First records of *Parergodrilus heideri* (Annelida: “Polychaeta”) from North America

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*Parergodrilus heideri* Reisinger, 1925 is one of two species of the family Parergodrilidae (together with the marine litoral, interstitial species *Stygocapitella subterranea* Knöllner, 1934) and one of only two truly soil-dwelling “polychaetes” (the other being *Hrabeiella periglandulata* Pižl and Chalupský, 1984) that are predominantly known from terrestrial habitats (Reisinger 1925, 1960; Römbke and Jans 1991; Chalupský 1992; Graefe 1993; Rota 1997, 1998; Purschke 1999; Rota et al. 2001; Beylich and Graefe 2007; Martinez-Ansemil and Parapar 2009; Rota et al. 2010). Due to its small body size (adults up to 1 mm) and sensitivity to dessication, the species has usually been found by researchers using some type of wet extraction for soil mesofauna, such as enchytraeids and free-living flatworms (“turbellarians”). However, due to its similar chaetae, *Parergodrilus heideri* can be easily mistaken for a freshly hatched enchytraeid, even by enchytraeid specialists without experience with this species.

Until recently, the species has been known only from Europe, ranging from southern Sweden in the north to southern Italy in the south and from north-eastern Spain in the west to northern Croatia in the east (an up-to-date overview of its distribution with references to published records was given by Rota et al. [2010]; see also references above). The first and only record outside of Europe was recently published by Dózsa-Farkas and Hong (2010) from Korea. That record from a single locality indicated that the genus and species have a much wider distribution than previously assumed.

We found *Parergodrilus heideri* at two sites within a study on the impact of earthworm invasion on enchytraeid assemblages (Annelida: Clitellata: Enchytraeidae) in northern hardwood forests of North America, previously devoid of any earthworms, conducted between autumn 2010 and summer 2011 (results to be published later, see also Eisenhauer et al. 2011). These are the first records from North America and thus of high faunistic importance. Together with the above-mentioned records from Europe and Korea they show that the species occurs on all three continents of the Holarctic.

Several papers have summarized and contributed to our knowledge on the morphology and systematic (phylogenetic) position of the species (Purschke 1999; Rota et al. 2001; Jördens et al. 2003) and we could not provide any new insights in this respect. However, we believe that our records not only substantially expand the known distribution area of the species but also provide important additional information on its range of habitats and thus autecology. In the following, we will provide details on the specimens and exact locations where these were obtained, sampling method, and a description of the habitats. Based on this information we will also advance some ideas on the origin of these populations and the species’ habitat requirements, comparing our data with those of other authors.

The two study sites were forests situated 250 km apart in northern Minnesota (Chippewa National Forest) and northern Wisconsin (Chequamegon section of Chequamegon-Nicolet National Forest), USA (Figure 1): The site within the Chippewa National Forest was situated on the Ottertail Peninsula at Leech Lake, being identical to the “Section 19” site in Hale et al. (2005), geographic coordinates: 47°16′0.00″ N, 94°23′48.60″ W (corresponding to the current position of the leading edge of earthworm invasion along the studied transect with a length of 390 m at 443–449 m a.s.l.; see explanation further below).

The other site, within the Chequamegon-Nicolet National Forest, was situated at Tower Lake in the Rainbow Lake Wilderness north of the town of Drummond, geographic coordinates: 46°26′3.06″ N, 91°19′36.00″ W (position of leading edge as above; length of transect 700 m from 380 m to 405 m a.s.l.).

Both study sites were covered with mesic forests approximately 80–100 years old after logging in the early 1900s.
At the Minnesota site, sugar maple (Acer saccharum) was dominant, with yellow birch (Betula alleghaniensis) and basswood (Tilia americana) as secondary species in the tree layer. Soil was a deep, well-drained and light-colored silty clay loam Eutroboralf (Warba series) associated with the Guthrie Till Plain (USDA 1997). The plots with P. heideri had a mean soil pH (H₂O) of 6.1 and silt loam texture with percentages of 26–41%, 51–64%, and 7–12% sand, silt and clay, respectively. The climate is humid, continental, and cold temperate with a mean annual temperature of 3.9°C and mean annual precipitation of 672 mm; mean monthly temperatures range from -5°C in January to 19.8°C in July (30-year averages for 1971–2000; PRISM Climate Group; see also Daly et al. 2008).

FIGURE 1. Location of the two study sites (black dots) in Minnesota (Ottertail Peninsula on Leech Lake, Chippewa National Forest) and Wisconsin (vicinity of Tower Lake within the Rainbow Lake Wilderness, Chequemegon section of Chequamegon-Nicolet National Forest), USA, where Parergodrilus heideri was recorded.

FIGURE 2. Micrograph of live specimen of Parergodrilus heideri collected on Sept. 26, 2010, at the study site on the Ottertail Peninsula on Leech Lake, Chippewa National Forest, Minnesota, USA.
At the Wisconsin site, sugar maple was again dominant, followed by aspen (*Populus tremuloides* and *P. grandidentata*), basswood, red maple (*A. rubrum*) and ash (*Fraxinus* spp.). The plots with *P. heideri* had a mean soil pH (H₂O) of 4.5 and loam to silt loam texture with percentages of 27–52%, 37–56% and 11–17% sand, silt and clay, respectively. The soils in the wider area are Fragiorthods and Haplorthods (Albert 1995), but no information was available for the exact study area. The climate is milder than at the above site, with a mean annual temperature of 5.2 °C and mean annual precipitation of 843 mm; mean monthly temperatures range from -0.3 °C in January to 25.4 °C in July (30-year averages for 1971–2000; source as above).

At both sites the invasion by European lumbricid species was underway. Under worm-free conditions there was a thick forest floor composed of L, F and H organic horizons. These layers were reduced at the leading edge of earthworm invasion and missing in most of the area with established *L. terrestris* populations (except the organic material of the middens above its burrows), whereas mineral soil was increasingly enriched with humus material into greater depths. For details on the impact of earthworms on soil properties and vegetation at these and similar sites see Hale at al. (2005, 2006) and Holdsworth et al. (2007). We took soil samples along transects (one transect per site) perpendicular to the leading edge of earthworm invasion. These transects had been established in preceding studies (Hale at al. 2005;
Holdsworth et al. 2007) and lengthened by us to reflect the advance of the leading edge since these studies had been conducted. Soil cores of 4.8 cm in diameter were taken down to a depth of 12 cm (rarely 9 or 15 cm) at three positions along the transects: un-invaded (or with a low density of the epigeic earthworm Dendrobaena octaedra only), leading edge (with established populations of epigeic and endogeic earthworm species) and invaded (with established populations of all three ecological groups of earthworms, including adults of the anecic Lumbricus terrestris). In autumn 2010, six soil cores from each position of the transect were extracted (3 x 6 = 18 soil cores per site). In spring–summer 2011 four soil cores per transect position (3 x 4 = 12 soil cores in total) were extracted from the Minnesota site and six soil cores per transect position (3 x 6 = 18 soil cores in total) from the Wisconsin site. These soil cores were subdivided into 3 cm layers. Microannelids were extracted from these layers by a modified O’Connor wet funnel extraction (24 h without heating with subsequent heating of the soil surface up to 44°C within 4 h) as developed for the quantitative extraction of enchytraeids (for a comparison of extraction efficiency of the original O’Connor method and some modifications see Kobetičová and Schlaghamerský 2003); extraction efficiency for Parergodrilus might be somewhat lower than for enchytraeids (see Reisinger 1925). At both sites the numbers of Parergodrilus heideri specimens obtained were comparable with those of the scarcer enchytraeid species, but many enchytraeid species reached much higher abundance (to be published elsewhere).

In total we found five specimens of Parergodrilus heideri at the two study sites. At the Minnesota site, one specimen (8 chaetigerous segments, 0.77 mm long, 0.14 mm wide, immature but already rather large, probably female – no egg but also no male copulatory chaetae; for micrograph of live specimen see Figures 2–3) was collected on Sept. 26, 2010 in the 3–6 cm soil layer in the non-invaded part of the transect and two specimens (1 mm and 0.95 mm long, respectively, 8 chaetigerous segments, both female adults with yolky egg) were collected on June 2, 2011 (in the 0–3 cm and the 3–6 cm soil layer, respectively) at the leading edge of earthworm invasion. At the Wisconsin site, one specimen (1 mm long, female adult with yolky egg) was collected on Oct. 3, 2010, in the 0–3 cm soil layer in the heavily earthworm-invaded part of the transect, near the shore of Tower Lake; another specimen (7 chaetigerous segm., ca 1 mm long, dead when examined), was collected on July 4, 2011 in the 0–3 cm soil layer at the leading edge of earthworm invasion. There were no apparent differences of our specimens compared to the specimens described from Europe. The maximum number of 8 chaetigerous segments, found in all specimens but one with 7 segments, corresponds with the maximum known number described for adult females (Reisinger, 1960) and even the specimens without eggs were most probably females. The lack of males is not surprising, as females have dominated the populations in previous studies. According to Reisinger (1960), males have a very short life span restricted to from early to mid summer, whereas females occur year-round with constant abundance (however, the lack of any seasonal variation in abundance of a species dwelling in the desiccation-prone organic soil layer seems improbable). Reisinger (1960) reported the first males ever found, with a male : female ratio of 1 : 70; however, once he learned more about the behaviour of the males (which cling to dead leaves with the help of excreta, whereas females let go when disturbed) and was more successful in finding them, he assessed a sex ratio ranging from 1 : 8 to 1 : 15 (with reference to the very same work of Reisinger, Chalupský (1992) and Rota (1998) interpreted the different estimates as a seasonal variation of the sex ratio between 1 : 70 and 1 : 8-15, or 1 : 10). Using a wet funnel extraction (as we did), Purschke (2002) got only two mature males but 293 mature females from leave litter collected in a beech forest in northern Germany (Purschke 2002).

As summarized by Rota et al. (2010), in Europe the species had originally been found in the organic soil layers of montane beech forests and it was reported that the species avoided permanently waterlogged soils (Reisinger 1925). Later, specimens were found near running water or even in sediments of their hypotheic zone (e.g., Martínez-Ansemil & Parar 2009), as well as in different types of waterlogged soils. Although it had been characterized as a dweller of damp but never wet soils with null humus and of a slightly alkaline to moderately acid pH (Graefe, 1993; Graefe & Schmelz 1999), it was also found in more acidic soil with moder humus and a pH of 3.6–4.5 (measured in 1N KCl and thus ca 0.5 lower than in H2O) of a spruce forest (located, however, on limestone, Römcke & Jans 1991). Although most records come from montane conditions, some are also from lowlands, for instance from the Elbe floodplain in northern Germany (Beylich & Graefe 2007). Our records from North America are again from rather well-drained soils (terrain depressions with waterlogged soil were present at both sites but not sampled) of deciduous forests, in our cases dominated by sugar maple. The elevation of around 400 m a.s.l. at both sites is considered upland habitat in the given geographic context, but is definitely not montane. However, the sites are located in the temperate-boreal transition zone, and the climate is rather harsh. In agreement with the observations of many other authors, we found all specimens in the upper six centimetres of soil and all but one in the upper three centimetres; in the given soil cores these layers corresponded with both the organic layer and the upper-most, humus-rich mineral soil. Due to the original absence of earthworms, the humus form originally present at the sites had been very different from mul, with a thick duff layer little mixed with the underlaying mineral soil and thus resembling moder to mor, even though the soil pH was only moderately acidic. This situation was still
present in the non-invaded parts of the study transects. As we found *Parergodrilus heideri* specimens along the entire gradient of earthworm invasion, including non-invaded areas of the forest, mull humus can not be considered a precondition for the presence of the species. There are no agricultural soils in the vicinity of the forests studied and European earthworms have reached them presumably as commercial fish bait of anglers (Holdsworth et al. 2007). No such transport of microannelids is to be assumed. The enchytraeid assemblages of both sites also included a number of species of a wide distribution range including such known from the arctic tundra, boreal and temperate forests of Europe (own unpublished data). Thus we consider *Parergodrilus heideri* a native species at these North American sites. Nevertheless, an initial introduction to North America with soil from Europe can not be fully excluded and Rota et al. (2010) suggested (referring to its distribution in Europe) that *P. heideri* might spread through waterlogged soils along hydrographic systems. A study of genetic distances between and among the European and the few known extra-European populations could shed light on their relationships, origin, and the time of their separation.

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References


**Parergodrilus heideri** FOUND IN NORTH AMERICA

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