

## ENGLISH TRANSLATION

This translation is intended to act as a supplement to the Dutch publication, to which reference should be made for photographs and figures. Page numbering is specific to the English version. To speed access, to species descriptions, these are included in the index on page 3 & 4. (See page 117 in the Dutch Version).

# De Nederlandse hooiwagens (Opiliones)

Hay Wijnhoven



3  
2009

ENTOMOLOGISCHE TABELLEN

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## Table of Contents

<b>INTRODUCTION</b> .....	2
CHARACTERISTICS OF HARVESTMEN .....	2
GROUPS SIMILAR TO HARVESTMEN .....	3
PREVIOUS PUBLICATIONS .....	3
<b>BIOLOGY</b> .....	3
LIFE CYCLE .....	3
MATING AND EGG-LAYING .....	4
FOOD .....	4
DEFENCE.....	4
PHORESY, PARASITES AND PREDATORS .....	5
DISTRIBUTION .....	5
<b>HABITATS</b> .....	6
<b>STUDY</b> .....	7
FIELD OBSERVATIONS .....	7
HANDLING .....	7
COLLECTING .....	7
STORAGE AND DISSECTION.....	8
PHOTOGRAPHING .....	8
<b>BODY PLAN</b> .....	8
CEPHALOTHORAX.....	8
ABDOMEN .....	9
JUVENILE OR ADULT?.....	10
MALE OR FEMALE?.....	10
<b>SYSTEMATIC REVIEW</b> .....	11
<b>HOW TO USE THE KEY</b> .....	13
LENGTHS.....	13
COLOUR.....	13
GEOGRAPHICAL AREA COVERED.....	13
<b>IDENTIFICATION KEY</b> .....	14
<b>SPECIES ACCOUNTS</b> .....	18
<i>Nemastoma bimaculatum</i> .....	18
<i>Nemastoma lugubre</i> .....	19
<i>Nemastoma dentigerum</i> .....	20
<i>Paranemastoma quadripunctatum</i> .....	21
<i>Mitostoma chrysomelas</i> .....	22
<i>Trogulus tricarinatus</i> .....	23
<i>Trogulus nepaeformis s.l.</i> .....	24
<i>Anelasmacephalus cambridgei</i> .....	25
<i>Ischyropsalis hellwigi</i> .....	26

<i>Phalangium opilio</i> .....	27
<i>Opilio parietinus</i> .....	28
<i>Opilio saxatilis</i> .....	29
<i>Opilio canestrinii</i> .....	30
<i>Platybunus pinetorum</i> .....	31
<i>Megabunus diadema</i> .....	32
<i>Rilaena triangularis</i> .....	33
<i>Lophopilio palpinalis</i> .....	34
<i>Oligolophus tridens</i> .....	35
<i>Oligolophus hanseni</i> .....	36
<i>Paroligolophus agrestis</i> .....	37
<i>Lacinius horridus</i> .....	38
<i>Lacinius ephippiatus</i> .....	39
<i>Odiellus spinosus</i> .....	40
<i>Mitopus morio</i> .....	41
<i>Dicranopalpus ramosus</i> .....	42
<i>Homalenotus quadridentatus</i> .....	43
<i>Astrobunus laevipes</i> .....	44
<i>Leiobunum limbatum</i> .....	45
<i>Leiobunum rotundum</i> .....	46
<i>Leiobunum blackwalli</i> .....	47
<i>Leiobunum rupestre</i> .....	48
<i>Leiobunum sp. A</i> .....	49
<i>Nelima sempronii</i> .....	50
<i>Nelima doriae</i> .....	51
<b>APPENDIX I. Glossary</b> .....	<b>52</b>
<b>Legends to Figures</b> .....	<b>54</b>

**NOTE: Page numbering** – ‘p.16’ refers to a page in the original work whereas ‘Tp.16’ refers to a page number in this translation.

## FOREWORD

Members of the British Arachnological Society's Harvestman Recording Scheme (HRS) were so impressed with the quality of Hay Wijnhoven's *De Nederlandse Hooiwagens (Opiliones)* that it was felt an English translation was highly desirable. This would greatly enhance the available literature for identifying these most interesting creatures in Britain and also aid the detection of future introductions from the continent.

After discussions with the author and the British Arachnological Society (BAS), the organisation under which the HRS operates, it was agreed to seek a grant from The Open Air Laboratories (OPAL) to fund a translation. This was successfully achieved by Mike Davidson whose hard work is much appreciated. With the OPAL grant and funding from the BAS the task of translation and editing was shared by Hay Wijnhoven, Jinze Noordijk (the current coordinator of the Opiliones study group of EIS-Netherlands) and myself. Thanks also to Geoff Oxford and Helen Smith for support and proof reading.

The cost of producing an English version as an independent publication was considered to be too expensive so it has been designed as a supplement to the Dutch publication. All diagrams, photographs and bibliography are referenced directly to the original. The object being that the original must be purchased and that the supplement is made available to those requiring it in English.

It would be interesting to compare our findings in Britain with those described in this publication, and to this end I would very much welcome feedback. Of particular importance is to ascertain how quickly introduced species adapt to their new conditions, how fast they spread and to what extent, if any, they interact with our native species.

I hope this is a successful venture, not only in broadening our knowledge of harvestmen and the sharing of this with our Dutch colleagues, but also in stimulating renewed interest in the ecology and distributions of species in Britain. Many thanks go to the author, EIS-Netherlands, OPAL and the BAS for their support in bringing this project to fruition.

Peter Nicholson  
Harvestmen Recording Scheme Organiser  
October 2014



## INTRODUCTION

Harvestmen are known in Holland colloquially as ‘balls on stilts’ or ‘shepherds on stilts’ (Figs 1-4). They are as commonly seen in gardens and on walls of buildings as in nature reserves. But for most people, their knowledge of this group stops here. What harvestmen do exactly, and how many species there are, is often unknown. This is disappointing given the diverse and interesting way these creatures live. There is much still to be discovered about this group, even in the Netherlands: small species hide under bark and mysterious giant species have invaded the country in recent years.

Harvestmen form an order within the class Arachnida. Globally, around 6,000 species have been described. Estimates of the true number of species suggest about 10,000. Harvestmen are therefore the third largest order within the Arachnida, after the mites (Acarina) and spiders (Araneae). In central- and northwest-Europe, around 110 species occur, of which 30 are found in the Netherlands.

The oldest fossils of harvestmen originate from the early Devonian, around 400 million years ago. Back then, species lived that are more or less comparable to the species found today. Because of the lack of older fossils phylogenetic relationships with other arachnids are largely unknown. A combination of DNA-analyses, comparative morphological research and paleontological studies has recently indicated that harvestmen are more closely related to scorpions (Scorpiones), pseudoscorpions (Pseudoscorpiones) (Fig. 5) and Solifugae than to spiders.

The Dutch name ‘hooiwagens’ [hay wagons] is probably derived from the fact that many species reach adulthood, and are thus conspicuously present, around September during hay-making. In Germany they are called ‘Weberknechte’ [weavers' servants], in the UK ‘harvestmen’ or ‘harvest spiders’, and in the USA and Australia ‘daddy longlegs’ (a name that is used in the UK for Tipulidae). The scientific name, Opiliones, is derived from the genus *Opilio* (Latin for shepherd). In ancient Roman times, herdsmen walked on stilts to have an overview of their herd.

Although harvestmen are known to many biologists and entomologists, their distribution over the country is not thoroughly studied. The main cause – derived from a traditional lack of interest in this group – is the absence of a recent identification key. This publication gives an overview of the 30 species that are found in the Netherlands. After the species list, an identification key and species descriptions are provided, with information on habitat and occurrence in the Netherlands. I hope that this guide will stimulate research on this interesting animal group and will lead to a better understanding of the species distribution, biology and ecology. Hopefully, this will also help to better protect the most vulnerable species.

## CHARACTERISTICS OF HARVESTMEN

When people think about harvestmen, the image of a ‘ball on stilts’ emerges: small round bodies that flee quickly on long thin legs. There are, however, those that do not meet this description at all (Figs 1-4). One of the characteristics of the Class Arachnida, to which harvestmen belong, is their eight legs. This is the main characteristic separating them from insects and other invertebrates. The Order of harvestmen is characterised by the following combination of features:

- four pairs of legs;
- cephalothorax and abdomen are unified over the entire body;
- presence of an ocularium on the cephalothorax;
- presence of internal sexual organs.

## GROUPS SIMILAR TO HARVESTMEN

Harvestmen are mainly confused with spiders (Araneae), especially with the indoor species *Pholcus phalangioides* (Fig. 6). The most obvious difference is the absence of a constriction between the cephalothorax and abdomen in harvestmen. Spiders have spinnerets and poison glands, which are also lacking in harvestmen. Additionally, spiders have six or eight eyes, while harvestmen only have two. Some species of large mites (Acari) may look like harvestmen, because the cephalothorax and abdomen are fused (Fig. 7) but they lack the ocularium which harvestmen have.

## PREVIOUS PUBLICATIONS

There has not been a great deal written about harvestmen in the Netherlands. Loman (1900) mentions nine species. Ger Spoek made important contributions to the current knowledge of this group. He mentions 19 species in 'De hooiwagens van Nederland' (Spoek 1964), a publication based on his article in *Zoölogische Verhandelingen* (Spoek 1963). In a second, revised print of his identification key Spoek (1975) added *Nemastoma dentigerum* and *Ischyropsalis hellwigi*. Since then, several authors have recorded the presence of nine other species: *Nemastoma bimaculatum* (Van der Hammen 1983, Wijnhoven & Koomen 1997), *Opilio canestrinii* (Van der Weele 1993), *Dicranopalpus ramosus* (Cuppen 1994, Noordijk *et al.* 2007), *Platybunus pinetorum* (Wijnhoven 1998b), *Trogulus nepaeformis* s.l. (Wijnhoven 1998a, 1998b), *Astrobinus laevipes* (Wijnhoven 2003), *Nelima sempronii* (Wijnhoven 2005a), *Nelima doriae* (Wijnhoven 2007) and *Leiobunum* sp. A (Wijnhoven 2005b, Wijnhoven *et al.* 2007).

## BIOLOGY

### LIFE CYCLE

Harvestmen moult seven or eight times between hatching from their eggs and reaching adulthood. The young animals closely resemble the adults in form, but the legs are relatively short. During moulting the exoskeleton bursts open on the dorsal-side, so that the body can emerge. With the pedipalps and chelicerae, the legs are pulled out of the old exoskeleton (Fig. 8). In most cases, the old exoskeleton remains for some time attached to the last sternite. Sometimes, individuals with this exuvium can be found in the field (Fig. 9). After moulting, harvestmen are vulnerable; the new exoskeleton needs to harden and reach its true colour (Fig. 4).

**Stenochronous species.** Most harvestmen have a life cycle of one generation per year (univoltine). The reproduction is stenochronous, which means that it occurs within a limited period. The eggs are laid in autumn or the beginning of winter, and they hatch in spring. In these species, the egg-period is relatively long and the juvenile period relatively short. After seven or eight moults, they are fully grown; dependent on the species, this can be from June to August onwards. After egg-laying the females die. This is due to exhaustion, lack of food, predation, diseases or cold periods; the number of individuals decreases in autumn. Periods of slight frost can be withstood, but when temperatures reach 5° C below freezing point most individuals die. In mild winters, several species can survive to the end of December and occasionally adults can be found until the end of February (Wijnhoven 2006).

*Platybunus pinetorum* and *Rilaena triangularis*, although having a stenochronous reproduction cycle, overwinter as juveniles (Fig. 10). The egg stage in this case is short in comparison to the long juvenile period. The adults appear from April until July. At the beginning of July, the eggs are laid and the animals die. In August, the new juveniles appear.

A new species to the Netherlands, *Nelima doriae*, has a unique life cycle. Juveniles overwinter, maturing in March, and give rise to a second generation in autumn. *Nelima doriae* is the only multivoltine (more than one generation per year) species in our country. The generations overlap, so that juveniles can be found all year round.

**Eurychronous species.** Within the Troglidae and Nemastomatidae, adults can be found all year. They have one generation per year, but reproduction is eurychronous, which means that it is not limited to a certain period in the year. Members of this family live approximately two years, so generations overlap. *Homalenotus quadridentatus* and *Astrobonus laevipes* (both belonging to the Sclerosomatinae (Phalangiidae)), are eurychronous as well. They apparently live up to 15 months.

The phenological data on Dutch harvestmen are summarised in Figure 11.

## MATING AND EGG-LAYING

Harvestmen are probably the first group within the invertebrates where internal fertilisation evolved by means of a sperm transferring apparatus, the penis, and a sperm storage and egg laying organ, the ovipositor (Pinto-da-Rocha *et al.* 2007). Since both sexes can mate several times, this group forms the ideal organism for studying sexual evolution. Harvestmen mate frontally, head-to-head (Figs 12-13). The male grasps the female with the pedipalps. This may go together with courtship rituals. The penis is pushed forward between the pedipalps and chelicerae of the female, under her genital plate, and into her ovipositor. Sperm cells are deposited in the seminal receptacles (storage organs in the tip of the ovipositor; Fig. 50) and can stay there viable possibly for months (Juberthie 1964). The eggs are only fertilised when they are laid and thus move through the ovipositor (Pinto-da-Rocha *et al.* 2007, Wijnhoven 2008a). Eggs are laid in multiple clusters under bark, in the soil, in moss or in dead wood. Troglidae are different, in that they mate in a belly-to-belly position and lay their eggs in empty snail shells. It is of note that snails form their main food source.

## FOOD

Harvestmen are nocturnal predators that hunt for all sorts of invertebrates such as earthworms, insect larvae, flies, mosquitoes, isopods, springtails, mites, spiders and other harvestmen (Fig. 14; Adams 1984, Bristowe 1949, Halaj & Cady 2000, Phillipson 1960a, 1960b). They use the ambush technique for hunting. They wait until a potential prey appears and try to catch it with their chelicerae, pedipalps and legs. Harvestmen have no poison glands, so they usually start eating while the prey is still alive. The prey is cut or torn into pieces and eaten with the chelicerae.

The Troglidae are specialised snail eaters and eat their way into a snail without damaging the shell. *Ischyropsalis hellwigi* is also a snail-eating specialist, but it is able to break the shell with its formidable chelicerae. Many harvestmen species also eat all sorts of carrion, faeces (of birds), sugary substances (rotting or over-ripe fruit) and living or dead plant material.

## DEFENCE

A simple strategy that harvestmen use, so as not to be noticed during the day, is to choose a suitable resting place on a tree trunk, on a wall, in shrubbery, or in the litter layer. They often position themselves in a characteristic way and stay still all day (Figs 15-18, 282). Many species have excellent camouflage (Fig. 19). The Troglidae and Sclerosomatinae (Phalangiidae) excrete a sticky substance by which soil, litter and clay particles may become attached to the body. Camouflaged like this, they can barely be found on or in the soil.

The soil-dwelling Trogulidae, Sclerosomatinae (Phalangiidae) and Nemastomatidae freeze upon disturbance in a typical position, pretending to be dead (thanatosis) (Figs 20-24). *Nemastoma* species fold their legs up against their body (Fig. 24). They easily roll away amongst the leaf litter and thus may escape predators (and researchers). Other species also pretend to be dead for some time after disturbance, like *Paroligolophus agrestis* and *Odiellus spinosus* (Fig. 22-23).

The glands that excrete a stinking substance (see Body Plan, p.21, Tp.8) are apparently used to repel other invertebrates (Machado *et al.* 2005). The chemical composition of the volatile components is very diverse (e.g. ketones, alkylphenols and even nicotine). Some people appear to be able to smell these strange odours.

*Leiobunum* species may form large clusters (Figs 33-34). Possibly this behaviour serves as a defence mechanism, perhaps because the combined effects of the stinking substances is better protection against predators (such as spiders).

When threatened, *Leiobunum* species start shaking, a phenomenon called 'bobbing'. The animal moves so fast that the body is probably unrecognisable and uncatchable to predators. Some Phalangiidae have another strategy when disturbed: they drop from their location to safety, or they run away. It is amazing to see how agile and fast they can be when moving through vegetation on their long legs. An example is *Leiobunum blackwalli* which uses its long prehensile-like tarsi to grasp the vegetation like a monkey's tail. When catching a harvestman, the legs break off easily. Each leg has spiracles, openings enabling it to breathe, and can keep on twitching for a long period after detachment. This distracts attention from the animal itself. Legs that are detached do not grow back. At the end of the season, more and more individuals can be found that are missing one, two or more legs. They do not seem to be hampered by this very much. However, individuals that have lost the second pair of legs, which are important for sensing their surroundings, have lost much of their ability for orientation.

## PHORESIS, PARASITES AND PREDATORS

Some less mobile invertebrate species make use of the fact that harvestmen can move considerable distances. They catch a lift with the harvestmen by holding temporarily on to the body, a leg or pedipalp. This phenomenon occurs in many animal groups and is called phoresis. Well known examples of this involve pseudoscorpions. A harvestman with a pseudoscorpion on its leg has even been found in amber of 40 million years old. There is not much known about phoretic mites on harvestmen.

There are several internal parasites known for harvestmen, including Nematoda, Trematoda and Mermithida (Pinto-da-Rocha *et al.* 2007). Certain fungi can also be harmful (Fig. 25). The most conspicuous external parasites are mites (Acari) belonging to the family Erythraeidae, Trombiidae and Trombiculidae, especially species from the genus *Leptus* (Erythraeidae), which are common. These small, bright red mites drill their mandibles in the body or leg of their host (Fig. 26). The connection is 'glued', after which the parasite feeds on the haemolymph of the host. Only the larval stages of these mites are parasites, the nymphs and adults are free-living predators.

Harvestmen are eaten by a myriad other animals (Pinto-da-Rocha *et al.* 2007). Important predators are birds, shrews, frogs and toads, and especially spiders. Cannibalism is a frequent phenomenon.

## DISTRIBUTION

One of the most interesting developments of the last two decades is the northward spread of many invertebrates from south and central Europe. This tendency can also be seen in harvestmen. Since 1991 the following species from south and central Europe have been found in the Netherlands for the first time: *Platybunus pinetorum*, *Opilio canestrinii*, *Dicranopalpus ramosus*, *Astrobinus laevipes*, *Nelima sempronii* and *Nelima doriae*. In the species texts this is discussed further. Since there are several other species

occurring within 150 km of the Dutch borders, more species are to be expected in due course. In most cases, these new-comers succeed in finding new ecological niches, apparently without influencing the presence of other species. An exception is *Opilio canestrinii*. This species is extremely successful and this has led to the dramatic decline of *Opilio parietinus* (Reemer 2003). It remains uncertain what the influence of *Dicranopalpus ramosus* will be, a species that is spreading swiftly (Noordijk *et al.* 2007). The invasion of *Leiobunum sp. A* in Western Europe could also have negative effects on other species (Wijnhoven *et al.* 2007).

Another interesting pattern is that quite a few species reach the (northern, north-western or western) limit of their geographic range in the Netherlands: *Nemastoma bimaculatum*, *Nemastoma dentigerum*, *Paranemastoma quadripunctatum*, *Trogulus nepaeformis* s.l., *Ischyropsalis hellwigi*, *Platybunus pinetorum*, *Odiellus spinosus*, *Homalenotus quadridentatus*, *Astrobus laevipes*, *Nelima sempronii* and *Nelima doriae* (Weeda 2006).<sup>1</sup>

Because distributions of harvestmen in the Netherlands are not that well-known, no distribution maps are presented in this publication. In Great Britain (National Biodiversity Network, [www.nbn.org.uk](http://www.nbn.org.uk))<sup>2</sup> and Belgium (Vanhercke 2004), distributions maps are available, and much of this data are online. In Germany, increasing numbers of faunistic records have been assembled in recent years (Blick & Komposch 2004).

## HABITATS

The diversity in form within harvestmen is matched only by the diversity of habitats in which they occur and their distinct life styles (Figs 27-30). In general, it can be said that species with short legs live on or in the soil, while species with long legs occur in the vegetation and on walls and tree trunks. Trogulidae, Nemastomatidae, and Sclerosomatinae (Phalangiiidae) live exclusively in the soil layer, in litter and under dead wood and stones. Because they require moist environments, they live principally on water-holding soils, like clay, loam and silty loams (loess). They are often dependent on deciduous forests. At the other end of the spectrum, thermophilic species can be found, like *Phalangium opilio* and *Odiellus spinosus*, which live in dry, sun-exposed areas such as dunes, heathlands, ruderal (disturbed areas), open biotopes and urban areas.

Juvenile stages are especially vulnerable to dehydration and stay in the litter layer and under wood. When they grow older, they are more resistant to dry circumstances and can be found higher in the vegetation. The adults hunt and rest in herbs, in bushes, on walls and on tree trunks, up into the tree canopy. For this reason, species-rich habitats are often characterised by a well-developed vertical (vegetation) structure. Amongst other habitats are, forest edges, wood banks, roadside verges, and old deciduous and mixed forests with a thick litter layer and a well-developed moss, herb and shrub layer. Ruderal and urban habitats can however also be rich in species: bramble bushes, patches of stinging nettle, abandoned industrial sites, brick factories along rivers, park landscapes, ruins, old walls, cemeteries and estates.

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<sup>1</sup> Note: of these species, *Nemastoma bimaculatum* and *Odiellus spinosus* are on the British list, while *Platybunus pinetorum* is a recent introduction.

<sup>2</sup> Note: also Harvestmen Recording Scheme (SRS/HRS) <http://srs.britishtspiders.org.uk/portal/p/Welcome>

## STUDY

### FIELD OBSERVATIONS

Harvestmen are easily surveyed by field observations. In vegetation with a searchable structure (like patches of stinging nettle, ivy, or Japanese knotweed), species like *Phalangium opilio*, *Opilio canestrinii*, *Rilaena triangularis*, *Mitopus morio* and *Leiobunum rotundum* can be easily be found (Fig. 31). Stinging nettles especially can harbour a surprisingly large number of species. Searching walls may provide several species: *Phalangium opilio*, *Opilio canestrinii* (Fig. 32), *Dicranopalpus ramosus*, *Leiobunum rotundum*, and occasionally *Opilio saxatilis*, *Oligolophus hansenii* and *Paroligolophus agrestis*. On walls, *Leiobunum* sp. A can form huge tangles (Fig. 33). Lifting ivy and bending aside grasses and herbs from the base of walls, posts etc., often reveals *Phalangium opilio*, *Opilio saxatilis*, *Oligolophus tridens*, *Paroligolophus agrestis* and *Mitopus morio*. Large numbers of *Leiobunum rotundum* can be found from June onwards under bridges, gutters, on trees and against posts in agricultural fields (Fig. 34).

Many species are to be found under loose dead wood and stones on the ground. This microhabitat includes some difficult-to-identify juveniles, especially specialised soils dwellers: *Nemastoma* and *Trogulus* species (Fig. 35), *Paranemastoma quadripunctatum*, *Anelasmacephalus cambridgei*, *Ischyropsalis hellwigi*, *Lacinius ephippiatus*, *Odiellus spinosus*, *Homalenotus quadridentatus* and *Astrobus laevipes*. It is worthwhile to carefully check the underside of stones or wood lying on the ground, including the soil underneath (always replace the item afterwards). Especially attractive are the bark fragments that lay with their rougher-outer-side on the soil, as here more cervices are to be found for resting harvestmen to hide away. Beware that many species do not move at low temperatures. Adult harvestmen species to be found in this microhabitat are *Mitostoma chrysomelas*, *Phalangium opilio*, *Rilaena triangularis* (mostly juveniles and subadults), *Lophopilio palpinalis*, *Oligolophus tridens*, *Paroligolophus agrestis*, *Odiellus spinosus*, *Mitopus morio*, *Leiobunum rotundum*, *Leiobunum blackwalli*, *Nelima sempronii* and *Nelima doriae*. On tree trunks several species can be found, amongst these are *Phalangium opilio*, *Opilio canestrinii*, *Platybunus pinetorum*, *Rilaena triangularis*, *Lophopilio palpinalis*, *Oligolophus hansenii*, *Paroligolophus agrestis*, *Mitopus morio*, *Dicranopalpus ramosus*, *Leiobunum rotundum* and *Leiobunum blackwalli*.

### HANDLING

The chelicerae of harvestmen are too small and weak to penetrate the human skin, although they do try. In large species this only gives a tickling feeling. All harvestmen can therefore easily be handled for study. Catching long-legged species requires some practise. The best method is to try to grab two or more legs at once, reducing the chance of amputation. Because many species let themselves drop upon disturbance, it is best to hold a jar under the animal. Soil dwelling species are more sclerotized, making them less vulnerable and more easily handled.

### COLLECTING

With the exception of the strict soil-dwelling species, many species can be caught using a sweep net in tall vegetation like grassland, thicket, shrubbery, or small trees. By using a stick to beat on branches of trees while holding a white umbrella or sheet under it, harvestmen can be collected from forest edges and scrub as well. Additionally, using pitfall traps is a good way to catch harvestmen. Of course this technique is most suitable for soil dwelling species and juveniles that are harder to identify. Identifying harvestmen from pitfall traps may form part of a survey where other invertebrates are collected.

A sieve with an eight millimetre mesh is suitable for collecting soil dwellers. Just take a hand full of moist litter from the base of walls or tree trunks, or from under stones or dead wood. Shake the sieve thoroughly

above a white sheet or tray. Large litter particles remain in the sieve, while harvestmen fall through. They play dead for a while (see Defence, Tp.4), but will start walking within a few minutes.

Sometimes harvestmen are attracted by the sugaring solution used to attract moths. There are also reports of harvestmen being attracted to rotten bananas. These techniques can lead to simple observations in one's own garden (Wijnhoven 2008a).

## **STORAGE AND DISSECTION**

Killing and preserving harvestmen can best be done in jars with 70% alcohol. Do not place too many individuals in one jar, because the legs will tangle and fall off. Harvestmen will lose their colours in alcohol; they eventually turn pale yellow. When kept in the dark, they retain their colour longer. A label should be placed in each jar, indicating locality (coordinates), habitat, date and recorder / identifier. The collection can later be given to a museum.

The dissection of the pedipalp, chelicera and penis can easily be done with two pairs of fine forceps (tweezers). They can be examined with a stereo binocular microscope (30-60x) and the fine details can be studied with a compound microscope (30-100x). The dissected parts can be placed on hollow glass slides, in a drop of water (or glycerine) and under a cover slip. The material does not need to be stained.

## **PHOTOGRAPHING**

A harvestman resting during the day does not move much when not disturbed. The animal can be looked at with a loupe (hand lens) and be photographed. A simple camera with a macro function renders acceptable results, as many of the photographs in this publication show. By making a photographic archive, a good overview is obtained of the natural colours and patterns, which may be lost in the alcohol collection. It is recommended to add locality and date in the file name of the photo, so it serves as the equivalent of a label in collection material, for example, 20080814\_01\_Beuningen\_Wijnhoven\_specimen8.

Adult harvestmen can often be identified from photos. It is therefore possible to obtain a name when the picture is placed on an internet forum. It may be important to not only photograph the complete animal, but also some details of the ocularium, and the area in front of it.

## **BODY PLAN**

### **CEPHALOTHORAX**

Harvestmen are characterised by a cephalothorax that is completely fused with the hind body into a single unit, without a spider-like waist (Fig. 36). The cephalothorax or fore-body bears all appendages: jaws (chelicerae), pedipalps and legs. On top of the cephalothorax there is an ocularium or eye tubercle with two eyes; spiders have six or eight eyes at the front of the cephalothorax. The ocularium is an important structure for species identification. It often has a distinctive shape or colour pattern and/or is provided with tubercles and setae. Figures 37-44 show some examples demonstrating the remarkable diversity harvestmen have developed.

The ocularium usually occurs at one to two times its length from the front margin. In Nemastomatidae the ocularium is weakly developed and situated near the front margin (Fig. 40). In Trogulidae the eyes are located even further forward (Fig. 37).

Most Phalangiinae and Oligolophinae have a group of three tubercles called the trident, near the midsection of the frontal margin, which is in some species accompanied by additional tubercles (Figs 36, 39). *Opilio* species also have tubercles near the front margin, but in these species a central tubercle is missing, leaving a smooth central area bordered by groups of tubercles (Fig. 44). Phalangiidae can usually be identified with a hand lens (10x) by the characteristics of the ocularium in combination with angle and relative length of trident tubercles (Figs 82-84, 89-93). On either side of the cephalothorax above the first leg, oval-shaped odoriferous or repugnatorial glands occur. These are glands that produce a secretion for defence and intraspecific communication, and also contain chemicals with a powerful antibacterial effect (Pinto-da-Rocha *et al.* 2007).

At the front of the cephalothorax are two chelicerae, each with a single basal (first) segment and a second segment having a fixed digit and movable digit, which act like a pincer. In males of Nemastomatidae the first segment has a dorsal apophysis which is species-specific (Figs 70-72). This contains glands which play a role in courtship behaviour. In *Phalangium opilio* males, the first cheliceral segment is elongated forming a horned process (Figs 99, 177). Oligolophinae are characterised by a small ventral hooked process on the first cheliceral segment (Fig. 101). The region between the chelicerae and the front margin is occupied by the so-called supra-cheliceral lamellae. In *Phalangium opilio* the midsection has two small, pointed tubercles (Fig. 98).

The pedipalps are located next to the chelicerae. They are leg-like sensory structures with segments: trochanter, femur, patella, tibia and tarsus (Fig. 36). The tarsus terminates in a toothed (or pectinate) claw in Leiobunidae and Sclerosomatidae (Fig. 95). Other families have a smooth claw (Fig. 94; visible at magnification of about 30x), while in Trogulidae and Nemastomatidae a tarsal claw is absent. Different segments of the pedipalps can have prominent bulges (apophyses) or distinctive tubercles which are important for species diagnosis. In most species these characters are fully developed only in males.

The eight legs consist of a coxa, trochanter, femur, patella, tibia, metatarsus and tarsus. In Trogulidae the tarsus has two to four segments, while in the long-legged species (like Leiobunidae) these can have over a hundred segments. Leg lengths are highly variable, from about twice the body length in soil-dwelling species like Trogulidae, to more than ten times the body size in Leiobunidae. The legs of the second pair are always the longest and act as sensory organs. *Leiobunum* species have rows of stout denticles at the front and rear sides of at least some coxae.

In a small area of the ventral cephalothorax region a large number of structures are concentrated (Figs 45-53). Between the leg coxae are the genitalia, anatomically derived from the segments of the abdomen. The base (coxae) of the pedipalps and first pair of leg coxae are modified into a mouth (maxillary lobe of the pedipalps and maxillary lobe coxa I; ‘mondopening’ (mouth opening) in Fig. 45). In Phalangiidae the second leg coxae have a large projection (maxillary lobe coxa II). A rectangular plate forms the labium.

## ABDOMEN

The abdomen (or opisthosoma) is segmented but in many species (like Trogulidae and Nemastomatidae) the segments are fused into a scutum. The original segmentation of ten segments is in most harvestmen only recognisable by transverse rows of small denticles bordering the tergites. The micro-sculpture of the dorsal side is variable: smooth with tubercles (e.g. *Opilio saxatilis*), granulated (*Nemastoma*) or finely granulated with rows of large conical bumps (*Astrobus*). The last, tenth, tergite covers the anus and is called the anal plate (anal operculum).

Many species have a characteristic patterning on the dorsal surface (saddle). The saddle can be distinct and with a silvery surface (e.g. *Platybunus* females), have irregular margins, or indistinct to almost absent. Colouring and contrast can be highly variable within one species, but in most cases the basic pattern is discernible, making it an important diagnostic character in the field.

Segments on the underside of the body are called sternites. As explained earlier (Cephalothorax, last para.) the second segment, which lies between the leg coxae, has developed into a large genital plate (genital operculum) that covers the reproductive structures. In some species it has a characteristic shape (Figs 52, 53). Harvestmen differ from all other Arachnid groups in that they use a copulatory organ (penis) for direct transfer of sperm to the female. The reproductive structures are homologous organs: the penis and ovipositor have the same embryonic origins. The penis consists of a long trunk and a movable glans with a pointed stylus (Figs 46-47). The seminal tract runs internally, terminating at the stylus tip. The basal part has an intrinsic penial muscle with a tendon that attaches at the base of the glans. Usually the glans has two pairs of sensory setae. The penial morphology is highly species-specific and it is a most important characteristic in Opiliones classification.

The female has an ovipositor (Figs 49, 50) consisting of a segmented (or non-segmented in the more primitive groups) tube. Each segment is provided with a complex muscle system enabling the ovipositor to be moved in all directions and to evert to a considerable length (approximately 10 mm in *Leiobunum* species) for egg-deposition in crevices of rocks, tree bark or into the soil. Several ovipositor types can be recognised, but for species diagnosis their features play a minor role. In the top segments of the ovipositor are located a pair of seminal receptacles for the storage of sperm cells (Fig. 50). The shape and location of these organs are species-specific, but since they are delicate, non-sclerotised structures, they are often prone to slight deformations during the painstaking preparation and clearing process. Therefore, the seminal receptacles are not often used in species diagnosis.

## JUVENILE OR ADULT?

Harvestmen grow by moulting (shedding their skin) seven or eight times before becoming mature. In adult harvestmen the front side of the genital operculum is open. When the animals are sexually receptive, the penis or ovipositor can be everted through this opening. In juveniles the genital operculum is still fused to the surrounding tissue. As this character is hardly ever visible with a hand lens, you may not succeed in identifying a specimen because it is immature. Juveniles that just need one more moult before reaching maturity are called subadults. Generally these look very similar to adults but with some experience can usually be identified. The younger stages, however, often are quite different from adults and occasionally cannot be reliably identified (e.g. *Oligolophus hanseni/Oligolophus tridens/Paroligolophus agrestis*). Some juveniles can be easily recognised at every stage, like *Dicranopalpus ramosus* (forked pedipalps) and *Mitostoma chrysomelas* (shape of pedipalps).

## MALE OR FEMALE?

When starting to learn about harvestmen it can be confusing that many species (Phalangiidae and Sclerosomatidae) are incredibly sexually dimorphic (Fig. 32; see also drawings on left pages in the species descriptions). In *Leiobunum rotundum* and *L. blackwalli* for example, males are smaller and reddish-brown with contrasting black, long legs. Females are more robust, with a dark saddle pattern and lighter, somewhat shorter legs. A general feature of most males is that they are smaller, flatter, have a shorter, more rectangular abdomen (e.g. Figs 32, 280, 329) and have longer legs. Male pedipalps and chelicerae frequently have modifications (tubercles, protuberances) that usually play a role in courtship and mating behaviour or in male-male contests. The ventral region of the pedipalpal tarsus for example, can be provided with rows of stout, black spines to enable a firm grip of the female during mating. All pedipalp drawings in this book therefore are based on male specimens. In females, pedipalps and chelicerae have a more basic design. Females are usually larger and more rounded, especially when they have developing eggs (e.g. Figs 49, 210, 241).

## SYSTEMATIC REVIEW

The classification of harvestmen is still under investigation and adjustments may be necessary (for example *Dicranopalpus* belongs to the superfamily Phalangioidea but the genus currently has uncertain placement (*Incertae sedis* - Crawford, 1992) and for the present has been assigned to the family Phalangiidae). The list below is, with few exceptions, the classification of Martens (1978). Subfamilies Sclerosomatinae and Leiobuninae of Phalangiidae are presently treated as a separate family (Sclerosomatidae; Pinto-da-Rocha *et al.* 2007). Synonyms are only mentioned if they occur in publications from 1963 onwards. Some harvestmen species already have a Dutch name; for these species a Dutch name is shown. Native species are numbered. For the following species a note on taxonomy is included at the end of the species accounts: *Trogulus tricarinatus*, *Trogulus nepaeformis*, *Mitostoma chrysomelas*, *Opilio canestrinii*, *Leiobunum rupestre* and *Leiobunum* sp. A.

Class Arachnida		spinachtigen
Order Opiliones		hooiwagens
Suborder Palpatores		
Superfamily Troguloidea		aardhooiwagens
Family Nemastomatidae		
Subfamily Nemastomatinae		
Genus <i>Nemastoma</i> C.L. Koch, 1836		
1	<i>Nemastoma bimaculatum</i> (Fabricius, 1775)	
2	<i>Nemastoma lugubre</i> (Müller, 1776)	
3	<i>Nemastoma dentigerum</i> Canestrini, 1873	
Genus <i>Paranemastoma</i> Redikorzew, 1936		
4	<i>Paranemastoma quadripunctatum</i> (Perty, 1833)	
Genus <i>Mitostoma</i> Roewer, 1951		
5	<i>Mitostoma chrysomelas</i> (Hermann, 1804) = <i>Mitostoma confusum</i> Spoek 1963	
Family Trogulidae		kaphooiwagens
Subfamily Trogulinae		
Genus <i>Trogulus</i> Latreille, 1802		
6	<i>Trogulus tricarinatus</i> (Linnaeus, 1767)	
7	<i>Trogulus</i> c.f. <i>nepaeformis</i> (Scopoli, 1763)	
Genus <i>Anelasmacephalus</i> Simon, 1879		
8	<i>Anelasmacephalus cambridgei</i> (Westwood, 1874)	
Superfamily Ischyropsalidoidea		
Family Ischyropsalididae		slakkenhooiwagens
Subfamily Ischyropsalididae		
Genus <i>Ischyropsalis</i> C.L. Koch, 1839		
9	<i>Ischyropsalis hellwigi hellwigi</i> (Panzer, 1794)	slakkenhooiwagen
Superfamily Phalangioidea		
Family Phalangiidae		echte hooiwagens
Subfamily Phalanginae		
Genus <i>Phalangium</i> Linnaeus, 1758		
10	<i>Phalangium opilio</i> Linnaeus, 1761	gewone hooiwagen
Genus <i>Opilio</i> Herbst, 1798		
11	<i>Opilio parietinus</i> (De Geer, 1778)	
12	<i>Opilio saxatilis</i> C.L. Koch, 1839	

13	<i>Opilio canestrinii</i> (Thorell, 1876) = <i>Opilio ravennae</i> Spoek, 1962	rode hooiwagen
	Genus <i>Platybunus</i> C.L. Koch, 1848	
14	<i>Platybunus pinetorum</i> (C.L. Koch, 1839)	
	Genus <i>Megabunus</i> Meade, 1855	
-	<i>Megabunus diadema</i> (Fabricius, 1779)	
	Genus <i>Rilaena</i> Šilhavý, 1965	
15	<i>Rilaena triangularis</i> (Herbst, 1799) (Synonym <i>Platybunus triangularis</i> (Herbst, 1799))	voorjaarshooiwagen
	Genus <i>Lophopilio</i> Hadži, 1931	
16	<i>Lophopilio palpinalis</i> (Herbst, 1799) (Synonym <i>Odiellus palpinalis</i> Roewer, 1923)	
	Subfamily Oligolophinae	
	Genus <i>Oligolophus</i> C. Koch, 1872	
17	<i>Oligolophus tridens</i> (C.L. Koch, 1836)	drietandhooiwagen
18	<i>Oligolophus hanseni</i> (Kraepelin, 1896)	
	Genus <i>Paroligolophus</i> Lohmander, 1945	
19	<i>Paroligolophus agrestis</i> (Meade, 1855)	bonte hooiwagen
	Genus <i>Lacinius</i> Thorell, 1876	
-	<i>Lacinius horridus</i> (Panzer, 1794)	
20	<i>Lacinius ehippiatus</i> (C.L. Koch, 1835)	
	Genus <i>Odiellus</i> Roewer, 1923	
21	<i>Odiellus spinosus</i> (Bosc, 1792)	
	Genus <i>Mitopus</i> Thorell, 1876	
22	<i>Mitopus morio</i> (Fabricius, 1799)	
	Subfamily Gyantinae	
	Genus <i>Dicranopalpus</i> Doleschall, 1852 ( <i>Incertae sedis</i> )	
23	<i>Dicranopalpus ramosus</i> (Simon, 1909)	Strekpoot
	Subfamily Sclerosomatinae	
	Genus <i>Homalenotus</i> C.L. Koch, 1839	
24	<i>Homalenotus quadridentatus</i> (Cuvier, 1795)	
	Genus <i>Astrobunus</i> Thorell, 1876	
25	<i>Astrobunus laevipes</i> (Canestrini, 1872)	
	Subfamily Leiobuninae	
	Genus <i>Leiobunum</i> C.L. Koch, 1839	
-	<i>Leiobunum limbatum</i> L. Koch, 1861	
26	<i>Leiobunum rotundum</i> (Latreille, 1798)	
27	<i>Leiobunum blackwalli</i> Meade, 1861	
-	<i>Leiobunum rupestre</i> (Herbst, 1799)	
28	<i>Leiobunum</i> sp. A	
	Genus <i>Nelima</i> Roewer, 1910	
29	<i>Nelima sempronii</i> Szalay, 1951	
30	<i>Nelima doriae</i> (Canestrini, 1871)	

#### Addenda, 2014

1. Recently it has become evident that all drawings in this book concerning *Trogulus nepaeformis* s.l. have to be ascribed to *Trogulus closanicus* Avram, 1971. See the recent key to the Dutch *Trogulus* species *T. tricarinatus*, *T. closanicus* and *T. nepaeformis* (Wijnhoven H., J. Noordijk & Th. Heijerman 2014. Het hooiwagengenus *Trogulus* in Nederland (Opiliones: Trogulidae) *Nederlandse Faunistische Mededelingen* **42**: 1-9).

2. The north-western populations of "*Leiobunum rupestre*" are in fact *Leiobunum tisciae* (Figures 327 and 328 are *L. rupestre*).

## HOW TO USE THE KEY

Many harvestmen can easily be identified in the field, often with the naked eye. They have a distinct appearance, leg length, size, posture or colour pattern, but in most cases a combination of features needs to be considered. The classification in Opiliones is primarily based on genital morphology, which requires microscopic study. Also many other features of taxonomic importance are small, like the toothed pedipalpal claw of Leiobunidae. Instead of a taxonomic approach, in this key a more practical one is followed by using features that in the majority of cases can be judged with a 10x hand lens. For some species it will be necessary to take a look at the detailed drawings of the male pedipalps, chelicera or penis with the help of a microscope (30-60x). The key only can be used for adult specimens (Juvenile or adult? Tp.10).

## LENGTHS

The length of a harvestman is measured from the front margin of the fore body (the chelicerae are not included) to the rear end. The smallest measures indicated are for adult males and the largest are for females.

## COLOUR

Note the colours refer to adult animals only. Locally different colour patterns may occur. Some species are highly variable like *Mitopus morio* (Figs 54-56), *Phalangium opilio* and *Opilio canestrinii*. Individuals that have recently moulted have the most vivid colours, and get darker and less contrasting with age. This is different for each species. Juveniles and subadults usually are lighter and more contrasting, or they have not developed the typical saddle pattern. The drawings on the left-hand pages of the species accounts are mostly based on specimens with highly contrasting colour patterns. If males are clearly different from females, both sexes are depicted.

## GEOGRAPHICAL AREA COVERED

This book mentions all species from the Netherlands, neighbouring German states (Niedersachsen and Nordrhein-Westfalen) and Belgium, except for *Amilenus aurantiacus* (Simon, 1881) which is found in the far south of the Netherlands (Vanhercke 2004). *Platybunus bucephalus* (C.L. Koch, 1835) is also not included. This key also largely covers the harvestmen of Great-Britain and Ireland, although many continental species do not occur there while some others do, like *Paroligolophus meadii* (Pickard-Cambridge, 1890) and *Sabacon viscayanum ramblaianum* Martens, 1983. Four species that do not occur in the Netherlands have been included, as they may be expected in the future: *Megabunus diadema*, *Lacinius horridus*, *Leiobunum limbatum* and *Leiobunum rupestre*.

### Addenda, 2014:

1. For the *Trogulus* species see Wijnhoven H., J. Noordijk & Th. Heijerman 2014. Het hooiwagengenus *Trogulus* in Nederland (Opiliones: Trogulidae) *Nederlandse Faunistische Mededelingen* **42**: 1-9.
2. *Leiobunum rupestre* cannot be expected to occur in the Netherlands. It should be *Leiobunum tisciae*.
3. Another new species recently found in the Netherlands is *Leiobunum religiosum* (Noordijk, J. & J. Bink 2014. *Leiobunum religiosum* (Opiliones: Sclerosomatidae), een nieuwe hooiwagensoort voor de Nederlandse fauna. *Entomologische Berichten* **74**: 138-142).

## IDENTIFICATION KEY

- 1 Pedipalps and chelicera not visible from above, covered by a roof-like ‘hood’ (Figs 57, 58). Trogulidae. (2)
  - Pedipalps and chelicera visible from above. (4)
- 2 Body not strongly flattened, pear-shaped. All legs with large tubercles. Tarsi I and II with three segments (Fig. 59). Small, up to 3.9 mm. *Anelasmaocephalus cambridgei* (p.56, Tp.25)
  - Body very flattened. In adults, only the femur of the first leg with tubercles. Tarsi I and II with two segments (Fig. 60). Large species from 4.6 to 8.2 mm. (3)
- 3 Length 4.6 to 5.8 mm. Distance between the eyes approximately twice as broad as the diameter of the eye (Fig. 57). Tarsus II maximally 1.2 mm long. *Trogulus tricarinatus* (p.52, Tp.23)
  - Length 6.1 to 8.2 mm. Distance between the eyes approximately four times as broad as the eye (Fig. 58). Tarsus II ca. 1.6 mm long. *Trogulus nepaeformis* s.l. (p.54, Tp.24)[& *Trogulus closanicus*]
- 4(1) Palpal tarsus shorter than palpal tibia (Fig. 61). Sabaconidae, Ischyropsalididae, Nemastomatidae. (5)
  - Palpal tarsus longer than palpal tibia (Fig. 62). (10)
- 5 Chelicera conspicuously large, like the claws of a lobster and much longer than the body. *Ischyropsalis hellwigi hellwigi* (p.58, Tp.26)
  - Chelicera not conspicuously large, shorter than body. (6)
- 6 Body dark brown with ‘golden’ patches, in a variable pattern. Upper side of abdomen with transverse rows of anchor-like tubercles. Long, slender legs. Pedipalp long and slender, with a characteristic ‘folded’ positioning (Fig. 64). *Mitostoma chrysomelas* (p.50, Tp.22)
  - Body black, with or without paler spots. Upper-side of abdomen granulated, sometimes with tubercles or protrusions. Relatively short, stout legs and pedipalps. (7)
- 7 Larger, 3.5 to 4 mm. Black with two yellow-white 8-shaped patches (Fig. 65). Three pairs of stout protrusions on abdomen. *Paranemastoma quadripunctatum* (p.48, Tp.21)
  - Smaller, 1.5 to 2.7 mm. Black, with or without silver-white patches (Figs 66, 67). No protrusions on abdomen. (8)
- 8 Completely black. ♂: constricted base of apophysis on first segment of chelicera (Fig. 70), hook on the underside of palpal femur (Fig. 61). *Nemastoma dentigerum* (p.46, Tp.20)
  - Black with two silvery-white patches (Figs 66, 67) seldom without these patches. (9)
- 9 White patches on the outer-side with a notch (Fig. 66), seen from the side, mostly below the imaginary line from eye to the rear edge of the scutum (Fig. 68). ♂: apophysis on the first (basal) segment of chelicera split at the end (Fig. 71), palpal tibia curved, with a prominent bulge at its base (Fig. 73). *Nemastoma bimaculatum* (p.42, Tp.18)
  - White patches on the outer-side without a notch (Fig. 67), seen from the side, mostly above the imaginary line from eye to the rear edge of the scutum (Fig. 69). ♂: apophysis on the first (basal) segment of chelicera with a flat or slightly dented top (Fig. 72), palpal tibia only weakly curved, base with a slight bulge (Fig. 74). *Nemastoma lugubre* (p.44, Tp.19)
- 10(4) Abdomen with large cone-shaped tubercles (Figs 75, 76). Relatively short legs. (11)
  - Abdomen without cone-shaped tubercles. Short to long legs. (12)

- 11 Rear of abdomen with four large, backward pointing cone-shaped tubercles (Fig. 75). Body strongly flattened. Ocularium bears several tubercles, with some in front of the eye (missing in older specimens). *Homalenotus quadridentatus* (p.92, Tp.43)
- Rear of abdomen with large, oblique-pointing cone-shaped tubercles (Fig. 76). Body not strongly flattened. Ocularium with crest of 5-6 white tubercles, but no tubercles in front of the eyes. *Astrobunus laevipes* (p.94, Tp.44)
- 12(10) Patella of pedipalp on the inside with a very long apophysis, pedipalp seems ‘forked’ (Fig. 77). All legs stretched parallel to each other in rest (Fig. 15). *Dicranopalpus ramosus* (p.90, Tp.42)
- Pedipalps different. In rest, legs spread out more or less radially. (13)
- 13 Patella and tibia of pedipalp with apophysis with a length respectively one third of their segments (Figs 78, 79). (14)
- Patella and tibia of pedipalp without apophysis or apophysis is a short, blunt bulge. (17)
- 14 Length 3.5 to 8 mm. Ocularium with seven to ten pairs of tubercles. (15)
- Length 2.6 to 4 mm. Ocularium with four or five pairs of tubercles. (16)
- 15 Palpal femur with tubercles that are shorter than the width of the femur (Fig. 78). Apex of palpal femur on the inside has a conspicuous bulge. Ocularium about as long as wide, not strongly furrowed, to the front almost none at all (Fig. 80). ♂: pale yellow-brown. ♀: saddle shape without silver border. 3.5 to 7 mm. *Rilaena triangularis* (p.72, Tp.33)
- Palpal femur with tubercles that are at least as long as the width of the femur (Fig. 79). Ocularium broader than long, clearly furrowed throughout (Fig. 81); ♂: black saddle with unclear edges, reddish legs. ♀: saddle shape with clear silver border. *Platybunus pinetorum* (p.68, Tp.31)
- 16 (14) Ocularium large, with two rows of five very long tubercles (Fig. 82). In front of the ocularium, at most one tubercle. *Megabunus diadema* (p.70, Tp.32)
- Ocularium small, with two rows of four to five tubercles, the central pair larger than the others (Fig. 83). In front of the ocularium is a trident, the central member being the longest. *Lophopilio palpinalis* (p.74, Tp.34)
- 17 (13) Trident in front of ocularium. (18)
- Scattered tubercles or no tubercles at all in front of ocularium. (23)
- 18 Ocularium pale and smooth, without tubercles, only small hairs Fig. 84). ♀: top of genital operculum incised (Fig. 86); ♂: hollow (Fig. 85). *Paroligolophus agrestis* (p.80, Tp.37)
- Ocularium with two rows of tubercles. Genital operculum with rounded top. (19)
- 19 Femur of legs with longitudinal rows of hairs and denticles (Fig. 87). (20)
- Femur of legs only with rows of hairs (Fig. 88). (21)
- 20 Ocularium with two rows of five small tubercles. Trident members point upwards, tubercles quite small and in line (Fig. 89). The femur of the legs has rows of small denticles. Small, 3.7 to 4.8 mm. *Lacinius ephippiatus* (p.84, Tp.39)
- Ocularium with two rows of four very large tubercles. Trident oblique, tubercles are very long and accompanied by other large tubercles (Fig. 90). The femur of the legs has rows of robust denticles. Large, 4 to 6.9 mm. *Lacinius horridus* (p.82, Tp.38)
- 21 (19) The trident strikingly large in relation to small ocularium, tubercles broad cone-shaped (Fig. 91). Large, robust species, to 9.5 mm. *Odiellus spinosus* (p.86, Tp.40)
- Trident smaller, tubercles more slender. Smaller, slimmer species, 3.3 to 5.2 mm. (22)

- 22 No additional tubercles next to the trident (Fig. 92). Two to five tubercles behind the trident. The palpal patella has a blunt apophysis at the top. Frontal part of the ocularium rises vertically, with two rows of 4 to 7 tubercles. *Oligolophus tridens* (p.76, Tp.35)
- At least one additional tubercle adjacent to each side of the trident (Fig. 93). A group of four to seven tubercles are found behind the trident. Palpal patella without an apophysis, top only thickened. The lateral view of the front face of ocularium is inclined obliquely, with two rows of five to six tubercles. *Oligolophus hanseni* (p.78, Tp.36).
- 23 (17) Area in front of ocularium with tubercles. Ocularium with tubercles. Claw of tarsus smooth (30x, Fig. 94). (24)
- Area in front of ocularium smooth. Ocularium smooth or with very small spines. Claw of tarsus with teeth (30x, Fig. 95). (28)
- 24 Genital operculum at the top not spoon-shaped (Fig. 96). Tibia of legs in cross-section strongly angular. (25)
- Genital operculum at the top spoon-shaped (Fig. 97). Tibia of legs in cross-section circular to weakly angular. (26)
- 25 Two small tubercles on the front of the cephalothorax, above the chelicerae and below the fore edge (Fig. 98). Many large tubercles in front of the ocularium. Ocularium large, with 4 to 7 large, pointed tubercles. ♂: second segment of chelicera with a prominent horn, variable in length (Fig. 99), pedipalps conspicuously long. *Phalangium opilio* (p.60, Tp.27)
- No tubercles above the chelicerae (see above). Scattered, small tubercles are found in front of the ocularium (Fig. 100). The ocularium is quite small, with 6 to 7 small tubercles. Chelicerae and pedipalps of ♂ are normal (Fig. 101). *Mitopus morio* (p.88, Tp.41)
- 26 (24) The ocularium has two rows of 7 to 10 robust tubercles. The palpal femur of ♂ has denticles. *Opilio parietinus* (p.62, Tp.28)
- Ocularium with two rows of 4 to 6 tubercles. The palpal femur of ♂ is with or without denticles. (27)
- 27 Relatively long, slender legs. Femora of legs not thickened. The palpal femur of the ♂ is without denticles. ♂: evenly coloured, yellow-brown to red-brown. ♀: variable, pale yellow-brown with thin white-bordered black lines. *Opilio canestrinii* (p.66, Tp.30)
- Relatively short legs. Femur I and II thickened (most obvious in ♂), and densely covered with denticles. The palpal femur of ♂ has denticles. The abdomens of both sexes have dark markings. *Opilio saxatilis* (p.64, Tp.29)
- 28 (23) Ocularium with two rows of small spines, pale yellow, the eyes with black rim (Fig. 102, 103). All coxae without rows of small denticles (30x). Legs relatively short, length of leg II maximally 35 to 47 mm. (29)
- Ocularium smooth, only with several very small hairs, black or pale coloured with a contrasting mid-stripe (Figs 104-106). At least the first coxa at the front, and the fourth at the back, with rows of small denticles (30x). Very long legs, length of leg II 45 to 90 mm. (30)
- 29 Ocularium pale yellow, front part slightly darker, covered with two rows of small spines (Fig. 102). ♂: palpal tarsus strongly curved inwards, under side with a row of denticles. Underside of palpal femur and tibia without tubercles. *Nelima sempronii* (p.106, Tp.50)
- Ocularium pale yellow, front part darker, with two rows of relatively large spines (Fig. 103). ♂: palpal tarsus almost straight, underside without row of denticles. Palpal femur and tibia on the underside have cone shaped tubercles. *Nelima doriae* (p.108, Tp.51)
- 30 (28) Adult ♂: smaller, rear-end of the abdomen is quite truncated (e.g. Fig. 317 left). (31)

- Adult ♀: larger, rear-end of the abdomen is more rounded (e.g. Fig. 317 right). (35)
- 31 Main colour of abdomen is red-brown. (32)
- Main colour of abdomen is black. (34)
- 32 Abdomen red-brown with striking black rim, cephalothorax yellow-brown with dark patches. *Leiobunum limbatum* (p.96, Tp. 45)
- Abdomen red-brown, at most with small black edge, cephalothorax red-brown, with unclear markings in front of ocularium. (33)
- 33 Ocularium black with thin pale mid-stripe (Fig. 104). No dark translucent patches on genital operculum. A robust species. *Leiobunum rotundum* (p.98, Tp. 46)
- Ocularium pale yellow with thin black mid-stripe, eyes with black ring (Fig. 105). Two black patches on the penis shine through the genital operculum. A smaller and less robust species. *Leiobunum blackwalli* (p.100, Tp. 47)
- 34 (31) Abdomen is black with clear blue metallic sheen. Leg II up to 90 mm. Pedipalps largely yellow-brown. Trochanters of the legs are black, strongly contrasting with yellow-white coxae and underside of abdomen. Legs brown to black. Sometimes there is a small pale patch on both sides of the ocularium (Fig. 106). *Leiobunum sp. A* (p.104, Tp. 49)
- Abdomen black with weak blue-green metallic sheen. Leg II maximally 66 mm. Pedipalps are dark brown to black. The trochanters of the legs are yellow-brown and do not contrast with yellow-brown coxae and underside of abdomen. Legs pale brown. There are large pale patch on both sides of the ocularium. *Leiobunum rupestre* (p.102, Tp. 48)
- 35 (30) Ground colour of abdomen red-brown to yellow-brown, with a dark saddle. No metallic sheen. (36)
- Ground colour of abdomen yellow-brown to grey-brown, with many dark markings. Saddle not clearly delineated and without a metallic sheen. (37)
- 36 Ocularium black with a pale mid-stripe (Fig. 104), sometimes almost completely black. Saddle runs backwards with parallel sides, ending in two sideways pointing markings. In most cases a dark triangular patch in front of ocularium. Appears more robust than *Leiobunum blackwalli*. *Leiobunum rotundum* (p.98, Tp. 46)
- Ocularium yellow with black mid-stripe, eyes with black rim (Fig. 105). Saddle is broad at the rear and ends at the front end in a point. A dark patch, with often a pale mid-stripe, in front of ocularium. Smaller and more elegantly built. *Leiobunum blackwalli* (p.100, Tp. 47)
- 37 (35) Body with dark grey patches, especially on the margins, with vivid blue-grey and ochre colourings, saddle is indistinct. Small round black spots can be found in front of the ocularium,. The abdomen has no metallic sheen. *Leiobunum limbatum* (p.96, Tp. 45)
- Mainly with black patches, dark saddle and a triangular patch just before the ocularium. Abdomen has a green sheen. (38)
- 38 Trochanters of legs black, with strongly contrasting yellow-white coxae and underside of abdomen. The tibia of legs II and IV has a conspicuous white ring. Length of leg II is up to 85 mm. *Leiobunum sp. A* (p.104, Tp.49)
- Trochanters of legs yellow-brown, not contrasting with yellow-brown coxae and underside of abdomen. The tibia of legs II and IV has no conspicuous white ring. Leg II up to 65 mm. *Leiobunum rupestre* (p.102, Tp. 48)

## SPECIES ACCOUNTS

### *Nemastoma bimaculatum*

**Length:** 2.0-2.6 mm.

**Recognition:** Small, black and short-legged, with two white spots on cephalothorax with a large notch on the outside edge (Figs 107, 108). Compared with *N. lugubre*, the body of *N. bimaculatum* is more dorsally flattened. As a result, as seen from the side, the main part of the white spot lies below an imaginary line from the eye to the rear edge of the scutum (Fig. 68). Back fairly finely granulated (compare Figs 109 and 115).

♂ Chelicerae have on the first segment an anterodorsal prominent projection (Figs 71, 107, 113). The tibia of the palp is strongly curved and at its base there is a large, granulated projection (Fig. 110). The top of the penis has about ten small spines on both sides (Fig. 112).

**Habitat:** Soil and litter dweller. It requires environments with high relative humidity. Especially in the litter of moist, shady deciduous forests with clay or silty, loamy soils, but it is also found in forests on sandy soils and virtually open areas. Remarkably, *N. bimaculatum* and *N. lugubre* often occur together, for example under pieces of bark or on tree trunks.

**Phenology:** Adults throughout the year.

**NL:** Quite rare in parts of southern Holland. It appears to be more frequent in the Netherlands than is suggested by the limited literature available. This is mainly because *N. bimaculatum* has long been considered a subspecies of *N. lugubre*, and is rarely named (Spoek 1963). It was only recognised when *N. bimaculatum* was first confirmed as present by Van der Hammen (1983), from South Limburg. Wijnhoven & Koomen (1997) provide an overview of the then-known Dutch sites. Experience shows that the species occurs not only in South Limburg but in the whole province of Limburg, as far as the moraine at Nijmegen (Wijnhoven 1998a), and almost always in the same habitat as *N. lugubre*. Found in Noord-Brabant and Zeeland which suggests that *N. bimaculatum* is widespread in the southern half of the country. Found in isolated sites above the rivers in Wassenaar (Zuid-Holland), Scharmer (Groningen) and Hengelo (Overijssel).

**EU:** Distribution Atlantic. Found in areas contiguous with mainland western Europe, northern Spain, through France and Belgium to the Netherlands (Martens 1978). Also known from Britain, Germany, Norway and Iceland. Only known in a very few places in Germany, in the region east of South Limburg and in Belgium.

## *Nemastoma lugubre*

**Length:** 1.5-2.4 mm.

**Recognition:** Small, black and short-legged. Two white spots, rounded rectangular or irregularly edged, but almost never nicked from the outside (Figs 67, 114). In rare cases, the white spot outline is broken, or two spots are connected together to form a horseshoe-shaped spot. The abdomen of *N. lugubre* is dorsally slightly more arched than *N. bimaculatum*. As a result, the main part of the white spot lies above an imaginary line from the eye to the rear edge of the scutum, when seen from the side (Fig. 69). The dorsal area of the abdomen is fairly coarsely granulated (compare Figs 109 and 115).

♂ Has a prominent projection on the anterior surface of the first or basal segment of the chelicera, which is slightly indented (Figs 72, 114, 119). Tibia of the palp weakly curved at the base with a small, finely-granulated thickening (Fig. 116). Top of the penis is very characteristic with an asymmetrical tip, with two large, downward-pointing spines (Fig. 118).

**Habitat:** Soil and litter dweller which requires environments with high relative humidity. Found in deciduous and coniferous forests, rugged terrains, and ribbon-shaped valleys. Landscape elements are parks, meadows and ditches and ponds, on both clay and sandy soils. Open areas are not avoided, provided that the surface remains moist enough. Remarkably *N. lugubre* and *N. bimaculatum* are often found together, for example under pieces of bark or on tree trunks.

**Phenology:** Adults throughout the year.

**NL:** Probably widespread throughout the country.

**EU:** From the Netherlands, Belgium, Luxembourg and the east of France well into Russia, throughout Scandinavia and south into Bulgaria. It is also found in a few areas of Germany as far as Bonn. In Belgium and the Netherlands there are overlapping areas of *N. bimaculatum* and *N. lugubre* (Martens 1978, Van der Hammen 1983).

## *Nemastoma dentigerum*

**Length:** 1.4-2.0 mm.

**Recognition:** There are very few characters for recognition; it is all black and short legged (Fig. 120). The skin folds between segments are translucent greyish, especially in females. The dorsal area is finely granulated.

♂ First segment of the chelicera has a cylindrical projection which is constricted at the base (Figs 70, 122). The femur of the palp is club-shaped and at the anterior end it has a hook-shaped projection (Fig. 125). The patella of the palp is widened in a spoon-shape at its anterior end. The tip of the penis has a curved point, with rows of long hairs (Figs 123, 124).

**Habitat:** Soil and litter dweller. It prefers open areas and thickets with moist clay soils, under wood, stones, among clumps of grass and rotting hay. Found along ditches and around ponds, by tidal rivers and flood-plains and moist litter of hedgerows. It has been found on only a few sites with sandy soils (Wijnhoven 1998a), including in a city park. Occasionally it is found together with *N. lugubre*.

**Phenology:** Adults throughout the year.

**NL:** Generally around rivers and with areas of clay. It was first found in 1961 (Spoek 1975). Since the early 1990s, an increasing number of observations have been made (Wijnhoven 1998a, 2005b). The most northern records are from North Holland and Flevoland.

**EU:** Known from Germany, Netherlands, Italy, Slovenia, Croatia and Switzerland (Buick & Komposch 2004, Martens 1978, Novak 2004, Spoek 1975). It is found in contiguous areas of the central Mediterranean. In Germany, as in Netherlands, it is being found in more and more places. Probably *N. dentigerum* has expanded to the north in recent decades (Baumann *et al.*, 1992).

### *Paranemastoma quadripunctatum*

**Length:** 3.5-4.0 mm.

**Recognition:** Quite big, black, short-legged (Fig. 127). It has the typical 8-shaped yellow spots on the cephalothorax and small spots on the back of the abdomen (Fig. 126). The yellow pattern can extend to the front of the carapace as a continuous cord (Fig. 128). It has remarkably small, pale-yellow contrasting palps. Three paired bumps on the abdomen (sometimes fairly flat). The first segment of the chelicerae has a dorsal conical protrusion at its anterior end (Fig. 129). The penis has a characteristic tip (Figs 131, 132) which is diagnostic.

**Habitat:** It is found in the litter of moist deciduous and mixed forests, often in the vicinity of open water. A critical habitat requirement for this species is constant high humidity and the presence of dense undergrowth, with thick litter layers of moss and dead wood. It is also found in caves and limestone quarries (Spoek 1957).

**Phenology:** Adults throughout the year.

**NL:** Very rare. The east bank of the Meuse in Limburg defines a sharp north-western border (Spoek 1957). There are only a few sites in the province of Limburg and the Achterhoek (province of Gelderland) (Spoek 1975). Recent discoveries have been made in Tegelen, Roermond, Wellerlooi, Ruurlo en Winterswijk. Possibly there are more locations in the Achterhoek.

**EU:** Eastern France, Belgium, the Netherlands, Germany, Czech Republic, Slovakia, Hungary, Switzerland, Austria, Slovenia and northern Italy (Buick & Komposch 2004, Martens 1978) and also in Croatia and Bosnia-Herzegovina (Novak 2004). Twenty species of the genus *Paranemastoma* occur in south-eastern Europe, many with very limited distributions.

## *Mitostoma chrysomelas*

**Length:** 1.3-2.0 mm.

**Recognition:** Small, very long thin, black legs (Figs 133, 134). Palps are held up in a typical folded position (Figs 64, 134). It therefore cannot be confused with other species occurring in the Netherlands. The palp has glandular hairs or capitate setae (Fig. 139). The dorsum and ocularium have cup or bifid shaped tubercles, which are arranged in rows (Figs 133, 135). The dorsum of the juvenile is smooth and without tubercles.

♂ The top of the penis is a complex, three-dimensional structure (Figs 136, 137).

**Habitat:** It is found in all kinds of moist forests, on the edges of freshwater bodies and in rugged terrain, where it occurs in undergrowth, in litter and under loose stones. One of the most important habitat requirements appears to be richly textured mulch, with lots of moss, dead vegetation, leaves, and wood. Often it is found in small groups

**Phenology:** Adults throughout the year.

**NL:** It is relatively common and found scattered throughout the Netherlands, but some small sites may often be overlooked because the species lives in the litter layer.

**EU:** It is distributed over a significant area of Europe, stretching from Ireland, Great Britain and Scandinavia to Bulgaria (Blick & Komposch 2004, Martens 1978).

**Taxonomy:** Spoek (1964) recognises two subspecies in the Netherlands: *M. chrysomelas chrysomelas* (Hermann, 1804) and *M. chrysomelas confusum* Spoek, 1963. Martens (1978) however, states that there are no subspecies of *M. chrysomelas* because the variations described so far are only individual variations in genital-morphology and can be found to coexist within all populations. Synonym: *Mitostoma saxonica* (Hnatewytsh) in Spoek (1957).

## *Trogulus tricarinatus*

**Length:** 4.6-5.8 mm.

**Recognition:** *Trogulus tricarinatus* (Fig. 141) is small, usually fairly lightly-coloured compared to the dark brown *T. nepaeformis* s.l. (Fig. 150). Distance between the eyes about twice as large as the eye diameter (Figs 57, 140, 142). Tarsus of leg II has two segments which are up to 1.2 mm long (Fig. 143). Juveniles light brown (Fig. 3). Shape of the penis is an important identification feature (Figs 144, 145). Remarkably, however, in our country only one male of *T. tricarinatus* has ever been found. For identification, we therefore rely on the tarsi length of the leg II and the height and the distance between the eyes. It is very likely that the majority of the Dutch animals reproduce parthenogenetically (asexual propagation). Martens (1978) reported that this phenomenon, which is rare in harvestmen, occurs in populations from the Danube to Vienna. Also in central Germany parthenogenetic populations are found (pers. comm. Theo Blick 2006, Komposch & Gruber 2004).

♂ Top of the penis is slender, without cavity, and with a transparent membrane (Fig. 145).

**Habitat:** While the habitat of *T. nepaeformis* s.l. seems to be a true forest dweller, *T. tricarinatus* in our country is predominantly found in relatively open areas near the river, such as levees, banks, hawthorn thickets, roadsides, quay roads in floodplains, or ditches. It is found in leaf and grass litter, under rocks, rubble and wood, and in the upper soil layers of tide (flood) marks.

**Phenology:** Adults throughout the year.

**NL:** Quite rare, locally fairly high densities, for example, at the high-water mark of rivers. A large number of the classic Dutch sites of *T. tricarinatus*, as reported by Spoek (1963, 1964, 1975), must be attributed to *T. nepaeformis* s.l. (Wijnhoven 2005b). Up until now *T. tricarinatus* has only been reported with certainty from sites along rivers in the eastern parts of the Netherlands (Nijmegen, Ooij, Weurt, Wageningen, Rhenen, Driel, Wamel, Olst), from Central and South Limburg [Kessel, Wijlre] and Winterswijk). The re-examination of collected material and additional observations will provide greater clarity.

**EU:** Large contiguous areas of Spain, through France, southern England, the Benelux countries and Denmark, to the east of Poland, Slovakia, Romania, Hungary, into Greece.

**Taxonomy:** A revision of the genus *Trogulus* is in preparation (pers. comm. Axel Schönhofer 2007). One of the research questions is whether *T. tricarinatus*, like *T. nepaeformis* s.l., consists of a complex of species (Komposch & Gruber 2004).

## *Trogulus nepaeformis* s.l.

**Length:** 6.1-8.2 mm.

**Recognition:** More robust than *T. tricarinatus*. Distance between the eyes three to four times as large as the eye diameter (Figs 58, 149, 150, 151). Tarsus of leg II has two segments which are at least 1.6 mm long (Figs 148, 153). On average, individuals of *T. nepaeformis* s.l. are darker than *T. tricarinatus* and more males have been found than females. Juveniles are of a lighter colour.

♂ Top of the penis has a cavity, at the base of which are two spines raised on nodes (Fig. 157).

**Habitat:** Under dead wood and stones, in leaf litter and in the upper soil layers. While *T. tricarinatus* in our country seems tied to rivers, *T. nepaeformis* s.l. is possibly more dependent on the moist deciduous forests, such as beech forests on the moraines and calcareous forests on the loose, clay soils. The Nijmegen site though is on the clayey, reinforced gravel banks of a canal on moraine material.

**Phenology:** Adults throughout the year.

**NL:** Rare. *Trogulus nepaeformis* s.l. is very likely present in the Netherlands, but has been overlooked as *T. tricarinatus* (Oudemans 1916 and Spoek 1963, 1964, 1975). The first report under the generic *T. nepaeformis* (Scopoli, 1763) dates from 1998 (Wijnhoven, 1998b). Although the majority of museum specimens of *Trogulus* are still to be verified, *T. nepaeformis* s.l. seems to be restricted to the south-eastern provinces. In addition there are sites in South Limburg where it is known with certainty from Plasmolen, Wellerlooi, Beek (Gelderland), Nijmegen, Ubbergen, Berg en Dal, Reuver and near Winterswijk. The Meuse in Limburg possibly forms a barrier. In the Achterhoek, *T. nepaeformis* s.l. reaches the most north western boundary of its distribution.

**EU:** The area of distribution of *T. nepaeformis* s.l. includes northern Spain and Portugal, France and the Benelux countries, Germany, Switzerland, Austria, Poland, Czech Republic, Slovakia, Hungary, Italy, former Yugoslavia and Romania, where it reaches the eastern edge of its known distribution.

**Taxonomy:** The last few decades have shown that under the name *Trogulus nepaeformis* lies a complex of closely-related species. A number of species have recently been split: *T. closanicus* Avram, 1971, *T. martensi* Chemini, 1983, and *T. falcipenis* Komposch, 2000. A revision of the genus based on DNA analysis is being undertaken by A. Schönhofer (pers. comm. Axel Schönhofer 2007, Schönhofer & Martens 2008). Only after completion of this study can clarification be obtained on the status in the Netherlands, as it is extremely difficult to distinguish between species. It is very likely that at least two sister species will be found in our country (Wijnhoven 2008b). In this publication, this type of complex is indicated with the name *Trogulus nepaeformis* s.l..

### *Anelasmacephalus cambridgei*

**Length:** 2.6-3.6 mm.

**Recognition:** A very small Trogulidae which lives a hidden lifestyle. By covering itself with soil particles it is hard to find by sight alone. Compared with *Trogulus* species the body is not flattened and has a more pear-shaped outline (Fig. 160). On legs I and II, the tarsus has three segments; while the tarsus of legs III and IV has four segments (Figs 164-166). All legs with spines and long hairs (Fig. 160). The hood and eyes are unlike those of *Trogulus* (Figs 162, 163, compared with Figs 37, 155).

♂ The glans of the penis at the top is slightly curved (Fig. 168).

**Habitat:** Dependent on calcareous soils. Deciduous forests on moraines, grasslands and forests on chalk. The habitat is similar to that of *Trogulus nepaeformis* s.l. It is found under stones and wood in the upper soil layers. It hunts in the litter for snails and is sometimes caught in pitfall traps.

**Phenology:** Adults throughout the year.

**NL:** Very rare. Up to now only known in South Limburg, near Arnhem, Nijmegen, Wageningen and the Achterhoek (Spoek 1975, Wijnhoven 2005b).

**EU:** In northern Spain, France, southern England, Belgium, Netherlands, Germany (east to the Elbe), Switzerland and Austria.

## *Ischyropsalis hellwigi*

**Length:** 5.6-8.5 mm.

**Recognition:** Very sturdy, black, strikingly large chelicerae, which are much longer than the body and resemble the claws of a lobster (Figs 169-171). Because of its striking appearance *I. hellwigi* cannot be confused with other native harvestmen. Other sub-species of the genus occur only in central and southern Europe (Komposch & Gruber 2004, Martens 1978). For distinguishing these species it is mainly the shape and development of the first segment of the chelicerae that are most useful.

**Habitat:** It is very specific in its demands on the environment. The soil should be constantly moist. Mainly found in deciduous and mixed forests with rich undergrowth and lots of mossy stumps, dead wood and thick litter and humus layers. Because the main prey consists of snails, the soil must be calcareous.

**Phenology:** Adults throughout the year.

**NL:** Very rare. Only known from the vicinity of Winterswijk (Spoek 1975), where in the late 1960s three specimens were found in an oak forest. These finds are the most north-westerly records up to now.

**EU:** Central European, mainly montane in distribution. Reported from the Netherlands, Germany, Poland, Czech Republic, Slovakia, Hungary, Austria, Slovenia (Martens 1978), Croatia and Bosnia-Herzegovina (Novak 2004, 2005).

**Taxonomy:** The Dutch specimens belong to the subspecies *Ischyropsalis hellwigi hellwigi*

## *Phalangium opilio*

**Length:** 4.3 -7.7 mm.

**Recognition:** Large, robust, and with long legs. The body has numerous strong tubercles. For identification the two small tubercles on the supra-cheliceral (skin-fold above the jaws) are the best characters, but these are often difficult to see (Figs 98, 176, and 179). There is no trident. Populations from moorland have contrasting red-brown tints, whereas those from parks and floodplains have a more even tan.

♂ Easily recognizable by sickle-shaped extension of the second segment of the chelicera (length variable within populations, Figs 177, 180.) and the very long, leg-like palps (Figs 1, 177, 181). The dark saddle is variable in shape, has a reddish-brown to yellowish-brown colour but is sometimes almost absent.

♀ Underside a characteristically chalky-white, usually unspotted. Due to saddle having a zigzag outline it looks similar to that of the female *Mitopus morio*, the differences being: (1) The ocularium is much more robust and occupied with more and larger, acute, black-tipped tubercles (compare Figs 176 and 272, and Figs 98 and 100), and (2), the front area of the saddle occupied by the ocularium is usually paler than the remainder of the saddle (Fig. 178).

**Habitat:** Heat and drought-loving and found in a large variety of terrain types with an open or a semi-open nature: parks, gardens, cemeteries, industrial areas, heathlands, sand dunes, embankment slopes, river dunes, grasslands, forest edges, meadows and low-density woods. A dominant species on sandy soils, but can also live on clay soils. It occupies the herb layer, but can be found on structures including walls, tree trunks, heather, Scots pine (*Pinus sylvestris*), shrubs and timber posts.

**Phenology:** One of the earliest 'summer species'. Adults found from mid-May to early December, during mild winters until January. The main period is from August to October. Interestingly though, juveniles and subadults are found during the entire period of activity. Undoubtedly this is partly due to the occurrence of more than one generation. Wintering of juveniles has not (yet) been observed.

**NL:** Very widespread.

**EU:** Very large range. Found throughout Europe, with the exception of northern Scandinavia, the Alpine regions and the Mediterranean. It has been introduced to many parts of the world.

## *Opilio parietinus*

**Length:** 4.0-7.8 mm.

**Recognition:** Large, leggy. Legs longer than *Opilio saxatilis*, femora of legs I and III are not or only weakly thickened. The ocularium has two rows of seven to 10 teeth, (Figs 44, 185). Male and female with a blurred saddle outline and a slight median line (Fig. 184), lighter than *Opilio saxatilis*. Pedipalps and top of the first and second segment of the chelicerae equipped with black tipped tubercles (Figs 186, 190).

♂ Plates below the top of the penis do not have hairs (Figs 187-189, compare with Fig. 198).

**Habitat:** Prefers warm sites, only in habitats that are heavily influenced man, such as urban areas and villages, on farms, industrial areas. During the day they can sometimes be found on tree trunks, in hedges and bushes, but usually on walls, under windows and canopies.

**Phenology:** Adults from August to November.

**NL:** Very rare or extinct. According to Spoek (1975) *O. parietinus* “is common in the Netherlands, but numbers are reduced almost certainly in the sand dune areas, and there are also no records from the chalk area of South Limburg”. In recent years, there is increasing evidence that *O. parietinus* competes with the recent introduction *Opilio canestrinii* (Wijnhoven *et al.* 2007). It seems fairly certain that *O. parietinus* has now been completely displaced by *O. canestrinii* probably throughout much of western Europe (Komposch 1999). The last sighting dates back to 2006.

**EU:** It originated in Asia Minor (Martens 1978) and became well established throughout Europe (see above).

## *Opilio saxatilis*

**Length:** 3.0-5.8 mm.

**Recognition:** Smaller, darker and more compact construction than *Opilio parietinus* (Figs 192, 193). Femur of the first and third leg remarkably thickened, particularly in males (Fig. 197). Legs with rows of powerful black-tipped tubercles. Ocularium with two rows of 4 to 6 teeth (Fig. 194). Both sexes usually have a clear, light mid-stripe (Fig. 191). The pedipalps and the top of the first and second segment of the chelicerae are equipped with black-tipped tubercles (Figs 195, 196).

♂ The plates below the top of the penis have long hairs (Fig. 198).

**Habitat:** Preference for drier, more open terrain types than *O. parietinus*. Present in dunes, open woodlands, rivers, dikes, dunes and quayside roads in floodplains, including basalt stones along river banks, sometimes in gardens and homes. Found by bending aside grass/vegetation at the base of walls, trees, poles or posts; occasionally found with *O. parietinus* on walls.

**Phenology:** Adults from July to December.

**NL:** Probably generally everywhere. Distribution is not well known. *Opilio saxatilis* is better than *O. parietinus* at holding its own against the strong, offensive newcomer *Opilio canestrinii*. The main reason for this seems to be *O. saxatilis* is not strictly dependent on anthropogenic habitats, which are now completely dominated by *O. canestrinii*.

**EU:** It is originally from the eastern Mediterranean (Martens 1978); now reported from across Europe.

## *Opilio canestrinii*

**Length:** 3.8-8.0 mm.

**Recognition:** Medium sized, light coloured, leggy. Unlike *Opilio parietinus* and *O. saxatilis*, it has no spines on the jaws and palps (Figs 204, 206). Appears at first sight to be *Leiobunum*, but is usually paler (Fig. 201). The ocularium of *O. canestrinii* is very different; quite small and flat, light-coloured and with 4 to 6 acute black-tipped tubercles (Fig. 203).

♂ Trochanters of the legs light brown (*Leiobunum*, in contrast, are darker). The legs are dark brown, sometimes light brown, but ringed alternately with light and dark bands. The penis in cross-section is characteristically angular. On the dorsal side are two curved keel-shaped lines (Fig. 207).

♀ Colouring buff, often typically weak-green tinted. A good field characteristic is the black and white paired transverse stripes on the abdomen (Figs 200, 202). In some individuals (especially older ones) contrasting brown or orangey.

**Habitat:** In gardens and parks of towns and villages, areas containing landscaped elements but also in a variety of more natural habitat types, such as forest edges, rural areas, light woods and rugged wooded shores, also on herbs and shrubs, often on walls.

**Phenology:** Adults from the beginning of July, lasting during mild winters until February. The period of highest activity is usually from September to November.

**NL:** The first Dutch record was in 1991 (Van der Weele 1993). Nowadays it is one of the most abundant species in built-up areas. See also *Opilio parietinus*.

**EU:** Originally occurred in Italy, then, over the last two decades, it has spread over large parts of western Europe. Known from: Italy, France, the Benelux countries, Denmark, Sweden, Germany, Poland, Switzerland, Austria, Czech Republic, Slovakia (Blick & Komposch 2004) and Great Britain (Hillyard 2000).

**Taxonomy:** Spoek (1962) described this species under the name *Opilio ravennae* Spoek, 1962, based on material that was sent to him from Italy. However, it appeared later that Thorell had already described the species.

## *Platybunus pinetorum*

**Length:** 5-8 mm.

**Recognition:** Strong and impressive, long legs (Figs 19, 211). The ocularium is much broader than long, both in the centre and at the front, deeply grooved between eyes. Colour of ocularium reddish brown (Fig. Fig. 212), with black rimmed eyes. Tubercles on the femur of the palp are longer than the thickness of the femur (Figs 213, 214). Juveniles resemble those of *Rilaena triangularis* (see species text).

♂ Almost black with reddish legs, usually with an unclear saddle.

♀ Very marked contrast, a dark saddle with a sharply defined silver rim (Fig. 210). The genital morphology of this species is very similar for the whole genus of *Platybunus*. The shape of the palp and the placement of certain tubercles on the palp are important identification characteristics for separating the sexes.

**Habitat:** Juveniles and subadults in litter and herb layer, adults mainly on tree trunks, bushes and tall herbs. The site at Nijmegen consists of moist deciduous forest on clay with rich undergrowth at the base of a moraine. Populations at Loenen live in forests including larch, oak, birch and pine with a rich undergrowth of blueberry.

**Phenology:** Adults from late March to late June.

**NL:** Very rare. In 1998 for the first time in the Netherlands it was found in Beek-Ubbergen, east of Nijmegen (Wijnhoven 1998b). Since then observed there almost every year. In 2008 and 2009 also found at Beekbergen, Loenen and Meinweg (Limburg).

**EU:** European montane. Reported from the Netherlands, Belgium, Luxembourg, Germany, Austria, Switzerland, eastern France, northern Italy and Romania. The nearest populations are outside the Netherlands in the Eifel and the Black Forest. The species is increasingly reported in Germany, possibly extending to the north (Buick & Komposch 2004).<sup>3</sup>

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<sup>3</sup> Now found in Scotland (2014). See Harvestmen Recording Scheme (SRS/HRS)  
<http://srs.britishspiders.org.uk/portal/p/Welcome>

### *Megabunus diadema*

**Length:** 2.6-3.7mm.

**Recognition:** Small with long, thin legs (Fig. 217). Ocularium large, with a crown of two rows of five very long, pointed tubercles. (Fig. 43). In the palp the ventral side of the femur is covered with long tubercles. The patella and tibia of the palp have blunt projections (apophyses) to the distal ends. It cannot be confused with other species.

**Habitat:** Tied to places with high humidity. Found on rocks and tree trunks, often near seashores.

Parthenogenetic reproduction, males are very rare (Stol 2005).

**Phenology:** In the British Isles from early May to late August.

**NL:** Not recorded in this country. Possible on (basalt) dykes along the coast.

**EU:** Pyrenean, French Channel coast, Great Britain, Ireland, Iceland, west coast of Norway, Faeroe Islands (Martens 1978, Stol 1999).

## *Rilaena triangularis*

**Length:** 3.5-7.0 mm

**Recognition:** Quite distinctive with a light brown appearance and long legs (Fig. 219). The spine-tipped tubercles on the ventral side of the femur of the palp, shorter than the thickness of the femur (Fig. 223). On the inside of the palp at the distal end of the femur is a clear apophysis. Ocularium compared to *Platybunus pinetorum* narrows to the front, about as wide as, or wider, than long. The furrow between the two rows of seven to 10 acute tubercles does not significantly deepen to the front and is generally weak (Figs 220, 221) and the eye ring is tan (not brown). Juveniles of *R. triangularis* resemble those of *P. pinetorum*. The spine tipped tubercles on the femur of the palp in adult *Platybunus pinetorum* are noticeably longer, so much so that this feature can be used to separate adults of both species, but not noticeably larger in juveniles. The ocularium in young animals seems out of proportion with the rest of the body (Fig. 222). This easily distinguishes *Rilaena* and *Platybunus* from other harvestmen.

♂ The saddle is pale yellow-brown and the outline is vague or almost absent. There is a triangular shaped, dorsal apophysis on the distal end of the chelicerae (Fig. 224).

♀ The abdomen with a more-or-less clear saddle outline but without the sharply defined silver border seen in *P. pinetorum* (see female, Fig. 218). There is often a strong contrast but many forms are lighter and more evenly coloured.

**Habitat:** Found in a wide range of habitats, for instance, gardens, forests, parks, hedgerows, and thickets, and also in more open areas such as rivers, dikes, dunes and rough roadsides. Only dry habitats are avoided. Juveniles present in late summer, autumn and winter, and found under logs, in litter, hay or in field layers. Adults found in bushes and higher vegetation, such as nettles and bramble thickets, and on tree trunks.

**Phenology:** This is a common species and the only one in our country that matures in the spring. The main period is from April to July. Juveniles overwinter and can be seen from August.

**NL:** A widespread distribution.

**EU:** Atlantic. Widely distributed throughout Europe in a contiguous manner including Britain, France, the Benelux countries, Scandinavia, Poland, the Baltic States and western Russia, south into Bosnia. The southern boundary area is not well known. The species seems to be missing from Italy and Spain and is sporadic in the Alps.

### *Lophopilio palpinalis*

**Length:** 2.8-4.0 mm.

**Recognition:** Small, rather short-legged, with characteristic warm, reddish-brown base colour (Fig. 229). Saddle shape usually unclear, but often much less sharply defined than the ones shown (Fig. 228). Ocularium is distinctive: second spine clearly longer than the other (Figs 228, 230). Trident conspicuous, sharp spines inclined forward, central tooth longer than the lateral teeth. Femur of pedipalps has long, white, black-tipped tubercles on the ventral surface. On the inside of the pedipalp the femur, patella and occasionally the tibia, have an apophysis (Fig. 231). On top of the femur and patella, mainly on legs III and IV, are conspicuous long spines (Fig. 229).

♂ The penis has a broadened base (Fig. 232). The stylus tip is characteristically curved or twisted (Fig. 233). This and other species from the subfamily Oligolophinae are characterized by a hook on the basal segment of the chelicera: the ventral spur (for example, Figs 238, 245).

**Habitat:** Prefers moderately moist forests and grasslands, but also found on drier sites in the dunes. It is mainly found in the litter layer, in moss and beneath undergrowth, but sometimes on shaded vegetation (for example, bracken, ground elder or nettle) and on tree trunks.

**Phenology:** Adults in August to late December, during mild winters until January. The main period of activity falls in November.

**NL:** Probably rather common but little is known of the distribution.

**EU:** Spread over large parts of Europe: Britain, France, the Netherlands, Belgium, Germany, Denmark, southern Sweden, Latvia to the east of the Crimea, south into Bulgaria, Montenegro, Bosnia-Herzegovina.

## *Oligolophus tridens*

**Length:** 3.4-5.2 mm.

**Recognition:** Quite small, relatively short legs (Figs 26, 235.) Trident quite small, the members are close together and the middle member is often the longest in the female. Behind the trident are a few smaller tubercles (Fig. 236). *Lacinius ephippiatus* has a similar appearance, but a trident with three almost equally long, well separated, large members (compare with Figs 257, 259). The femur of the legs has longitudinal rows of short black spines (whereas in *L. ephippiatus* the femur has rows of acute, inclined tubercles). On the ventral surface of the first segment of the chelicerae there is a hook (Fig. 238).

♂ Although in this species the colour is quite variable, males are recognizable by the clear, black saddle. Often well behind the ocellarium the black outline of the saddle narrows to a parallel band running towards the rear, ending in two semi-circular patches (Fig. 234). The black saddle markings occasionally extend to the entire width of the abdomen. The penis is very long and slender (Figs 239, 240).

♀ The saddle outline is recognizable as a row of block-shaped spots.

**Habitat:** In woodlands, hedgerows, overgrown lawns, parks, gardens, and open wet places. Undergrowth, rocks, in clumps of grass, litter and higher in the vegetation (especially in nettles). Often found under stones and wood in small groups.

**Phenology:** Adults from August until December. The period of greatest activity is in November (Spoek 1975).

**NL:** Very common and widespread.

**EU:** Large areas of Europe; lacking only in the Mediterranean climate zone. Recorded from France, the Benelux countries, Great Britain and Ireland, Sweden, Norway, Iceland, Finland, Germany, Switzerland, Austria, Poland, the Baltic States, Russia, the former Yugoslavia, Italy, Czech Republic, Slovakia and Romania.

## *Oligolophus hanseni*

**Length:** 3.3-4.8 mm.

**Recognition:** Quite small, relatively short legs. The species is darker on average (more 'bluish') than the related species *Oligolophus tridens* and *Paroligolophus agrestis* (Figs 13, 14, 242). It is more compactly built compared with *O. tridens*, especially the male (compare Figs 234 and 241). The trident is fairly small with black-tipped tubercles. Directly on each side of the trident there is at least one additional tubercle (Fig. 243). Behind the trident is a group of four to seven black-tipped tubercles. Last segment of the pedipalps with ventral hook (Fig. 245). Ocularium is dark, the front face is inclined, with two rows, of five or six white tubercles which converge at the crown, the rear tubercles are usually more pronounced than the front.

♂ The saddle edge is unclear. Patella of palp without projection, only slightly thickened at the top. The underside of femur has spines. The movable digit of the chelicerae, has a rectangular ventral spur at its base (Fig. 244). Penis body has a characteristically folded structure (Figs 246, 247). Pattern usually contrasting light and dark mottled, especially on the abdomen, saddle with an indistinct outline.

♀ Some are very similar to a dark version of *Paroligolophus agrestis*, but the tubercles on the ocularium are a good distinguishing feature.

**Habitat:** General habitat is drier than for *O. tridens*. In coniferous and deciduous forests, parkland, heathland overgrown (Spoek 1997), in rural and anthropogenic habitats including, gardens and river banks with debris or rocks; very often on tree trunks.

**Phenology:** Adults from September to early February. The period of greatest activity is in November to December (Spoek 1963).

**NL:** Probably quite generally distributed, but the number of recorded locations is small.

**EU:** Atlantic distribution. Contiguous area from northern Spain, France, the British Isles, the Benelux countries, German lowlands and southern Scandinavia to the west of Poland; sporadically in Switzerland.

## *Paroligolophus agrestis*

**Length:** 2.8-4.6 mm.

**Recognition:** Quite small, stocky with relatively short legs (Figs 12, 249). It has similarities to *Lophopilio* and *Oligolophus* species. In the field it can be reliably recognized by the smooth ocularium, without tubercles, having only fine bristles (Figs 248, 250). Ocularium usually buff, with male and older specimens often dark brown. Trident quite small, the central member is the largest, usually in front of the two flanking members. Trident without any other tubercles directly to the sides (Fig. 250); usually there are two (or three) tubercles behind, giving a typical group formed of five (or six) teeth (Fig. 84) The first segment of the chelicerae has a ventral hook (Fig. 253). Often vividly coloured, the abdomen has a broad reddish-brown central stripe, which is enclosed by darker spots. On the last segments of the abdomen there is often a dark lateral band which strongly contrasts with the underlying light spots.

♂ Male genital plate hollowed out at the top (Figs 53, 252). The penis is long and slender with an extremely wide base. The glans has a very long stylus (Fig. 255).

♀ Unlike many other harvestmen, females have more contrast and are more richly marked than the male (*Oligolophus hansenii* may have a similar saddle). The top of the female genital plate has a deep trapezoidal notch (Figs 52, 251).

**Habitat:** Found in diverse habitats: parks, forests, dunes, grasslands and gardens in towns and cities. Adult animals are found in moist to fairly dry places, against walls, in the litter of light vegetation, in thickets and in the crown of trees.

**Phenology:** Adults from July to early February and during mild winters up to March. The period of greatest activity is in November and December (Spoek 1963, Wijnhoven 2008a).

**NL:** Very widespread.

**EU:** Atlantic: Britain, Ireland, Sweden, Norway, Denmark, the lowlands of Germany, Poland, Netherlands, Belgium, Luxembourg and France to northern Spain.

### *Lacinius horridus*

**Length:** 4.0-6.9 mm.

**Recognition:** Body and legs occupied by robust acute tubercles (Fig. 256; easily seen by eye). Ocularium has two rows of four large acute tubercles (Fig. 90). The trident has remarkably long, thin tubercles, diverging from the base outwards (Fig. 90). Not to be confused with other species.

**Habitat:** Heat and drought-loving. Found in open landscapes and anthropogenic habitats, at the base of walls, under-stones, undergrowth, in clumps of grass and dry litter.

**Phenology:** Adults from August until December.

**NL:** Not indigenous. To be expected in dry wasteland or poor habitats such as railway embankments or cemeteries.

**EU:** Southern Sweden and Finland, Germany, Poland, France, Switzerland, Italy, Czech Republic, Slovakia, Baltic States, Austria, in southern Europe in Greece. There is a site in Belgium (Vanhercke 2004).

### *Lacinius ehippiatus*

**Length:** 3.7-4.8 mm.

**Recognition:** Rather small to medium-sized, short-legged (Fig. 258). It can be confused with *Oligolophus tridens*. The trident has long, upward-pointing teeth (Figs 257, 259) but unlike *O. tridens* the trident is smaller with the middle tubercle longest. The ocularium has two rows of five or six fairly long tubercles. The femora of the legs have rows of setae and black-tipped tubercles (Fig. 260); *O. tridens* only has spines. The articulated segment of the chelicerae has a ventral tooth at its tip (Fig. 262). The femur of the palp has a knob-like projection on the inside near the top, which has spine-tipped tubercles (Fig. 261, right).

♂ The abdomen has a striking dark saddle, which narrows behind the ocularium and then runs parallel. The dark edges contrast with the light flanks (Fig. 257). The glans of the penis ends in a broad, knife-shaped stylus (Figs 264, 265).

♀ Saddle edges in the middle abdominal segments are less sharp.

**Habitat:** Moist; undergrowth and leaf litter, the herb layer of forests, coastal dunes and river areas (Spoek 1963, 1997).

**Phenology:** Adults from late May to early September. The period of highest activity falls in August (Spoek 1963).

**NL:** Relatively common.

**EU:** Widely distributed in Europe, with the exception of Spain, Mediterranean and Alpine climates and northern Scandinavia (Martens 1978).

## *Odiellus spinosus*

**Length:** 7.0-9.5 mm.

**Recognition:** Robust, with relatively short legs (Fig. 267). Saddle outline usually evident in male but sometimes only noticeable at the rear of the female. One of the best features is the trident. This is exceptionally robust, about as tall and wide as the relatively small ocularium (Figs 39, 268). Base of the first segment of the chelicera has a ventral hook.

♂ For male penis see figures 270, 271. In the male palp, the ventral surface of the femur has conspicuous spine-tipped tubercles.

**Habitat:** Heat and drought-loving. Found on sandy soils, heath land, barren roadsides, dunes with creeping willow vegetation, river dunes and open dunes with lichens, marram grass and sheep fescue, also sunny, open gardens and cemeteries (Spoek 1963, Wijnhoven 2005b). At a lower level, among pieces of dry wood, litter and low against walls.

**Phenology:** Subadults occur from June to August, adults from early July to late December. The highest activity is in November (Spoek 1963).

**NL:** Rare. In Holland it reaches the northern edge of its distribution. This is based on a small number of observations; in the past it was found at Veluwe, also in the North and South Holland dune area and in the North Brabant heathlands (Spoek 1975). It was found presumably in both types of habitat (urban area and open, rapidly-warming scanty vegetation).

**EU:** In Portugal, Spain, Corsica, France, southern England, Belgium, Netherlands, Germany, Switzerland, Italy, Slovenia, Croatia (Blick & Komposch 2004, Martens 1978).

## *Mitopus morio*

**Length:** 4.2-8.0 mm.

**Recognition:** Strongly marked with fairly long legs (Fig. 273). No clear trident, but a variable number of small tubercles, one of which is central to the ocularium (Figs 100, 272, 274.) The basal segment of the chelicera with ventral hook (Fig. 276).

♂ Easily recognizable by the yellow ground colour with jet black saddle outline behind the ocularium, sharply constricted then broad, tapering to rear. The dorsum is sometimes entirely black. The base of the glans of the penis has a fold of skin and a bladder that may become swollen (Figs 277, 278).

♀ Colour and contrast quite variable, saddle outline sometimes unclear (Figs 54-56). In the most highly contrasting specimens the shape is strongly angular and constricted; the 'zigzag' outline of the saddle is a good identification feature. Some individuals have a sharp, light, median stripe. Can be confused with *Phalangium opilio*, which has many more robust tubercles on its legs, body and ocularium (compare Fig. 272 with Fig. 176, or Fig. 100 with Fig. 98). Moreover, the front of the saddle of *M. morio* is better defined, not being as pale as the cephalothorax of *P. opilio*; to the rear, the saddle is more serrated.

**Habitat:** Has a preference for ribbon-shaped landscape elements such as hedgerows, rough verges, and humid corners in floodplains, along canals, in poplar forests and marshy places. The highest densities are to be found in rugged shoreline vegetation, on clay soils. In summer and autumn, often quite easily found by sight in large numbers on the top of brambles, nettles in fields and against posts and trunks in meadows and moist forest edges.

**Phenology:** Adults occur from mid-June to mid-November (Spoek 1963).

**NL:** Widespread

**EU:** A very large range. The area includes the temperate and arctic zones of Europe, Asia and North America.

## *Dicranopalpus ramosus*

**Length:** 3.0-6.0 mm.

**Recognition:** Medium size, leggy. Resting posture unmistakable, all legs parallel and extending laterally (Figs 15, 281). Ocularium wider than long, smooth, with a few small hairs (Figs 38, 283). The patella of the palps has a long projection (apophysis), which appears to give the palp a forked appearance (Figs 15, 284, 286). Even the smallest juveniles can be identified. The base of the femur of the palp has a small protrusion (Figs 284, 285). General colour tan, but older specimens can be reddish brown to almost black. There is a rare colour form with a black centre stripe.

♂ Brown to yellow with a black mask over the eyes ('Zorro', Fig. 280). Tip of papal patella apophysis is a yellow brown or tan. For inexplicable reasons, the shape of the penis (Figs 289-291) differs significantly from both the description and the drawing of Martens (Martens 1978; Figs 711 and 712).

♀ Yellow brown background with a saddle of dark and light patches in a typical pattern (Fig. 280). The tip of the papal patella apophysis is blunt and black. The abdomen has a hump to the rear (Fig. 282).

**Habitat:** Mainly in bushes and trees (managed or cultivated), in anthropogenic habitats such as gardens, parks and cemeteries. It seems to be able to maintain a hold further from buildings in moist deciduous forests, forest edges, hedgerows, and even river floodplains. Juveniles and subadults found in the herb layer (remarkably often on nettles), in shrubs, conifers, hedges, etc., often in fairly shady areas. They are easily found by sweeping a likely area of vegetation. The adults on average are higher in hot, sunny places, bushes, trees, hedges against posts in pasture, on walls of buildings, and occasionally indoors. Juveniles of this harvestman are sometimes windblown (Noordijk *et al.* 2007).

**Phenology:** Juveniles occur from mid-July, adults from mid-August. In mild winters it is occasionally seen until February (Wijnhoven 2004). The main period is from September to December.

**NL:** Widespread. In many places (such as Nijmegen, Ede and Wageningen) they are numerous. Initially found in the Netherlands in 1993 (Cuppen 1994). Since 2003, a rapidly growing number of domestic sites are known (Wijnhoven 2004, Noordijk & Wijnhoven 2006). It has also been recorded from the coastal provinces, although in 2007 there were no records from the coastal province of Flevoland (Noordijk *et al.* 2007).

**EU:** Known from Morocco, Spain, Portugal, France (Martens 1978), Belgium (Slosse 1995), England, Scotland, Ireland (Cawley 1995) and Germany (Schmidt 2004). It was originally found in Morocco, the Iberian Peninsula and France (Martens 1978). Found in the south of England from 1957 (Sankey & Storey 1969) and then from the mid-1990s it quickly advanced to the north, to Scotland and Ireland. Initial records reported from Germany in 2002 (Schmidt 2004).

### *Homalenotus quadridentatus*

**Length:** 3.0-4.5 mm.

**Recognition:** Characteristic species in our country only to be confused with *Astrobunus laevipes*. This species is light-coloured, short-legged, with a strongly flattened body. The abdomen has rectangular dark spots with white conical tubercles (Fig. 292). Four prominent white tubercles can be seen at the posterior margin. The leading edge of the carapace has a large tubercle and a smaller tubercle underneath (Figs 294, 295). The ocularium has two rows of two to five teeth, in juveniles often larger and more pointed than in adults (Figs 294, 295). Adult specimens are coated in adhering soil particles, thereby becoming uniformly light to dark brown (Fig. 293).

**Habitat:** It is restricted to calcareous soils where it is found in forest litter, under stones and dead wood in deciduous forests, calcareous grasslands, woodland edges and roadsides (according to Martens 1978). It is often found together with *Trogulus nepaeformis*. In South Limburg both species are found in the same habitats.

**Phenology:** As *H. quadridentatus* lives more than a year, there are overlapping successive generations. Adults occur through the whole year.

**NL:** The species is relatively common in South Limburg (Spoek 1975), elsewhere it is very rare. With regard to the European continent it is found to the south of a line drawn through our country's northern border. Isolated records are from in Kessel (Middle Limburg), Wageningen and Maarheeze (Noord-Brabant). It has been recently recorded in several places in Zeeland (Noordijk & Wijnhoven 2009).

**EU:** It has a relatively small range (Martens 1978). It is characterized as Atlantic-sub-Mediterranean. Outside the Netherlands, it is reported from the north of Portugal and Spain, France, Belgium, Switzerland and southern England. Not in Germany.

## *Astrobunus laevipes*

**Length:** 2.6-3.8 mm.

**Recognition:** Small, dark, short-legged. The abdomen has rows of cone-shaped tubercles (Figs 299, 300). The ocularium has "Tintin"<sup>4</sup> white tubercles, but only at the level of, and behind, the eyes (Figs 42, 300). Front edge of the carapace with two adjacent tubercles (Figs 42, 302). It remains motionless after being disturbed. Has excellent camouflage, often covered with adhering soil particles. Because the genital morphology differs little between the species of *Astrobunus*, external characteristics are mainly used for distinguishing species, such as the height of the cone-shaped dorsal spines and length and placement of the tubercles and the ocularium. In the Netherlands only *A. laevipes* is to be expected, so that the field attributes are sufficient for a certain determination.

**Habitat:** A large majority of sites are at or above the high-water level in river floodplains: on embankments, in peripheral areas of land above high tide, also at brickworks and on the higher wharf roads. Many habitats are open or semi-open, with few trees (such as willow, poplar) or shrubs (hawthorn, bramble and elder thickets). It is found in leaf litter, under rocks and dead wood in the drift line. Highest densities in ruderal (disturbed) habitats with heaps of old bricks, rubble or basalt stones.

**Phenology:** Adults have overlapping successive generations throughout the year. It lives for about 15 months (Martens 1978).

**NL:** Rare, generally local. It was first discovered in 2003 in the Netherlands (Wijnhoven 2003). It probably arrived on material floating on the Rhine. Since then found on the Waal (in Bemmelen, Millingen, Kekerdon, Ooij, Ubbergen, Nijmegen, Weurt, Beuningen, Druten and Haaften) and on the Lower Rhine near Wageningen and Rhenen. Probably many more places along the river have been colonized.

**EU:** Central and southern Europe. Outside the Netherlands reported from Germany (Baumann *et al.* 1992, Martens 1978), Austria, Czech Republic, Slovakia, Hungary, Romania, south Poland, Bosnia, Slovenia (Novak 2004, 2005) and northern Italy. Its north-western distribution is less well known. It has probably expanded to the north. The nearest northerly record outside the Netherlands is from Mainz, Germany (Hofer & Spelda 2001).

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<sup>4</sup> **Tintin** is a fictional comic character in *The Adventures of Tintin*. He has a quiff hairstyle.

## *Leiobunum limbatum*

**Length:** 3.9-7.4 mm. Leg II up to 92 mm.

**Recognition:** Large, with very long legs.

♂ Red-brown, dark brown to black edges (Fig. 307). Saddle shape can be seen as a slightly darker red-brown area in the centre. The area around the ocularium is light in colour with a few dark spots. The legs are dark brown to black. The ventral surface of the palpal femur has acute black-tipped tubercles at the base; in the middle is a row of black spines. On the ventral surface of the tibia of the palp is a very small area of spines. The tarsus of the palp curves inwards and has no spines on its ventral surface.

♀ Ground colour reddish brown with grey and dark patches behind the abdomen, which form a dark transverse band (Fig. 308). The ocularium is light in colour with a few dark spots.

**Habitat:** Found in moist to relatively dry deciduous and coniferous forests, but also in more open areas, for example against cliffs and eroded steep walls.

**Phenology:** Adults occur from July to late December.

**NL:** Not an indigenous species. It seems to have recently expanded its range, possibly in the eastern part of our country.

**EU:** Found in the Alps and Germany. The nearest sites to the Netherlands are in northern Germany and at Wuppertal.

## *Leiobunum rotundum*

**Length:** 3.0-5.5 mm. Leg II 45-60 mm.

**Recognition:** Noted for its very long legs (Fig. 310). Ocularium black with a light median band (Figs 104, 309, 312) sometimes with darker specimens entirely black. Very small teeth-like structures (denticles) on the cuticle in rows, on the front and back of the coxa I-IV but the row on the back of coxa III is missing.

♂ Smooth reddish brown, legs black. The trochanters are black (distinct from *Opilio canestrinii*). Shape of the penis and palp are important taxonomic characteristics for discriminating the species in the genus *Leiobunum* (Figs 315, 316).

♀ With a dark saddle with approximately parallel sides and ending in an anchor shape (Figs 309, 311). Rear of the abdomen is often a striking orange-red.

**Habitat:** Has no specific habitat requirements; inhabits all sort of areas with higher vegetation such as trees, shrubs and herbs, such as bramble thickets, forest edges and rugged river dune vegetation. Found in towns and villages, in gardens and parks, on walls, bridges, fences, hedgerows, under gutters and so on. It is regularly seen in aggregations of tens to about a hundred individuals (Fig. 34).

**Phenology:** Adults occur from late June to late November. The period of greatest activity is in August and September.

**NL:** Very widespread. In the last few years it seems to taken to urban areas in noticeable numbers, possibly due to competition with *Opilio canestrinii*.

**EU:** Atlantic. It is missing from the Mediterranean regions. Reported from Portugal and northern Spain, France, Ireland, Britain, the Benelux countries, Germany, Switzerland, Austria, Denmark, Norway, Sweden, Poland, the Baltic States, Hungary, Romania, Croatia and Slovenia (Novak 2004, 2005) and northern Italy.

## *Leibunum blackwalli*

**Length:** 2.5-5.2 mm. Legs II up to 50 mm.

**Recognition:** Medium size with long legs. Resembles *L. rotundum*, but is usually clearly of a more slender build, especially the male. The ocularium light with dark mid-stripe, dark rimmed eyes (Figs 105, 317-320).

♂ Smooth reddish brown, often dark to the front of the carapace. Form of penis and palp are important taxonomic characteristics of the genus (Figs 321, 324, 325). There are two dark spots on the penis (Figs 324, 325), which can be seen from both sides. On the leading edge of the coxae there are rows of very small teeth-like structures in the cuticle.

♀ It has a conspicuous broad triangular-shaped saddle with base to rear of abdomen (Figs 317, 319); a 'pine-tree shape'. Again, rows of very small teeth-like structures in the cuticle, but this time on the leading and back edges of all the coxae.

**Habitat:** Is usually in more open habitats than *L. rotundum*: in fields, dunes, along canals, and forest edges, but also in shady deciduous forests with a dense undergrowth of ivy (*Hedera*), for example. Found in the herb and shrub layer, under loose pieces of wood, between rocks and tussocks of grass, sometimes in the company of *L. rotundum*. Found also in cities and towns but far less commonly than *L. rotundum*.

**Phenology:** Adults occur from late July to early January. Period of greatest activity is in September (Spöck 1975).

**NL:** Rather common, but not nearly as numerous as *L. rotundum*. Its distribution is insufficiently known. It has possibly decreased due to competition with *Opilio canestrinii*.

**EU:** Atlantic distribution. In the Mediterranean climate zone it is largely missing. Area covers the north of Portugal and Spain, France, Belgium, Netherlands, Luxembourg, the British Isles, southern Sweden, Denmark, Germany, Switzerland, Poland, Czech Republic and Slovakia.

## *Leiobunum rupestre*

**Length:** 3.6-6.4 mm. Leg II up to 65 mm.

**Recognition:** Noted for its very long legs.

♂ Black with a faint blue-green metallic lustre and a light area on the left and right of the ocularium (Fig. 327). Occasionally the light areas to either side of the ocularium merge with the abdomen. The palp has a dense patch of spines to the base of the tibia. The tarsus of the palp is weakly curved inward, no spines on the underside. Trochanters of the legs light coloured (in contrast to *Leiobunum* sp. A).

♀ A dark, irregular-shaped saddle, with random dark patches, especially on the rear half of the abdomen. The trochanters are light coloured (Fig. 328).

**Habitat:** Found in beech and coniferous forests, mountains rising above the tree line. In the north of the area (Germany, Denmark, Baltic Sea) it is mainly synanthropic in parks and gardens, against walls.

**Phenology:** Adults occur from early August to late October.

**NL:** Not native, possibly in the east.

**EU:** Originally found in the Alps and Carpathians: Switzerland, Austria, south Germany, Italy, and the former Yugoslavia into eastern Ukraine. It has recently expanded into Poland, south Scandinavia, Denmark, and the Baltic region of Latvia into northern Germany (Hamburg).

**Taxonomy:** Populations in northern Germany and Denmark are attributed by some to *Leiobunum rupestre* (Blick & Komposch 2004, Martens 1978), by others to *Leiobunum tisciae* Avram 1971 (Starega 2004).

## *Leiobunum* sp. A

**Length:** 4.0-6.4 mm. Leg II 80-90 mm.

**Recognition:** Large, dark, with very long legs. It has a leg 'span' of 18 cm and is by far the largest harvestmen of our country. Ocularium is black, sometimes with a slightly lighter midline (Fig. 106). There are rows of small denticles on the front and back of the coxae, except on the back of coxa III (Fig. 332). This is the same arrangement as in *L. rotundum*. It has a characteristic green metallic sheen (Figs 330, 331).

♂ Very dark grey to black (Figs 329, 330). There is a patch beside the ocularium which sometimes has an orange-brown to pale-yellow stain. The underside of the coxae and legs are a contrasting yellow. Legs from the trochanters are black with the tips of tibia I and IV in some instances white. Form of penis and palp are important taxonomic features (Figs 333-336). The tip of stylus has a small swelling (Fig. 336).

♀ Light spots/patches cover most of the top of the abdomen, and there is a dark saddle (Figs 329, 331). The underside is pale yellow to light orange-brown. The tips of tibia I and IV especially are extensively white-ringed. Juveniles have pairs of white spots in the saddle shape (Fig. 329).

**Habitat:** Associated with stony ground. It is also found in ruderal places (disturbed areas) and around houses, near rivers, by former brickworks, on walls, in old brick ovens, under window sills and gutters, under bridges, concrete blocks and the like. It forms impressive aggregations of 50, to more than 1000. There are instances where the bodies are crammed into a few thin layers (Fig. 33). The white tips of the tibiae of the legs are then easily seen.

**Phenology:** Adults occur from late June to late December. The greatest activity is in September.

**NL:** Rare, locally abundant. First found in Ooij, east of Nijmegen in 2004. Recently it was also found in Spijk, Ooij, Bommel, Beuningen, Deest, Druten, Westzaan, Asperen, Amsterdam, Schagen and Ruinerwold. The danger is that this invasive species in the coming years will greatly expand and then possibly pose a threat to other species of harvestmen.

**EU:** Now reported from the Netherlands, Germany, Austria and Switzerland (Wijnhoven *et al.* 2007).

**Taxonomy:** A *Leiobunum* which has yet to be determined to species. It could possibly be new to science. At present this a provisional *Leiobunum* species referred to as 'A'. Wijnhoven *et al.* (2007) describe the morphology and the European sites (under the name *Leiobunum* sp.).

## *Nelima sempronii*

**Length:** 3.5-6.6 mm. Leg II 35-47 mm.

**Recognition:** Medium, *Leiobunum*-like, with medium, slender legs. The coxae of the legs have no denticles (in contrast to *Leiobunum* sp.). Leg II is remarkably thin; the femur is twice as thin as the femur of the first leg. The ocularium is pale, with black-rimmed eyes and two rows of five to seven very small denticles (Figs 102, 339). These denticles are slightly finer than in *Nelima doriae*. The ground colour of both sexes is light brown to ochre. The back is covered with fine, dark denticles.

♂ Tan with small silver spots and dark markings on the carapace (Figs 337, 338). The legs are dark from femora to claw. The tarsi of the palps is notable (Fig. 340) and characteristically curved and thickened at the base. Leading up to the claw, on the underside, are rows of black spines (Martens 1969).

♀ In contrast has a richer pattern with silvery spots and dark areas. On the abdomen there are usually a few dark and light spots, separated by a slight median band (Fig. 337).

**Habitat:** More or less moisture-loving, occupying the river and shore line. In the northern part of the area often synanthropic (pers. comm. Komposch 2004). In the Netherlands it is found on river dunes, rugged overgrown summer dikes, and in small patches of woodland and ruderal (disturbed) areas with a lot of debris. It is also found in rough vegetation, particularly, willow, bramble, hawthorn, and nettle. Found also under basalt stones, rubble, in tall grass against timber posts, on concrete walls, exposed vertical soil faces, and in the vegetation at the base of walls.

**Phenology:** Adults occur from early August to late November. The period of highest activity is from mid-September to mid-October.

**NL:** Very rare but locally quite numerous. In 2004 it was discovered in Vlietberg in Ooijpolder east of Nijmegen (Wijnhoven 2005). It possibly arrived in the Netherlands from the Rhine on floating material. It was also found in 2006 in Bommel and Millingerwaard (Colenbranderbos). Since the rivers are increasingly suitable habitats because of large-scale nature conservation projects, it is expected that the species will establish in more places.

**EU:** Central European, south and east of the Alps. As far as is known the original range covered parts of Slovenia, Croatia (Novak 2004), Hungary, Czech Republic and northern Italy. *N. sempronii* has recently established itself in other locations, probably as a result of human transportation. These secondary areas of expansion are city parks in Warsaw (Starêga 1975) near Berlin and Leipzig (Martens 1978) and areas along the Saale in Saxony-Anhalt (Blick *et al.* 2002). The nearest site to the Netherlands is located in Wuppertal, Germany (Plates 1994).

## *Nelima doriae*

**Length:** 3.2-5.3 mm. Leg 11 24-34 mm.

**Recognition:** Medium, fairly short, slender legs. The coxae of the legs have no denticles (in contrast to *Leiobunum* sp.). Leg II much shorter than in *N. sempronii*. Ocularium pale, with black-rimmed eyes and with two rows of six to nine small denticles and accompanying spines (Figs 103, 347). These denticles are more robust than *N. sempronii*. In the dark areas in front of the ocularium, there are some black spines. The ground colour of both sexes is light brown to ochre. The surface of the dorsum has small denticles which, unlike *N. sempronii*, are not darker than the background colour.

♂ Tan with small silver spots and dark markings on the carapace (Figs 344, 345.). First two segments of the abdomen with pairs of oblique dark spots. The legs from the femora are dark brown. The tarsi of the palps are almost straight, without a patch of black spines at its base. The penis is characteristically shaped with broad wings at the top (Figs 350, 351).

♀ Pattern has a richer contrast with silvery spots and dark areas. At the back of the abdomen is usually a contrasting pair of dark and light spots, separated by a wide, pale median band (Figs 344, 346.).

**Habitat:** Mainly introduced in man-made habitats such as gardens and parks. The Dutch site is a rich, oak-wooded bank left by gravel works on the River Meuse. Found under wood, stones, waste, and at the foot of concrete blocks.

**Phenology:** This species has an unusual number of generations in Holland, with probably two generations per year. Adults occur throughout the year, except in January and February, with juveniles and subadults of all ages throughout the year, even in winter.

**NL:** Very rare. The only population known was discovered in 2006 (Wijnhoven 2007). It arrived at Kessel and now extends along the Maas in Central Limburg. It may already be established in more places.

**EU:** Originating from the Mediterranean, it is reported from Morocco, Spain, southern France, Italy, Croatia, the Caucasus and the islands of Corsica, Sardinia and Sicily; Crete (probably imported, Martens 1978). Introduced and established in Australia, New Zealand, and Argentina (Acosta & Cokendolpher 1990, Martens 1978). It is still unclear whether this is one and the same species as that found in the original Moroccan and Spanish populations, or differs from those in the Adriatic region (Acosta & Cokendolpher 1990, Martens 1969, 1978). Dutch examples, based on details of the male genital tract, may have come from Italy or Croatia.

## APPENDIX I. Glossary

anale plaat	anal plate	tenth tergite that covers the anus
apofyse	apophysis	protrusion on jaw or palp
basaal	basal	towards the base
cheliccer	chelicera	jaw consisting of three segments, of which the second and third segments act like scissors
corpus penis		shaft of the penis (= trunk)
coxa		first leg segment
dorn	spine	a pointed protuberance
dorsaal	dorsal	on the upper side (see also ventraal)
drietand	trident	a group of three tubercles in the middle of the front edge of the carapace
eurychroon	eurychrone	with reproduction throughout the year (see also stenochroon)
eurytoop	eurytopic	able to tolerate a wide range of habitats or ecological conditions (see also stenotoop)
femur		third leg segment, second segment of the palp
gegranuleerd	granulated	fine-grained micro-sculpted
genitale plaat	genital plate	second abdominal segment that covers the genitalia
glans		top of the penis
juveniel	juvenile	immature
kaak	jaw	see cheliccer
klauw	claw	tarsal claw, hook at the tip of the tarsus of leg or palp
kopborststuk	cephalothorax	carapace (= prosoma)
korrelrij		a row of spines, more specifically on the coxa (only <i>Leiobunum</i> )
labium		lower lip
labrum		upper lip
lateraal	lateral	located to the side (see also medial)
legbuis	ovipositor	female organ used for egg-laying
lobus maxilaris		projection on the bottom of the palp and coxa I and II
mediaal	medial	situated in the middle (see also lateral)
metatars	metatarsus	sixth segment of the leg, may consist of several (apparent) segments
multivoltien	multivoltine	with several generations per year (see also univoltien)
oogheuvel	ocularium	a raised structure carrying a pair of eyes
operculum anale	anal plate	tenth tergite that covers the anus
operculum genitale	genital plate	second abdominal segment that covers the genitalia
opisthosoma		abdomen
ovipositor		ovipositor, laying device
palp	pedipalp	leg-like structure at the anterior end
patella		third segment of the palp, fourth segment of the leg (kneecap)
penis		male genital organ
prosoma		carapace, cephalothorax
receptaculum seminis	seminal receptacle	sperm storage organ in the ovipositor of the female
scutum		a dorsal shield comprising the first five abdominal segments, which is usually fused with the carapace
stekel	spine	thick protruding hair, rigid pointed surface protuberance
stenochroon	stenochrone	with reproduction confined to within a certain period of the year (see also eurychroon)
stenotoop	stenotopic	able to tolerate only a restricted range of habitats or ecological conditions (see also eurytoop)
sterniet	sternite	ventral abdominal segment
stinkklier	stink gland opening	ozopore = opening of a defensive gland, gland at the lateral edge of the

stylus		carapace, approximately located between the first and second leg pair
subadult		spine-shaped motile tip of the penis
suprachelicerale lamel	supracheliceral lamella	stage prior to maturity
tergiet	tergite	a fold of skin between the jaws/palps and the front edge of the carapace (e.g. <i>Phalangium opilio</i> has two tubercles on this fold of skin)
tibia		dorsal abdominal segment
tars	tarsus	fifth leg segment, fourth segment of the palp
tarsklauw	tarsal claw	last part of the leg (can consist of two to many segments or apparent segments), or the last segment of the palp (always only one segment)
trochanter		a terminal claw on the tarsi
truncus	trunk	second leg segment, first segment of the palp
tuberkel	tubercle	shaft of the penis, penile corpus
univoltien	univoltine	nodule to long conical protuberance ending with a hair
ventraal	ventral	with one generation per year (see also multivoltien)
zadeltekening	saddle	on the underside (see also dorsal)
		(usually) dark, saddle-shaped rectangular mark on back
s.l.		The abbreviation s.l. stands for ' <i>sensu lato</i> ' (= in a broad sense).

## Legends to Figures

- Figs 1-4:** Some examples of harvestmen. Not all types have the classical look of a small body with very long legs. **1.** *Phalangium opilio* ♂, **2.** *Astrobunus laevipes* ♀, **3.** *Trogulus tricarinatus*, juvenile, **4.** *Opilio saxatilis*, newly moulted. Note the shed skin (exuvium) to the bottom left.
- Fig. 5:** The pseudoscorpion *Neobisium carcinoides*. Harvestmen are more closely related to scorpions and pseudoscorpions than to real spiders.
- Fig. 6:** The Daddy-longlegs spider *Pholcus phalangioides* is often confused with harvestmen. Spiders have a marked constriction between the carapace and the abdomen.
- Fig. 7:** Mites, in the superfamily Trombidoidea, also have the carapace and abdomen fused together, as in harvestmen. Mites, however, have no ocularium.
- Fig. 8:** *Leiobunum* sp. during its final moult.
- Fig. 9:** *Rilaena triangularis*, juvenile. After shedding, the old skin often stays attached for some time.
- Fig. 10:** *Rilaena triangularis*, juvenile. The vast majority of finds of this species are of juveniles from undergrowth during the autumn and winter.
- Fig. 11:** Phenology diagram of Dutch harvestmen. The bars represent the period of the year when the species is adult.
- Fig. 12:** *Paroligolophus agrestis*, mating pair, female left, male right.
- Fig. 13:** *Oligolophus hanseni*, mating pair, male left, female right.
- Fig. 14:** *Oligolophus hanseni* with a winged insect prey.
- Figs 15-18:** Resting positions **15.** *Dicranopalpus ramosus*, **16.** *Nemastoma lugubre*, **17.** *Mitostoma chrysomelas*, **18.** *Lophopilio palpinalis*
- Fig. 19:** *Platybunus pinetorum* ♀. This species often rests on tree trunks during the day and is well camouflaged.
- Figs 20-24:** Normal resting postures **20.** *Trogulus nepaeformis* s.l. pretending to be dead, **21.** *Trogulus nepaeformis* s.l. **22.** *Paroligolophus agrestis*, **23.** *Odiellus spinosus*, **24.** *Nemastoma dentigerum*.
- Fig. 25:** *Opilio saxatilis*, killed by a fungal infection.
- Fig. 26:** *Oligolophus tridens* ♀, with parasitic mites.
- Figs 27-30:** Some examples of habitats in which harvestmen occur. **27.** Old brick factory in a river valley, habitat for many species including *Leiobunum* sp. A, *Leiobunum rotundum*, *Dicranopalpus ramosus*, *Phalangium opilio* and *Trogulus tricarinatus*, **28.** Eroded cliffs along the River Waal, habitat for, among others, *Leiobunum rotundum*, *Phalangium opilio* and *Nelima sempronii*, **29.** High water refuge on the Waal in Beuningen, habitat for, among others, *Astrobunus laevipes*, *Nemastoma dentigerum*, *Trogulus tricarinatus*, *Mitopus morio* and *Leiobunum rotundum*, **30.** Stuwwalbos, with a lot of dead wood and bark, habitat for, among others, *Trogulus nepaeformis* s.l., *Nemastoma bimaculatum*, *Rilaena triangularis* and *Mitostoma chrysomelas*.

**Figs 31-35:** Many harvestmen are easy to find by sight. **31.** *Mitopus morio*, pair on nettle, male left, female right, **32.** *Opilio canestrinii*, pair on a wall, the male (right) guards a female (left), **33.** *Leiobunum* sp. A, a large aggregate on the wall of a brick factory, **34.** *Leiobunum rotundum* can form large groups under bridges, **35.** *Nemastoma bimaculatum* under a plank accompanied by woodlice *Oniscus asellus*. The photograph is printed at about life-size to show how small *Nemastoma* species are.

**Fig. 36:** A harvestman (*Oligolophus tridens* ♂) seen from the side with genital plate opened and penis displayed.

**Figs 37-44:** Ocularia (the front of the animal is always to the left), **37.** *Anelasmacephalus cambridgei*, **38.** *Dicranopalpus ramosus*, **39.** *Odiellus spinosus*, **40.** *Nemastoma dentigerum*, **41.** *Mitostoma chrysomelas*, **42.** *Astrobonus laevipes*, **43.** *Megabunus diadema*, **44.** *Opilio parietinus*.

**Fig. 45:** The underside of a harvestman (*Oligolophus tridens* ♂).

**Figs 46-48:** **46.** Schematic diagram of ♂ genital plate, **47.** Sideways view of the penis, **48.** Schematic diagram of the genital plate of ♀, with ovipositor.

**Figs 49-53:** The harvestman *Paroligolophus agrestis*. **49.** Underside of ♀, **50.** Tip of the ovipositor with sclerotized dark parts shown (left), **51.** ♀ ventral view front, schematic diagram, **52.** Genital plate ♀, **53.** Genital plate ♂.

**Figs 54-56:** *Mitopus morio* ♀, different colour forms.

**Figs 57-58:** Hood and ocularium, **57.** *Trogulus tricarinatus*, **58.** *Trogulus nepaeformis* s.l..

**Figs 59-60:** Tarsus II, **59.** *Anelasmacephalus cambridgei*, **60.** *Trogulus nepaeformis* s.l..

**Figs 61-62:** Palp, **61.** *Nemastoma dentigerum*, **62.** *Oligolophus tridens*.

**Fig. 63:** *Ischyropsalis hellwigi*, jaw.

**Fig. 64:** *Mitostoma chrysomelas*, attitude of the palps.

**Fig. 65:** *Paranemastoma quadripunctatum*.

**Fig. 66:** *Nemastoma bimaculatum*.

**Fig. 67:** *Nemastoma lugubre*.

**Fig. 68:** *Nemastoma bimaculatum* from the side.

**Fig. 69:** *Nemastoma lugubre* from the side.

**Figs 70-72:** First segment of jaw with prominent projection, **70.** *Nemastoma dentigerum*, **71.** *N. bimaculatum*, **72.** *N. lugubre*.

**Figs 73-74:** Palpal tibia and tarsus. **73.** *Nemastoma bimaculatum*, **74.** *N. lugubre*.

**Fig. 75:** *Homalenotus quadridentatus*.

**Fig. 76:** *Astrobonus laevipes*.

**Fig. 77:** Palp, *Dicranopalpus ramosus*.

**Figs 78-79:** Dorsal palp, palp femur (right), **78.** *Rilaena triangularis*, **79.** *Platybunus pinetorum*.

**Figs 80-81:** Top view of ocularium (anterior to the top), **80.** *Rilaena triangularis*, **81.** *Platybunus pinetorum*.

**Fig. 82:** Ocularium *Megabunus diadema*.

**Figs 83-84:** Ocularium and trident, **83.** *Lophopilio palpinalis*, **84.** *Paroligolophus agrestis*.

**Figs 85-86:** Top of the genital operculum *Paroligolophus agrestis*, **85.** ♂, **86.** ♀.

**Figs 87-88:** Details of femur II, **87.** *Lacinius ehippiatus*, **88.** *Odiellus spinosus*.

**Figs 89-93:** Ocularium and trident, **89.** *Lacinius ehippiatus*, **90.** *L. horridus*, **91.** *Odiellus spinosus*, **92.** *Oligolophus tridens*, **93.** *Oligolophus hanseni*.

**Figs 94-95:** Tarsal claw, **94.** *Phalangium opilio*, **95.** *Leiobunum rotundum*.

**Figs 96-97:** Tip of genital operculum, **96.** *Mitopus morio*, **97.** *Opilio*.

**Figs 98-99:** *Phalangium opilio*, **98.** Ocularium and forward edge, **99.** Jaw ♂.

**Figs 100-101:** *Mitopus morio*, **100.** Ocularium and forward edge, **101.** Jaw (with ventral hook).

**Figs 102-106:** Ocularia, **102.** *Nelima sempronii*, **103.** *N. doriae*, **104.** *Leiobunum rotundum*, **105.** *L. blackwalli*, **106.** *Leiobunum* sp. A.

**Fig. 107:** *Nemastoma bimaculatum*.

**Fig. 108:** *Nemastoma bimaculatum*.

**Figs 109-113:** *Nemastoma bimaculatum* ♂, **109.** Ocularium, **110.** Palp, **111.** Penis, **112.** Tip of penis, dorsal view (left), lateral view (right), **113.** Jaw, medial view.

**Fig. 114:** *Nemastoma lugubre*.

**Figs 115-119:** *Nemastoma lugubre* ♂, **115.** Ocularium, **116.** Palp, **117.** Penis, **118.** Tip of penis, dorsal view (left), lateral view (right), **119.** Jaw, medial view.

**Fig. 120:** *Nemastoma dentigerum* ♂.

**Figs 121-125:** *Nemastoma dentigerum* ♂, **121.** Ocularium, **122.** Jaw, **123.** Penis, **124.** Tip of penis, lateral view, **125.** Palp, medial view.

**Fig. 126:** *Paranemastoma quadripunctatum* ♂.

**Fig. 127:** *Paranemastoma quadripunctatum* ♀.

**Figs 128-132:** *Paranemastoma quadripunctatum* ♂, **128.** Example showing extended pale patterning, **129.** Jaw, **130.** Palp, **131.** Penis, dorsal view, **132.** Tip of penis.

**Fig. 133:** *Mitostoma chrysomelas* ♂.

**Fig. 134:** *Mitostoma chrysomelas* ♀.

- Figs 135-139:** *Mitostoma chrysomelas* ♂, **135.** Ocularium and front (leg removed), **136.** Penis, lateral view, **137.** Tip of penis, lateral view, **138.** Jaw, **139.** Palp, detail of palpal tarsus tip (left).
- Fig. 140:** *Trogulus tricarinatus* ♂.
- Fig. 141:** *Trogulus tricarinatus* ♀.
- Figs 142-148:** *Trogulus tricarinatus*, **142.** Ocularium, **143.** Tarsus II, **144.** Penis, two views, **145.** Tip of penis, **146.** Jaw, **147.** Palp, **148.** *Trogulus nepaeformis* s.l., tarsus II.
- Fig. 149:** *Trogulus nepaeformis* s.l. ♂.
- Fig. 150:** *Trogulus nepaeformis* s.l. ♂.
- Figs 151-159:** *Trogulus nepaeformis* s.l. ♂, **151.** Ocularium, **152.** Tarsus I, **153.** Tarsus II, **154.** Tarsus III, **155.** Hood, ventral view, **156.** Penis, **157.** Tip of penis of two ♂♂, **158.** Jaw, **159.** Palp.
- Fig. 160:** *Anelasmacephalus cambridgei* ♀.
- Fig. 161:** *Anelasmacephalus cambridgei*.
- Figs 162-168:** *Anelasmacephalus cambridgei* ♂, **162.** Ocularium, **163.** Hood, ventral view, **164.** Tarsus I, **165.** Tarsus II, **166.** Tarsus III, **167.** Penis, **168.** Tip of penis, two views.
- Fig. 169:** *Ischyropsalis hellwigi* ♂.
- Fig. 170:** *Ischyropsalis hellwigi* ♂.
- Figs 171-175:** *Ischyropsalis hellwigi* ♂, **171.** Jaw, **172.** Palp, **173.** Penis, dorsal view, **174.** Tip of penis, lateral view (left), dorsal view (right), **175.** Ocularium.
- Fig. 176:** *Phalangium opilio* ♂♀.
- Figs 177-178:** *Phalangium opilio*, **177.** ♂, **178.** ♀.
- Figs 179-183:** *Phalangium opilio* ♂, **179.** Ocularium, **180.** Jaw, left with a small extension, right with a massive elongation of the second segment, **181.** Palp, **182.** Penis, lateral view (left), ventral view (right), **183.** Tip of penis.
- Fig. 184:** *Opilio parietinus* ♂♀.
- Figs 185-190:** *Opilio parietinus*, **185.** Ocularium, **186.** Palp, **187.** Penis, lateral view (left), dorsal view (right), **188.** Tip of penis, dorsal view, **189.** Tip of penis, lateral view, **190.** Jaw.
- Fig. 191:** *Opilio saxatilis* ♂♀.
- Figs 192-193:** *Opilio saxatilis*, **192.** ♂, **193.** ♀.
- Figs 194-199:** *Opilio saxatilis* ♂, **194.** Ocularium, **195.** Palp, **196.** Jaw, **197.** Femur I, with detail (right), **198.** Penis, lateral view (left), dorsal view (right), **199.** Tip of penis.
- Fig. 200:** *Opilio canestrinii* ♂♀.

**Figs 201-202:** *Opilio canestrinii*, **201.** ♂, **202.** ♀.

**Figs 203-209:** *Opilio canestrinii* ♂, **203.** Ocularium, lateral and dorsal views, **204.** Palp, details of palpal tarsus (right), **205.** Tip of palpal tarsus, ventral view, **206.** Jaw, **207.** Penis, ventral view (left), lateral view (right), **208.** Tip of penis, **209.** Stylus on penis tip.

**Fig. 210:** *Platybunus pinetorum* ♂♀.

**Fig. 211:** *Platybunus pinetorum* ♀.

**Figs 212-216:** *Platybunus pinetorum*, **212.** Ocularium, viewed from the right, **213.** Palp, lateral view (above), dorsal view (below), **214.** Palp, lateral view (above), dorsal view (below), **215.** Penis, lateral view (left), dorsal view (right), with two cross-sections, **216.** Tip of penis.

**Fig. 217:** *Megabunus diadema* ♀.

**Fig. 218:** *Rilaena triangularis* ♂♀.

**Fig. 219:** *Rilaena triangularis* ♀.

**Figs 220-227:** *Rilaena triangularis* ♂ (except Fig. 221), **220.** Ocularium, **221.** Ocularium, ♀, **222.** Juvenile, dorsal view, **223.** Palp, medial view and palpal femur, dorsal view (left), **224.** Jaw, **225.** Penis, lateral view (left), dorsal view (right), **226.** Tip of penis, **227.** Stylus on penis tip.

**Fig. 228:** *Lophopilio palpinalis* ♂♀.

**Fig. 229:** *Lophopilio palpinalis*, sub-adult.

**Figs 230-233:** *Lophopilio palpinalis*, **230.** Ocularium, **231.** Palp, ♀, **232.** Penis, lateral view (left), dorsal view (right), **233.** Tip of penis.

**Fig. 234:** *Oligolophus tridens* ♂♀.

**Fig. 235:** *Oligolophus tridens* ♀.

**Figs 236-240:** *Oligolophus tridens* ♂, **236.** Ocularium, side and top views, **237.** Palp, **238.** Jaw, **239.** Penis, lateral view, with detail of the tip, **240.** Penis, dorsal view, with detail of the base.

**Fig. 241:** *Oligolophus hanseni* ♂♀.

**Fig. 242:** *Oligolophus hanseni* ♂.

**Figs 243-247:** *Oligolophus hanseni* ♂, **243.** Ocularium, side and top views, **244.** Jaw, with detail of the tip, **245.** Palp, **246.** Penis, dorsal view with detail of the tip, **247.** Penis, lateral view with detail of the tip.

**Fig. 248:** *Paroligolophus agrestis* ♂♀.

**Fig. 249:** *Paroligolophus agrestis* ♀.

**Figs 250-255:** *Paroligolophus agrestis* ♂ (except Fig. 251), **250.** Ocularium, **251.** Tip of the genital operculum, ♀, **252.** Tip of the genital operculum, ♂, **253.** Jaw, **254.** Palp, **255.** Penis, with detail of the tip.

**Fig. 256:** *Lacinius horridus* ♂.

**Fig. 257:** *Lacinius ehippiatus* ♂♀.

**Fig. 258:** *Lacinius ehippiatus* ♂.

**Figs 259-265:** *Lacinius ehippiatus* ♂, **259.** Ocularium, **260.** Details of femur I, **261.** Palp, lateral view (left), medial view (right) with detail of palpal tarsus, **262.** Jaw, **263.** Penis, dorsal view (left), lateral view (right), **264.** Tip of penis, **265.** Stylus on penis glans.

**Fig. 266:** *Odiellus spinosus* ♂.

**Fig. 267:** *Odiellus spinosus* ♂.

**Figs 268-271:** *Odiellus spinosus* ♂, **268.** Ocularium, **269.** Palp, with detail of palpal tarsus, **270.** Penis, lateral view, and detail of the tip, **271.** Penis, dorsal view.

**Fig. 272:** *Mitopus morio* ♂♀.

**Fig. 273:** *Mitopus morio* ♂.

**Figs 274-279:** *Mitopus morio* ♂, **274.** Ocularium, **275.** Palp, **276.** Jaw, **277.** Penis, lateral view (left), dorsal view (right), **278.** Tip of penis, with detail of the glans, **279.** Stylus on penis glans, with detail of the stylus tip.

**Fig. 280:** *Dicranopalpus ramosus* ♂♀.

**Figs 281-282:** *Dicranopalpus ramosus*, **281.** ♂, **282.** ♀.

**Figs 283-291:** *Dicranopalpus ramosus*, **283.** Ocularium, **284.** Palp, ♂, median view, **285.** Details of the base of the palpal femur, **286.** Patella of palp, ♂ and ♀, dorsal view, **287.** Claw of the palpal tarsus, **288.** Jaw, **289.** Penis, lateral view (left) dorsal view (right), **290.** Tip of penis, **291.** Two views of the stylus.

**Fig. 292:** *Homalenotus quadridentatus* ♀.

**Fig. 293:** *Homalenotus quadridentatus*.

**Figs 294-298:** *Homalenotus quadridentatus*, **294.** Ocularium from an old individual, **295.** Ocularium from a subadult, **296.** Palp, ♂, lower palpal claw, **297.** Jaw, **298.** Penis, dorsal view (left) with detail of the tip, lateral view (right).

**Fig. 299:** *Astrobunus laevipes* ♂♀.

**Fig. 300:** *Astrobunus laevipes* ♀.

**Figs 301-306:** *Astrobunus laevipes*, **301.** ♂, side view, **302.** Front carapace, dorsal view, **303.** Palp, with detail of palpal tarsus, **304.** Jaw, **305.** Penis, ventral view (left), lateral view (right), **306.** Tip of penis, lateral view (left), dorsal view (right).

**Figs 307-308:** *Leiobunum limbatum*, **307.** ♂, **308.** ♀.

**Fig. 309:** *Leiobunum rotundum* ♂♀.

**Figs 310-311:** *Leiobunum rotundum*, **310.** ♂, **311.** ♀ in the web of the Walnut Orb-weaver, *Nuctenea umbratica*.

**Figs 312-316:** *Leiobunum rotundum* ♂, **312.** Ocularium, **313.** Palp, **314.** Jaw, **315.** Penis, dorsal view, details of the tip (left), **316.** Penis, lateral view, details of the tip (right) and of the tip of the stylus (far left).

**Fig. 317:** *Leiobunum blackwalli* ♂♀.

**Figs 318-319:** *Leiobunum blackwalli*, **318.** ♂, **319.** ♀.

**Figs 320-326:** *Leiobunum blackwalli* ♂ (except Fig. 320), **320.** Ocularium, ♀, **321.** Palp, detail of lower side of palpal tarsus (right), **322.** Palpal tarsus claw, **323.** Jaw, **324.** Penis, dorsal view (left), lateral view (right), **325.** Tip of the penis, lateral view, detail of the tip of the stylus (right), **326.** Penis tip, dorsal view.

**Figs 327-328:** *Leiobunum rupestre*, **327.** ♂, **328.** ♀.

**Fig. 329:** *Leiobunum* sp. A ♂♀ and juvenile.

**Figs 330-331:** *Leiobunum* sp. A, **330.** ♂, **331.** ♀.

**Figs 332-336:** *Leiobunum* sp. A, **332.** Coxa I, frontal view, detail of denticle row (left), **333.** Palp, lateral view (left), medial view (right) with detail of the tarsal claw, **334.** Penis, dorsal view (left) lateral view (right), **335.** Tip of penis, dorsal view (left), lateral view (right), **336.** Tip of stylus.

**Fig. 337:** *Nelima sempronii* ♂♀.

**Fig. 338:** *Nelima sempronii* ♂.

**Figs 339-343:** *Nelima sempronii* ♂, **339.** Ocularium, **340.** Palp, with detail of the palpal tarsus, **341.** Penis, dorsal view (left), lateral view (right), **342.** Tip of stylus, **343.** Surface structure of penis (see arrow, Fig. 341).

**Fig. 344:** *Nelima doriae* ♂♀.

**Figs 345-346:** *Nelima doriae*, **345.** ♂, **346.** ♀.

**Figs 347-351:** *Nelima doriae* ♂, **347.** Ocularium, **348.** Palp, with detail of the palpal femur, **349.** Claw of the palpal tarsus, **350.** Penis, dorsal view (left), with detail of the tip, **351.** Penis, lateral view, detail of the tip (right).