SOME NOTES ON THE DISTRIBUTION AND ECOLOGY OF IRIDOVIRUS (IRIDOVIRUS, IRIDOVIRIDAE) IN TERRESTRIAL ISOPODS (ISOPODA, ONISCIDAE)

BY

H. WIJNHOVEN[1,3]) and M. P. BERG[2])

[1]) Groesbeeksedwarsweg 300, NL-6521 DW Nijmegen, The Netherlands

[2]) Section Soil Ecology, Department of Ecology and Ecotoxicology, Vrije Universiteit Amsterdam, De Boelelaan 1087, NL-1081 HV Amsterdam, The Netherlands

ABSTRACT

During an inventory of terrestrial isopods in the Ooypolder, east of Nijmegen, The Netherlands, terrestrial isopods infected with Isopod Iridescent Virus (IIV) or Iridovirus were collected. *Trichoniscus pusillus* was the most important host for Iridovirus; infected individuals and the focus of infection were found mainly between December and March. The symptoms and course of the disease, the route of infection, and the distribution of the virus are discussed. A number of isopod species, *Hyloniscus riparius*, *Trichoniscoides helveticus*, *T. albidus*, *Androniscus dentiger*, *Haplophthalmus mengii*, *H. danicus*, *Oniscus asellus*, and *Porcellio spinicornis* are added to the list of species known to be infected with Iridovirus.

RÉSUMÉ

Au cours d'un inventaire des isopodes terrestres d'un polder (Ooypolder), à l'est de Nimègue, Pays-Bas, des isopodes terrestres infectés par l'iridovirus (Isopod Iridescent Virus (IIV)) ont été récoltés. *Trichoniscus pusillus* était l'hôte le plus important pour l'iridovirus; des individus infectés et le foyer de l'infection ont été trouvés principalement entre décembre et mars. Les symptômes et le déroulement de la maladie, le chemin de l'infection et la répartition du virus sont discutés. Un certain nombre d'espèces d'isopodes, *Hyloniscus riparius*, *Trichoniscoides helveticus*, *T. albidus*, *Androniscus dentiger*, *Haplophthalmus mengii*, *H. danicus*, *Oniscus asellus* et *Porcellio spinicornis* sont ajoutées à la liste des espèces connues comme étant infectées par l'iridovirus.

INTRODUCTION

An Iridovirus (Iridovirus, Iridoviridae) was isolated from terrestrial isopods in 1980 and named after its host: Isopod Iridescent Virus (abbreviated IIV)

[3]) Corresponding author.

(Federici, 1980; Cole & Morris, 1980). The type-species of Iridovirus was isolated by Xeros in 1954 from larvae of the cranefly *Tipula paludosa* Meigen, 1835. Different types of Iridovirus have been reported for other insects since, mainly larvae of Diptera, Coleoptera, and Lepidoptera (Kelly & Robertson, 1973; Carey et al., 1978). The occurrence of Iridovirus is, however, not restricted to the Insecta and has been recorded in other arthropods, for instance in Chilopoda (Ohba & Aizawa, 1979) and Diplopoda (Hopkin & Read, 1992). Iridescent viruses have been found in several phyla of invertebrates, including molluscs and annelids, and in Protozoa (Devauchelle & Durchon, 1973; Fenner, 1976). Several crustaceans have been found to contain Iridoviruses. Also in decapod Crustacea (crayfish, lobsters, anomurans, and crabs) blue specimens have been reported (Holthuis, 1965, 1975; Federici & Hazard, 1975).

Little is known about the geographical distribution, the ecology, and epidemiology of IIV in natural populations of terrestrial isopods. Therefore, during a period of one-year and a half, terrestrial isopods infected with IIV were observed in the Ooypolder near Nijmegen, the Netherlands. Notes were taken on the ecology of IIV and the fate of infected animals was followed.

SYMPTOMS OF INFECTED ISOPODS AND COURSE OF THE DISEASE

Isopods infected with IIV are easily distinguished from healthy isopods or from those infected with other parasites or pathogens. The diagnosis is unmistakable: in time, infected animals change colour strongly. They become light blue to violet and are apparently totally covered with a pearl-shell glow. This symptom gives this group of viruses its name: Isopod Iridescent Virus. The discolouration originates from light reflection by para-crystalline virus particles in the tissue cells (Federici, 1984). Although the actual occurrence of IIV in the sampled isopods was not established in itself, we may assume that purple-blue coloured isopods are infected with IIV. According to Federici (1984) the blue colour can be taken as near-definitive evidence of Iridovirus infection.

To follow the development of the disease in time, slightly blue-coloured individuals of *Trichoniscus pusillus* Brandt, 1833 were sampled and kept in plastic containers under natural conditions. The visible development of IIV was followed daily. The first sign of IIV infection is a blue bloom on the unpigmented ventral side of the animals. The discolouration moved slowly to the dorsal, pigmented side of the isopods and clear light-blue to violet spots appeared locally on the epimera, the sides of the pleonites, the backside of the pereionites, and on the head.

In the next phase, the natural red-brown body pigment in the chromatophores of *T. pusillus* aggregated into dark patches. This forms the typical reticulate structure where unpigmented patches mark the attachment of muscle fibers. Thereafter the colour of the individuals changed to completely iridescent blue-violet. In the field this colour contrasted sharply to the dark colour of the soil. It seemed that, due to a high virus content, the cells responsible for the formation of body pigment lose their function followed by the disappearance of the typical, reticulate chromatophores. Besides various groups of cells and organs, the epidermic cells also became infected. The amount of discolouration and depigmentation was highly variable between individuals. The discolouration to blue was more pronounced in dry soil, presumably since, due to desiccation of the animals, the virus was aggregated in a smaller body volume resulting in a stronger discolouration.

In a more advanced stage the virus was also present in the cytoplasm of the hepatopancreas and, due to the rapid multiplication of virus particles, the animals eventually died. Some individuals had so much virus in the haemocoel that the decomposing animals showed a dark-blue haemocoel. Infected animals that were sampled alive all showed the described course of disease, although some animals died before the symptoms were fully developed. When the disease developed fully, pale light-blue patches in the center of the first four body segments were shown, at the location were the lobes of the hepatopancreas are situated. These animals stiffened and died a few days later. Their body was slightly curved downwards as a consequence of oedema (fig. 1). This could be seen dorsally, where the membranes between the tergites became visible. This array of symptoms was observed regularly.

During infection the behaviour of the animals changed: at the beginning of the infection individuals of *T. pusillus* seemed to behave normally with regard to stimuli, like light, touch, and water contact, although their movement in the field seemed to be slower in comparison to healthy animals. Heavily infected animals showed a decrease in phototactic response and/or no response at all when brought into contact with water. The amount of faeces produced by infected individuals was less than for healthy animals, suggesting a decreased food consumption. These increases in the stress levels of the animals resulted in accelerated death.

Longevity of infected individuals of *Trichoniscus pusillus* was followed. On an average they lived 32.8 ± 22.6 days ($N = 10$); the first died after 2 days, the last after 64 days at a temperature regime of 11.3 and 5.6°C during day and night, respectively. The observed longevity is much longer then reported by Federici (1980) who found for field collected infected animals of *Armadillidium vulgare* (Latreille, 1802) and *Porcellio dilatatus* Brandt, 1833, survival times of 9.1 and 4.5 days, respectively. In a separate study, Federici (1980) injected uninfected

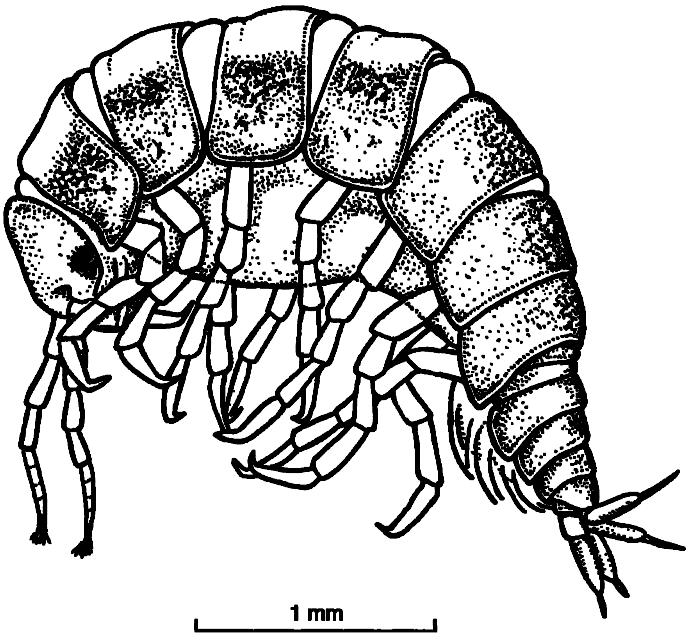

Fig. 1. Habitus of a dead IIV infested female of *Trichoniscus pusillus* Brandt, 1833, from the Ooypolder near Nijmegen, the Netherlands (UTM-coordinates 31 U GT 02 48), with characteristic oedema, stiffening of the body, and central white patch on the first four body segments (drawing H. Wijnhoven).

isopods with a culture of pure virus. Discolouration was noticed after 11 and 14 days for *A. vulgare* and *P. dilatatus*, and after the first sign of discolouration the animals died 17 and 20 days later, respectively. The whole cycle from infection to mortality was completed with 31 days. The length of the cycle seems to depend on temperature, as infected animals of *T. pusillus* lived longer during winter than in summer.

In contrast to infected animals, healthy individuals of *T. pusillus* all formed marsupia and reproduced. In November, an infected female of *Ligidium hypnorum* (Cuvier, 1792) was collected that had produced a marsupium. The oostegites were wide, maybe this female was infected after the marsupium was formed while eggs or embryos might have been resorbed. An infected female with a developed marsupium was also collected in the field for *T. pusillus*, as well as two females with developing oostegites.

TERRESTRIAL ISOPODS ACTING AS HOSTS FOR IIV

A list of species known to be infected with IIV, together with geographical locations, is presented in table I. Seven additional species of terrestrial isopods, of

which the occurrence of infection with IIV was not known previously, are added to this list: *Hyloniscus riparius* (Koch, 1838), *Trichoniscoides albidus* (Budde-Lund, 1880), *Trichoniscoides helveticus* (Carl, 1908), *Androniscus dentiger* Verhoeff, 1908, *Haplophthalmus mengii* (Zaddach, 1844), *H. danicus* Budde-Lund, 1880, and *Porcellio spinicornis* Say, 1818. As the virus does not seem to be species specific or even order specific, this list probably is a poor representation of the real number of species which act as hosts for IIV.

In the older literature some blue coloured 'species' or 'varieties' were described which were almost certainly animals infected with IIV. Schöbl (1861) described *Trichoniscus violaceus* from Bohemia, Vandel (1960) described a variety, *T. pusillus* var. *violaceus*, and mentioned that this "variety seems to be very common on the British Isles". Probably in both cases it is *T. pusillus pusillus* or *T. pusillus provisorius.* Vandel (1960) found an amethyst-coloured female of *T. pusillus alticola* in France. The same author published a variety of *Ligidium hypnorum*, *L. hypnorum* var. *coeruleum* or *L. hypnorum* var. *amethisticum* and mentioned that "a blue or violet colour is regularly seen in certain individuals of *L. hypnorum*".

In all probability IIV has an extensive geographical distribution being found in Africa, North America, and Europe (table I). Although little attention has been paid to IIV in the Netherlands, IIV infected isopods are known from many locations (especially *Porcellio scaber* Latreille, 1802, often in gardens).

THE OCCURRENCE OF IIV IN A DUTCH POLDER

The distribution and ecology of terrestrial isopods was studied in the Ooypolder and records on IIV infected isopods were collected in 1993 and 1994 (Wijnhoven, in prep.). The Ooy is an old clay polder situated along the river Waal. On the south side the polder is bounded by a lateral moraine deposited during the second last ice-age and on the north and west side by the river Waal (fig. 2). A winter dike divides the polder into two parts. The river foreland lays north of the dike, between the dike and the river, and is flooded on an average once a year. The remaining part of the polder is situated between the dike and the lateral moraine.

In the area under investigation IIV is wide-spread in the polder, with *Trichoniscus pusillus* being the most important host, but it is absent from the river foreland and the moraine (fig. 2). Only two species of terrestrial isopods are common in the river foreland, *Hyloniscus riparius* and *Trachelipus rathkii* (Brandt, 1833) and the chance of the two species being infected by *T. pusillus* is low.

Usually only a single infected individual of *T. pusillus* was observed at a site, while in some cases it was possible to locate more infected individuals in the

TABLE I

A list of terrestrial isopods from which infection with IIV is recorded; listed species without references have been recorded by the authors; * = 'species' and 'varieties' described in older literature which are certainly species infected with IIV

Species	Geographic location	Reference	Remarks
Ligidium hypnorum (Cuvier, 1792)	France	Lereboullet (1843, 1853)	var. *coeruleum*
	Europe	Schöbl (1861)	var. *amethystinum*
	Czechoslovakia	Fric (1872)	var. *amethystinum*
	USSR	Semenkeivitsch (1931)	var. *coeruleum*
	France	Legrand (1948)	var. *coeruleum*
	The Netherlands		Several locations
Trichoniscus pusillus Brandt, 1833	Czechoslovakia	Schöbl (1861)	var. *violaceus*
	England	Norman & Brady (1911)	var. *violaceus*
	England	Standen (1917)	var. *violaceus*
	England	Sutton (1972)	var. *violaceus*
	The Netherlands		Several locations
Hyloniscus riparius (Koch, 1838)	The Netherlands		
Trichoniscoides albidus (Budde-Lund, 1880)	The Netherlands		
Trichoniscoides helveticus (Carl, 1908)	The Netherlands		
Androniscus dentiger Verhoeff, 1908	England		Several locations
Haplophthalmus mengii (Zaddach, 1844)	The Netherlands		
Haplophthalmus danicus Budde-Lund, 1880	The Netherlands		
Oniscus asellus Linnaeus, 1758	England	Hopkin (1992)	
Philoscia muscorum (Scopoli, 1763)	England	Standen (1917)	var. *violaceum*
	England	Collinge (1918)	var. *violaceum*
	France	Vandel (1962)	var. *violaceum*
	The Netherlands		Several locations
Mauritaniscus littorinus (Miller, 1910)	California	Schultz et al. (1982)	

TABLE I
(Continued)

Species	Geographic location	Reference	Remarks
Armadillidium vulgare (Latreille, 1802)	Turkey	Ermin (1943)	
	Texas	Hess & Poinar (1985)	
	California	Federici (1980)	
	California	Cole & Morris (1980)	
	California	Schultz et al. (1982)	
	The Netherlands	Hess & Poinar (1985)	
	The Netherlands	Poinar et al. (1985)	
	Virginia	Hess & Poinar (1985)	
	The Netherlands		Several locations
	California	Grosholz (1993)	
Cylisticus convexus (De Geer, 1778)	Virginia	Schultz et al. (1982)	
Porcellionides pruinosus (Brandt, 1833)	California	Schultz et al. (1982)	
Porcellio laevis Latreille, 1802	California	Schultz et al. (1982)	
	California	Grosholz (1992, 1993)	
Porcellio spinicornis Say, 1818	The Netherlands		
Porcellio dilatatus Brandt, 1833	California	Federici (1980)	
	California	Hess & Poinar (1985)	
	California	Grosholz (1993)	
Porcellio scaber Latreille, 1802	California	Cole & Morris (1980)	
	California	Schultz et al. (1982)	
	The Netherlands	Poinar et al. (1985)	
	California	Grosholz (1992, 1993)	
	The Netherlands		Several locations
Trachelipus rathkii (Brandt, 1833)	Virginia	Schultz et al. (1982)	
	The Netherlands		Several locations

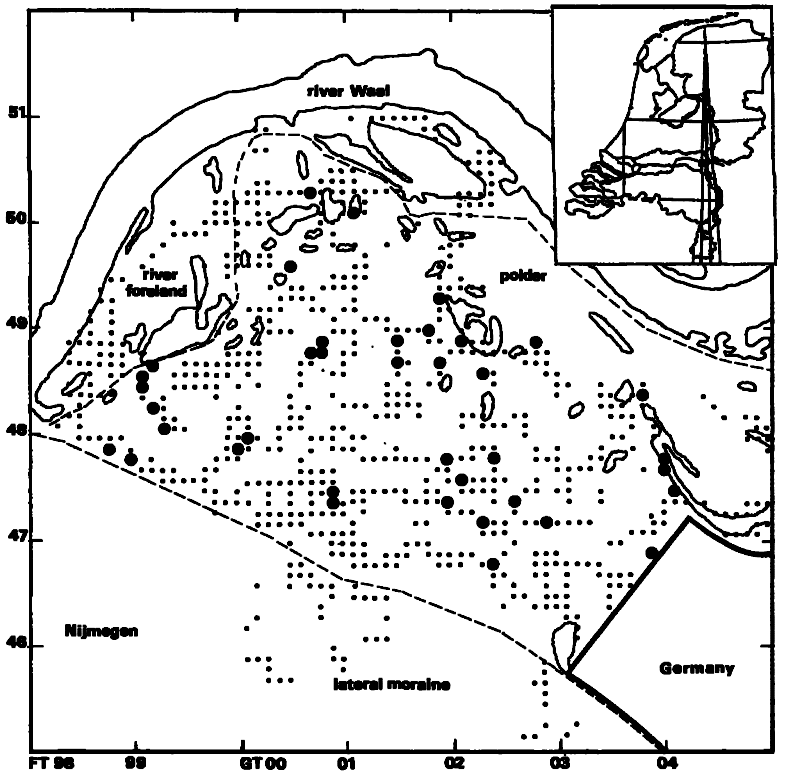

Fig. 2. Map of the research area with UTM-coordinates. The dots represent the sampling sites: small dot, no IIV infection; large dot, IIV infection.

vicinity. In this case we speak of a focus of infection. The sites with a high degree of infected individuals were mostly small in area (on the average 1 dm^2) and strongly bounded. In several cases they were found in mole-hills, with a high density of *T. pusillus*. At one site eight infected individuals were found alongside a ditch over a distance of 4 meters, while at the bottom of the ditch fifteen individuals could be observed over 3 dm^2 organic matter. At another site, with a small population of *T. albidus*, a significant focus of infection over a surface area of 5 m^2 was localized. At this particular site one-third of the population of *T. pusillus* was visually infected with the virus. Five other infected species were found as well: *Ligidium hypnorum*, *Trichoniscoides albidus*, *Haplophthalmus danicus*, *Trichoniscoides helveticus*, and *Oniscus asellus*. The virus has had a hold at this site for months, from April 1993 to February 1994. In July the infection had disappeared but within 20 meters five new focuses of infection were observed.

In the Ooypolder, 77.2% of all infected animals was collected in the months December to April (table II). This is in agreement with data collected by Federici

TABLE II

Total numbers of individuals with observed IIV infection per month, for seven species of terrestrial isopods in the Ooypolder near Nijmegen. The species names are abbreviated as follows: L.hyp., *Ligidium hypnorum*; H.rip., *Hyloniscus riparius*; T.pus., *Trichoniscus pusillus*; T.hel., *Trichoniscoides helveticus*; T.alb., *Trichoniscoides albidus*; H.men., *Haplophthalmus mengii*; and O.ass., *Oniscus asellus*

	L.hyp.	H.rip.	T.pus.	T.hel.	T.alb.	H.men.	O.ass.	Individuals total	Species total
January	2	1	13	–	–	–	–	16	3
February	1	1	11	1	–	–	–	15	4
March	–	2	24	1	–	–	–	27	3
April	1	–	8	–	–	–	–	9	2
May	–	1	1	–	–	–	–	2	2
June	–	–	12	–	–	–	–	12	1
July	1	–	4	–	–	–	–	5	2
August	–	–	3	–	–	–	–	3	1
September	–	–	–	–	–	–	–	–	0
October	–	–	2	–	–	–	–	2	1
November	1	–	1	–	–	–	–	2	2
December	3	–	11	–	1	4	2	21	5

(1980) who found most infected individuals between January and March, the coldest and wettest months in southern California. Federici (1980) mentions that, from an apparently healthy population of *Armadillidium vulgare* and *Porcellio dilatatus*, 5% and 45% of the individuals, respectively, were infected with the virus and developed the symptoms of the disease. From these results it appears that estimates of the amount of infected individuals based on blue discolouration alone give a substantial underestimation.

DISCUSSION

Transference of IIV between isopods

The transfer mechanisms for IIV in free-living populations between infected and uninfected individuals is insufficiently known. The isopod *Porcellio scaber,* when infected with virus through injection or by feeding on infected material, developed the disease within 7-12 days (Cole & Morris, 1980). After 11-16 days of injection with virus, *Porcellio dilatatus* and *Armadillidium vulgare* showed discolouration, while 11 days later the first individuals died (Federici, 1980). Cole & Morris (1980) suggest the possible transfer of virus via small wounds or through feeding on infected isopods. Other food sources, like dead soil organisms and faeces, might also cause infection. It is not known if coprophagy of isopod faeces is an important source of infection. Healthy individuals of *Trichoniscus*

pusillus fed with algae and faeces of infected individuals showed no infection. This could either be due to the absence of virus in the faeces or to the digestion of the virus by uninfected animals.

It would be interesting to study the faeces of isopods for the occurrence of IIV. The same applies for the faeces of small insectivore mammals, like shrews and hedgehogs. Transference of virus from males to females via spermatozoids also is a possibility, although in a parthenogenetic species like *T. pusillus* this plays no role. In the Ooypolder the effect of IIV on the population dynamics of terrestrial isopods seems of no importance. In summer IIV seemed to balance on the edge of extinction. The type of landscape, soil texture and water content, the amount of isolation of subpopulations, abundances and competition for food, are factors which could influence the distribution of Isopod Iridescent Virus.

The hosts

The present list of terrestrial isopods acting as a host for Iridescent Virus is far from complete and no doubt more infected species will be discovered. The possibility of an individual becoming infected with IIV seems to be a summation of chances. Not coincidentally IIV infection is found in species with a preference for humid habitats. According to Federici (1984) fluctuations in moisture seem necessary for infection. This explains the high occurrence of infection by *Porcellio scaber* in gardens which are periodically sprayed with water and show a strong fluctuation in soil moisture. The second criterion is the occurrence of a high population density of isopods.

The number of infected individuals is high in winter and early spring. Low temperatures and frost decrease the number of possible hiding places, animals aggregate in the remaining suitable places in high densities, and food availability decreases. Infected food, such as faeces or dead animals, might be an important transfer source. Consumption of this kind of food might explain the spreading of the virus infection among populations in winter. Infection, incubation, and distribution of the virus take time, and as a consequence the epidemic shifts to spring.

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