DISTRIBUTION AND ECOLOGY OF TWO ENIGMATIC SPECIES, *TRICHONISCOIDES SARSI* PATIENCE, 1908 AND *T. HELVETICUS* (CARL, 1908) (CRUSTACEA, ISOPODA) IN THE NETHERLANDS

Matty P. Berg

Department of Animal Ecology, Institute of Ecological Science, Vrije Universiteit Amsterdam, The Netherlands. E-mail: matty.berg@falw.vu.nl

INTRODUCTION

Specimens of *Trichoniscoides* are tiny and often live deeply hidden in the soil. Their small body size and concealed way of life makes them not easy to discover, especially during dry summer periods when most surveys are done. Once a specimen is discovered it is often difficult to determine the species directly in the field. The genus *Trichoniscoides* Sars, 1899 has three native species present in the Netherlands, i.e. *Trichoniscoides albidus* (Budde-Lund, 1880), *T. sarsi* Patience, 1908 and *T. helveticus* (Carl, 1908). Only specimens of *T. albidus* are easy to distinguish. The dull wine-red colour, in combination with the contrasting white under parts, and one brownish ocellus, sets this species apart from the other two species that both have an orange colour and a reddish ocellus. It is, however, not easy to distinguish *T. sarsi* from *T. helveticus* (photo 1). The males can only be separated after close microscopic examination of the pleopods, while determination of females to the species level is currently not possible.

Photo 1: Habitus of *T. sarsi* (left) and *T. helveticus* (right). Photos © Theodoor Heijerman.

The similar appearance of *T. sarsi* and *T. helveticus* might be one reason for the relatively late discovery of *T. sarsi* in many countries, such as Germany (Allspach, 1989), The Netherlands (Berg, 1997), and Belgium (Lock, 2001). Species of *Trichoniscoides* are poorly recorded, which makes the true extent of their distribution and habitat uncertain, especially at the borders of their geographical range. In Great-Britain *T. sarsi* and *T. helveticus* reach the western extreme of their range (Hopkin, 1991; Oliver & Meechan 1993). They are only known from a few locations in south east England (Gregory, 2002) and the Dublin area, Ireland (Cawley, 2001). From the distribution map published by Gregory (2002) it is apparent that *T. sarsi* and *T. helveticus* are mutually exclusive species, as their British ranges do not overlap. It was questioned why overlap in ranges did not occur. Both species occupy different habitats. *Trichoniscoides sarsi* is found in synanthropic sites, like gardens, while *T. helveticus* lives in calcareous grassland and open woodland on limestone. These habitat types are widely dispersed in south east England.

Therefore, difference in habitat occupancy does not seem to explain the observed exclusion (Gregory, 2002). What factors are at play? Can a comparison between British and Dutch records throw some light on this enigmatic range question? In the Netherlands the status of both species is relatively well known (Berg, Soesbergen, Tempelman & Wijnhoven, 2008). Both are scarce to common, can locally occur in high densities, and are close to the centre of their geographic range.

DISTRIBUTION IN THE NETHERLANDS

Over the last 15 years the members of the Isopod Survey Group of the European Invertebrate Survey, division the Netherlands, have made surveys all over the country. The database of the Isopod Survey Group contains 735 records of *T. helveticus,* and 1980 records of *T. sarsi*. The records of the two species are plotted on a single map in Figure 1. The distribution of Holocene and Pleistocene geological formations are added to the background of the map, and indicate the areas of the country that are below and above mean sea level, respectively. In the Holocene part, the soil consists mainly of sea clay, mixed with smaller areas of lowland peat. Sand dunes along the coast prevent flooding of the hinterland. The Pleistocene part consists mainly of tertiary sand, on which river clay has been deposited along the river areas. In the extreme south east of the Netherlands loess can be found. The coverage of isopod records over the country is mapped in Figure 2, using 10 km grid squares of the Universal Transverse Mercator (UTM) grid as mapping units. Circular

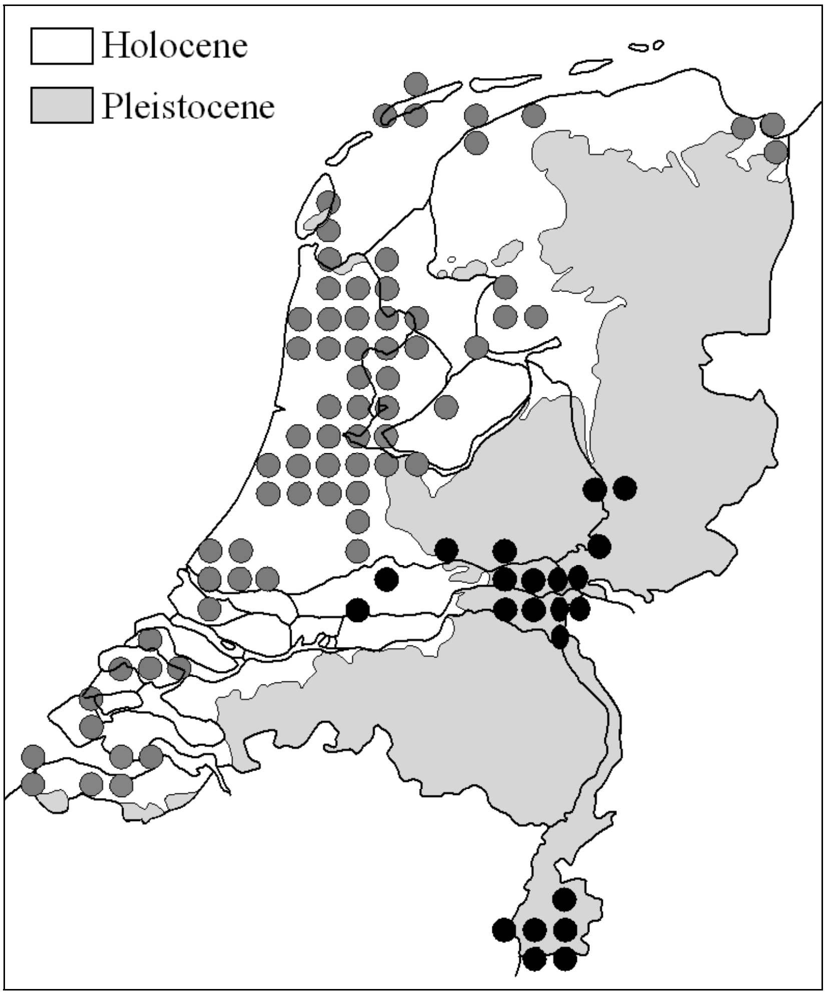

Figure 1: Distribution of *Trichoniscoides sarsi* (grey dots) and *T. helveticus* (black dots) in the Netherlands (grid cells are 10x10 km).

symbols increasing in diameter are used to differentiate the total number of species recorded per grid square. Blank squares indicate that there are no records of terrestrial isopods due to an absence of recording. Figure 2 might help to evaluate whether *T. sarsi* and *T. helveticus* are absent for a certain area due to absence of recordings or in all probability due to absence of the species.

Like in Great-Britain, *T. sarsi* and *T. helveticus* have never been recorded together. Their ranges are clearly divided (see Figure 1). *Trichoniscoides sarsi* is restricted to the western part of the country, and is recorded only from the Holocene region. Most records are from sea clay soils or from synanthropic sites with rich soil types, for instance sea clay mixed with (a little) sand. This species has been recorded from above the supralittoral zone, but never for the dunes nor for lowland peat. *Trichoniscoides helveticus* is more restricted to the eastern part of the Netherlands, but does not occur in the north east. Its distribution is not limited to the Pleistocene area, although most records are from this area. What the records do have in common is that *T. helveticus* only occurs on geologically young, river clay soil and loess soil. However, *T. helveticus* seems to be absent in river estuaries, near the sea, the trajectory of the tidal rivers or the former tidal rivers. It has never been found on sandy soils nor in lowland peat. In Europe, *T. sarsi* has a more 'atlantic' distribution, while *T. helveticus* has a more 'continental' distribution (Schmalfuss, 2003).

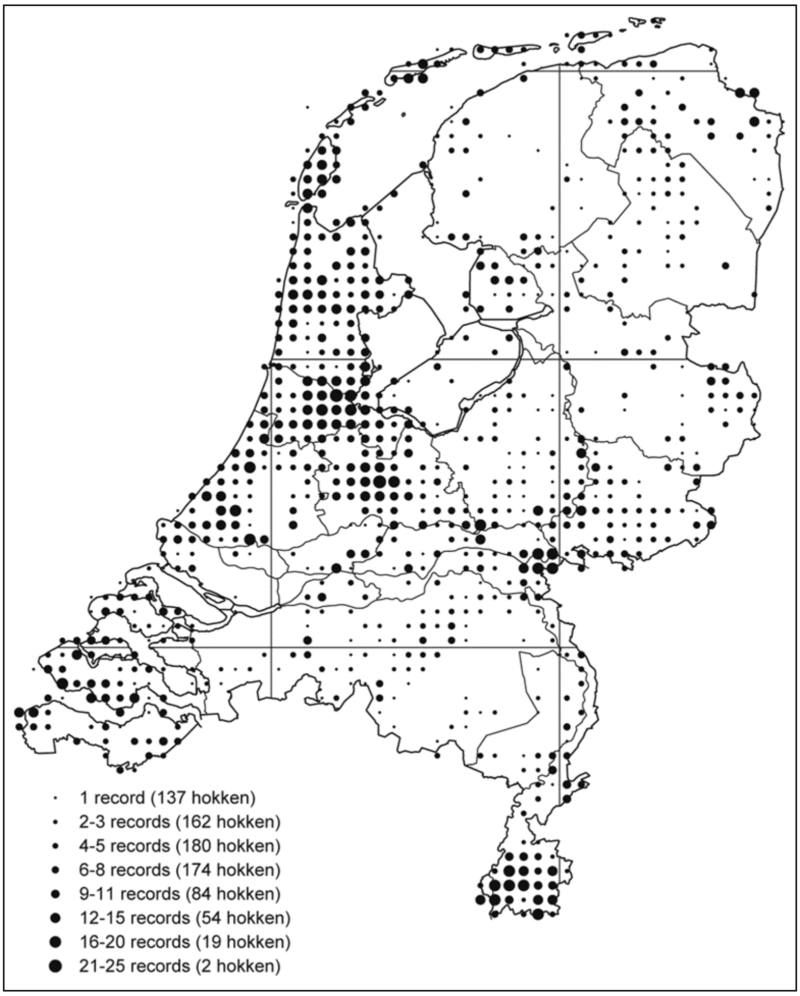

Figure 2: Number of species per grid cell (5x5 km). Between brackets the number of grid cells with a particular species richness is given. The number of species in a grid cell is significantly correlated with the number of records per grid cell. Absence of dots indicate areas that are not surveyed.

HABITAT AND MICRO SITE

Records of the habitat of the mutually exclusive species *T. sarsi* and *T. helveticus* in the Netherlands provide no explanation why their geographical ranges in Great-Britain do not overlap. Their habitat preferences are not different from the habitats already given by Gregory (2002) for Great-Britain. Both species prefer calcareous sites. *Trichoniscoides sarsi* is found in sites of ditches next to grasslands, in drains of road sites, on dikes near fields and lakes, in flowerbeds of gardens, parks, greens and graveyards. This species is often found under synanthropic conditions, and is usually absent from forests. *Trichoniscoides sarsi* often co-occurs with other hygrophylic isopods, such as *Trichoniscus provisorius, T. albidus*, *Haplophthalmus mengii*, *Metatrichoniscoides leydigii* and *Trachelipus rathkii*.

Trichoniscoides helveticus is found in sites of ditches and drains next to fields and rivers, on the shores of lakes, in wooded banks and in moist deciduous forests (Wijnhoven, 2000). Occasionally this species is recorded from gardens, but in general *T. helveticus* avoids synanthropic conditions. Accompanying species are mostly *Haplophthalmus mengii*, *Trichoniscus pusillus*, *T. provisorius*, *Trachelipus rathkii* and *Hyloniscus riparius*.

The micro sites where *T. sarsi* and *T. helveticus* have been found are rather similar. Both species can easily be observed under buried stones and logs, under root mats on concrete culverts and abutments, on the interface between soil and stone walls, and under organic ditch marks. They prefer moist and rather light clay soils with an open texture, in which earthworms are frequently present. Here, they can be found in wormholes, former root channels, between roots, and in larger clay aggregates. They are often observed deeply hidden in the soil profile. Inundation by salt water, fresh water or seepage water is not tolerated. In conclusion, it seems that the non-overlapping ranges of *T. sarsi* and *T. helveticus* can not be explained by habitat or micro site preferences.

SOIL TYPE AND CLIMATE

Trichoniscoides sarsi and *T. helveticus* both prefer moist, base-rich clay soils. However, *T. sarsi* has a strong preference for sea clay, while *T. helveticus* is predominantly found in river clay. Chemically, sea clay and river clay are not very divergent (Locher & de Bakker, 1993). Sea clay has a slightly higher soil pH (5.2 to 7.6) than river clay soil (4.8 to 7.0). The large overlap in soil pH between the two clay types and the small differences in pH at the extremes of the pH range suggest that soil pH does not explain the distribution of *T. sarsi* and *T. helveticus*. Recent deposited or newly reclaimed sea clay soil contains a high sodium content. Although *T. sarsi* does occur in young sea clay soil it is also found in relatively old sea clay soil, with a sodium content not very different from river clay, while *T. helveticus* is absent in old sea clay. Therefore, chemical differences between the two clay soil types does not seem to explain the different ranges of *T. sarsi* and *T. helveticus*.

Soil moisture content affects the suitability of soils as a habitat for soil fauna, especially for isopods with a low drought tolerance. Sea clay has, on average, a significantly higher groundwater level (GWL) and a higher fraction of fine sand than river clay (de Bakker & Locher, 1992; Locher & de Bakker, 1993). As GWL is positively related to soil moisture content, differences in GWL may explain the observed distribution of the two *Trichoniscoides* species. In summer, the GWL for sea clay is 80-120cm below the soil surface, while river clay has a GLW of 120cm. In late summer, the driest period of the year, the low average GWL of river clay might result in soil moisture contents that are too low for *T. sarsi*, but not for *T. helveticus*. However, desiccation measurements under standardized laboratory conditions (measuring mass loss of field collected animals at 15º C and 40% relative humidity, after acclimatization for two days without food) revealed a higher water loss rate for *T. helveticus* (24.3 ml water g^{-1} dry weight h^{-1}) than for *T. sarsi* (20.8 ml water g^{-1} dry weight h^{-1}). If we assume an equal minimum threshold level for the amount of water that can be lost before mortality occurs than *T. helveticus* is reaching this threshold faster under dry conditions than *T. sarsi*, just the opposite of what you would expect. An alternative explanation might be that the minimum threshold level differs for the species.

In winter, the average GWL for sea clay is less than 40cm below ground level, while river clay has a GWL of 40-80cm. A high GWL forces isopods to the soil surface, and this is the reason why tiny, deeply living isopods are easier to collect during winter than in summer. In mid winter, when the GWL is at its highest, river clay soil has more pore space to offer to soil fauna than sea clay. The geographic location of river clay and sea clay in the Netherlands coincide with differences in the long-term yearly minimum temperature and with the long-term monthly minimum temperature from October till January (KNMI, 2007). The minimum temperature in the Pleistocene part of the country, with river clay, is 1.0-1.5 ºC lower than in the Holocene part, with sea clay. This means that sub-zero temperatures occur more often in river clay areas than in sea-clay areas. When the temperature drops below zero for a prolonged period of time, river clay offers better protection than sea clay because animals can crawl deeper into the ground due to a lower GWL. Moreover, isopods probably crawl more easily through river clay than sea clay due to a higher fraction of course sand (De Bakker & Locher, 1992), resulting in a lighter soil type. If extremes at the low temperature range explains the exclusive distribution patterns of the two *Trichoniscoides*-species one would expect the more 'continental' *T. helveticus* to be more tolerant to sub-zero temperatures than the more 'Atlantic' *T. sarsi*. Unfortunately, information on cold tolerance is not available for both species.

DISCUSSION AND CONCLUSION

Trichoniscoides sarsi and *T. helveticus* are rather similar in choice of habitat and micro sites, but they prefer different soil types, predominantly sea clay and river clay, respectively. Geographic separation of these clay types may result in the mutually exclusive range, with *T. sarsi* occurring in the western part of the Netherlands, and *T. helveticus* in the eastern part. The exclusive presence of *T. sarsi* in sea clay and *T. helveticus* in river clay suggests that explanatory factors for their distribution are related to clay type dissimilarities. On the one hand, sea clay and river clay vary in chemical, physical, and morphological characteristics. Acidity and mineral content are not that different between both clay types, but river clay has a more open texture and has a lower GWL. On the other hand, sea clay is located in the western part of the country, while river clay is found predominantly in the eastern part. Their geographic location coincides with a climatic gradient; more 'maritime' or 'Atlantic' in the west and more 'continental' in the east. In winter, the average minimum temperature significantly declines from the west coast to the eastern border, while the amount of precipitation is about 20mm higher in the west than in the east. Proximity of the North Sea causes relatively cool summers and mild, wet winters in the western part compared to the eastern part. Moreover, the amplitude of the daily temperature fluctuation is smaller in the west than in the east. The correlation between geographic location of clay types and climatic conditions during winter makes it difficult to unravel the observed separation in *T. helveticus* and *T. sarsi*. *Trichoniscoides helveticus* can overcome warm and dry summer conditions by crawling to deeper soil layers that are cool and moist. River clay with its lighter soil, and a lower GWL gives better opportunities to crawl deep into the soil and escape detrimental environmental conditions than sea clay. River clay might give better protection against water loss under dry conditions because animals can crawl deeper into the soil. This could also explain the lower water loss rate of *T. sarsi* compared *T. helveticus*, because *T. sarsi* is more exposed to dry conditions. Similarly, river clay can protect species better to exposure to sub-zero temperatures in winter, which are often accompanied by a low relative humidity. On the other hand, observations in Britain suggests that both species can be found close to the surface in heavy frost (S.J. Gregory, personal communication). It could also be that *T. helveticus* is simply adapted to the colder continental winters, while *T. sarsi* prefer warmer, damper winters. If this argument holds, then *T. helveticus* should have a higher cold tolerance than *T. sarsi*.

Although these factors can explain why *T. helveticus* is not found in the west, it does not give a proper explanation for the absence of *T. sarsi* in the east. For a true understanding why the range of both *Trichonisocides*-species do not overlap, and to be able to differentiate between effects of soil type and climatic factors, we need more physiological information. For instance, how dissimilar are *T. sarsi* and *T. helveticus* in pH-preference, cold-tolerance, drought-tolerance, and vertical stratification along the soil profile? The boundary between sea and river clay areas are particularly attractive to survey in this respect. Here, climatic conditions are equal and it would be interesting to find out if the two species are mutually exclusive too. Quantifying physiological traits of specimens collected in this boundary region, in combination with competition experiments might give an answer to the enigmatic ranges of *T. sarsi* and *T. helveticus*. Nevertheless, the observed differences in the distribution of the two species and their niche in the Netherlands might give some clues why the species have non-overlapping ranges in Great-Britain.

ACKNOWLEDGEMENTS

I am grateful to all the members of the Isopod Survey Group of the European Invertebrate Survey, division The Netherlands for the many records they have gathered over the last 17 years and to Steve Gregory for his constructive comments on an earlier version of the manuscript.

REFERENCES

Allspach, A. (1989) Neunachweise von vier Landasselarten (Isopoda: Oniscidea) für Deutschland. *Stuttgarter Beitr. Naturk. Ser. A* **436**: 1-8.

Berg, M.P. (1997) Naamlijst van de Nederlandse landpissebedden (Crustacea: Isopoda: Oniscidea). *Nederlandse Faunistische Mededelingen* **7**: 31-34.

Berg, M.P., Soesbergen, M., Tempelman, D. & Wijnhoven, H. (2008) *Verspreidingsatlas pissebedden, duizendpoten en miljoenpoten*. EIS-Nederland, Leiden. (in press).

Cawley, M. (2001) Notes and records on the Irish woodlice (Crustacea: Isopoda), including new sites for *Halophiloscia couchi* (Kinahan). *Bulletin of the Irish Biogeographical Society,* **25**: 211-217.

De Bakker, H. & Locher, W.P. (1992) *Bodemkunde van Nederland*: *Bodemgeografie*. Malmberg, Den Bosch.

Gregory, S. (2002) Exclusive *Trichoniscoides*. *Newsletter of the British Myriapod and Isopod Group* **4**: 1-2. Unpublished.

Gruner, H.E. (1966) *Isopoda. Krebstiere oder Crustacea*. Die Tierwelt Deutschlands **53**, Jena.

Harding, P.T. & Sutton, S.L. (1985) *Woodlice in Britain and Ireland: distribution and habitat.* Huntingdon, Institute of Terrestrial Ecology.

Hopkin, S.P. (1991) A key to the woodlice of Britain and Ireland. *Field Studies* **7**: 599-650.

KNMI (2007) Climate atlas of the Royal Dutch Meteorological Society 1971-2000 (In Dutch). *http://www.knmi.nl/klimatologie/normalen1971-2000/index.html*.

Locher, W.P. & de Bakker, H. (1993) *Bodemkunde van Nederland: Algemene bodemkunde*. Malmberg, Den Bosch.

Lock, K. (2001) *Trichoniscoides sarsi* (Patience, 1908): a new species for the fauna of Belgium (Isopoda Trichoniscidae). *Bull. Annls. Soc. R. belge Ent.* **137**: 29-31.

Oliver, P.G. & Meechan, C.J. (1993) *Woodlice*. Synopses of the British Fauna (New Series) **49**. Field Studies Council.

Schmallfuss, H (2003) World catalog of terrestrial isopods (Isopoda: Oniscidea). *Stuttgarter Beiträge zur Naturkunde Series A*. **654**:1-341.

Wijnhoven, H. (2000) Landpissebedden van de Ooijpolder. Deel 1: Verspreiding. *Ned. Faun. Mededel.* **11**: 55-131.

Wouters, K, Tavernier, J.M. & Meurisse, L. (2000) Distribution and bibliography of the terrestrial Isopoda (Crustacea) of Belgium. *Bull. Kon. Bel. Ins. Natuur. Biol.* **70**: 193-205.