. asellus, C. convexus and T. rathkei and P. pictus, Ph. muscorum, Tr. demivirgo. The species connected by "and" are essentially equal. This order differs from that reported by Herold, especially in the difference between P. pictus and O. asellus. The superior resistance of O. asellus to low moistures at high temperatures was, however, very marked in these experiments. It is possible that dependence upon soil moisture is not directly correlated with dependence upon high relative humidity. This might explain the discrepancy. Except for these two species the order of dependence upon soil moisture is correlated with the respiratory structures of the species. The two most resistant species have the pseudo-tracheae best developed. C. convexus and T. rathkei have less well developed pseudo-tracheae. O. asellus is probably resistant because of its comparatively large size. The other two species have simple respiratory systems, but Philoscia has the advantage of a water conducting system, and also of size.

The order of dependence is about the same at low temperatures as at high, but the distinctions between species are less well marked. The relative humidity of the system would not be expected to change greatly with temperature, but the absolute humidity, the rate of water absorption, and the rate of metabolism would change. Absorbable soil moisture seems to be fairly good index of the biological effects of a soil on animals as well as on plants. Thus resistance to cold in sandy soil of 5% moisture content and in loam of 39% is about the same. The amount of absorbable water in the two soils is of the same order of magnitude. The effects of cold in sandy soil of 15% moisture are comparable with those in loam of 100% moisture. The physical qualities of a soil are probably of great importance, for a coating of dust on the moist surface of an animal takes up moisture, and causes drying. This appeared to be a factor in the death of woodlice at low soil moistures. A microscopic examination of dead animals showed fine dust covering the respiratory apparatus. It is probable that soil moisture becomes a limiting factor for land isopods before the relative humidity falls to a limiting value. This is certainly true at high temperatures. Woodlice are not, however, entirely dependent upon absorbing moisture from the substrate. Oniscus asellus has been kept alive in a wire cage over water in a desiccator for over a week. In a few experiments the animals scarcely made contact with the soil, but remained on the sides of the containers. Animals manifesting this avoidance reaction generally lived longer than those who did not, and it may be considered as a protective reaction against the drying effect of the soil.

The resistance of young animals to dryness is much less than that of adults. This fact is of importance in the ecology and distribution of the species. Of the young tested, only two species, A. vulgare and P. scaber, appeared to be less dependent than other species upon soil moisture. The aggregations of young animals are less dense than those of adults, and the protection against dryness afforded by them would be small. As for the protective value of such aggregations as those described by Allee in nature, there can be little doubt. It may be pointed out, however, that at high temperatures when moisture is most essential, the animals are stimulated to great activity and do not readily collect into quiet groups.

PART VI

REACTION OF WOODLICE TO CHLORIDES

Blake (unpublished) and Herold (1930) have noted the association of Philoscia muscorum with soils of definite salinity. Blake compared the distribution of this species with the ground water isochlors of the State of Massachusetts, and found that the isochlor of 2.5 parts per million coincided almost exactly with the western limit of Ph. muscorum. It is apparent from the New England distribution maps that certain other species are found much more commonly near the coast than away from it. Even though winter conditions inland might prevent certain species from becoming abundant as free living species, they might be expected to occupy protected niches more completely than they do. Their failure to do so might be explained if it could be shown that they reacted in favor of high chloride concentrations in soil, or unfavorably towards low chloride concentrations. Experiments to determine this reaction were carried out on the adults and young of four species, Ph. muscorum, Porcellio scaber, Oniscus asellus and Trachelipus rathkei.

Methods

Covered glass dishes 5" square and 2½" high were used as experimental containers. Each dish was divided into two equal parts by a glass partition 1" high sealed in place with paraffin. Washed and dried sand was placed in each side of the container level with the top of the partition. To the sand on each side were added 50 ml. of distilled water or salt solution according to the plan of the experiment. The sand in each case had been washed with distilled water until the wash water gave no cloudiness upon the addition of silver nitrate. The animals were then added, an equal number on each side. Observations weremade daily, or in some cases more often. Soil, moisture conditions, and temperature were the same on both sides of the container. The source of light was above the experiments, and was presumably the same in all parts of the dishes. These were turned at each observation, so that if light was a determining factor in any cases, it would be as favorable for one side as another.

Since it was possible that any reaction to chloride concentration might be induced either by external contact or by enteric contact, but not necessarily by both, an attempt was made to provide for both possibilities. In the first experiments an attempt was made to soak thin slices of potato in several changes of chloride solution of the desired strength. The potato slice was then placed on sand which was saturated with the same solution. Unfortunately the potato was usually soon overgrown by bacteria, and did not attract the isopods. Acid washed filter paper soaked in salt solution was then substituted for it. This was used for protection from light, but was apparently not used for food. The experiments, then, do not exclude the possibility of a reaction to enteric stimulation.

Pure sodium chloride was used in making up the test solutions. A 3% solution of salt in distilled water was made, and this was twice successively diluted 1:100 to make solutions of 300 p.p.m. and 3 p.p.m. of chloride ion. The 3 p.p.m. solution is close to the value of the ground water isochlor which coincides with the western limit of Philoscia in Massachusetts. The 300 p.p.m. solution is intermediate between the weaker solution and conditions in a salt meadow. It certainly is not too salt for land isopods, since P. scaber and Ph. muscorum are common in the sale meadows of eastern Massachusetts.

In observing the experiments the difference between the numbers of animals on the two sides was recorded. The number on the low salt side was algebraically subtracted from the number on the high salt side. Controls were carried out in which there was no difference between the salt concentration on the two sides. In these cases one side was arbitrarily chosen at the start as the one to be treated like the high salt side.

The significance of the mean difference between the numbers of occurrences on the two sides was determined by the method of "Student" as given by R. A. Fisher (1930). "If x_1, x_2,..........x_n is a sample of n^1 values of a variate x, and if this sample constitutes the whole of the information available on the point in question, then we may test whether the mean of x differs significantly from zero by calculating the statistics

$$\bar{x} = \frac{1}{n'} \sum x$$

$$\frac{s^2}{n'} = \frac{1}{n'(n'-1)} \sum (x-\bar{x})^2$$

$$t = \frac{\bar{x}\sqrt{n'}}{s}$$

$$n = n'-1$$

End quote

Tables are available which show for each value of n, the values of t for which, in a population distributed normally about zero, P, the probability of falling outside the range ± t, takes the values 0.9..........0.01. In this work a probability of less than 0.05 was considered to indicate probable significance of results. In other words, this meant that there was less than one chance in twenty of the difference being due to chance alone.

Behavior of Woodlice in Chloride Experiments

The adults and, to a lesser extent, the young of P. scaber, O. asellus, and T. rathkei to aggregate in one corner of the container. These groups, when broken up, showed a marked tendency to come together again in the same place in which they had originally aggregated. Sometimes there would be two groups, one on each side of the container. These aggregations introduced an unforeseen complication, since the side on which they were formed might be determined solely by chance. Downs (Allee, 1931) found that land isopods tended to congregate about any less active individual, and that the choice of the precise spot on which the first animal stopped often seemed to be due to internal factors.

Eventually such aggregations break up and may be renewed in another place. In many cases an attempt was made to break up the groups mechanically, in the hope that the position of their renewal might be dictated by chloride concentration. The effect of such disturbances wore off quickly, and the position of the new aggregation was often the same as that of the old one. It is interesting to note that the most consistent results were obtained with *Ph. muscorum* which does not form close aggregations, and that this species shows no marked preference for one side or the other in any experiment. This suggests that the preferences apparently shown in certain experiments, may be actually due to the chance formation of an aggregation on one side at the start.

Results of Experiments

The results of the experiments are summarized in the following tables. For each experiment are given the total number of occurrences on each side, the difference between the two numbers, the means of these values, and the probability that the mean does not differ significantly from zero. Significant probabilities are underlined.

Table 44

Experiments on P. scaber, adult

Expt. No.	Salt P.P.M. Side 1	Salt P.P.M. Side 2		Occurrences Side 1	Occurrences Side 2	Diff.	Probability
C3	0	3	Total	43	53	10	
			Mean	4.3	5.3	1.0	.5 P .4
C16	3	300	Total	39	31	-8	.6 P .5
			Mean	4.33	3.44	-.888	
C5	0	300	Total	14	70	56	
			Mean	1.4	7.0	5.6	.01 P
C10	0	0	Total	33	59	26	
			Mean	3.3	5.9	2.6	.3 P .2

Table 45

Experiments on P. scaber, young

Expt.	Salt P.P.M.			Occurrences			Probability
No.	Side 1	Side 2		Side 1	Side 2	Diff.	
C26	0	3	Total	15	24	9	
			Mean	1.88	3.00	1.12	.5 P .4
C11	3	300	Total	28	22	-6	
			Mean	3.11	2.44	-.67	.6 P .4

Table 46

Experiments on T. rathkei, adult

Expt.	Salt P.P.M.			Occurrences			Probability
No.	Side 1	Side 2		Side 1	Side 2	Diff.	
C8	0	3	Total	41	69	28	
			Mean	3.72	6.27	2.54	.1 P .05
C17	3	300	Total	23	49	26	
			Mean	2.88	6.13	3.25	.05 P .02
C15	3	3	Total	34	33	-1	
			Mean	4.25	4.12	-.13	P .9

Table 47

Experiments on T. rathkei, young

Expt.	Salt P.P.M.			Occurrences			Probability
No.	Side 1	Side 2		Side 1	Side 2	Diff.	
C12	0	3	Total	39	25	-14	
			Mean	4.87	3.12	-1.75	.1 P .05
C4	3	300	Total	66	26	-40	
			Mean	5.08	2.00	-3.08	.02 P .01
C21	3	3	Total	38	35	-3	
			Mean	3.8	3.5	-.3	.8 P .7

Table 48

Experiments on O. asellus, adult

Expt.	Salt P.P.M.			Occurrences			Probability
No.	Side 1	Side 2		Side 1	Side 2	Diff.	
C7	0	3	Total	30	75	45	
			Mean	2.72	6.81	4.09	.05 P .02
C18	3	300	Total	32	42	10	
			Mean	4.0	5.25	1.25	.6 P .5
C13	0	0	Total	40	43	3	
			Mean	4.44	4.77	.33	.9 P .8

Table 49

Experiments on O. asellus, young

Expt.	Salt P.P.M.			Occurrences			Probability
No.	Side 1	Side 2		Side 1	Side 2	Diff.	
C19	0	3	Total	32	13	-19	
			Mean	3.55	1.44	-2.11	.2 P .1
C6	3	300	Total	49	52	3	
			Mean	4.46	4.73	.273	.9 P .8
C20	300	300	Total	25	12	-13	
			Mean	3.1	1.5	-1.6	.4 P .3

Table 50

Experiments on Ph. muscorum, adult

Expt.	Salt P.P.M.			Occurrences			Probability
No.	Side 1	Side 2		Side 1	Side 2	Diff.	
C2	0	3	Total	26	34	8	
			Mean	2.88	3.77	.88	.5 P .4
C9	0	300	Total	24	25	1	
			Mean	2.4	2.5	.1	. P .9
C23	300	300	Total	20	27	7	
			Mean	2.22	3.00	.78	.5 P .4

Table 51

Experiments on Ph. muscorum, young

Expt. No.	Salt P.P.M. Side 1	Salt P.P.M. Side 2		Occurrences Side 1	Occurrences Side 2	Diff.	Probability
C22	0	3	Total	36	32	-4	
			Mean	3.6	3.2	-.4	.6 P .5
C14	0	300	Total	39	49	10	
			Mean	4.33	5.44	1.11	.6 P .5
C24	300	300	Total	12	15	3	
			Mean	1.71	2.14	.43	.7 P .6

Discussion

A glance through the probability column of the above tables shows that in only four of the experiments are the means significant from a statistical point of view. This is due largely to the fact that the individual observations from which the means were computed varied so greatly. A large standard deviation reduces the probability of the results being significant according to the procedure used here. We may consider, therefore, that the results may be explained by chance in all but these four cases.

Does the statistical significance of the results in these four experiments indicate that in them, the woodlice did react to the difference in chloride concentration between two sides of the container? In the writer's opinion, it does not. The results are better explained by the tendency of land isopods to form aggregations in definite places which are chosen by chance. The results are contradictory. For example, the means in experiments C17, with adult T. rathkei, and C4, with young T. rathkei, are both statistically significant, but one mean is positive while the other is negative.

If the above conclusion is accepted, we shall see that it is unlikely that the chloride concentration of the soil influences the distribution of land isopods. The chloride gradient in nature must be very gradual except near the coast. Since the animals do not react to larger differences, it is unlikely that small natural differences would have any effect on the choice of a habitat. To be sure the experiments do not exclude the possibility of a reaction to enteric stimulation. Chlorine is found in many plant tissues, though it does not seem to be an essential part of them. Strasburger (1898, p. 176) gives the chlorine content of several plant tissues. Calculated in parts per million of dry weight, some of these are: rye straw, 960; pea straw, 2800; potato tubers, 1300; tobacco leaves, 11,500; spruce wood, 1.5. Except for spruce wood, the chlorine content is high. Animal tissues would be expected to contain considerable amounts of chlorine. It is difficult to conceive of the lack of sufficient chlorine in the food as a limiting factor in distribution.

Summary

1. Four species of land isopods were tested with respect to their reaction to differences in the chloride concentration of their substrate.

2. The results were measured as the excess of occurrences

on the side of the experimental container with high salt concentration, over the number of occurrences on the side with low salt concentration.

3. In most cases the mean differences are not statistically significant. In those cases which are statistically significant, the results can be explained as due to the tendency of the animals for aggregation.

4. It is concluded that low chloride concentration of the soil is not likely to be a limiting factor for the distribution of land isopods.

PART VII

PHYSIOLOGY, ECOLOGY AND DISTRIBUTION COMPARED

DISCUSSION AND CONCLUSIONS

We are now in a position to bring together the information which has been collected, and to compare the results of laboratory experiments with field observations, and the assigned climatic limits. It will be convenient to treat each species separately, and to summarize the results at the end. Before proceeding with this comparison, it will be well to examine the relationship of climate, as measured at weather bureau stations, to the microclimate which has been considered in the experimental work. Precipitation will not vary much within a limited area, although the amount of water reaching the soil, and the amount retained by it depend upon vegetational and physiographic factors as well as upon the type of soil. We shall, therefore, consider chiefly the relationship between temperatures in various environments.

Relationship between Climate and Microclimate

It will be realized at once that the mean temperatures calculated from weather bureau records are not the temperatures to which animals in nature are subjected. The inadequacy of an average to represent the extreme conditions at any point is obvious. Oceanic islands and coastal regions have climates varying less from year to year than do continental areas. Likewise, continental climates are usually characterized by more marked diurnal fluctuations than are oceanic climates.

Animals which live in protected situations are not exposed to the full vigor of weather conditions, and the environment of the woodlice is more constant than, for example, that of a sand dune inhabitant.

During the summer, temperature in soil, in logs and in similar situations depends upon a complex of factors. Important ones are: solar radiation, absorption characteristics of the surface, heat conductivity, air temperature, air movement, evaporation from the substrate, and the proximity of other radiating or absorbing surfaces. (Graham, 1920). Insolation is generally the most important factor. Thus great differences in temperature may exist within a few inches. Graham found that the subcortical temperature on the upper surface of a white pine log exposed to the sun was above 45°C. for four hours of a summer day. The maximum air temperature this day was 40°C., but the subcortical temperature on the lower side of the log rose to a maximum of 32-33° for about two hours. Under white pine logs in three-quarters shade the temperature of no part rose above 35°C. during the hottest part of summer. Graham's work was done with fresh logs, which are not used as habitats by woodlice. Old rotting logs would, however, afford an opportunity for the animals to retire further from the surface, and thus escape even better from excessively high temperatures.

Chapman and others (1931) compared the temperatures of widely different environments of the same climatic area during the warmest six weeks of the year. The records of the

St. Paul and Minneapolis weather stations were compared with thermograph readings on a sand dune, a pine plantation, an oak forest, a basswood-maple forest and a tamarack bog. All were located near the 45th parallel of latitude at about the same altitude. It was found that the mean daily temperatures in the different environments did not vary much from those of the weather bureau, although the two forests and the tamarack bog averaged about 2°F. less. The mean daily temperatures of the bog, basswood-maple forest, and sand dunes were compared by means of regression lines. There is a high correlation between these environments, but the forest and bog tend to be cooler on warm days and warmer on cool days. A comparison of the temperatures at different strata brings out interesting differences. On one afternoon these were:

Table 52 (Chapman, 1931)

Temperatures in Deg. Cent. at Distances from Soil Surface

	Above			Below			
	5'	6"	Surface	1"	6"	12"	18"
Tamarack bog	28	27	26.5	22.5	21.5	18	17.5
Basswoods	25	24.5	24.5	18	17.5	17	16
Sand dunes	30	31	41	35	29.5	25.5	24

It will be noted that the temperature at the soil surface and at 1" to 6" below is much more suitable for woodlice in the case of the bog and forest.

We may conclude that in temperate climates the high air temperatures sometimes recorded at weather stations are buffered by features of the environment such as forests and logs. In exposed situations the soil temperature may often rise above the lethal point for land isopods.

The actual temperatures attained in the hibernacula of woodlice are also of interest. The data of Holmquist (1931) is probably the most pertinent available. The environments studied were piles of leaves, and the interior and exterior portions of two logs in the middle and late stages of decay, respectively. In late fall and early spring the temperature of these hibernacula fluctuated with the air, but less widely. The upper surface of the logs showed most variation, the under surface least, while the leaves were intermediate. A remarkably constant zero temperature was maintained in all hibernacula when covered with snow. The lowest temperature recorded under the bark of the under side of the basswood log was -4.0°C. The lowest temperature in the top of the log was -8.4°, and in the leaves -5.3°C. Land isopods would choose the under side of a log for hibernation. A temperature of -4.0° for even one day would probably be fatal to all species studied except P. pictus and T. rathkei. It is evident that low winter soil temperatures must be very important in limiting the distribution of the members of this group.

The results of Mail (1930 and 1932) bring out the protective value of snow very clearly. In Montana in 1931 there was a continuous snow blanket from December 1 to March 31. During this time the air temperature fluctuated between -26.5°C. and 7.8°C. During this time the surface of the soil was never colder than -4.0°C. At a depth of 6 inches the temperature was -0.3° on a day when the air temperature was -26.5°. In his first study he found that even one inch of snow kept the soil temperature nearly constant despite fluctuations in air temperature. A thaw followed by a freeze destroyed the gradient, and brought low temperatures to the deeper layers of the soil. Thus the actual air temperatures recorded during the winter may not be as important as the amount of snow on the ground at the time of the severest cold.

We may conclude that weather bureau records give a fair picture of the average temperature conditions in various environments in the same locality during the summer. Animals living on the forest floor are, however, protected from extremely high temperatures. The hibernacula chosen by woodlice offer considerable protection from low temperatures, but the cold must often be sufficient to kill non-resistant species, and non-hardy individuals of resistant species. It would seem from present evidence, that the direct lethal effect of cold would be more of a limiting factor, than the direct lethal effect of high temperatures. The floor of the tropical rain forest is an extraordinarily constant environment, and the temperature in many places does not rise above 27°C. (Allee, 1926b). In these places the limiting effect of high temperature is probably through its modification of the general environment.

Consideration of Individual Species

Trichoniscus demivirgo

In the laboratory this species is shown to be most dependent upon moisture of the eight species studied. It is resistant to low temperatures (-2.0°C.) in a moist environment, but is otherwise susceptible to them. It does not withstand a constant temperature of over 25°C. for a week, being the least resistant species in this respect. Thus it appears to have the poorest tolerance of extreme physical conditions of any of the eight species considered.

These findings check with the ecology and distribution of the species. Trichoniscus is found in wet situations, and in these only when they are protected from excessive insolation. Thus it is protected both from dryness and high temperatures. We have seen that a bog is perhaps the most constantly cool terrestrial environment in summer. In winter the freezing of the surface of the wet soil protects the lower layers from cold. Thus Trichoniscus finds suitable conditions only in its own niche. Its climatic limits are also narrow, and it is unlikely that they will be extended to any great extent, even if the geographical distribution of this species is found to be wider than we now know it.

Oniscus asellus

The experimental results on Oniscus prove it to be moderately cold hardy, resistant to dryness at moderate temperatures, but susceptible to high temperatures. We find that its habitat is usually in moist, shaded places, though it is is not restricted to them as much as is Trichoniscus. The absence of Oniscus from the Mediterranean region and from the southern United States is perhaps due to its lack of toleration for high temperatures. Its more or less synanthropic habits in the north also fit its physiological characters. We have seen that excessive moisture generally reduces cold tolerance. Thus the preference of this species for moisture actually works to its disadvantage at the approach of winter. It would be expected that Oniscus might be found in areas where moderate seasonal moisture deficiencies occurred. In the original list of localities, no such place appeared, but I have been told by Professor Blake that he has taken Oniscus at Garberville, California, where two months are normally deficient in rainfall. Garberville is in the Coast Range, where summers are cool and the annual rainfall heavy. Thus no severe drought condition results. The distribution predicted from the laboratory proves to be actually true.

Philoscia muscorum

As compared with Oniscus, Philoscia is slightly less cold resistant, has the same lack of tolerance for high temperatures, and is much more dependent upon soil moisture. Its choice of habitat fits its laboratory characteristics. Its northern limit has been set slightly farther north than that of Oniscus as a free living species in North America, and slightly farther south than that of Oniscus in Europe. These differences can be reconciled by considering the interaction of the summer temperature on the limiting winter temperature. The southern distribution of Philoscia presents a problem. This species is found in southern Spain and in northern Africa, both of thich have not and dry summers. Its habitat in such places is apparently moss beds which are permanently moist. Just why Philoscia should be able to extend its range farther south than Oniscus is a problem. It is very likely that the varieties of "Philoscia muscorum" inhabiting hot, dry regions are at least physiologically, and possibly systematically distinct from the one studied here. This genus is widely distributed in the tropics, while Oniscus and the Porcellionidae are largely wanting as natives.

Cylisticus convexus

This species has been shown to be resistant to high temperatures, dependent upon moderate soil moisture, and generally very susceptible to cold. Its habitat preferences and distribution agree with the first two characteristics. This species is, however, found commonly in New England, in eastern Canada and in the east Baltic region, all of which have severe winters. The discrepancy may be due to the fact that a fair sample of the population was not used in the experimental work, or it may be due to special means of protection from the cold. The number of Cylisticus available was small, and thus the number of animals used in the study was fewer than with most of the other species. The experimental results, however, were very sharp. It was noted that old females were more cold resistant than other individuals. Possibly they tide the species over severe winters, although some males would also have to survive. We know of no special hibernating adaptations of this species, but it is quite possible that such exist. It seems doubtful that protection by synanthropism can entirely explain this problem. Herold, a careful observer, does not mention it in the east Baltic region. Certainly this is not the case at Orange, Mass., where the writer has had an opportunity to observe Cylisticus. Possibly drifts of snow afford special protection from the cold in the habitats selected by this species.

Porcellio pictus

In the laboratory P. pictus is shown to be very resistant (for a land isopod) to low temperatures, dependent upon moderate soil moisture, and susceptible to the effects of high temperatures. According to the author's observations, the habitat chosen by this species fits these characteristics. The only way to reconcile Herold's physiological results, and his ecological observations on this species with the work reported here, is to assume that P. pictus actually is resistant to low atmospheric relative humidity, although it is injured by contact with a dry substrate. According to the writer's observations, the only places where P. pictus can be said to occupy a xeric habitat is among stones which would not absorb water from the body of an animal as would soil. The fact that P. pictus is found in no places with periodic deficient rainfall substantiates the argument that it is not actually a xeric species. The occurrence of free living

P. pictus in regions with very cold winters, and its absence from the southern United States and from the Mediterranean region are in accord with its physiological characteristics.

Porcellio scaber

This species, the most widely distributed of those studied, is found in the laboratory to have the widest range of physiological tolerance. It is markedly resistant to high temperature and to low moisture, and is one of the more cold hardy species. Climatically we have seen that as a free living species it extends somewhat farther north than does O. asellus which has an equivalent cold tolerance. This is possibly because of its tendency to choose drier places for hibernation. Because of its tolerance for high temperatures this species might be expected to range farther south than appears to be the case. All authors speak of it as a northern species, yet it would seem to be much better adapted for hot, dry climates than Philoscia muscorum, which apparently extends farther to the south. The causes for this discrepancy are perhaps to be found in the biotic rather than the physical environment.

Trachelipus rathkei

The abundance of this species in regions with severe winters would be expected from its toleration for low temperature. Field observations and climatic indices agree with the laboratory findings that this species is dependent upon a fair amount of soil moisture. T. rathkei has been reported reliably from more southern points in the United

States than has P. scaber, yet the latter species is found to be more tolerant for high temperatures. In Europe, however, P. scaber has penetrated farther south than has T. rathkei.

Armadillidium vulgare

This species is both the least tolerant of low temperatures, and the most tolerant of high temperatures of any of the eight studied. Its dependence upon soil moisture is less than that of any species except P. scaber. Its habitat under rocks and logs in moderately dry situations, and its occurrence in regions with marked periodic deficiencies in rainfall check with these characteristics. The distribution of A. vulgare in relation to temperature also fits its physiological characteristics, for it is the species which penetrates farthest south, and has the most southern-northern limit.

Characteristics of the young as limiting factors

Since in nature very young animals do not hibernate, their resistance to low temperatures is of purely physiological interest. We have seen that the tolerance of the young animals for high temperatures is as good or better than that of adults of the same species. Because of their small size and soft bodies, young animals are more susceptible to dryness.

It will be noted that A. vulgare and P. scaber which tolerate the greatest rainfall deficiencies have young which are less dependent than others on soil moisture. The young of A. vulgare are also the most resistant class studied with respect to high temperatures. It would be interesting to know whether broods are released during dry periods. Possibly the reproductive cycle would be adapted to fit the special conditions of the climate. Philoscia muscorum, which is also found in regions with rainfall deficiency, has young which are very dependent upon soil moisture. This difficulty must be overcome by a specialization of habitat as is apparently the case with the adults.

Thus, the chief way in which the physiological characteristics of the young animals influence the distribution of a species is in raising the moisture requirements. If a periodic shortage of soil moisture does not coincide with the breeding season, its effects will be less noticeable than if it did coincide.

Discussion

In a general way the laboratory tolerance of a species for extreme conditions fits its distribution according to climate. It does not seem possible at the present time, however, to state that a species which will tolerate -3.0°C. at 39% moisture in loam for a week will be limited by a definite winter isotherm. The discrepancy between the susceptibility of Cylisticus to cold, and its northern limit demonstrates this. When sufficient data on the annual cycle of temperature in comparable environments in different parts of the world have been accumulated, it may be possible to prepare isotherms for the actual habitations of animals, so that the biologist will not have to depend upon weather bureau data which has been prepared for other purposes.

A range of difference between the absolute temperature limits of eight species of only about two degrees seems a very small one to account for the differences between the northern boundaries of the various species. The absolute limit of a species, however, applies only to the most resistant animals after a preliminary hardening period. The resistance of a species to sudden drops in temperature before it has had an opportunity to become hardened, may actually be more important in determining its limits. This characteristic seems to divide the species more sharply than the absolute limits. The percentage of survivors after prolonged exposure to cold, and the resistance of a species to sudden exposure to low temperature have both been considered in determining the position of each species in cold tolerance. The same principle has been applied to the assigning of position in laboratory high temperature tolerance. Positions are numbered in the order of decreasing tolerance for severe conditions. In Table 53 we compare the order of the assigned limiting winter isotherm with the laboratory order of cold tolerance. Only one value is used for the mean temperature of the coldest month. This is the lowest one found for the species in a free living state. It happens that all of these values are from New England to Canada, so that they would be expected to check with experimental work done on New England animals.

Table 53

Species	Coldest month: Temp. C°.	Position	Approx. Lab. limit: 7 days-C°.	Position
P. pictus	-11.4	2	-4.0	1
T. rathkei	-12.4	1	-3.5	2
P. scaber	-6.4	3	-3.0	3
O. asellus	-4.7	7	-3.0	3
Ph. muscorum	-6.0	5	-2.0	5
Tr. demivirgo	-6.4	3	-2.0	6
C. convexus	-5.7	6	-2.0	7
A. vulgare	-2.8	8	-2.0	8

Upon actual examination it is found that the agreement is by no means perfect. Three factors contribute to the failure to match. In the first place there is no justification for distinguishing between winter limits of -6.4°C. and -6.0°C. So small a difference might occur within the limits of one city, because of different hours of observation, differences in the location of instruments, or because the averages represent a different series of years. If we group the climatic limits more broadly, T. rathkei and P. pictus are in the first group; P. scaber, Ph. muscorum, O. asellus, Tr. demivirgo and C. convexus in the second group; while A. vulgare is alone in the third group. Each group then contains the same position numbers for both climatic index and laboratory tolerance, though the numbers are paired in only three cases.

It must also be remembered that for P. scaber, O. asellus and C. convexus the assigned northern limit is the boundary between the range of the animal as a free living species and as a synanthropic species. The determination of this boundary was somewhat arbitrary, since it is sometimes difficult to know just how much protection an animal receives from association with man. Since seeing the data on the protective qualities of snow, the author wonders if deep snow in forests may not afford as effective protection against cold as the environs of human habitations. Occupied houses, themselves, would be warmer in winter than outside, but it is unusual for woodlice to be found in them. The study of winter temperatures in a wide variety of environments in various climatic regions would throw light on this question. Until such an investigation, the winter temperature controls of the three species named above must be regarded as provisional. It is possible that the association of woodlice with man is for reasons other than protection from winter cold.

Finally, there may be differences between species in the site and depth chosen for hibernation. Elucidation of this point would require a careful field study such as Holmquist carried out in the Chicago region.

A similar comparison may be made between the limiting temperature of the warmest month (under favorable rainfall conditions) and the laboratory tolerance for high temperatures. This is done in Table 54.

Table 54

Species	Warmest month °C.	Position	Approx. Lab. Limit. 7 days °C.	Position
A. vulgare	28.4	1	35.0	1
P. scaber	25.3	3	35.0	2
T. rathkei	26.6	2	32.5	3
C. convexus	24.9	5	32.5	4
O. asellus	23.3	6	30.0	5
Ph. muscorum	25.3	3	30.0	5
P. pictus	23.1	7	30.0	7
Tr. demivirgo	21.8	8	25.0	8

The species at the extremes of this table have their climatic and laboratory positions in agreement, and this is so in the median range, except for Phioscia muscorum.

Differences in the habits of species undoubtedly accounts for some of the disagreement between laboratory tolerance and climatic boundaries. The writer has not had the opportunity of studying these animals at their southern limits, and cannot say how their habits are affected by the warmer climate.

Another factor influences the applicability of the high temperature tolerance of a species as a means of predicting its southern distribution. We have seen that it is very likely that the southern boundary of a species may not be determined by the limit of lethal temperatures, since it is generally possible to escape from extremes of heat. High temperature may affect other physiological processes such as reproduction, though young were borne normally by P. scaber at 32.5°C. In the southern part of their range these woodlice are brought into competition with other species, some undoubtedly better adapted for high temperatures. Biotic pressure in general becomes more severe in warm regions. It is probable that high temperatures modify the environment and cause an increase in competition, so that the northern species of woodlice are crowded out before actual physical limiting factors are reached. Physical conditions may be limiting factors in some cases, however, and the question should not be closed until field studies are carried out in the south.

General Conclusions

In the introduction to this paper, four general questions were put. We shall now see whether it is possible to give satisfactory answers to all of these.

Question 1. Is climatic control of the distribution of woodlice due chiefly to the direct lethal action of low and high temperatures, and of dryness upon the animals?

With the exception of Cylisticus, there is good correlation between the cold tolerance of a species and the mean temperature of the coldest month at the free living limit. Because of this, and because the temperatures reported from the type of hibernacula frequented by woodlice are close to the lethal temperatures for them, it appears that the northern limits of these animals are largely determined by the lethal effects of low temperatures. In some regions where the winters are mild, the coolness of the summer may be the actual limiting factor. No experimental evidence for this theory has been presented, but an analysis of the climatic data substantiates it.

It seems far less likely that the southern limits of the woodlice are determined by the lethal action of high temperatures. We have seen that even in a tropical forest there are environments whose temperature does not rise to the lethal temperature of most of the species tested. There is abundant moisture in this environment. Nevertheless, none of these species are found in such tropical environments. Possibly ecological isolation explains their absence, but at least two species, P. scaber and A. vulgare, have been carried across the entire tropical zone, and have become established in the south temperate regions of Africa, Australia and South America. It is probable that the high temperatures in the tropics are a limiting factor, although their effect may be indirect. There is, nevertheless, a positive correlation between the limiting summer isotherm for a species and its tolerance for high temperatures determined in the laboratory, and the question is not closed.

The tolerance of different species for various degrees of deficient soil moisture is closely correlated with their choice of habitat, and with the number of months of deficient rainfall tolerated.

Question 2. Is a wide ranging species more or less tolerant of extreme conditions than a more restricted one?

Insofar as there is evidence to answer this question, wide spreading species have a wider range of physiological toleration than do narrowly limited ones. Trichoniscus demivirgo is the least widely distributed both geographically and ecologically. It tolerates the narrowest range of temperature, and is most dependent upon soil moisture. Porcellio scaber and Armadillidium vulgare are the two most widely distributed species. They are also the most resistant to high temperatures and to low soil moisture. Wide ranging species tolerate extreme conditions, while species with a restricted distribution have a lesser range of tolerance, and require a more or less specialized environment.

Question 3. Does the same species in different parts of the world show different climatic limits to its distribution?

The climatic requirements of a species in different parts of its range are very nearly the same, but it is impossible to select a single control, such as the mean temperature of the warmest month, as a limit. Rather one must consider all the climatic factors, and the possible interactions between them.

Question 4. Does a wide ranging species necessarily inhabit regions with somewhat varying climatic characteristics; and does a more restricted species occur only in regions with rather sharply defined climatic characteristics?

It appears probable that the reason certain species have been able to spread more widely than others is because of their ability to withstand variable climates, especially in the matter of rainfall. There is no real evidence on the second part of this question. The only studied species, which is not widely distributed, occurs in a region (New England) which is characterized by abundant rainfall, warm summers and cold winters. There is no proof that it would not survive perfectly well if transferred to a suitable environment in a place with considerably different climate.

Finally, it must be emphasized that, although the climatic controls do check in many cases with experimental data, several problems of distribution remain unsolved by any of the means of analysis used here. The absence of P. scaber, even in synanthropic environments, from the western part of Massachusetts is not explained by climatic limits, since it occurs along the Maine coast where winters are colder. The difference in chloride concentration of the soil is also ruled out as a direct cause. Why has this species not gained a foothold away from the coast in New England, and also in northern Europe? The absence of Trachelipus rathkei from the region south of the Cohasset, Mass.- Westport, R. I., line is another unsolved problem. Blake has hypothesized from the characteristics of the flora that the soil south of the line is more acid than that north of it. The writer is at present experimenting with an apparatus to test the reaction of different species of woodlice to differences in the pH of soils.

Other Results

The preceding section summarizes the results of the primary objectives of this research. Certain secondary results are enumerated below.

1. The known distributions of eight species of land isopods have been mapped, and a number of erroneous or doubtful records deleted.

2. The interrelations between five climatic controls have been studied.

3. Observations have been made on the physiology of cold hardiness in woodlice, and the results on these land crustacea have been compared with those of other investigators on insects.

4. The reactions of four species to differences in chloride concentration of the soil have been studied, and it is concluded that this is not a direct factor in the distribution of woodlice.

PART VIII

SOME RELATED LITERATURE AND AN APPRAISAL OF METHOD

In the preceding seven parts we have considered the distribution of eight species of land isopods, and have sought for an explanation of the distributions based upon the tolerance of the different species for extremes of temperature and moisture. The literature on the climatic factors limiting distribution, and on the effects of extreme temperatures and moisture upon animals is voluminous. It would be impossible to do it justice without expanding this treatise unduly. For this reason it has been decided to limit the discussion of related literature to typical studies of the relationship of physiological characteristics of animals to their distribution. In addition, we shall attempt an appraisal of the experimental methods as a tool for the understanding of animal distribution.

Physiological Characteristics and Habitat

Few papers could be found which compare the physiological adaptations of closely related animals with their habitats. More often zoologists have stressed structural adaptations, and have neglected what may be more important from an ecological viewpoint, the adaptations of habit and cellular physiology.

Shelford (1913) studied the reaction and survival of animals collected from different environments in air of high evaporating power. Animals from moist habitats reacted negatively to the high end of the gradient, while those from dry environments did not. There was only a rough relationship between the survival time of animals with similar integuments and their reaction. Plethodon glutinosus (salamander), an inhabitant of moist woods, was more sensitive to dry air than P. cinereus which lives under leaves in drier places. P. glutinosus lived longer, however, due probably to its protective dermal secretions. All arthropods lived much longer than did amphibians, but those from moist habitats reacted to dry air almost as definitely as did the salamanders.

J. R. Parker (1930) determined the optimum developmental temperatures for Melanoplus femur-rubrum, M. mexicanus and M. packardi. He found that the first has a lower optimum temperature for development. This was correlated with the habitat of M. femur-rubrum which is found in bushy areas along streams or in rank growing grass, while the other species are inhabitants of open ground where they are exposed to higher temperatures.

Williams (1934) reported upon the moisture requirements of two species of termites, Reticulitermes hesperus of moist regions, and R. tibialis of more arid regions. He found that the former required 1.0% of moisture in sand, while the latter would survive with 0.8%. The small difference between these moisture values suggests that they are in the critical range in which the relative humidity of the soil atmosphere is changed greatly by a small variation in soil moisture. R. hesperus also required more moisture in its food.

Davies(1928) studied the effects of various relative humidities upon species of Collembola under starvation conditions. He concluded that in general organisms with tracheal respiration are less susceptible to low humidities than are those with cutaneous respiration. One of his species, Entomobrya multifasciata, has cutaneous respiration, but lives as long as Sminthurus viridis which has trachael respiration. Difference in survival time was definitely related to the habitats of the several species.

Talbot (1934) compared the duration of life in dry air of five ant species of the genus Formica. She found a definite correlation between the habitat frequented by a species and its tolerance for air of high evaporating power. In the genus Lasius there was no significant difference between the tolerance of varieties from the exposed dunes and from moist woods. She did not test the reactions of these species in a moisture gradient, so that the moisture of the air may be a factor influencing the choice of habitat.

It is probable that in general animals from moist habitats react negatively to the dry end of a moisture gradient. In many other cases no such correlation can be demonstrated as, for example, in Lasius and Plethodon. Among the land isopods, species living in moist environments are injured by dryness, but the converse of this statement is not true.

Climate and Distribution

The literature contains many studies on the effect of climate on the limitation of animals and plants. We are not particularly concerned with the life zones of various authors. The method for predicting the probable future distribution of introduced species has been outlined by Cook (1931). Data on distribution and abundance is collected, and sorted into the categories of common, occasionally common, and rare. Climatic data for these regions is collected, plotted as climographs and studied to determine the limiting factors. If any physiological data is available it is also studied. Finally, the climate in the area of present distribution is compared with that in a new area, and the expected future distribution can be estimated. This method requires no experimental work to be successful. It has been applied by Cook (1924) to the pale western cutworm (Porosagrotis orthogonia), and by Gjullin (1931) to the Mediterranean fruit fly (Ceratitis capitata). Graf (1925), however, decided that climate had very little to do with the control of the Mexican bean beetle.

Appraisal of Methods

Cook's method for predicting the future distribution of economically important insects can be extended to the prediction of the abundance of a particular pest in any year, by studying the abundance of the species for a few years in relation to weather conditions. Cook (1926) reports good results with such methods on the pale western cutworm. If it is possible to obtain satisfactory results simply by letting nature perform experiments, and treating the observations statistically, will detailed studies of the physiological characteristics of animals in any way facilitate the solution of practical problems of control? Do studies made under controlled constant temperature and humidity apply in nature where conditions are variable? V. E. Shelford (1934) in a recent symposium stated that the physiological results of the Illinois codling moth investigation were so complicated, that in spite of the fact that they cost many thousands of dollars, no one could use them. The one observation of great practical value was that heavy spring rains decreased infestation, and this result was the result of a "natural" experiment. He suggests that climate simulation experiments should be undertaken only after fifteen years study of the life history and habits of an animal.

On the other hand, P. A. Buxton (1933) is enthusiastic over the possibilities for the application of knowledge gained in the laboratory to the control of insects of medical and agricultural importance.

Shelford's present viewpoint represents a modification of his earlier views, in which the laboratory for climate simulation played a very important part. Naturally, he does not now condemn laboratory contributions to ecology, but he does feel that the blind application of physiological data obtained under unnatural conditions is a hindrance.

It seems to the writer that this is a sane viewpoint. There is a great deal to be done on the exact measurement of environmental factors in the field. This is true in the case of the woodlice. A study of the numbers of each species found in a certain area, and a comparison of annual fluctuations with weather records will undoubtedly help our understanding of the climatic factors operating in the control of these animals. The most promising field for future laboratory work seems to be an analysis of the factors which cause woodlice to choose the habitats they do, and of the reaction of woodlice to various features of the environment.

If further studies on physiological tolerance are made, it will be important to control the past history of the experimental animals by maintaining them in the laboratory as was done in this series. More information can be obtained in the same time by running all high temperature and low moisture experiments in the definitely lethal range, so that survival times are cut down. The severity of different combinations might be measured by a standard evaporimeter. At low temperatures, the time required for the hardening process offers an interesting problem, as does the physiological nature of this process.

In the tremendous complex which is the environment of every animal, it is impossible to determine the exact way in which each factor operates without recourse to laboratory experiments. Field observations and field measurements of conditions of existance are necessary preliminaries. Natural conditions must be simulated as nearly as possible. Even if such studies do not have an immediate application, they aid in the understanding of the mechanism of climatic control. Possibly we shall some day be able to measure the biotic factors in the environment in some quantitative way, so that a satisfactory statement on the subject of competition can be made to replace the rather indefinite ones made in this paper. Gause (1934) is proceeding with the experimental study of the struggle for existance between competing animals; the question of animal distribution is linked with this problem as well as with the physical environment.

BIBLIOGRAPHY

Allee, W. C. (1926a)
Studies in Animal aggregations: causes and effects of bunching in land isopods.
Jour. Expt. Zool. 45:255-277.

Allee, W. C. (1926b)
Measurement of environmental factors in the tropical rain-forest of Panama.
Ecology 7 (3):273-302. 9 fig.

Allee, W. C. (1931)
Animal Aggregations, A Study in General Sociology.
431 pp. Bibliography.
Univ. Chicago. 1931.

Arcangeli, Alceste (1924)
Contributo alla conoscenza degli Isopodi della Catalogna.
Trabajos del Museo de Ciencias Naturales de Barcelona. Vol. 4, No. 12, p. 1-29. 5 pl.

Arcangeli, Alceste, (1925)
Isopodi terrestri della Spagna settentrionale ed orientale, raccolti dal Dr. F. Haas negli anni 1914-1919.
Abhandl. Senckenbirgischen Naturforsch. Gesel. Vol. 39 (2):131-137.

Arcangeli, Alceste, (1927)
Isopodi terrestri raccolti nell' Estremo Oriente dal Prof. Silvestri.
Boll. d. Laborat. zool. gen. e agraria di Portici 20.

Arcangeli, Alceste, (1931)
Isopodi terrestri raccolti in Albania dal dott. Pietro Parenzan.
Atti Accad. Sci. Veneto-Trentino-Istriana, 22:79-85. 1 pl.

Arcangeli, Alceste (1932)
Isopodi terrestri raccolti dal Prof. Silvestri nel Nord-America.
Boll. Lab. Gen. e Agraria (Portici) 26:121-141, 7 fig.

Bepler, H.
Uber die Atmung der Oniscideen.
Griefswalder dissertation. 1909.

Blake, C. H. (1931)
New Land Isopods from New England. On Isopoda Oniscoida II.
Occ. Papers, Boston Soc. Nat. Hist. 5:341-348.

Blake, C. H. (1931)
Distribution of New England Woodlice. On Isopoda Oniscoida III.
Occ. Papers, Boston Soc. Nat. Hist. 5:349-355.

Blake, C. H. (1933)
Unpublished talk in M.I.T. Biological Seminar.

Bodine, Joseph Hall (1923)
Physiological Changes in Certain Orthoptera during Hibernation.
Jour. Exp. Zool. 37:457-476.

Budde-Lund, Gustave (1885)
Crustaceae Isopoda terrestria per familias et genera et species descripta.
Hauniae.

Buxton, Patrick A. (1933)
The effect of climatic conditions upon populations of insects.
Trans. Roy. Soc. Trop. Med. & Hyg. 26 (4):325-364. 5 fig.

Carl, J. (1908)
Monographie der schweizerischen Isopoden.
Neue Deukschr. Schweiz. Natur f. Ges. Vol. 42.

Chapman, Royal N. (1931)
Animal Ecology with special reference to Insects. 464 p.
McGraw-Hill. N. Y. and London.

Chapman, Royal N., Wall, R., Garlough, L., Schmidt, C. (1931)
A Comparison of Temperatures in Widely Different Environments of the Same Climatic Area.
Ecology 12:305-322.

Clayton, H. Helm (1927)
World Weather Records Collected from Official Sources.
Smithsonian Miscellaneous Coll., Whole Volume 79, Washington.

Clayton, H. Helm (1934)
World Weather Records - 1921-1930.
Smithsonian Miscellaneous Coll., Whole volume 90, Washington.

Collinge, Walter E. (1917)
A Check-list of the British terrestrial Isopoda (Woodlice).
Scottish Naturalist. No. 65.

Collinge, Walter E. (1917)
Some Remarks upon the Occurrence of Two Rare Woodlice in Scotland.
Scottish Naturalist. No. 65, 137-139.

Cook, W. C. (1924)
The Distribution of the Pale Western Cutworm, Porosagrotis orthogonia, Morr. A Study in Physical Ecology.
Ecology, 5:60-69.

Cook, W. C. (1926)
Some Weather Relations of the Pale Western Cutworm.
Ecology 7:37-47.

Cook, W. C. (1931)
Notes on Predicting the Probable Future Distribution of Introduced Insects.
Ecology 12:245-247.

Dahl, Friedrich (1916a)
Die Asseln oder Isopoden Deutschlands. 90 p. 107 fig.
Gustave Fischer, Jena.

Dahl, Friedrich (1916b)
Die Verbreitung der Landasseln in Deutschland.
Mitt. Zool. Mus. Berlin, Bd. 8. S. 149.

Dahl, Friedrich (1919)
Reihenfange und die Okologie der deutschen Landisopoden.
Zool. Anz. 50:193-203; 209-218.

Davies, Maldwin W. (1928)
The Effect of Variation in Relative Humidity on Certain Species of Collembola.
Brit. Jour. Exp. Biol. 6:79-86.

Dollfus, Adrien (1892)
Catalogne raissonnè des Isopodes terrestres de l'Espagne.
Anal. Soc. Esp. d'Hist. Nat. T. 21:161-190. 13 fig.

Dollfus, Adrien (1893a)
Sur deux isopodes terrestres d'Islande recueillis par M. Gaston Buchet.
Bull. Soc. Zool. Franc. Vol. 17:231.

Dollfus, Adrien (1893b)
Catalogue raissone des Isopodes terrestres de l'Espagne. Premier Supplement.
Anal. Soc. Esp. N. H. 22:47-51.

Dollfus, Adrien (1896a)
Land Isopoden der Balkans region im Landesmuseum zu Sarajevo.
Wissensch. Mittheil. aus Bosnien und Hercegovina Vol. 4:583-586. Vienna.

Dollfus, Adrien (1896b)
Les Isopods terrestres du Nord de l'Afrique.
Mem. Soc. Zool. France. 9:523-553.

Dollfus, Adrien (1897a)
Tableau Iconographique des Philoscia d'Europe.
Feuille des Jeune Naturalistes. Ser. 3, 70-73; 91-95.

Dollfus, Adrien (1897b)
Les Crustaces Isopodes Terrestres a grand dispersion.
Feuille des Jeune Naturalistes. Ser. 3, No. 324, 205.

Dollfus, Adrien (1899)
Catalogue des Crustaces Isopodes terrestres (Cloportides) de France.
Feuille des Jeune Naturalistes. 29:347-348.

Dollfus, Adrien (1901)
Catalogue des Isopodes terrestres de Hongrie, appartenant au Museum National de Budapest.
Termes zetrajzi Fuzetek. Budapest. Vol. 24: 143-151.

Fabricius, J. C. (1793)
Entomologica systemica. Vol. II. Hauniae.

Fink, D. E. (1925)
Physiological Studies on Hibernation in the Potato Beetle, Leptinotarsa decemlineata.
Biol. Bull. 49:381-404.

Fisher, R. A. (1930)
Statistical Methods for Research Workers. 3rd Ed.
Oliver & Boyd. London.

Gause, G. F. (1934)
The Struggle for Existence. 163 pp.
Williams & Wilkins. Baltimore.

Gjullin, C. M. (1931)
Probable distribution of the Mediterranean fruit fly (Ceratitis capitata Weid) in the United States.
Ecology 12:248-259.

Goodnough, X. H. (1915)
Rainfall in New England.
Jour. N. E. Water Works Assn. Vol. 29:237-438.

Graf, J. E. (1925)
Climate in relation to Mexican bean beetle distribution.
Jour. of Ec. Ent. 18:116-121.

Graham, S. A. (1920)
Factors influencing the Subcortical Temperatures of Logs.
Minn. State Ent. Rept. 18:26-42.

Hann, Julius (1911)
Handbuch der Klimatologie. Ed. 3, Bd. 3. Klima der gemässigten zonen und der polarzonen.
Stuttgart, Engelhorn.

Hansen, H. J. (1887) (1888)
Oversigt over det vestlige Groenlands Fauna af Malakostrake Havkrebsdyr.
Vid. Medd. fra den Natur. For. Kjøbenhagen.
p. 177-198.

Harger, Oscar (1880)
Report on the marine Isopoda of New England and adjacent waters.
Rept. U. S. Comm. Fish. 6:297-462.

Hellen, W., and Ehrstrom, K. E. (1919)
Zur Kentniss der Isopoden Finnlands.
Meddelanden af Societas pro Fauna et Flora Fennica, 45.

Herold, Werner (1913)
Beitrage zur Anatomie und Physiologie einiger Land Isopoden.
Zool. Jahr. Abt. Anat. 35 (4).

Herold, Werner (1925)
Untersuchungen zur Okologie und Morphologie einiger Landasseln.
Zeit. Morph. und Okol. Tiere 4:337-415.

Herold, Werner (1929)
Zur Landasselnfauna Pommerns.
Abh. u. Berichte d. Pommerschen Naturforsch. Ges.
Bd. 10:109-113.

Herold, Werner (1930)
Beiträge zur Verbreitung u. Okologie der Landisopoden des Ostbaltikums.
Zeit. fur. Morph. u. Okol. Tiere 18 (3):474-536.

Herold, Werner (1932)
Isopoden des Dümmersdorfer Traveufers.
Lubeck, 3 pp.

Herold, Werner (1933)
Die Isopodenfauna Hiddensees.
Archiv. fur Naturgesch. Neue Folge, Bd. 2(1):
97-123.

Hoek, P. P. C. (1888)
Crustacea Nederlandica.
Tijdschr. Nederl. Dierk. Vereenig. Ser. 2, Vol. 2,
Leyden.

Holmquist, A. M. (1931)
Studies in Arthropod Hibernation. Temperatures in
Forest Hibernacula.
Ecology 12 (2): 387.

Jennison, M. W. (1932)
Critical Study of the effect of temperature upon
certain aspects of bacterial growth curves.
M.I.T. Thesis. Biology.

Johansen, Frits (1922)
On the Woodlice Occurring in Canada and Alaska.
Canad. Field Nat. Vol. 36:156.

Johansen, Frits (1924)
A Biological Excursion to Anticosti Is.
Canad. Field Nat. Vol. 38:161-164.

Johansen, Frits (1929)
Further Observations on Canadian Land and Fresh
water Crustacea made in 1928.
Canad. Field Nat. Vol. 43.

Johnsson, A. (1858)
Synoptisk framställning af Sveriges Oniscider.
Akad. abhandl. Uppsala.

Kunkel, B. W. (1918)
The Arthrostraca of Connecticut.
Conn. Geol. Nat. Hist. Surv. Bull. 26.
261 p. Fig. 1-84.

Lebedeff, A. F. (1928)
The Movement of Ground and Soil Water.
First Int. Congress Soil Sci. Proc. & Papers.
p. 459-494. Washington.

Livingston, B. E. (1931)
Soil Point Cones and Their Use.
Mimeographed bulletin. Johns Hopkins Lab. Plant Physiology.

Mail, G. Allen (1930)
Winter Soil Temperatures and their Relation to subterranean insect survival.
Jour. Agric. Res. 41 (8): 571-592. 11 fig.

Mail, G. Allen (1932)
Winter Temperature Gradients as a Factor in Insect Survival.
Jour. Econ. Ent. 25 (5):1049-1053.

Maury, Andre (1930-1931)
Crustaces Isopodes de Normandie (Formes Terrestres).
2^{e} Liste.
Bull. Soc. Linn. Normandie. 8th series.
Trav. Orig. 40-50.

Meinertz, Thysden (1934)
Die Landisopoden Dänemarks. II. Die Onisciden.
Zool. Jahr. Abt. Syst. Bd. 66, H3/4: S.211-284.
39 Ahb.

Merriam, C. H. (1898)
Life Zones and Crop Zones of the United States.
U. S. Dept. Agr. Bull. Biol. Survey.
Bull. 10, p. 9-73.

Miers, E. J. (1877)
On a collection of Crustacea, Decapoda and Isopoda, chiefly from South America, with descriptions of new Genera Species.
Proc. Zool. Soc. London. p. 653-678.

McDougall, E. (1925)
The Moisture Belts of North America.
Ecology 6:325-332.

Norton, A. H. (1909)
Some aquatic and terrestrial crustaceans of the State of Maine.
Proc. Portland Soc. Nat. Hist. 2:245-255. 1 fig.

Parker, J. R. (1930)
Some Effects of Temperature and Moisture upon Melanoplus mexicanus, mexicanus and Cannula pellucida Scudder (Orthoptera).
U. of Mont. Agr. Expt. Sta. Bull. 222, p. 132.

Payne, Nellie M. (1926)
The Effect of Environmental Temperatures upon Insect Freezing Points.
Ecology 7:99-106.

Pierce, W. D. (1911)
Notes on the Economic importance of sowbugs.
U. S. Bureau of Ent. Bull. No. 64, p. 15-22.
Issued separately in 1907.

Proctor, William and others (1933)
Biological Survey of the Mt. Desert Region.
Wistar Inst., Philadelphia.

Rathbun, M. J. (1905)
Fauna of New England. 5. List of the Crustacea.
Occ. Papers, Boston Soc. Nat. Hist. 7, No. 5:1-117.

Richardson, Harriet (1905)
A Monograph on the Isopods of North America.
Bull. of the U. S. Nat. Museum. No. 54. Washington.
liii + 727 p.

Robinson, Wm. (1927)
Water Binding Capacity of Colloids, a definite factor in winter hardiness of insects.
Jour. Econ. Ent. 20:80-88.

Sars, G. A. (1896)
Crustacea of Norway. Vol. 2 Isopoda. Bergen.

Shelford, V. A. (1912)
Animal Communities in Temperate America.
Univ. of Chicago.

Shelford, V. E. (1913)
The reactions of certain animals to gradients of evaporating power of air. A study in experimental ecology.
Biol. Bull. 25:79-120.

Shelford, V. E. (1929)
Laboratory and Field Ecology.
Williams & Wilkins. Baltimore. 608 pp.

Shelford, V. E. (1934)
Faith in the Results of Controlled Laboratory Experiments as Applied in Nature.
Ecol. Monograph. 4 (4):491-498.

Stephenson, K. (1913)
Grølands Krebsdyr og Pycnogonider.
Medd. Groenland. Vol. 22, p. 1-479.

Strasburger, E. (1898)
A Textbook of Botany.
Macmillan Co. New York.

Stuxberg, A. (1873)
Tvenna nya Onisclder beskrefna Oefvers Klg.
Akad. Foerhandl for 1872, No. 9, p 305.
Stockholm.

Stuxberg, A. (1876)
Om Nord-Ameridas Onisclder.
Oefvers Kgl. Vet. Akad. Foerhandl. for 1875,
No. 2, p 43-63. Stockholm.

Talbot, Mary (1934)
Distribution of Ant Species in the Chicago Region
With Reference to Ecological Factors and Physiological Toleration.
Ecology 15 (4):416-439.

Thompson, W. R. (1934)
The Tachinid Parasites of Woodlice.
Parasitology, Vol. 26:378-448.

The Times Atlas. London, 1922.

Tua, P. (1900)
Contribuzione alla conoscenza degli Isopode
Terrestria Italiani.
Boll. Mus. Torino. Vol. 15, No. 374.

U. S. Dept. of Agriculture
Atlas of American Agriculture. Part II: Climate.
Sect. A. Precipitation and Humidity.
Sect. B. Temperature, Sunshine, Wind.

Vandel, A. (1925)
Recherches sur La Sexualite des Isopods.
Bull. Biologique de La France ed de la Belgique.
T. 59:318-371.

Verhoeff, K. W. (1917a)
Germania zoogeographica. Die Verbreitung der
Isopoda terrestria im Vergleich mit derjenigen
der Diplopoden. Uber Isopoden 18 Aufsatz.
Zool. Anz. Bd. 48; S. 347-376.

Verhoeff, K. W. (1917b)
Uber einige niederosterreische Diplopoden und Isopoden.
"Verhandlungen" der k. k. zoologischen-botan. Gesell. in Wien (Jahrgang 1917) p. 220-223.

Verhoeff, K. W. (1917c)
Zur Kenntnis der Entwickelung der Trachealsysteme und der Untergattungen von Porcellio und Tracheoniscus. (Uber Isopoden 22 Aufsatz)
Sitzungberichten der Gesell. naturforsch. Freunde. Jahr. 1917, No. 3, p. 195-223. 7 fig.

Verhoeff, K. W. (1917d)
Uber Mediterrane Oniscoideen, namentlich Porcellioniden.
Jahresh. Ver. Naturk. Würrtbg. 73:161.

Verhoeff, K. W. (1920a)
Zur Kenntnis der Larven, des Brutsackes, und der Bruten der Oniscoidea.
Zool. Anz. Bd. 51. 28 Isopoden. Aufsatz. p. 169-190.

Verhoeff, K. W. (1920b)
Uber die Atmung der Landasseln.
Zeit. fur. wissen. Zool. Vol. 118: p. 365-447.

Verhoeff, K. W. (1923)
Zur Kenntnis der Landasseln Palestinas. 30 Isopoden Aufsatz.
Archiv. fur Naturges, 89: Abt. A. 206-231. 13 fig.

Verhoeff, K. W. (1929)
Uber Isopoden der Balkan Halbinsel gesammelt von Herrn Dr. I. Buresch. Teil II. 33 Aufsatz.
Königl. Naturwiss. Inst. Sofia. 2:129-139.

Verhoeff, K. W. (1931a)
Vergleichende Geographische Okolgische Untersuchungen über die Isopoda terrestria von Deutchland, den Alpenländern, und Anschliessenden Mediterrangebiet. 46 Aufsatz.
Ztschr. Morph. Okol. Tiere. 22:231-268.

Verhoeff, K. W. (1931b)
Zur Kenntnis alpenlandisches und Mediterraner Isopoda Terrestria. 47 Aufsatz.
Zool. Jahr. Abt. Syst. 62:15-52.

Verhoeff, K. W. (1933)
Zur Systematik, Geographie und Okologie der Isopoda terrestria Italiens und über einige Balkan Isopoden. 49 Isopoden Aufsatz.
Zool. Jahr. Abt. Syst. 65:1-64.

Walker, E. M. (1927)
The Woodlice or Oniscoidea of Canada (Crustacea, Isopoda).
Canad. Field Nat. 41:173.

Wallace, N. A. (1919)
The Isopoda of the Bay of Fundy.
Univ. of Toronto Stud. Biol. Ser. No. 1.

Webb, M. W. and Sillem, Charles (1906)
The British Woodlice, a monograph of the Terrestrial Isopod Crustacea. London.

Williams, O. L. (1934)
Termites and Termite Control. Chapter 4.
Univ. Calif. Press.

APPENDIX A

CLIMATOLOGICAL DATA

In this table are given the values of the five climatic controls for each station considered in Part IV. The numbers at the heads of the columns correspond to the numbers of the controls. These are:

I. Sum of the mean temperatures of the four warmest months in degrees Centigrade.

II. Mean temperature of the coldest month in degrees Centigrade.

III. Mean annual precipitation in decimeters.

IV. Number of months ordinarily deficient in rainfall.

V. Mean temperature of warmest month in degrees Centigrade.

Station	I	II	III	IV	V
Akhiar, U.S.S.R.	84.7	1.8	3.9	0	23.1
Algiers, Algeria	96.0	11.9	7.5	4	25.3
Anticosti Island,	46.0	-17.6	7.9	0	13.7
Athens, Greece	99.5	9.1	3.9	4	26.6
Austin, Texas	110.3	9.7	8.6	0	28.8
Baltimore, Md.	92.2	1.1	11.0	0	25.2
Barcelona, Spain	87.1	8.0	5.4	2	23.3
Beirut, Syria	108.7	14.3	9.0	5	28.4
Belgrade, Jugoslavia	80.3	- 1.6	6.2	0	22.0
Besancon, France	69.5	0.4	7.1	0	18.8
Bilbao, Spain	77.6	8.1	12.5	0	20.5
Bodo, Norway	43.0	- 2.3	9.1	0	12.5
Boston, Mass.	78.2	- 2.8	11.2	0	21.8
Budapest, Hungary	77.0	- 2.1	6.0	0	21.3
Burgas, Bulgaria	84.3	0.8	4.5	0	23.0
Burlington, Vt.	74.5	- 7.8	8.2	0	21.1
Cape Town, Africa	82.4	12.6	6.4	4	21.3
Casablanca, Morocco	86.0	11.9	4.2	4	22.9
Cernauti, Roumania	70.2	- 4.9	6.3	0	19.5
Cetinje, Jugoslavia	79.6	- 1.7	15.3e	0	22.0
Charleston, S.C.	103.7	9.9	12.3	0	27.0
Chatham, N.B.	66.0	-11.8	11.1	0	19.3
Cincinnati, Ohio	93.6	0.4	9.8	0	25.3
Concord, N.H.	72.5	- 6.1	10.0	0	21.1
Copenhagen, Denmark	56.4	- 0.7	5.7	0	15.4
Danzig	64.1	- 1.3	6.4	0	17.8
Dunedin, New Zealand	54.9	5.8	5.8	0	14.3
Eastport, Maine	56.9	- 6.4	11.0	0	15.9
Edinburgh, Scotland	54.9	3.9	6.6	0	14.7
Fitchburg, Mass.	76.8	- 4.7	10.5	0	21.7
Fredericton, N.B.	66.0	-11.2	11.1	0	18.9
Genoa, Italy	90.7	7.5	13.1	0	24.1
Georgia, State of	102.7	8.2	12.6	0	26.6
Greenville, Maine	64.4	-12.4	10.5	0	18.6
Hamburg, Germany	63.0	0.3	6.7	0	17.2
Hammershus, Denmark	59.3	0.3	6.4	0	16.6
Hankow, China	107.2	3.8	13.8	0	28.6
Helsingfors, Finland	56.5	- 6.6	6.2	0	16.6
Honolulu, Hawaii	102.1	21.5	8.6	0	25.9
Huesca, Spain	80.1	2.9	5.9	0	21.8
Ivigtut, Greenland	30.7	- 7.6	11.7	0	9.7
Juneau, Alaska	49.3	- 2.9	20.0	0	14.1

Station	I	II	III	IV	V
Karlsruhe, Germany	69.4	0.5	8.2	0	19.0
Key West, Florida	113.0	20.7	9.7	0	28.6
Kiew, U.S.S.R.	69.6	- 6.0	5.9	0	19.3
Königsberg, Germany	62.4	- 2.8	5.2	0	17.4
Kola, U.S.S.R.*	40.6	-11.8	---	0	12.7
Leningrad, U.S.S.R.	58.3	- 8.0	5.2	0	17.4
Los Angeles, Cal.	77.3	11.7	2.6	7	20.3
Las Vegas, New Mexico	75.2	0.3	4.2	0-1	20.5
Lyon, France	77.6	2.4	8.7	0	21.2
Madrid, Spain	87.5	4.3	4.2	2	24.3
Mandal, Norway	57.2	- 0.4	10.0	0	15.8
Marseille, France	82.3	6.8	5.8	2	22.1
Mariehamn, Finland	52.4	- 4.5	5.6	0	15.3
Melbourne, Australia	75.5	9.3	6.5	0	19.7
Montreal, Que.	70.8	-10.9	11.0	0	20.5
Morrison, Illinois	84.4	- 3.7	9.5	0	23.3
Nantucket, Mass.	73.0	- 1.6	11.0	0	19.9
New Orleans, La.	106.6	11.7	14.7	0	27.4
New York, N.Y.	84.9	- 1.0	11.4	0	23.1
Nice, France	81.8	6.5	8.7	2	21.9
Nuwara Eliya, Ceylon	63.6	14.1	25.0	0	16.5
Orkney Islands	55.7	3.7	8.0e	0	12.2
Oslo, Norway	59.9	- 4.0	5.6	0	17.4
Palermo, Italy	93.9	10.3	7.6	0	24.8
Paris, France	68.5	2.5	6.6	0	18.6
Petropavlosk, Siberia	38.9	-11.2	11.9	-	11.8
Portland, Maine	71.2	- 5.3	11.2	0	20.0
Port Arthur, Ont.	56.7	-15.1	6.0	0	16.7
Port-au-Prince, Haiti	109.2	24.5	13.7	0-1	27.8
Potenza, Italy	75.0	2.9	6.4	0	20.5
Quebec, Que.	64.4	-12.4	10.5	0	18.7
Riga, Latvia	63.6	- 5.1	5.4	0	17.9
Rockport, Mass.*	70.3	- 2.8	10.0	0	19.9
St. Paul Is., Alaska	27.1	- 5.4	8.0	0	7.9
Sandesund, Norway	59.4	- 2.2	5.6	0	16.5
San Diego, Cal.	76.4	12.2	2.4	8	20.4
San Francisco, Cal.	59.0	9.7	5.6	4	15.5
San Marino*	86.4	4.6	6.8	0	23.6
Sapporo, Japan	70.4	- 6.2	9.8	0	20.6

---

* Rockport - figures for 1926 only.

San Marino - temperature estimated from that of Siena at about the same altitude. Rainfall estimated from that of Ancona.

Kola - Values for January, April, July and October available. Other months estimated from these.

Station	I	II	III	IV	V
Sarajevo, Jugoslavia	71.0	- 2.6	8.4	0	19.4
Saraisk, U.S.S.R.*	67.9	-11.4	6.0	0	20.0
Sortavala, Finland	58.2	- 9.7	6.5	0	17.3
Stettin, Germany	66.6	- 0.7	6.0	0	18.4
Stykkisholm, Iceland	37.1	- 2.1	6.5	0	10.6
Thorshavn, Faroes	39.4	3.0	14.5	0	10.6
Tokio, Japan	92.0	2.8	14.9	0	25.4
Toronto, Ontario	73.5	- 6.1	7.9	0	20.6
Trondhjem, Norway	48.4	- 2.9	11.5	0	14.0
Turin, Italy	83.3	0.6	8.6	0	22.9
Turners Falls, Mass.	80.3	- 5.7	9.8	0	21.1
Upsala, Sweden	55.6	- 4.8	5.4	0	16.6
Vaasa, Finland	52.4	- 7.6	5.5	0	15.3
Valparaiso, Chile	68.2	12.9	6.0	7	17.5
Vestmanno, Iceland	41.0	1.4	13.7	0	11.5
Victoria, B.C.	58.3	3.8	8.1	2	15.7
Victoria, Texas	112.8	13.3	9.1	0	28.9
Washington, D.C.	91.2	0.5	10.9	0	24.9
Wilno, Poland	65.5	- 5.7	6.7	0	18.8

---

* Saraisk - Estimated from records for Moscow, Saratov, Kursk and Kasan.

APPENDIX B

TABULATION OF EXPERIMENTS OF SERIES A

This tabulation is arranged by species in order first of descending temperatures, and secondarily of ascending soil moistures. Its purpose is to facilitate looking up the characteristics of each species. The arrangement is essentially that of the textual tables. The columns from left to right give for each experiment:

1. Its number.
2. The number of animals used.
3. The temperature in degrees Centigrade.
4. The soil moisture in percent of dry weight.
5. The type of soil. S-sandy; L-loam.
6. Preliminary treatment to increase hardiness.
7. Minimum, average, and maximum survival times in days.
8. Duration of experiment in days.
9. The number of survivors.

Trichoniscus demivirgo

Expt. No.	No.	Temp. °C.	Moist. %	Soil	Hard-ened	Survival Time Min.	Ave.	Max.	Dura-tion	Survi-vors
A61a	1	2.2	39	L	No	2	2	2		0
A62a	2	2.2	100	L	No	4	#	#	6	1
A106a	3	0.5	100	L	No	7	#	#	7	2
A62b	1	-1.0	100	L	Yes	4	4	4		0
A106b	2	-1.0	100	L	Yes	1	1	1		0
A75a	2	-1.0	200	L	No	4	#	#	6	1
A75b	1	-1.0	200	L	Yes	8	8	8		0
A86a	3	-3.0	39	L	No	1	1	1		0
A89a	3	-3.0	200	L	No	1	1	1		0

Oniscus asellus

Expt No.	No.	Temp. °C.	Moist. %	Soil	Hard-ened	Survival Time			Dura-tion	Survi-vors
						Min.	Ave.	Max.		
A28a	3	4.5	5	S	No	#	#	#	12	3
A29a	3	4.5	15	S	No	#	#	#	12	3
A30a	3	4.5	25	S	No	#	#	#	12	3
A52a	2	2.2	12	L	No	1	1.5	2		0
A53a	2	2.2	20	L	No	4	5	6		0
A54a	3	2.2	39	L	No	#	#	#	6	3
A105a	3	0.5	39	L	No	1	#	#	7	2
A28b	3	-1.0	5	S	Yes	6	#	#	14	2
A38a	5	-1.0	5	S	No	#	#	#	14	5
A29b	3	-1.0	15	S	Yes	#	#	#	14	3
A39a	5	-1.0	15	S	No	13	#	#	14	4
A30b	3	-1.0	25	S	Yes	#	#	#	14	3
A64a	2	-1.0	12	L	No	2	3	4		0
A70a	2	-1.0	20	L	No	4	#	#	6	1
A54b	3	-1.0	39	L	Yes	#	#	#	8	3
A105b	2	-1.0	39	L	Yes	#	#	#	7	2
A74a	2	-1.0	100	L	No	#	#	#	6	2
A75a	2	-1.0	200	L	No	2	4	6		0
A70b	1	-1.8	20	L	Yes	#	#	#	9	1
A80a	3	-1.8	20	L	No	2	5	7		0
A54c	3	-1.8	39	L	Yes	4	#	#	7	2
A105c	3	-2.0	39	L	Yes	#	#	#	2	2
A74b	2	-1.8	100	L	Yes	1	1.5	2		0
A28c	2	-2.0	5	S	Yes	1	2.5	4		0

Expt. No.	No.	Temp. °C.	Moist. %	Soil	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
A38b	5	-2.0	5	S	Yes	1	2.6	5		0
A29c	3	-2.0	15	S	Yes	1	1	1		0
A39b	4	-2.0	15	S	Yes	1	1	1		0
A30c	3	-2.0	25	S	Yes	1	1	1		0
A70c	1	-3.0	20	L	Yes	1	1	1		0
A85a	3	-3.0	39	L	Yes(?)	4	#	#	7	1
A95a	3	-3.0	39	L	No	1	1	1		0
A87a	3	-3.0	250	L	No	1	1	1		0
Philoscia muscorum										
A31a	3	4.5	5	S	No	4	4.3	5		0
A32a	3	4.5	15	S	No	#	#	#	12	3
A55a	2	2.2	12	L	No	1	1.5	2		0
A56a	2	2.2	20	L	No	5	#	#	6	1
A57a	3	2.2	39	L	No	#	#	#	6	3
A103a	2	0.5	15	S	No	#	#	#	7	2
A104a	2	0.5	39	L	No	5	#	#	7	1
A40a	3	-1.0	5	S	No	13	#	#	14	2
A32b	3	-1.0	15	S	Yes	7	#	#	14	1
A103b	2	-1.0	15	S	Yes	#	#	#	7	2
A41a	3	-1.0	15	S	No	4	#	#	14	1
A68a	2	-1.0	12	L	No	1	2.5	4		0
A56b	1	-1.0	20	L	Yes	1	1	1		0
A71a	2	-1.0	20	L	No	2	#	#	6	1
A57b	3	-1.0	39	L	Yes	1	3	5		0
A104b	1	-1.0	39	L	Yes	7	7	7		0

Expt. No.	No.	Temp. °C.	Moist. %	Soil	Hardened	Survival Time			Duration	Survivors
						Min.	Ave.	Max.		
A74a	2	-1.0	100	L	No	#	#	#	6	2
A75a	2	-1.0	200	L	No	2	2.5	3		0
A71b	1	-1.0	23	L	Yes	7	7	7		0
A81a	3	-1.8	23	L	No	1	1	1		0
A82a	4	-1.8	39	L	No	#	#	#	5	4
A74b	2	-1.8	100	L	Yes	3	3	3		0
A40b	2	-2.0	5	S	Yes	1	1.5	2		0
A32c	1	-2.0	15	S	Yes	1	1	1		0
A103c	2	-2.0	15	S	Yes	1	1	1		0
A41b	1	-2.0	15	S	Yes	1	1	1		0
A83a	3	-3.0	39	L	Yes	1	1	1		0
<u>Cylisticus convexus</u>										
A58a	1	2.2	13	L	No	1	1	1		0
A59a	1	2.2	20	L	No	7	7	7		0
A60a	2	2.2	39	L	No	1	#	#	6	1
A108a	2	0.5	39	L	No	1	#	#	7	1
A42a	3	-1.0	5	S	No	1	1	1		0
A43a	3	-1.0	15	S	No	1	1.7	2		0
A60b	1	-1.0	39	L	Yes	#	#	#	9	1
A108b	1	-1.0	39	L	Yes	6	6	6		0
A72a	1	-1.0	20	L	No	1	1	1		0
A74a	1	-1.0	100	L	No	1	1	1		0
A75a	1	-1.0	200	L	No	1	1	1		0
A60c	1	-1.8	39	L	Yes	8	8	8		0

Porcellio pictus

Expt. No.	No.	Temp. °C.	Moist. %	Soil	Hardened	Survival Time			Duration	Survivors
						Min.	Ave.	Max.		
A44a	3	-1.0	5	S	No	#	#	#	14	3
A45a	3	-1.0	15	S	No	13	#	#	14	2
A65a	2	-1.0	12	L	No	5	7	9		0
A69a	2	-1.0	20	L	No	#	#	#	7	2
A73a	2	-1.0	39	L	No	#	#	#	7	2
A74a	2	-1.0	100	L	No	#	#	#	6	2
A75a	2	-1.0	200	L	No	#	#	#	6	2
A69b	2	-1.8	20	L	Yes	#	#	#	9	2
A73b	2	-1.8	39	L	Yes	#	#	#	9	2
A74b	2	-1.8	100	L	Yes	#	#	#	9	2
A75b	2	-1.8	200	L	Yes	2	3	4		0
A44b	3	-2.0	5	S	Yes	1	#	#	7	1
A45b	2	-2.0	15	S	Yes	1	1	1		0
A69c	2	-3.0	20	L	Yes	5	#	#	6	1
A73c	2	-3.0	39	L	Yes	#	#	#	7	2
A93a	3	-3.0	39	L	No	1	#	#	2	1
A74c	2	-3.0	100	L	Yes	1	1.5	2		0
A90a	3	-3.0	260	L	No	1	2	3		0
Porcellio scaber										
A22a	3	4.5	5	S	No	11	#	#	12	2
A23a	3	4.5	15	S	No	#	#	#	12	3
A24a	3	4.5	25	S	No	#	#	#	12	3
A46a	2	2.2	12	L	No	1	3.5	6		0
A47a	3	2.2	20	L	No	#	#	#	6	3

Porcellio scaber

Expt. No.	No.	Temp. °C.	Moist. %	Soil	Hardened	Survival Time Min.	Ave.	Max.	Duration	Survivors
A48a	3	2.2	39	L	No	#	#	#	6	3
A107a	3	0.5	39	L	No	5	5.7	6		0
A22b	2	-1.0	5	S	Yes	8	9	10		0
A34a	5	-1.0	5	S	No	2	#	#	14	2
A23b	3	-1.0	15	S	Yes	13	#	#	14	2
A35a	5	-1.0	15	S	No	7	#	#	14	4
A24b	3	-1.0	25	S	Yes	12	#	#	14	2
A67a	2	-1.0	12	L	No	1	2.5	4		0
A47b	3	-1.0	20	L	Yes	2	#	#	7	1
A48b	3	-1.0	39	L	Yes	5	#	#	7	2
A110a	3	-1.0	39	L	No	1	#	#	7	1
A74a	3	-1.0	100	L	No	5	#	#	6	2
A75a	2	-1.0	200	L	No	1	1	1		0
A47c	1	-1.8	20	L	Yes	6	6	6		0
A77a	3	-1.8	20	L	No	#	#	#	7	3
A48c	2	-1.8	39	L	Yes	8	#	#	9	1
A76a	3	-1.8	39	L	No	#	#	#	6	3
A110b	1	-2.0	39	L	Yes	#	#	#	2	1
A74b	2	-1.8	100	L	Yes	1	2	3		0
A34b	2	-2.0	5	S	Yes	2	3	4		0
A23c	2	-2.0	15	S	Yes	1	1	1		0
A35b	4	-2.0	15	S	Yes	1	2.3	3		0
A24c	2	-2.0	25	S	Yes	1	1	1		0
A77b	3	-3.0	20	L	Yes	2	4.3	7		0

Porcellio scaber

Expt. No.	No.	Temp. °C.	Moist. %	Soil	Hard-endd	Survival Time Min.	Ave.	Max.	Duration	Survivors
A48d	1	-3.0	39	L	Yes	6	6	6		0
A84a	3	-3.0	39	L	Yes(?)	1	2	4		0
A92a	3	-3.0	39	L	No	1	#	#	2	1
A86a	3	-3.0	250	L	No	1	1	1		0
Trachelipus rathkei										
A25a	4	4.5	5	S	No	8	#	#	12	2
A26a	3	4.5	15	S	No	#	#	#	12	3
A27a	3	4.5	25	S	No	#	#	#	12	3
A49a	2	2.2	12	L	No	2	2	2		0
A50a	2	2.2	20	L	No	#	#	#	6	2
A51a	3	2.2	39	L	No	#	#	#	6	3
AD1a	5	2.0	40	L	No	#	#	#	7	5
AD2a	6	2.0	110	L	No	1	#	#	7	5
A109a	3	0.5	100	L	No	#	#	#	7	3
A25b	2	-1.0	5	S	Yes	1	2.3	4		0
A36a	5	-1.0	5	S	No	8	#	#	14	4
A26b	3	-1.0	15	S	Yes	#	#	#	14	3
A37a	5	-1.0	15	S	No	#	#	#	14	5
A27b	3	-1.0	25	S	Yes	#	#	#	14	3
A66a	3	-1.0	12	L	No	2	4.3	6		0
A50b	2	-1.0	20	L	Yes	5	7	9		0
A51b	3	-1.0	39	L	Yes	#	#	#	8	3
A74a	2	-1.0	100	L	No	6	#	#	6	1
A109b	3	-1.0	100	L	Yes	1	#	#	7	1
A75a	2	-1.0	200	L	No	4	4	4		0

Trachelipus rathkei

Expt. No.	No.	Temp. °C.	Moist. %	Soil	Hardened	Survival Time			Duration	Survivors
						Min.	Ave.	Max.		
A78a	3	-1.8	20	L	No	2	4	6		0
A51c	2	-1.8	39	L	Yes	4	6	8		0
AD1b	5	-2.0	40	L	Yes	1	#	#	7	2
A79a	4	-1.8	39	L	No	3	#	#	7	2
AD5a	5	-2.0	40	L	No	7	#	#	7	3
A109c	1	-2.0	100	L	Yes	1	1	1		0
AD2b	5	-2.0	110	L	Yes	6	#	#	7	3
A74b	1	-1.8	100	L	Yes	#	#	#	9	1
AD6b	5	-2.0	110	L	No	3	#	#	7	4
A36b	4	-2.0	5	S	Yes	1	4.5	7		0
A26c	3	-2.0	15	S	Yes	1	3.0	5		0
A37b	5	-2.0	15	S	Yes	1	2.0	3		0
A27c	3	-2.0	25	S	Yes	1	1.7	2		0
A79b	2	-3.0	39	L	Yes	5	#	#	7	1
A94a	3	-3.0	39	L	No	2	2	2		0
A74c	1	-3.0	100	L	Yes	#	#	#	7	1
A88a	3	-3.0	250	L	No	1	1	1		0
AD1c	2	-4.0	40	L	Yes	1	1.5	2		0
AD5b	3	-4.0	40	L	Yes	1	2.6	5		0
AD10a	3	-4.0	40	L	No	1	1	1		0
AD2c	3	-4.0	110	L	Yes	1	1	1		0
AD6b	4	-4.0	110	L	Yes	1	1	1		0

Armadillidium vulgare

Expt. No.	No.	Temp. °C.	Moist. %	Soil	Hardened	Survival Time			Duration	Survivors
						Min.	Ave.	Max.		
AD3a	7	2.0	40	L	No	2	#	#	7	4
AD4a	6	2.0	110	L	No	3	#	#	7	4
A100a	3	0.5	5	S	No	2	2	2		0
A101a	3	0.5	10	S	No	6	#	#	9	1
A102a	3	0.5	15	S	No	2	2	2		0
A97a	3	0.5	20	L	No	2	#	#	9	1
A98a	3	0.5	39	L	No	2	2.3	3		0
A99a	3	0.5	100	L	No	1	1.7	2		0
A101b	1	-1.0	10	S	Yes	1	1	1		0
A97b	1	-1.0	20	L	Yes	2	2	2		0
AD3b	4	-2.0	40	L	Yes	3	#	#	7	1
AD7a	3	-2.0	40	L	No	1	1.3	2		0
AD4b	4	-2.0	110	L	Yes	1	1.2	2		0
AD3c	1	-4.0	40	L	Yes	1	1	1		0

(Abstract)

A COMPARISON OF THE PHYSIOLOGY, ECOLOGY AND DISTRIBUTION OF SOME NEW ENGLAND WOODLICE

by

John Langworthy Fuller

B. S., Bates College

1931

Submitted in Partial Fulfillment of the Requirements
for the degree of
DOCTOR OF PHILOSOPHY
from the
Massachusetts Institute of Technology
1935

Signature of Author.......Signature redacted.......
Department of Biology and Public Health, May 9, 1935

Signature of Professor in Charge of Research...Signature redacted

Signature of Chairman of Departmental Signature redacted
Commmttee on Graduate Students...

(Abstract)

A COMPARISON OF THE PHYSIOLOGY, ECOLOGY AND DISTRIBUTION OF SOME NEW ENGLAND WOODLICE

The fact that every organism has a more or less restricted range is a commonplace. It has been suggested by Herold and Blake that the limit of the northward spread of land isopods is determined by the winter temperatures. The present study is a more complete investigation of the limiting climatic factors for eight species, and for each species a comparison of its climatic limits with its tolerance for high and low temperatures, and for deficient soil moisture.

As a result of a zoogeographical and ecological survey it is possible to characterize the habitat and distribution of each species.

Trichoniscus demivirgo Blake is an inhabitant of swampy places. It ranges in New England from Bar Harbor to Nantucket, but has not been found more than ten miles inland.

Oniscus asellus Linne is found under stones in moist places. It is distributed throughout central Europe, but is absent from the Mediterranean region, and is synanthropic in northern Europe. In North America it ranges from the eastern part of Canada to Pennsylvania.

Philoscia muscorum sylvestris (Fabricius) is found in moist woods under leaves and in grass. Its range includes the western Mediterranean basin, and central Europe as far east as Danzig. In North America this species is found along the coast south from Bar Harbor with its southern limit uncertain.

Cylisticus convexus (De Geer) occurs under boards and stones. It is found in eastern Europe from Latvia to Bulgaria, and in central Europe. In eastern North America Cylisticus ranges from New Brunswick to Virginia.

Porcellio pictus Brandt is found under stones associated with lime soils. It ranges from Finland to northern Italy. In eastern North America it ranges from Quebec City south to Pennsylvania.

Porcellio scaber is found under logs and stones in fairly dry situations. It has spread to many parts of the world. P. scaber is abundant along the coasts of Norway, New England and British Columbia, and has its southern boundaries in northern Italy, southern Ohio, and middle California.

Trachelipus rathkei is found in moderately moist woods and in gardens. It ranges throughout central Europe, though more abundant in the east, and is absent from the Mediterranean basin and the southern Balkans. This is the most common woodlouse inland in New England and eastern Canada, and extends as far south as Georgia.

Armadillidium vulgare Latreille is a wide ranging species, but it occurs in warmer countries than does P. scaber. This species is found in every part of the Mediterranean basin, and throughout Europe as far north as Denmark. In North America it ranges from southern New England to Texas, and is also common along the California coast.

A study of the limiting climatic conditions yielded results of general application. The limiting winter temperature is higher in regions with cool summers. The limiting summer temperature is higher in regions with abundant rainfall. Three species, P. scaber, A. vulgare and Ph. muscorum were found to occur in regions with periodic rainfall deficiency. Table 1 compares the climatic indices for temperature with the tolerations found by experiment.

Table 1

Species	Winter Index °C.	Cold Tol.	Summer Index °C.	High Temp. Tol.
Tr. demivirgo	- 6.4	Moderate	21.8	Very poor
O. asellus	- 4.7	Moderate	23.3	Poor
Ph. muscorum	- 6.0	Moderate	25.3	Poor
C. convexus	- 5.7	Poor	24.9	Moderate
P. pictus	-11.4	Good	23.1	Poor
P. scaber	- 6.4	Moderate	25.3	Moderate
T. rathkei	-12.4	Good	26.6	Moderate
A. vulgare	- 2.8	Poor	28.4	Good

In the experimental work at low temperatures, each species was exposed in soils of low and high moisture content. In low moisture soil preliminary exposure to low temperatures increased cold hardiness. In moist soil this adaptation did not occur. There were characteristic differences between the cold resistance of the several species, the minimum for the most resistant being about -4°C.

Experiments at high temperatures were carried out in a similar manner. High moisture was favorable to survival at high temperatures. Again the species differed in their tolerations for extreme conditions, the maximum temperature endured being 40°C.

Species found in the driest habitats were most tolerant of low soil moisture. P. scaber and A. vulgare were very resistant to dryness, but Ph. muscorum which also occurs in regions with deficient rainfall was not.

There is a positive correlation between the survival of a species under extreme conditions in the laboratory, and its geographical and local distribution. The fact that correlation is not perfect is explained by our incomplete knowledge of distribution, and by ecological adaptations. Unstudied factors may also influence distribution. The chloride concentration in the soil, suggested as an influence, was found to have no effect on the reaction of woodlice.

It is concluded that the limiting action of climate is probably due to the lethal action of low temperatures, and possibly of high temperatures also. The doubt in the latter case is occasioned by the fact that an active animal might escape from dangerously high temperatures, whereas it would be inactivated at low temperatures and could not escape from cold. It is also concluded that no single climatic index will account for the distribution of the woodlice, but that the interaction of several controls must be considered.