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Previous volumes (2010-2017): 250 € / year (4 issues)

Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d’avenir » programme (Labex Agro: ANR-10-LABX-0001-01)

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THE BIOLOGY OF CERATOZETES CISALPINUS BERLESE, 
SCHELORIBATES LAEVIGATUS KOCH, 
AND OPPIA NEERLANDICA OUDEMANS (ORIBATEI), 
WITH A DESCRIPTION OF ALL STAGES 1

BY


The biology of oribatids was first investigated by Michael (1883-1888), followed by Jacot (1936 b) and Frenzel (1936), and most recently by Grandjean (1948), Riha (1951), Sengbusch (1954) and Pauly (1956). For this work, the three most common oribatids in a moist meadow were selected as a study group for investigations into the life cycles, habits, reproduction, and nutrition of sod-living oribatids. To illustrate how common these three species can be, sod samples from a dry pasture during the latter part of April and early May yielded up to 150 S. laevigatus per square foot. At the same time, up to 100 C. cisalpinus were obtained from a square foot sample of moist meadow sod. An effort was also made to determine the importance of and the interrelationships of fungi and oribatids to sod humus formation. Since the three species have been poorly described, especially the immature stages, a complete description of all stages is presented.

Ceratozetes cisalpinus Berlese 1908.

Plates 1-3, figs 1-16.

Family Ceratozetidae Jacot (1925). C. cisalpinus Berlese (1908), Ewing (1909) (C. minnesotensis ?), Sellnick (1928), Willmann (1931). No known holotype. Plesiotypes of all stages are deposited at the University of Minnesota.

Adult color ranges from a light yellowish-brown through a rich mahogany brown to an almost blackish brown. The old, very dark individuals tend to develop a whitish spot on the anterior third of the notogaster, and a whitish border along

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Acarologia, t. IV, fasc. 1, 1962.
the exterior edge of the pteromorph. The lateral suture disappears just before contacting the notogastral suture.

The three nymphal stages differ essentially only in size (fig. 14), and only the tritonymph is illustrated completely (fig. 9). Differences in leg setation, anal and genital plate setation, and the number of genital discs easily separate the nymphal stages. The proterosomal plate is distinct in all stages, but the pygidium only in nymphs. All non-sensory setae are black. In decreasing intensity of immature sclerotization, the sclerotized areas are the gnathosoma, legs, and the proterosomal plate. The legs are a light reddish brown. The limits of coxal sclerotization mesally are distinct. The body of the immature stages is milky white, smooth, and slightly transparent. The cuticle of all stages is smooth on both the legs and the body.

Ventral setal rows F through H are retained from the larva to the tritonymph. Dorsal setal row F is lacking in the larva. The anal and genital setal numbers agree with that found to be general for Ceratozetes spp. by Grandjean (1950 b).

Some tritonymphs lack adgenital setae, and some have 6 genital setae on one side or both.

The chela muscles (fig. 2) are predominantly levators, but at least one depressor is present.

Slits or deep grooves appear on the femora and trochanters of legs III and IV of nymphs and adults. Not all of the porose areas are illustrated on the legs. A chitinous band encircles the genu of legs I and II of all nymphal stages, and is thickened around the seral sockets of genu setae I and II.

The ovipositor is of the typical oribatid type (fig. 8), and is very similar in size and setation to that of Galumna spp. drawn by Jacot (1937). Only the distal portion of the ovipositor is shown; that is, the innermost part when the ovipositor is retracted. The single posterior finger is actually a fusion of two fingers, each of which lost the zeta setal row. Grandjean (1956) finds only two setal rows on each of the three fingers in Eremaeus spp., but finds a kappa setal row at the junction of the distal and proximal ovipositor. C. cisalpinus has no kappa setae.

The spermatophore (figs 5, 45, and 46) is composed of a noncellular stalk, and a packet of sperm (or spermatids) suspended in a clear fluid. The stalk generally has a foot and granules appear throughout its length. At the top of the stalk there are two short lateral supports, and a medial, central support which deeply indents the sperm sac.

Adult genital plate measurements were made with special care, because these are used to sex living adults. The genital plate is the most easily measured structure on a living mite that can be used determine the sex of the individual. In mounted, cleared specimens, the presence or absence of an ovipositor is used. There is little chance of error due to measurement on an angle since the genital plates are in the middle of the venter. The genital plates are relatively flat, and can therefore be measured accurately. Immature stages are best distinguished by the number of genital discs or the number of genital setae. In order of reliability, from most
to least, the immature measurements are: the width of the proterosomal plate (at the widest point), the genital slit length, the anal slit length, the first tarsal segment length (without claws), and the total length. All measurements of the immature stages are averages. All measured specimens were laboratory reared, and each sample contained from 10 to 20 specimens. All measurements are given in mm, with the width taken at the widest point.

<table>
<thead>
<tr>
<th>Immature stages</th>
<th>proterosomal width</th>
<th>genital slit length</th>
<th>anal slit length</th>
<th>first tarsal segment length</th>
<th>total length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larvae</td>
<td>.100</td>
<td>.065</td>
<td>.065</td>
<td>.055</td>
<td>.26</td>
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<tr>
<td>Protonymphs</td>
<td>.125</td>
<td>.035</td>
<td>.100</td>
<td>.065</td>
<td>.34</td>
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<tr>
<td>Deutonymphs</td>
<td>.180</td>
<td>.060</td>
<td>.135</td>
<td>.085</td>
<td>.47</td>
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<tr>
<td>Tritonymphs</td>
<td>.240</td>
<td>.075</td>
<td>.170</td>
<td>.105</td>
<td>.60</td>
</tr>
</tbody>
</table>

**Scheloribates laevigatus** Koch 1836.

Plates 3-4, figs 17-26.

Family Scheloribatidae Grandjean (1933). Koch (1836), Sellnick (1928), Willman (1931), Kates and Runkel (1948), Grandjean (1933, 1942, 1950 b, and 1958). The holotype is unknown to us, if such were ever designated. Plesiotypes are deposited at the University of Minnesota.

The adult color is yellowish brown when very young and becomes reddish brown within a short time. Adults darken with age, but never get black.

The ovipositor is identical to that of *C. cisalpinus* but smaller in size. The spermatophore also is very similar but for smaller size and a darkening of the lower portion of the sperm sac.

The cuticle of all stages is smooth on both the legs and the body.

Only the deutonymph is illustrated (fig. 26). A pygidium is lacking. The sclerotized legs are a light, orange brown, as are the mouth-parts, while the proterosomal plate is hardly sclerotized at all. The proterosomal plate is still easily
 delimited from the white cuticle of the remainder of the body. The extent of the coxal sclerotization mesally is clear. Most setae of the dorsal hysterosoma and ventral idiosoma appear to be sensory. The larvae have an extra seta on the proterosomal plate. Porose areas appear on the proterosomal plate, especially around the pseudostigma. Grandjean (1938) distinguishes Scheloribatidae larvae from Oribatulidae larvae on the basis of palpal setal characteristics.

Grandjean’s (1942) chaetotaxic formula for the legs of this species does not seem to fit the authors’ observations (fig. 21).

Essential measurements are given in Table 2.

<p>| Table 2. |
| --- | --- | --- | --- |</p>
<table>
<thead>
<tr>
<th>Adult body</th>
<th>average</th>
<th>s</th>
<th>largest</th>
<th>smallest</th>
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</thead>
<tbody>
<tr>
<td>Female length</td>
<td>.58</td>
<td>.02</td>
<td>.63</td>
<td>.55</td>
</tr>
<tr>
<td>Female width</td>
<td>.38</td>
<td>.02</td>
<td>.41</td>
<td>.36</td>
</tr>
<tr>
<td>Male length</td>
<td>.54</td>
<td>.02</td>
<td>.57</td>
<td>.50</td>
</tr>
<tr>
<td>Male width</td>
<td>.35</td>
<td>.02</td>
<td>.38</td>
<td>.33</td>
</tr>
<tr>
<td>Adult genital plate</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Female length</td>
<td>.077</td>
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<td>.083</td>
<td>.070</td>
</tr>
<tr>
<td>Female width</td>
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<td>.078</td>
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<tr>
<td>Male length</td>
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<td>.003</td>
<td>.073</td>
<td>.064</td>
</tr>
<tr>
<td>Male width</td>
<td>.063</td>
<td>.003</td>
<td>.068</td>
<td>.060</td>
</tr>
<tr>
<td>Immature stages</td>
<td>proterosomal width</td>
<td>genital slit length</td>
<td>anal slit length</td>
<td>first tarsal segment length</td>
</tr>
<tr>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Larvae</td>
<td>.09</td>
<td>---</td>
<td>.055</td>
<td>.030</td>
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<tr>
<td>Protonymphs</td>
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<td>.070</td>
<td>.034</td>
</tr>
<tr>
<td>Deutonymphs</td>
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<td>.043</td>
<td>.070</td>
<td>.038</td>
</tr>
<tr>
<td>Tritonymphs</td>
<td>.17</td>
<td>.055</td>
<td>.150</td>
<td>.044</td>
</tr>
</tbody>
</table>

Oppia neerlandica Oudemans 1900.

Plate 5, figs 27-36.

Family Opiiidae Grandjean (1953). Oudemans (1900), Paoli (1908), Sellnick (1928), and Willman (1931). The holotype, if it exists, was not examined. Plesiotypes are deposited at the University of Minnesota.

Only females of this species have been found and only two pairs of genital discs are present.

Young adults are pale yellow, with the cuticle almost transparent. Older adults become progressively more orange. The cuticle is smooth, but for an area of large tubercles extending from coxal cavity I to coxal cavity IV above and between each coxal cavity. Adult notogastral setae are nonsensory, unlike those of S. laevi-
The number of spines on the edge of the adult pseudostigmatic organ is variable.

Aside from the smaller size of the ovipositor of this species, the only difference from that of *C. cisalpinus* is the lack of one zeta seta on each of the anterior fingers. There are no kappa setae.

Immature stage legs are not conspicuously more sclerotized than the rest of the body, but are covered with small tubercles as on much of the immature stage's body. Slits and porose areas, which appear on adult legs, are not present on the legs of immature stages. Immature stage notogastral setae are similar to those of immature stage *C. cisalpinus*, but smaller. The ventral setae are sensory. The proterosomal plate is distinct, but hardly sclerotized at all. In the larvae, the plate is short and the posterior limit is very indistinct. The podosomal gland opening is more anteriorly placed than in the other two species.

Measurements of the adult and immature stages are given in Table 3.

**Table 3.**

<table>
<thead>
<tr>
<th></th>
<th>Adult body (female)</th>
<th>Adult genital plate (female)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>average</td>
<td>s</td>
</tr>
<tr>
<td>length</td>
<td>.28</td>
<td>.01</td>
</tr>
<tr>
<td>width</td>
<td>.14</td>
<td>.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Immature stages</td>
<td>proterosomal</td>
<td>genital slit</td>
</tr>
<tr>
<td></td>
<td>width</td>
<td>length</td>
</tr>
<tr>
<td>Larvae</td>
<td>.044</td>
<td>—</td>
</tr>
<tr>
<td>Protonymphs</td>
<td>.050</td>
<td>.012</td>
</tr>
<tr>
<td>Deutonymphs</td>
<td>.060</td>
<td>.015</td>
</tr>
<tr>
<td>Tritonymphs</td>
<td>.075</td>
<td>.023</td>
</tr>
</tbody>
</table>

**Biology.**

**Culturing Techniques.**

To culture a species of organism implies the rearing of successive generations and an increasing number of specimens. MICHAEL (1883) had moderate success in rearing 4 species of oribatids, but was only really successful with *Damaeus nitens*. JACOT (1936) reared phthiracarid mites that burrowed inside soft, punky spruce needles. KRULL (1939) reared a number of sod mites, but was not successful in culturing any. GRANDJEAN (1950 a) reared several camisid species in an effort to prove parthenogenesis. RIHA (1951) reared some primitive oribatids on a diet of rotting wood.
and Rhode (1955) cultured three phthiracarids on a moss diet. Sengbusch (1954) was the first to really, successfully rear oribatids, culturing successfully three Galumna spp. Pauly (1956) cultured three Belba spp., and Sitnikova (1959) cultured another Belba sp.

This study was restricted to the three most common oribatids found in moist meadows in the St. Paul, Minnesota area. These are S. laevigatus, C. cisalpinus, and O. neerlandica. S. laevigatus was more common in dryer pastures, up to 300 often being found per square foot. The meadow that supplied the specimens for this study was never dry and was almost completely shaded the year round. C. cisalpinus was the most abundant oribatid here, up to 100 per square foot. A modified Berlese funnel was used to extract the mites from the sod samples.

Huber (1958) discusses the use of plaster of paris and activated charcoal as a substrate for rearing mites. The relative humidity is supposed to remain near 95% in the culture tubes, and it actually does, even when the dish containing the tubes becomes dry. Though activated charcoal was supposed to restrict fungal growth, no effect on fungal growth could be demonstrated, so plain charcoal was used for the most part in these experiments. The addition of 1 part charcoal to 9 parts of plaster of paris makes it easier to see the eggs and immature stages, and imparts a more even texture to the plaster of paris and indirectly produces a more stable relative humidity.

Individual culture tubes (fig. 37) were preferred to Rhode’s (1956) method of sealing several or more tubes in one block of plaster-charcoal. The use of plastic culture tubes prevented excessive water condensation. The culture tubes were kept in glass dishes 12 1/2 cm. in diameter and 6 1/2 cm. high, covered with a dish 13 1/2 cm. in diameter and 3 1/2 cm. high. Moisture was supplied by 4-5 layers of filter paper. A change of the filter paper every two weeks kept the influence of fungal and bacterial products on the culture tubes at a minimum. Each dish
held 10 culture tubes arranged around the circumference. The open center made watering (once every other day) easier, and kept the culture cleaner with less water condensation. If a smaller volume of air than this were allowed a dish of culture tubes or individual tubes, then water vapor condensed on the surfaces. With this method, individual culture tubes were easy to clean and reuse, discard, or remove to new conditions. Manipulation for viewing and feeding were much simplified.

Above 15° C., water condensation was no problem because of the plastic culture tube and the breathing tube. With glass culture tubes, water condensation was a problem even with the breathing tube at all temperatures. Below 15° C., water condensation could only be prevented, even in plastic culture tubes, by very careful daily watering of the dishes. The top half of a or no. 5 rubber stopper was used for the culture tube lid, because they fit better than cork and fungi will not grow on rubber. Cork may permit more air transfer, but it crumbles, gets moldy, and does not seal well.

The use of filter paper (or anything else a specimen might eat or crawl under) for a substrate is inadequate. Stender dishes or other glass containers, regardless of substrate, are also inadequate.

*Life cycles.*

All timed cultures were kept continuously at 25° C., at about 90-95 % relative humidity, and fed with what was found to be an optimum diet for each species. These diets are discussed under nutrition. The life cycles are presented graphically in figures 38-40. The time figures are averages under the above conditions, which are close to the minimum time possible for each species. Under these conditions, the average time for the life cycle of *C. cisalpinus* was 32 days, for *S. laevigatus* 64 days, and for *O. neerlandica* 23 days from egg deposition to adult emergence. The life cycle of *C. cisalpinus* can be extended to 70 days by a minimum diet alone, and a low temperature (5° C.) will extend the life cycle to from 70 to 80 days.

In nature, the temperature of the habitat is likely to average less than 25° C., so the life cycle probably takes longer to complete than is indicated in figures 38-40. It is estimated that in the field *S. laevigatus* would have about 3 complete generations per year, *C. cisalpinus* about 4-5, and *O. neerlandica* 6-7 in Minnesota.

The ordinate is total body length rather than body volume, because the total body length of each stage is proportional to the body volume of that particular stage, and total body length is more easily and accurately obtained than the body volume.

The length of the life cycles of *C. cisalpinus*, *S. laevigatus*, and *O. neerlandica* compares well with other oribatids that have been cultured. The time from egg deposition to adult emergence for *Oppia (= Damaeus) nitens* was 40 days, for *Ceratoppia (= Notaspis) bipilis* 79 days, and for *Cepheus palmicinctum* 375 days according to MIChael (1883). PAULY (1956) determined the life cycle for *Belba clavipes*
as 75 days, *B. gracilipes* 75 days, and *B. geniculosa* 150 days. According to Sitnikova (1959), it took 120 days for *Belba boreus*. Sengbusch (1954) determined that *Galumna nervosus* took 47 days, *G. longipluma* 60 days, and *G. eliminatus ithacensis* 87 days. All of the above species were cultured at 25°C, and at a relative humidity of about 95%.

Sengbusch (1954) was the only author to give the percent survival in his cultures. He found that 42% survived, which he considered excellent. If over-
crowding was avoided and food and moisture were adequate but not excessive, over 90% of the eggs deposited by the three species studied here survived to become reproducing adults.

None of the three species studied had a deutovum stage. The eggs are much smaller when first deposited than older eggs, and they have been squeezed into an elongate form while being deposited. This is especially true with *O. neerlandica*. To illustrate that eggs, as they appear in the body of a female, may be considerably wider than the ovipositor or genital plates and can still be deposited normally, the measurements of the genital plates and ovipositor are included with the measurements of the eggs of the three species. Eggs inside of a female are difficult to measure accurately, but rough measurements indicate that the mature eggs inside of a female are the same as the eggs when first deposited. In the table below, all measurements are in mm., and length is the first figure given. The ovipositor is measured when fully extruded.

<table>
<thead>
<tr>
<th></th>
<th>Just laid eggs</th>
<th>Ready to hatch eggs</th>
<th>Ovipositor</th>
<th>Genital plate</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. cisalpinus</em> ....</td>
<td>.180 x .105</td>
<td>.225 x .135</td>
<td>.62 x .08</td>
<td>.097 x .113</td>
</tr>
<tr>
<td><em>S. laevigatus</em> ....</td>
<td>.187 x .095</td>
<td>.195 x .105</td>
<td>.55 x .05</td>
<td>.077 x .072</td>
</tr>
<tr>
<td><em>O. neerlandica</em> ....</td>
<td>.083 x .063</td>
<td>.120 x .075</td>
<td>.14 x .025</td>
<td>.035 x .035</td>
</tr>
</tbody>
</table>

Pauly (1956) estimated total egg production as 70 for *Belba gracilipes*, 60 for *B. clavipes*, and 40 for *B. geniculosa*. Belbid eggs are deposited singly throughout the life of the adult.

*C. cisalpinus* females preferred ground, dried leaves of any kind for oviposition, and, as a second choice, the cast nymphal skins. If neither were present, then the driest spot available seemed to be acceptable. Eggs were usually laid under a flake of leaf, never deeply inserted. All the fertilized eggs the female contained (10-16) were deposited at once, usually in one place, seldom in more than two places. It took females 15 to 20 days after emergence to mature eggs, fertilize them, and finally deposit them. The female would not then lay eggs again until she had been subjected to cold (less than 5°C) for at least 2 1/2 months. If the female were removed to a higher temperature before 2 1/2 months had elapsed, eggs were not produced. Hundreds of adults were kept at 25°C for 10 to 12 months after they had produced their first batch of eggs, and all died without producing any more eggs.

*S. laevigatus* females deposited their eggs in the tissue of decayed grass, or apparently into anything soft and punky. These eggs are inserted very deeply, and are, therefore, difficult to find. The eggs are laid in batches of 3 to 8 in several different locations. Up to 12 eggs can be matured and deposited at one time, but the average is 8. Females began to deposit eggs 20 days, on the average, after emergence. The length of adult life and number of eggs batches matured could
not be determined as precisely as in the case of the previous species. It appears that *S. laevigatus* can mature more than one batch of eggs without the necessity of cold treatment. At 25° C., the adults seldom live more than 4 months.

*O. neerlandica* preferred massed fungal hyphae for oviposition, but when such were not present they would oviposit almost anywhere. These lay their eggs singly, since only one egg was matured completely at one time. Females deposit an average of 12 eggs over a period of a week, and seldom depositing more than 3 eggs in any one place. Egg production commenced on the average 7 days after adult emergence. Adults were short lived, seldom surviving more than a month at 25° C.

*Microenvironment.*

Immature stages of *S. laevigatus* are burrowers, and will not survive if prevented from burrowing. In order to check on the immature stages it is necessary to disrupt their habitat, often to the extent of ruining it. They work in small groups and undermine patches of punky debris, rather than making long, thin tunnels. The only way a good medium for *S. laevigatus* could be obtained, was to culture it with *O. neerlandica* which controlled fungal growth. Though the immature stages of *S. laevigatus* would develop alone in culture, the culture would soon be overgrown with fungi that observation became impossible. It requires about 100 *O. neerlandica* to produce a suitable medium for two dozen adult *S. laevigatus* and all the immature stages they can produce. In sod, according to Jacot (1936 b), the top surface is dry and free from fungal hyphae, while one or two millimeters below is a pylpy, half decomposed grass litter layer. Using food, as described under nutrition for *S. laevigatus* cultures, *O. neerlandica* produces a condition whereby the surface is dry and free from fungal growth, while less than a millimeter below this surface is punky food material. Adult *S. laevigatus* are surface dwellers and feeders, but are easily enmeshed in fungi and water condensation. They cannot tolerate entrapment, and die within a day or two if not released. Since fungal growth restricts the free movement of adult *S. laevigatus* in a culture, without the presence of *O. neerlandica* to restrict fungal growth, *S. laevigatus* adults would never have the opportunity to deposit spermatophores, become fertilized, or to deposit eggs.

*O. neerlandica* feed extensively on fungal hyphae, and are not enmeshed in it. All stages can feed and move freely through fungal growth; however, they are only slightly less susceptible to entrapment in water condensation than *S. laevigatus*. Their small size permits them to work through and out of fungal hyphae. They are not as good burrowers as immature *S. laevigatus*, and need a rather loose food substrate to penetrate. It is their small size that allows them to penetrate loose material, and they do not actually burrow into a solid substrate. Immature *O. neerlandica* can produce a cavity in solid food, but access to the surface is open, whereas immature *S. laevigatus* hatch from the eggs and complete their development without ever producing access to the surface.
C. cisalpinus are surface feeders in all stages, except larvae and protonymphs may burrow into very loose material. Immature stages are never trapped in fungal hyphae unless it becomes almost solid. The long, black setae of the immatures seem to assist them in avoiding entrapment by water droplets and fungal growth. Adults seem to avoid these two major survival problems by sheer bulk and strength. This species is the least apt to be trapped in water condensation of the three species studied. Adults alone, although not trapped by fungi, are prevented from feeding by it. Unless immature C. cisalpinus or any stage of O. neerlandica are present to keep the fungi down, adults of C. cisalpinus apparently starve.

Immature stages of all three species feed continuously, except when molting. After emergence, adult female C. cisalpinus feed continuously for about 2 weeks. Males feed continuously for about a week. O. neerlandica adults actively feed for 7 to 10 days after emergence. S. laevigatus adults feed actively for about 15 to 20 days after emergence, and will resume active feeding for short periods at apparently unpredictable intervals. Just before C. cisalpinus females deposit their second batch of eggs food uptake is increased. Adults of the three species feed continuously just after emergence, and thereafter seem to feed only occasionally. This reduction in food intake occurs gradually over a period of days.

Molting.

Molting in these three species is quite normal externally. An active immature stage oribatid feeds until the cuticle is quite distended. It then becomes quiescent and proceeds to molt. C. cisalpinus and O. neerlandica immatures then seek a dry, protected spot such as dried ground leaves or cast nymphal skins. Partially decomposed tree leaves or grass, thoroughly dried and rough ground, provided an excellent material in which molting or oviposition can occur for many sod-inhabiting oribatids. A small pile of such material in a culture offers protection in its loose structure, and is usually the dryest spot available. S. laevigatus molts in the burrow it has produced by its feeding.

After the immature specimen finds a suitable spot it becomes quiescent. This is called the pre-ecdysial-resting-stage (pers) (fig. 44), and it will not move even if violently disturbed. By definition here, pers is both singular and plural, and may be used as a noun or suffix. The duration of the pers varies from species to species, and from stage to stage, but invariable the larvapers is the shortest, and the tritopers the longest.

At the end of the premolt period, the old cuticle splits on what would be the notogastral membrane from posteriormost region to the level of the fourth leg. The next stage expands and protrudes from the split, and then remains that way until the legs and mouthparts have hardened. This is called the hardening period. The C. cisalpinus adult hardening period takes about 12 to 24 hours, and is longer than the hardening period for any immature stage. If, for example, an adult is removed from the split tritonymphal skin before the hardening period is com-
pleted, it is able to move about and feed, but the legs bend and it dies within a day or two.

Most of the pressure to split the old cuticle is supplied by the expanding body. The expansion is rapid, and the adults harden in an expanded state. Probably water uptake provides the pressure for expansion. The legs are not used until they are hardened, and then they are used to extract the individual from the old cuticle. The new legs, as usual for oribatids, are extracted from the old leg cuticle about half way through the premolt period.

Only the legs, gnathosoma, and proterosomal plate of the immatures harden, while the rest of the body expands to a definite shape and size. Figure 11 schematically illustrates the manner of growth of *C. cisalpinus* during each immature stage. The hardened regions expand very little, but the hysterosoma enlarges throughout that stage in a distinctive manner as a consequence of feeding. In the recently emerged immature the hysterosoma overlaps the proterosomal plate and a hysterosomal, crescent-shaped groove is present. Expansion in that stage results in the elimination of the crescent-shaped groove and the hysterosomal overlap and enlargement towards a globular form.

The manner of growth of *O. neerlandica* and *S. laevigatus* within any one immature stage is slightly different (fig. 32). The hysterosoma folds over the proterosomal plate, as in *C. cisalpinus* when recently emerged, but the hysterosomal folds are transverse rather than crescent shaped. Expansion results in elongation of the immature rather than in its becoming more globular.

Feeding *C. cisalpinus* and *O. neerlandica* of all stages have a definite tendency to feed together. With two identically prepared piles of food they will invariably all feed on one pile only. With overcrowding of the cultures, they feed all over at once.

Feeding immature *S. laevigatus* have no grouping tendencies.

*C. cisalpinus* very strikingly molt in groups (fig. 44), even when all parts of the culture tube are equally dry and clean. Sometimes this group molting reaches the point where they are piled on top of one another. *O. neerlandica* does not exhibit this tendency.

In cultures of both sexes and mixed ages of *C. cisalpinus*, frequently a group of adults will congregate on the side of the culture tube. It is always the cleanest spot in the culture. When moved away, very often tremendous numbers of spermatophores are revealed. Sometimes only a few spermatophores are revealed, and this is thought to be because the adults were either simply seeking a dry spot to rest upon or they were not there long enough to produce many spermatophores.

A few miscellaneous activities have been observed which are worth recording here briefly. *C. cisalpinus* adults clean their first two pairs of legs in much the same way as roaches, and they clean the last two pairs of legs by scraping them on each other in much the same manner as a fly. They clean those parts of the body that can be reached with their legs, especially the sides of the proterosoma and the anal and genital plates. Adult *S. laevigatus* and *O. neerlandica* as well as some
of the immature stages of the three species have been observed to clean their legs and body in a manner such as described for *C. cisalpinus*.

The first pair of legs of adult *C. cisalpinus* are used almost like feelers, and the reaction of a hungry individual waving its foremost legs in the air and often going directly towards the food leaves little doubt that PAULY (1936) was correct in his determination that chemoreceptors are present on those legs. Most stages of all three species have been observed to react in this manner upon the addition of fresh food.

Feigning death by *C. cisalpinus* occurs only rarely in any stage, but occurs more often in adults. Most of the time, if disturbed, pushed, or rolled over they immediately resume activity when the disturbance ceases. A death feign seldom lasts more than 1 or 2 seconds. If touched lightly, they simply move away; but, if roughly shoved, they are still when being moved, but resume activity almost as soon as the shoving stops. Even when picked up with a moist brush, they resume activity as soon as they are set down. This is true for both freshly caught or cultured specimens. *O. neerlandica* feigns death as infrequently as *C. cisalpinus*, but *S. laevigatus* exhibits a more typical and lasting feign of death in all stages when disturbed. This death feigning was discussed thoroughly by RIHA (1951) for a number of oribatid species.

The speed of the various stages of all three species were measured by placing the individual to be tested on a bulls-eye surrounded by measured concentric circles. This experiment was run to obtain an approximation of how far an oribatid could move under its own power. This would be important when considering dispersal of the species. The circles were traced on plaster-charcoal, and a temperature of 25° C. and a relative humidity of about 90 % were maintained. All measurements are in cm/sec., and averaged for three replicates on five different individuals.

<table>
<thead>
<tr>
<th>Table 5.</th>
<th>slow walk</th>
<th>normal pace</th>
<th>excited</th>
<th>very excited</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. cisalpinus.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults.............</td>
<td>.09</td>
<td>.11</td>
<td>.14</td>
<td>.22</td>
</tr>
<tr>
<td>Tritonymphs.........</td>
<td></td>
<td>.08</td>
<td>.11</td>
<td>.17</td>
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<tr>
<td>Protonymphs..........</td>
<td></td>
<td>.022</td>
<td>.05</td>
<td></td>
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<tr>
<td><em>S. laevigatus.</em></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Adults.............</td>
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<td>.04</td>
<td>.05</td>
<td>.065</td>
</tr>
<tr>
<td>Deutonymphs.........</td>
<td></td>
<td>.009</td>
<td>.02</td>
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<tr>
<td><em>O. neerlandica.</em></td>
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</tr>
<tr>
<td>Adults.............</td>
<td>.028</td>
<td>.04</td>
<td>.06</td>
<td>.075</td>
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<tr>
<td>Deutonymphs.........</td>
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<td>.025</td>
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</tr>
<tr>
<td>Larvae.............</td>
<td></td>
<td>.010</td>
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With some stages, 4 distinct speeds could be determined consistently, but with other stages 2 or even 1 speed was all that could be elicited. A camel hair brush...
was used to stimulate them for excited or very excited speeds. The slow walk was mostly exploring. The normal pace is the easiest to get, because it is the speed most often used in open places. This normal pace is remarkably consistent. The excited pace is obtained by touching the rear end of the specimen, but the very excited pace could only be obtained by almost squashing the specimen with the brush.

A remarkable waggle movement is exhibited upon occasion in culture tubes by adult *C. cisalpinus*. It was never seen in other species or other stages of this species, and was never observed in an open dish or bare culture. It is unpredictable, but has occurred often enough when deliberately provoked to be certain it was not a freak occurrence. Upon opening a healthy colony and finding many adults on the pile of ground leaves provided, a mere touch on one individual will send it off at an excited pace through the surrounding group of individuals, wagging its body furiously. This waggle resembles the dance of a foraging honeybee on a hive frame very closely. Others contacted by the wagging individual either waggle in place or set off wagging at an excited pace for a short distance. The original wagging individual never goes far, but goes farther than the others. It appears in a group of mites like a wave of vibration passing through the group. Most of the group generally quickly resume normal activities again. A waggle prone group can be made to go through the mass wagging several times before the response is not elicited any more. By this time, all the individuals in the group are moving in all directions at a normal pace. This may be some primitive form of communication.

*Dispersal and Natural Enemies.*

It is the author's opinion that the three studied species, like most sod-inhabiting oribatids, are dispersed over short range (cm. to m.) mostly by mammals and birds using dry grass that contain oribatids for nesting material. *Jacot* (1930) discusses bird dispersal, and *Willmann* (1931) mentions that *S. laevigatus* is common in small mammal nests. Most of the long range dispersal, and much of the short and intermediate range also, is accomplished by water. Since excess moisture drives the adults up, and since they can float very well and tolerate extended periods of submersion (see under bioclimatics), water dispersal is likely to be the most important of all. In the spring, with a combination of high population and much rainfall, one would expect most of the water dispersion to take place. A few samples of floating debris, composed mostly of grass and twigs, taken from the St. Croix river in May, 1960, produced at least one dozen different oribatid species (all adults), one of which was *S. laevigatus*.

The behavior of predators, mostly mesostigmatids, in a petri dish is artificial, but it does give some indications as to their effect in the field. The most obvious fact is that the heavy armor of the large adult oribatids is ample defense against even the largest of mite predators. The armor of adult *O. neerlandica* is too light to protect them from many of the large mite predators. Immature stages of all
species are completely helpless in the open, and just 1 or 2 predators will kill every one in a culture. *S. laevigatus* immatures are much better protected than the other two species, and since they do not leave openings to their burrows even small predators have to dig them out. The small size of *O. neerlandica* immatures allows them to escape many of the large predators. The predators found in the study field in conjunction with the three studied oribatids have not yet been determined to species. The most efficient control of the population of these three species, aside from climatic factors, is mite predation. Characteristically, there seems to be no specificity of predator for prey.

If fungal hyphae are not consumed quickly enough by oribatids, they act as an entanglement and may cause the death of an individual. Parasitic fungi may exist, but none could be proven in the cultures studied here. A dead oribatid in culture sprouts fungi out the mouthparts, anal and genital plates, and even the tarsal segment tips. The fungi that sometimes grow from dead *C. cisalpinus* adults in the cultures used were occasionally different from those that grow on the food, but are most likely other saprophytic fungi. Immature *C. cisalpinus* very rarely supported fungal growth, as they decomposed with no evidence of fungal activity. The only postulation offered for this difference in decomposition between adults and immatures, is that bacterial activity is so much more efficient in dead immatures than in dead adults.

Nematodes were always present in the culture tubes unless special precautions were taken. The young worms could penetrate the plaster-charcoal and spread from culture to culture in any one dish. These nematodes, a *Rhabditis* sp., fed on all the foods offered the mites or on other invertebrates offered as food for the three studies oribatids. These worms appeared in the mites as soon as they died, and sometimes when the mites were moribund. In moribund oribatids, the nematodes are first detected in the food bolus of the gut. They probably only move to the mites flesh when the mite is dead, since sections of active adults never revealed any worms. Fungal and bacterial activity did not seem to interfere with the activity of these nematodes.

Pieces of immature setae and cuticle were occasionally found in the food bolus of sectioned adult *C. cisalpinus*. This may have been due to dead immatures or their cast skins becoming mixed with the normal food and consumed. Cannibalism is not a factor with any of these three species.

What is sometimes called a cerotegument is present at certain times on adult *C. cisalpinus*. This layer on top of the cuticle has been discussed by Grandjean (1951) and Winkler (1957) for several other oribatid species. Where it comes from, and what it is is uncertain according to these authors. In adult *C. cisalpinus* (never immature stages) it only appears in older individuals, at least three months old. It appears occasionally as an isolated spot in the middle of the notogaster, but most often on both notogaster and venter in the posteriormost region. When first noticed, it is no larger than the genital plates, but slowly spreads anteriorly until the mite dies. The beginning of the formation of the cerotegument varied
from three months to ten months. Once started, the specimens die in less than two months, usually much less. Very few adults die before the cerotegument is formed when reared in culture tubes.

The cerotegument is a black, crustose, cement-like substance that varies greatly in thickness according to age and the place on the specimen's body. If it is in the form of a spot, it is thinner at the edges. When this substance forms over the anal and genital plates, these structures are sealed shut. In extreme cases, the leg movement is impaired and death results within a day or two. Sometimes debris sticks to the cerotegument, and the specimen is forced to carry a burden up to five times its own volume.

Very noticeable is the fact that the substance forms much more slowly and less extensively in clean culture tubes. The cerotegument does not increase on dead individuals. A specimen with a spot of cerotegument appears dull, in contrast to the normal shiny surface, and is much more apt to be caught in water condensation. In the author's opinion, the cause of the formation of this material is that wax layers of the cuticle are lost, dermal glands fail to function properly, or both. Fine debris then clings to the cuticle and hardens.

Reproduction.

The spermatophoric method of fertilization appears to be quite common for soil inhabiting arthropods. PAULY (1956) describes spermatophores for Belbidae; SCHALLER (1952) for Collembola; SCHALLER (1954) for Diplura; ANDRÉ (1953) and LIPOVSKY et al (1957) for Trombiculids. PAULY's (1956) illustration of a belbid spermatophore is slightly different from that of C. cisalpinus (fig. 5), being more similar to that of S. laevigatus (fig. 21) with the dark material being present in the bottom half of the spermatophore. LIPOVSKY, et al (1957) found that trombiculid spermatophore stalks could be multiple, and that the sperm sac rested on a fork at the top of the stalk. They believed the sperm sac to be uniform throughout, though it certainly is not in C. cisalpinus and S. laevigatus. When the sperm sac is removed by a female trombiculid, a forked structure remains, but when a female oribatid removes a sperm sac (fig. 46), an unforked stalk with the central and lateral supports is easily visible (fig. 45).

LIPOVSKY, et al describe how trombiculid males produce a spermatophore in a few seconds. PAULY's (1956) description of male spermatophore deposition for three belbid species is very close in time and procedure to that for C. cisalpinus. The male oribatid first lowers its body, and extrudes the penis. A bit of stalk material is fixed to the substrate, and the body is raised almost as high as it can go. The body of C. cisalpinus is not angled (anterior end down) as drastically to the substrate as with Belba gracilipes, certainly never more than 30°. The raising of the body either draws the stalk material out, or the stalk is drawn out between the penal sclerites. The latter is most likely, because the bit of stalk material first fixed to the substrate appears too small to provide enough material for the
The entire stalk. The penis appears to be extruded all this time. The stalk hardens almost immediately, and the mite retracts the penis and settles down on the stalk with the genital plates almost closed. The body is horizontal now, and this position is held for at least several minutes. The body is then quickly raised, revealing a complete spermatophore.

In picking up the spermatophore the female raises its body as high as possible, moves over the spermatophore, opens the genital plates, and then settles down on it. The genital plates are closed and the female remains still for a few seconds, then, with a visible jerk, rises and moves off.

Female uptake of spermatophores was only observed once, in contrast to the many observations of male spermatophore deposition. About half the time the females upon encountering a spermatophore would feel it with her first pair of legs, then pass on. The rest of the time she would completely ignore the spermatophore.

As Jacot (1934) demonstrated, most oribatid species can be sexed on the basis of the female specimen being statistically larger than the male. Aside from very few species of the genera *Galumna*, *Hydrozetes*, and *Anisochthodes* that Newell (1957) listed as exhibit obvious external sexual dimorphism, dead cleared oribatids can only be sexed on the basis of the presence or absence of an ovipositor or when not properly cleared, on minute size differences.

In order to segregate living, virgin, adult female *C. cisalpinus*, and young, adult males one must collect premolt tritonymphs and wait for each to emerge. When an adult emerges, it is placed ventral side up on a slide, inside a glued-down, plastic ring; water is added; and a coverslip is slid on. With the proper thickness of the plastic ring, the specimen is immobilized, yet not squashed. The genital plates can then be measured with an ocular scale. There is overlap between the measurements of male and female genital plates, but beyond a certain range they are easily identified (table 1).

Individual males vary greatly in how many and how long spermatophores are produced. They start producing a few about 10 days after emergence, and full production is usually attained at 20 days of age. The maximum produced by one male was about 20 in 5 hours. For the rest of the males life, the number produced varies greatly with time. Males were still producing a few spermatophores when over a year old.

Males by themselves produce only about 20 % of the number of spermatophores that they will if females are also present in the culture. In mixed cultures, congregateing groups show a great abundance of spermatophores when they are caused to move away. Somehow, the presence of the females stimulates the males to produce more spermatophores.

With about six of each sex in a culture tube, about 30 to 40 spermatophores would be produced in 2 to 3 days fairly regularly. These culture tubes were kept almost bare in order that the adults could be removed and egg checks easily made. Upon removal of the adults, a clean culture with a number of spermatophores was
then available for the introduction of virgin females. These virgins were never in the same culture with a male. After the virgin females were 20 days old, they were introduced to the spermatophores alone, and left for about a week. After two days, all spermatophores were gone. Though most of the sperm sacs were accidently dislodged and destroyed, some of the fresher sperm sacs were probably taken up by females. At the end of a week, the same virgins were introduced to more fresh spermatophores alone. The final proof that sperm transfer in *C. cisalpinus* is by spermatophores, was the fact that eggs were produced after four introductions of fresh spermatophores (never any males present) by 10 to 15% of the virgin females.

Males would only deposit a spermatophore on a clean dry surface, and preferred a smooth surface. They deposit very few in very dirty cultures which contain many fecal pellets.

Sperm in both the male and in the spermatophore is inactivated by temperatures of 35° C. and probably less (see under bioclimatics). The sperm sac takes up moisture very rapidly and often ruptures, and it is easily dislodged and destroyed by a passing mite as it is rather sticky. It is likely the spermatophores are quickly penetrated by bacteria, for they are often found in squashed slide preparations. With low relative humidity, less than 50% R. H., the sperm sac shrivels within a day.

Spermatophores standing out in the open in a culture are almost always ignored by females. These spermatophores are at least several hours old. When transferring virgin females, it takes them some time to settle down, and many of the spermatophores in the culture into which they are introduced are much older than several hours. This is probably the reason it has taken at least four introductions of fresh spermatophores to obtain even the low percentage of eggs produced. It is believed that the sperm must be very fresh, not more than an hour or so old, before they are picked up by females. This would account for the fact that most spermatophores are produced in groups of both sexes, as described above, and that nearly 100% of the females produce eggs under these conditions.

Grandjean found parthenogenesis in *Dameobolba minutissimus* (1955), in several *Nothrus* spp. (1947 b), and in *Camisia segnis* (1947 a). He discusses parthenogenesis of oribatids in general (1941 and 1952). It is apparently a common phenomenon in certain families of oribatids, especially Camisiidae and Eremaeidae. Grandjean (1941) assumes that if only females were found, the likelihood of parthenogenesis is very high.

Parthenogenesis was definitely proved in *O. neerlandica* by placing a solitary egg in a fresh culture tube (never used before), and observing that in less than 30 days a lone female resulted. This female then proceeded to lay eggs which hatched and developed into more adults. In 12 cultures, each originally with a solitary egg, the results were the same.

*O. neerlandica* cultures, containing roughly 50 females each, were subjected
to many combinations of cold temperatures and restricted light, but males were never produced. The indication is that males probably do not exist.

Cultures of virgins alone of *C. cisalpinus* were kept until they died of old age (8 to 10 months), and eggs were never produced.

*Strenzke* (1949) discusses the various types of reproduction in oribatids, and includes normal oviparity, viviparity, parthenogenesis, and aparity. Viviparity was listed as occurring in certain *Ameronothrus* spp. Aparity is development wherein the eggs hatch in the dead female with the resulting larvae forced to eat their way out. *Jacot* (1933) claims aparity occurs in several species of higher oribatids, especially galumnids, and he further states that aparity or viviparity must take place because the eggs are too large to be deposited in the normal fashion. A comparison of the egg size with genital plate size of *O. neerlandica* in table IV illustrates that aparity cannot be assumed simply on the basis of large eggs relative to genital plate size.

A number of workers have reported finding immatures inside of dead adults, but, as *Strenzke* points out, the gnathosoma is usually lacking in these dead adults. Immature *S. laevigatus* will feed on dead adults, mostly on exudates and fungi growing from the dead adult. *O. neerlandica* in all stages would feed on dead house fly maggots. Most cases of finding immatures in dead adults are probably simply cases of saprophytic feeding. It is possible that if eggs were just ready to be laid and the female died, the eggs could mature, hatch and the larvae could force their way through the decaying body. Dead adults are hollowed out very quickly by bacteria, nematodes, and fungi. In the author's opinion, if aparity and viviparity do exist in oribatids, it is very rare. Oviparity is certainly by far the most common mean of producing young.

Normal copulation has never been observed in oribatids, so spermatophoric insemination is likely to be the only means of sexual reproduction.

**Bioclimatics.**

A systematic study of temperature, light, humidity or submersion tolerances was not made for all stages of *C. cisalpinus, S. laevigatus,* and *O. neerlandica.* However, general observations and some experiments revealed some interesting biological data.

Temperature, as high as those found in their normal habitat has no direct effect on the life of an individual. Cultures of *C. cisalpinus* were maintained at 35° C for two months, and though reproduction did not occur, activity appeared normal. As *Shaldybina* (1956) states, the relative humidity, as influenced by temperature, affects the movement of soil mites in general. Adults are more influenced by relative humidity than immatures, and move up when it becomes too wet, and down when it is too dry. In the study cultures, immature *S. laevigatus* would not leave their burrows no matter what the temperature or relative humidity was.
Cultures containing *C. cisalpinus* virgin females and males kept at 33° C. had an abundance of spermatophores, but never produced any eggs. Even if the temperature is raised to 35° C. for 6 hours once every 4 to 6 days, spermatophores are produced without any egg production. If these same cultures are placed and kept at 25° C. for a week, eggs are produced at the end of that week. This seems to indicate that eggs were matured by the females, but that the sperm in the spermatophores was non-viable. Control cultures containing virgin females and males kept at 25° C. from the time emergence of these adults started to produce eggs in 20 days.

To check on any adverse effect high temperature might have on females, virgin females, raised and kept at 25° C., were introduced to spermatophores produced by males at 35° C. Eggs were never produced, even though the virgin females were provided with fresh spermatophores, which were produced at 35° C., every week to ten days for two months. Virgin females reared and kept at 25° C. that were placed in cultures containing spermatophores only, that were produced also at 25° C., produced eggs (see under reproduction). A few attempts to introduce virgin females alone to spermatophores produced by males maintained at 25° C., but subjected to 35° C. for two hours prior to the introduction of the virgin females, resulted in no egg production.

A temperature of 35° C. for 1-2 hours will kill all the sperm in a male *C. cisalpinus*, as well as in any spermatophores produced. Probably lower temperatures will inactivate the sperm, but this was not tested. Field temperatures seldom reach 35° C. at the sod level. The maturation of eggs by females is not influenced by temperatures up to 35° C. A heat sterilized male is not likely to produce viable spermatophores for at least 5 to 6 days.

Acclimatization is very distinct with *C. cisalpinus*. When first moved to 5° C. from 25° C., they are immobilized, but after a day or two activity is again near normal.

Just a few experiments were done with low temperatures. Activity and feeding is continued for all species and all stages down to 2 to 3° C. *C. cisalpinus* males will even produce a few spermatophores at 3° C. The developing eggs of *C. cisalpinus* could be kept at 4° C. for several weeks, but the developing eggs of *S. laevigatus* died at 4° C. within a week. Both *C. cisalpinus* and *O. neerlandica* eggs would complete development and hatch at 4° C. Freezing killed all eggs of the three species. *O. neerlandica* deposited about as many eggs at 5° C. as they did at 25° C., *C. cisalpinus* deposited very few eggs at 5° C. and *S. laevigatus* were never observed to deposit eggs at 5° C.

Sod samples taken from the center of a field that was flooded and used for ice skating all winter, produced large populations of *S. laevigatus*. The samples were taken as soon as the ice thawed and most of the water was drained off. Immatures were completely lacking.

Sod samples taken from a moist meadow in St. Paul during February and March showed almost 95% adults of all species. In April, the total number of oribatids
in the samples had increased greatly, and of that total half or more were immatures.

Haarlov (1942) found that most Greenland oribatids overwinter as nymphs, mostly tritonymphs, and that they molt to adults almost immediately in the spring and produce eggs. There was only one generation per year in this case. Rha (1951) indicates that most oribatids in Europe overwinter as adults. Both are probably correct for their regions. In any case, the three species studied here overwinter predominantly as adults in St. Paul, Minnesota. As winter approaches, the last group of immatures continued feeding and development, but spermatophore deposition and uptake are curtailed. The result would be a large majority of adults in early spring samples. O. neerlandica can lay eggs below 5° C., though immatures in early spring are rare.

Cultures of C. cisalpinus containing only females that had already produced one batch of eggs, and with plenty of males and spermatophores present, would not produce more eggs at 25° C. These cultures were kept for between 10 to 12 months, and most of the specimens had died of old age without producing more than a few eggs. A number of cultures containing nonvirgin females and males were placed at 5° C. and none of the cultures removed before 2 1/2 months had elapsed produced eggs. At the end of 2 1/2 months, the cultures that were removed produced enough eggs to average close to 10 eggs per female. Cultures were not kept longer than 2 1/2 months. Actually, in cultures of nonvirgin females with active males maintained at 25° C., about one egg batch for every 10 to 20 females appeared without the cold treatment. Whether these eggs were the result of a second batch by some females, or were simply the result of a delayed egg deposition is unknown. There is indication that an adult egg deposition diapause is present in C. cisalpinus. This diapause is broken by subjection of the adults to less than 5° C. for 2 1/2 months.

Rha (1954) found that S. laevigatus adults could stand up to 24 hours of complete dryness. The author found that adults of C. cisalpinus and O. neerlandica could tolerate as much desiccation as S. laevigatus adults. As expected, in cultures that were allowed to slowly dry out, immatures were the first to die. Out in the open the immatures of all three species died at the same rate, but with food material present the ability of O. neerlandica and especially S. laevigatus immatures to burrow into the more moist areas permitted them to survive longer than C. cisalpinus immatures. The amount of material present to burrow in had to be large enough so that it was the last thing to dry out. The habits of the immatures supply the key to the ability of the species to survive in any given area. The burrowing habits of immature S. laevigatus are an asset in dry pastures, but in more moist meadows there would be no advantage. In dryer grass fields, such as lawns and pastures, C. cisalpinus was much rarer than the other two species, frequently missing altogether, and S. laevigatus was much more abundant than O. neerlandica. In the more moist meadows, all three species were present, but C. cisalpinus was dominant.

The tolerance for complete submersion was remarkable. In a droplet of water, where movement of the individual was almost completely restricted, all stages of
the three species died within 1 to 3 days. Adults could tolerate this entrapment better than the immatures. With complete submersion in larger quantities of water *S. laevigatus* resumed an almost normal existence. They could eat and move about for up to 2 months, provided the surface of the water was open to the air. Even in a container with a top allowing no air over the water surface they could survive for a month. Reproduction and molting, however, did not occur. The other two species were somewhat less tolerant to complete submersion, seldom surviving more than a week or two. *O. neerlandica* adults could deposit eggs that would hatch, and the resulting larvae could survive for as long as a week.

Sperm inactivation due to high temperature and female second egg batch diapause probably greatly influence populations of *C. cisalpinus* in the field. Too few continual field samplings were made to verify this statement in this study, but these factors may be utilized to help explain summer oribatid population decreases as found by RIHA (1951).

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Nutrition.

The study of the nutrition of the three species can be divided into two parts, natural and cultural. An attempt was made to determine what the diet is in the natural habitat, and to determine the role played by fungi. The culture diets were mostly of materials not normally found in the natural habitat.

It was found that the oribatids studied would nibble at almost anything, including filter paper, pencil erasure, wool, wood, and even powdered charcoal. They never ate much of these materials, and only occasionally did so when they were starved. What a species might be eating when seen in Berlese funnel renderings is therefore often misleading.

MICHAEL (1883) reared *Oppia nitens* in moldy cheese and rotten wood, *Cepheus palmicinctus* on lichen, and *Ceratoppia bipilis* probably also on lichen. JACOT (1936a) reared phthiracarids on punky spruce needles, and RHODE (1955) reared other phthiracarids on moss. GRANDJEAN (1950a) used lichen for several camisid species. SENGBUSCH (1954) used moss for the adults and an alga for the immature stages of *Galumna nervosus*, *G. longipluma*, and *G. eliminatus iihacensis*. PAULY (1956) used a diet of green algae (in addition to the fungal hyphae that grew thereon) for *Belba gracilipes*, *B. geniculosa*, and *B. clavipes*, while SITNIKOVA (1959) used a diet of rotten oak leaves and moldy potatoes for *Belba boreus*.

Those species that are found in very restricted habitats, such as a moss bed, or burrowing in pine needles, wood or, lichen can be assumed to feed primarily on the material that makes up just about 100% of their environment. Sod-inhabiting species present a more difficult problem. An excellent method is to analyze the fecal pellets of freshly caught oribatids as did FORSSLUND (1939). He found mostly fungal hyphae, with smaller amounts of fungal spores, solid pieces of unknown origin, and a few pieces of arthropod cuticle. The fungal hyphae was almost exclusively white or hyaline. Fecal pellets of freshly caught specimens in the-
The present study revealed much the same, except that the solid portion constitutes a larger percentage of the total, especially in *C. cisalpinus*.

The next step was to try to culture *C. cisalpinus*, *S. laevigatus*, and *O. neerlandica* on materials derived solely from the sod in which they were extracted. Sod and sod products do not make good culture media. All three species would grow and develop on fresh green grass, but the cultures soon died out. Combinations of green grass, grass roots, fungi, and decaying sod debris produced better results, but only with *O. neerlandica* could a continuous succession of generations be obtained. This combination of sod products was very difficult to work with, and much of the lack of successful rearing with this medium is attributable to mechanical difficulties. Sod is a living unit in which the mites live, and breaking off small bits and placing them in culture tubes did not supply a suitable environment or diet.

A simple diet upon which these species could be easily reared through continuous generations was desired. After trying everything from raisins to algae and slime molds to caterpillars, three materials, either singly or in combinations, were found that could support these oribatids indefinitely. The three materials were, 1) a *Coprinus* sp. which is a mushroom found commonly in grass fields, 2) a lichen of the genus *Physcia* (probably *P. adglutinata*) found on the bark of elms near lakes, and 3) an artificial diet given to the authors by Dr. M. A. Brooks of the University of Minnesota, and based on a diet developed by Gordon (1959).

The directions for preparing the artificial diet used here are:

- **Glucose** (dextrose) ground and sifted........... — 360.0 g.
- **Casein** (vitamin free)........................................— 300.0 g.
- **Salt mixture**........................................— 40.00 g.
- **Vitamin mixture**........................................— 40.00 g.
- **Choline mixture**........................................— 25.00 g.
- **Corn oil**........................................— 30.00 g.
- **Cholesterol**........................................— 10.00 g.

Dissolve the corn oil and cholesterol in reagent grade acetone by means of a hot water bath, then pour into the dry mixture of all the other ingredients in a shallow pan. Mix it all with a fan blowing over the pan to remove the acetone. Add 174.78 g. of celluflour to get a one kg. total.

The choline mixture is obtained by dissolving 2.8 g. of choline chloride in 25 ml. of hot absolute ETOH, then adding 22.2 g. of celluflour. Dry this mixture at 120° C. with stirring for 4-6 hours. The choline mixture is kept dry until the final mix with the other ingredients.

There are two groups of salts, the macrosalts and the microsalts.

<table>
<thead>
<tr>
<th>Macrosalts</th>
<th>Microsalts</th>
</tr>
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<tbody>
<tr>
<td>CaCO₃</td>
<td>CaSO₄ · H₂O</td>
</tr>
<tr>
<td>MgSO₃</td>
<td>Fe (NH₄) (SO₄)₂ · H₂O</td>
</tr>
<tr>
<td>K₂SO₄</td>
<td>Mn SO₄ (anhydrous)</td>
</tr>
<tr>
<td>KH₂PO₄</td>
<td>Zn SO₄ · H₂O</td>
</tr>
<tr>
<td>NaHCO₃</td>
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</table>
Dissolve the microsalts in 15 ml. of double distilled water and add 12 g. of cellulour, then mix and oven dry at 120° C. Grind the macrosalts in a mortar and pestle and mix perfectly, then add to the dried microsalts.

The vitamin mixture is prepared as follows:

1. Dissolve 3.6 g. of inositol in 15 ml. of hot water, then add 16.4 g. of cellulour. Dry at 120° C. for 4-6 hours and keep it dry until used.

2. Dissolve the following in 3 or 4 ml. of hot water and add 9.8 g. of cellulour. Dry at 50° C. in a vacuum oven for 2 hours.
   - Thiamin ............... 68 mg.
   - Nicotinic acid ........... 98 mg.
   - Pyridoxine HCl ........... 82 mg.
   - Ca pantothenate.
   - Cyanocobalamin (B_{12}) 2 mg.

3. Dissolve 12 mg. of biotin in a few ml. of hot 95% ETOH and add 5 g. of cellulour. Dry at 50° C. in a vacuum oven for 2 hours.

4. Add 88 mg. of folic acid to 5 ml. of hot water containing one drop of concentrated (28%) NH_{3}, then add 4.9 g. of cellulour. Dry at 50° C. in a vacuum oven. Mix 2), 3), and 4) and then add 7.6 mg. of riboflavin (weigh and keep in a dim light). Add 1) to this and mix the whole thing thoroughly.

With these three foods, the amount provided in each culture had to be very close to the amount they could consume before the fungal hyphae grew. The unused artificial diet was removed every other day, and the unused mushroom and lichen once a week. The artificial diet became rancid in two days. In well balanced cultures, even the unused food seldom developed fungal growth by the time it was changed. It was found better to provide somewhat less food than the mites could consume in a given period, since the cultures were then kept free of fungal growth.

The success of a particular food or combination was evaluated on the duration of the life cycle and the number of eggs produced. If continuous generations were not produced, the diet was judged to be unsuccessful.

The mushrooms were oven dried at 100° C., and ground slightly. The lichen was scraped from the bark and oven dried at 100° C. The artificial diet is passed through a 100 mesh screen after preparation and stored in a deep freeze until used.

It was impossible to prevent fungi, chiefly various Mucor and Rhizopus species from developing on the culture foods. Various colored fungi also grew occasionally, but never flourished. The colored fungi grew mostly on the filter paper in the culture dishes. Other white or hyaline hypha-producing fungi were undoubtedly present in the cultures, but since the oribatids specimens fed on them all alike, the fungal hyphae are treated as a group.

It was observed that the fungal hyphae were eaten by all stages of all three species studied in varying degrees. A healthy colony of G. cisalpinus or O. neerlandica had very little apparent fungal growth, so that each individual could get very little fungal hypha to feed on. Examination of the fecal pellets from these colonies revealed virtually no fungal hyphae. In cultures of S. laevigatus alone,
fungal hyphae grow freely, since the immature mites are under the surface, and
the adults gradually decrease their food intake and do not consume enough to reduce
the amount of fungus present.

In order to determine whether fungi were necessary at all, an aseptic rearing
technique was attempted (figs 41 to 43). Only *C. cisalpinus* was used. It could
be determined when eggs were ready to hatch by the presence of black larval setae
seen through the chorion. The eggs were then placed on the colored cotton in
the glass tube, and a cotton plug inserted. Bright orange-dyed cotton was used
to provide a background against which the whitish eggs were easily visible. Hypo-
chlorite (1.0 %) is introduced for 10 to 15 seconds, removed, and then distilled
water is introduced for 15 seconds. The short piece of glass tube containing the
surface sterilized eggs is then placed in the sterile box. The eggs are always visible,
and are easily removed with a brush.

The dimensions of the sterile box are not important. The floor is of glass, for
ease in swabbing with an antiseptic, and a bactericidal ultra-violet lamp is mounted
on the inside top. Elastic cuff sleeves should be used over both openings.

![Fig. 41](image1)

**Fig. 41.** Egg surface sterilization device. — **Fig. 42.** Sterile box.
**Fig. 43.** Detail of microscope fitting on the sterile box.

Glass culture tubes were used since plastic tubes could not withstand either
heat or chemical sterilization. The mushroom and lichen used were sterilized
in an autoclave or chemically with propylene oxide. Malt agar in stender dishes
was used to test the sterilized food and the surface sterilized specimens. Surface
sterilized eggs produced larvae that could walk around on the malt agar for hours.
without producing any fungal or bacterial growth. The malt agar dish remained clean for weeks after the larvae died. The aseptic larvae placed in the culture tubes with sterilized food would walk around for up to two days, but would not feed on any of the solid foods offered. Every larva so treated died without feeding. Aseptic larvae placed in a culture tube with a little growing fungal hyphae ate and continued to develop.

Premolt period tritonymphs were successfully surface sterilized, and when placed on the malt agar adults emerged. The tracks of the adult could be followed for the three days they wandered about and remained aseptic. This was also done with premolt deutonymphs. Since neither the tritonymphs nor adult can feed on the malt agar, no fecal pellets are voided, and no fungi develop. Premolt period individuals only have food in the midgut, and only more feeding in the next stage will push it through.

Placing of surface sterilized premolt deut and tritonymphs in aseptic cultures containing sterilized food resulted in adults and tritonymphs emerging and feeding upon the food provided. Pieces could be seen to be chewed off the sterilized food. Naturally, fecal pellets were voided shortly, and fungi grew freely in a short time.

It is concluded that larval *C. cisalpinus* must have fungal hyphae on which to feed upon hatching, but that nymphs and adults can survive very well with very little or none. Older larvae can ingest solid food, as evidenced by the appearance in older larvae of green and dark brown food boli. The outline of the gut can be seen through the cuticle of all immature stages, and the color of the food boli are clearly distinguishable. This color was a good indicator of the food consumed. The food bolus was white when the specimen was feeding upon the artificial diet, green when feeding on the lichen, dark brown on the mushroom, and whitish-yellow when feeding on fungal hyphae.

None of the species studies survived long on any of the animal tissue used. Using housefly maggots, it was found that *O. neerlandica* in all stages ate more than either of the other two species. *C. cisalpinus* ate the least, which was virtually none at all. Dead, soft mites and springtails were not eaten any more than the fly maggots. Even in combinations with other foods, the animal food was little eaten.

Vitzthum (1943) states that the parasitic hymenopteran *Polygnotes zosini*, which attacks the pupae of the ceccidomyid fly *Mayetica destructor*, is eaten in the pupae of the flies by *S. laevigatus*. It is most likely that the oribatid was feeding on fungi or exudates that result from decay, and may or may not have incidentally killed the hymenopteran with none too judicious use of its chelicerae. *S. laevigatus* and other oribatids superficially appear to be feeding on dead invertebrates, especially in Berlese funnel renderings, but are simply taking up the juices that result from decay.

The nutrition of *S. laevigatus* was the most difficult to study because of the secretive habits of the immature stages. The adults preferred and reproduced best on a mixture of mushroom and lichen when the fungal growth was kept down
by O. neerlandica. On mushroom or lichen alone, mortality was high and egg production poor. The artificial diet was only nibbled at, and the adults did not survive long on this alone. Immature S. laevigatus could only be successfully reared on mushroom, either alone or in combination with artificial diet or lichen. The combination of mushroom and lichen, with adequate numbers of O. neerlandica present, produced the greatest number of immatures per adult present.

O. neerlandica could not be reared on the artificial diet alone, but either mushroom or lichen alone provided a food upon which continuous generations could be cultured. Comparatively, a combination of mushroom and lichen was the most successful, while the mushroom alone was the least successful. The artificial diet added to either mushroom or lichen was eaten a little, but no improvement was noted. Fungal hyphae alone proved to be almost as successful a diet for O. neerlandica as the mushroom-lichen combination.

Living, feeding C. cisalpinus were examined under 90 × magnification in order to observe the action of the mouthparts on various foods. A fungal hypha is cut with the chelicerae and the end is conducted between the endites with the help of the palps into the oral orifice. The hypha is sucked in rapidly, and the mite moves along the hyphal strand. When enough is sucked in, the chelicerae clip it off, and the end disappears quickly into the mouth. The chelicerae and endites are used to scoop bits of either artificial diet or mushroom into a small pile. This small portion is pushed into the mouth cavity by the palps or forward body motion, and is quickly sucked in. Sometimes the entire gnathosoma is shoved into the food. The chelicerae nip into a piece of lichen once or twice, then seize a piece and pull it off. This piece is then worked between the endites, and shoved into the oral orifice by the palps. The lingula could never be seen in the feeding operation.

C. cisalpinus could be successfully cultured on either mushroom, lichen, or artificial alone, or upon any combination of the three foods. The best single food used was the artificial diet, and the life cycle (fig. 40) is based on individuals reared on this diet. Only 1/10th as many eggs were produced on mushroom or lichen alone as were produced on the artificial diet, though the duration of the life cycle is only slightly longer with mushroom or lichen. A mushroom-lichen combination was far better than either mushroom or lichen alone, but was not as good as artificial diet-mushroom or artificial diet-lichen combinations. With the artificial diet alone or in combinations with mushroom or lichen, egg production averaged almost 20 per female. On a mushroom-lichen combination about one half the eggs are produced that are produced on the artificial diet. With all of the above diets, more than 90 % of the eggs deposited would hatch, develop through the immature stages, and become adults. On a diet of fungal hyphae alone, only 10 % of the eggs that hatch would complete immature development to become adults. The adults that did develop were short lived, and never produced any eggs. The duration of the life cycle on fungal hyphae was more than twice that on the artificial diet, or about 70 days.
Lichen is preferred fresh by all three species, and rotten, moldy lichen is eaten only if nothing else is available.

Nutrition is definitely a factor in egg production and influences the duration of the life cycle. Some oribatids are quite specific in their food requirements, but others are not. Neither chlorophyll nor fungi were necessary to complete the life cycle, though \textit{C. cisalpinus} larvae needed fungal hyphae to feed on initially. The success of the artificial diet provides an opportunity to study more critically the nutritional requirements of free living mites.

It is the author's opinion that sod-inhabiting oribatids contribute to humus formation by direct consumption of fallen plants, eating and churning up of fungal decayed materials, and by eating and spreading the fungi. The relative importance of the oribatid's contribution compared to that of other animals cannot be determined at this time. Though fungi and bacteria are the most important contributors to humus formation in sods, (Waksman, 1952), oribatid mites may be considered among the most important animals. In various kinds of sod throughout the world, tremendous numbers of oribatids are found. Kates and Runkel (1948) calculated there were 9 million \textit{S. laevigatus} per acre in a pasture in North Dakota, and the author estimates this species at about 6 million per acre in a pasture in St. Paul, Minnesota. Many workers throughout the world have noted the large numbers of oribatids present in various kinds of sods.

\textit{Albinism.}

An interesting byproduct of the nutritional studies was the discovery of the occurrence of albinism in \textit{C. cisalpinus} (fig. 49). Actually albinism, which means lack of pigment, as it is found in this species appears to be mostly a lack of sclerotization. An albino immature stage lacks all sclerotization, even in legs and gnathosoma. The whole body appears almost glasslike, instead of the normal milky white. The legs are weak, often bending and movement is difficult and awkward. They are easily entrapped in fungi and water, and have great difficulty in molting. Extreme albinos never survive molting, since they cannot get out of the old cuticle. The setae, however, are still black. Albinism can become apparent in any immature stage, including just hatched larvae. It is progressive (fig. 49), but also reversible. Usually an individual is doomed when it becomes an albino, seldom reaching the adult stage; because, though all degrees of albinism are present, most albinism observed was extreme. Reversing from albino to normal took place only with immatures, but occurred in less than 5\% of all albinos produced. Only 1 to 2\% of the albino immature observed became adults, but these adults never deposited eggs or spermatophores and always died within 2 or 3 days after emergence. Figure 47 shows an albino and normal adult from the same egg batch. Both are four days old.

The very young larval albinos that occur may indicate maternal dietary deficiency. Generally, when albinism occurs not all of any one batch of eggs pro-
duces albino immature stages. The problem is that albinism could not be consistently produced deliberately. All sorts of minimal diets were tried to no avail. The two factors, not always together, that produced 80% of the albinoes were overcrowding and a diet of lichen alone for over one generation. Over 50% of all the albinoes observed occurred in overcrowded cultures, especially if that culture contained no artificial diet. Unfortunately, one or two albinoes would crop up inconsistently in other cultures also. Possibly, with manipulation of the artificial diet, albinism may be traced to a specific deficiency. However, it was impossible to determine at this time whether dietary deficiencies or genetics was more important in the occurrence of albinism.

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The Biology of Ceratozetes cisalpinus Berlese, Scheloribates laevigatus Koch, and Oppia neerlandica Oudemans (Oribatei), with a description of all stages.

Abstract.

All stages of Ceratozetes cisalpinus, Scheloribates laevigatus, and Oppia neerlandica are described and illustrated. At 25°C, about 95% relative humidity, and with what was found to be an optimum diet, O. neerlandica took 12 days, C. cisalpinus 24 days, and S. laevigatus 54 days to go from egg hatch to adult emergence. Under the above conditions and with the culturing methods used here, over 95% of all eggs deposited resulted in reproducing adults. Egg production, the microenvironment of the immature stages, growth and molting, movement and motion, natural enemies, and the bioclimatics of these three species were investigated. C. cisalpinus cerotegument formation was investigated. Water is postulated as the most important means of dispersal for sod inhabiting oribatids. The mechanics of C. cisalpinus spermatophoric reproduction, and the influence of various physical factors and the presence of both sexes on spermatophoric reproduction were investigated. Second batch egg deposition diapause in C. cisalpinus is suspected. Parthenogenesis was definitely proven in O. neerlandica. C. cisalpinus could be reared on an artificial diet, lichen, or mushroom; S. laevigatus on a mushroom-lichen combination; and O. neerlandica on fungal hyphae, lichen, or mushroom. By means of aseptic culturing, it was determined that newly hatched larvae of C. cisalpinus required growing fungal hyphae for initial feeding. Albinism occurred in C. cisalpinus, and its occurrence was partially correlated with overcrowded cultures.