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Morphological anomalies in a Polish population of *Stigmatogaster subterranea* (Chilopoda: Geophilomorpha): a multi-year survey

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Abstract

After a multi-year survey of the centipede fauna in the city of Poznań (Poland), we document here the high frequency of naturally occurring anomalies in an isolated population of the geophilomorph *Stigmatogaster subterranea* (Shaw, 1794). Out of 809 specimens collected in 1991 to 2007, 25.8 % are affected by anomalies of either the appendages or the trunk. In particular, 6.4 % of the specimens have anomalous features in the trunk, 18.9 % on the legs, and 2.5 % on the antennae. Anomalies are found in juveniles and adult specimens as well, and the frequency of defects does not differ between sexes. Preliminary observations indicate that similar anomalies occur with comparable high frequency also in other populations of *S. subterranea*. This suggests the possibility that a constitutional high level of developmental instability could be a distinctive feature of the species.

Keywords: developmental stability, segmental anomaly, teratology

1. Introduction

The occasional occurrence of specimens with anomalous morphological features has been recorded in natural populations of several species of geophilomorph centipedes. Besides minor trunk anomalies and defects confined to the appendages, only thirteen cases of conspicuous anomalies affecting the segmental pattern of the trunk have been described in scientific literature to date (reviewed in Leśniewska et al. 2009). The most commonly reported kinds of anomalies include the so-called ‘spiral segmentation’ (helicomery) and partially reduced trunk segments (Balazuc & Schubart 1962, Minelli & Pasqual 1986, Pereira & Minelli 1995, Simaiakis et al. 2007).

Here we present data on the occurrence of numerous morphological anomalies, affecting either the main body axis or the appendages, in a single, isolated population of the geophilomorph species *Stigmatogaster subterranea* (Shaw, 1794) living in Poznań (W Poland). *S. subterranea* occurs in natural sites from the Pyrenees (Brolemann 1930), across western Europe (Berg 1995, Lock 2000) and the British Isles (Eason 1964, Barber & Keay

1988), to north-western Germany (Jeekel 1964) (reviewed by Lindner 2007). In Denmark, Scandinavia, the Czech Republic and eastern Germany, it is found exclusively in synanthropic sites (Palmén 1949, Enghoff 1973, Olsen 1995, Lindner 2007). The species has also been introduced to Newfoundland (Palmén 1954).

A population of a geophilomorph species, characterised by such a large number of anomalous specimens, had never been found before. Outstanding for a single geophilomorph population is also the total number of specimens secured by our survey, as well as the multi-year duration of the survey. To the best of our knowledge, only some populations of *Strigamia maritima* (Leach, 1817), *Orya barbarica* (Gervais, 1835) and *Orya panousei* Demange, 1961 have been sampled as intensively as the population of *S. subterranea* from Poznań, but these were not specifically examined for the occurrence of anomalous specimens (Demange 1961, Lewis 1961, Kettle & Arthur 2000, Vedel et al. 2008).

2. Materials and methods

Site

The investigated population is found in the 'Citadel Park', situated in the city centre of Poznań (W Poland). The population lives on the bank of a deep moat, with a slope of about 35–40° SSE (Fig. 1). The area occupied covers about 3400 m^2 (170 x 20 m). The slope is covered by a ruderal community Chelidonio-Robinietum with a regeneration tendency towards a sloping elm and ash marshy meadow Querco-Ulmetum violetosum odoratae. Anthropogenically transformed brown soil and deluvial soil are found in the area.

The Poznań population is far beyond the borders of the natural range of *S. subterranea* (see under Introduction), and thus we can assume that it has been accidentally introduced into this area – most probably with garden soil. It was first recorded in 1991 (Leśniewska & Wojciechowski 1992), and since then it has remained confined to the same area of the park.

The Citadel, the area where the investigated population lives, is situated on a hill, where in the XIXth century the Prussians erected a massive complex of military buildings. The fort was substantially damaged during the city's liberation in 1945. Some parts of the Citadel were demolished in 1956 to 1959. Only fragments of the fort have survived; the remaining area is occupied by a large park (about 1 km^2) and cemeteries. The area of the Citadel has never been a place for storing potentially teratogenic materials (Biesiadka et. al. 2006, J. Biesiadka pers. comm.). The Citadel is surrounded by a quiet residential district. There are no industrial plants which could produce and discharge pollutants.

Fig. 1 Habitat of the population of *S. subterranea* living in the Citadel Park, Poznań. The localisation of the site in the city of Poznań is indicated on the map.

Collection methods

The material used in this study includes 809 specimens of *S. subterranea* (442♂♂, 363♀♀, 4 early juv.) collected in 1991 to 2007. Most specimens were secured by intense and systematic sampling started in 2003 (Tab. 1). These were collected by direct sampling from litter, soil, or under stones, loose bark of trees, logs, stumps, or by taking either quantitative or qualitative litter-soil samples (Tab. 1). Litter-soil samples were taken to the depth of 30 cm and subsequently sorted by hand. Each quantitative sample involved 16 random samples, each with a surface area of 1/16 m^2 (1 m^2 in total). A total of 16 quantitative samples was collected – three in summer, three in autumn, three in winter, and seven in spring (Tab. 1).

All specimens were examined by one of us (M. Leśniewska) with a stereoscopic light microscope up to 80x magnification. L. Bonato and G. Fusco examined only the anomalous specimens.

Tab. 1 Samples of *S. subterranea* used in the study (abbreviations: dc: direct capture; qual: qualitative soil sampling; quan: quantitative soil sampling).

	Date	Number of specimens (estimated density: specimens m^{-2})	Sampling method
1	25/05/1991	3	dc
2	15/05/1993	10	dc
3	19/05/1995	27	dc
4	16/10/1996	1	qual
5	13/05/1998	1	dc
6	21/06/2001	8	dc
7	21/05/2003	35 (19)	dc; quan
8	28/05/2003	3	dc
9	17/04/2004	14	dc
10	08/05/2004	19	dc
11	22/05/2004	3	dc
12	26/05/2004	72 (54)	dc; quan
13	29/05/2004	6	dc
14	31/05/2004	5	dc
15	01/06/2004	3	dc
16	02/06/2004	6	dc
17	29/10/2004	7 (5)	dc; quan
18	13/01/2005	2 (1)	dc; quan
19	01/03/2005	2 (2)	quan
20	28/04/2005	64 (54)	dc; quan
21	05/05/2005	5	dc
22	19/05/2005	31	dc
23	24/05/2005	77 (39)	dc; quan
24	01/06/2005	66 (31)	dc; quan
25	08/06/2005	5	dc
26	28/06/2005	8 (7)	dc; quan
27	25/07/2005	9 (8)	dc; quan
28	08/08/2005	11 (7)	dc; quan
29	27/09/2005	29 (11)	dc; quan
30	01/10/2005	11	dc
31	08/10/2005	10	dc
32	27/10/2005	7 (1)	dc; quan
33	29/12/2005	2 (2)	quan
34	25/04/2006	50 (22)	dc; qual, quan
35	20/05/2006	21	dc
36	27/05/2006	10	dc
37	30/05/2006	86 (78)	dc; quan
38	03/06/2006	11	dc
39	06/06/2006	31	dc
40	30/06/2006	12	dc; qual
41	20/09/2006	12	dc
42	25/04/2007	14	dc

Comparative materials

We examined additional specimens of *S. subterranea* from several populations from four main areas: Copenhagen (Denmark) (53 specimens); West Cornwall and SW Devon (England) (35); Leipzig, Rudolstadt and near Hagen in Westphalia (Germany) (112); Amsterdam, Muideberg, Ulvenhout and other few localities nearby (The Netherlands) (35). The specimens were collected in natural and synanthropic habitats in years 1994 to 2007.

Tab. 2 Frequency of anomalous centipede specimens from the Citadel Park of Poznań (Poland) for species other than *S. subterranea.*

Species	Number of specimens	Number of anomalous specimens (affected body part)	% anomalous specimens
Cryptops hortensis	63	0	0.0
Geophilus alpinus	53	2 (legs)	3.8
Geophilus flavus	178	4 (legs)	2.3
Geophilus truncorum	4	0	0.0
Lithobius crassipes	2	0	0.0
Lithobius forficatus	260	0	0.0
Lithobius melanops	5	0	0.0
Lithobius microps	382	0	0.0
Schendyla nemorensis	128	1 (antenna)	0.8
Total	1075	7	0.7

Additionally, we checked for morphological anomalies all the other centipede species collected in the Citadel Park during our survey in years 1991 to 2007: *Lithobius melanops* Newport, 1845, *Lithobius crassipes* L. Koch, 1862, *Lithobius forficatus* (Linnaeus, 1758), *Lithobius microps* Auct. nec Meinert, 1868, *Schendyla nemorensis* (C. L. Koch, 1837), *Geophilus alpinus* Meinert, 1870, *Geophilus truncorum* Bergsøe & Meinert, 1866, *Geophilus flavus* (De Geer, 1778), *Cryptops hortensis* (Donovan, 1810) (see Tab. 2 for sample sizes).

Chemical analysis of the soil

Heavy metal content in the soil was determined by the atomic absorption spectrometry method using the Varian atomic spectrometer AA-200 (Tab. 3). A soil sample collected on 01/03/2005 (Tab. 1) was used for the analysis.

Tab. 3 Heavy metal content in the soil from the investigated site.

Heavy metal	Content (mg kg^{-1})	Polish standard for protected areas (max mg kg^{-1})
Pb	8.47	50
Cd	0.51	1
Cu	5.16	30
Ni	7.35	35
Cr	2.67	50
Zn	15.50	100

3. Results

Population density and structure

The average density of the population was estimated at 21.3 specimens m^{-2} by 16 quantitative soil samplings (range 1 to 78 spec. m^{-2}; Tab. 1). The highest densities were recorded in spring (average 42.4 spec. m^{-2}, range 19 to 78), whereas the lowest in winter (average 1.7 spec. m^{-2}, range 1 to 2). For comparison, recorded average population densities of the other centipede species living in the same site varied between 0.1 and 25 spec. m^{-2} (range 0 to 62) (Fig. 2).

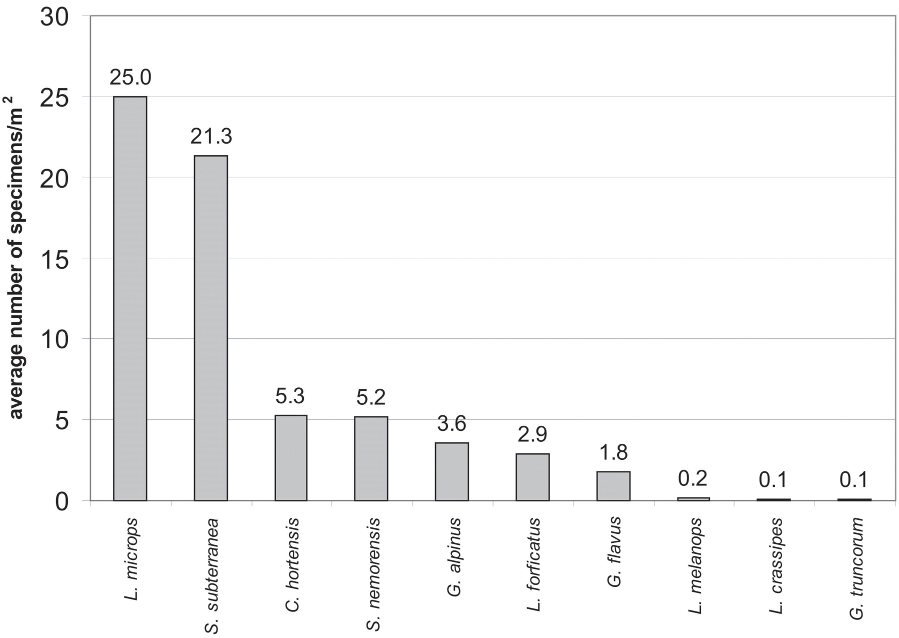

Fig. 2 Average densities of the centipede species from the Citadel Park, Poznań.

For the whole *S. subterranea* sample, males/females ratio was 1.22 (54.9 % males, 45.1 % females; n = 805). Body length varied in the range 13 to 58 mm for males and 12 to 70 mm for females. The number of leg-bearing segments varied in the range 75 to 83 for males and 77 to 87 for females (Fig. 3).

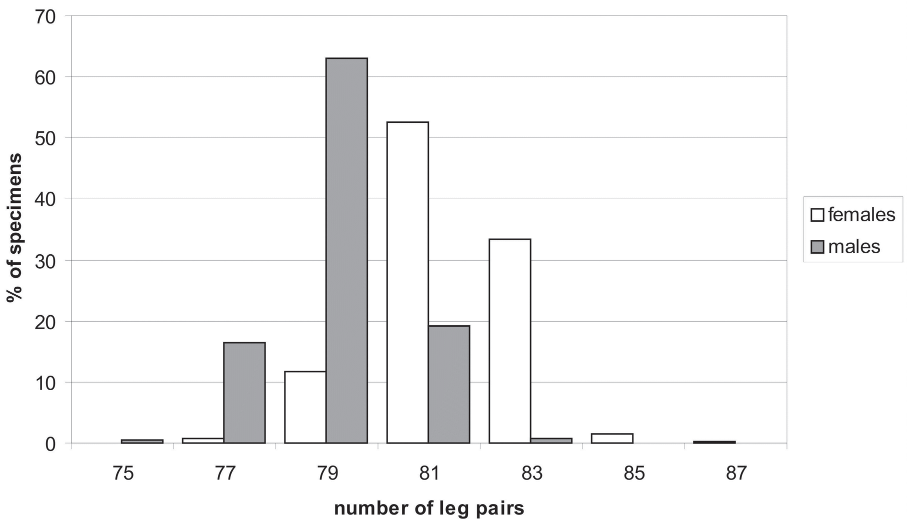

Fig. 3 Frequency distribution of the number of leg pairs in the population of *S. subterranea* from Poznań (n = 804). A single anomalous specimen with 80 pairs of legs is not included.

Anomalies

Morphological anomalies on the body trunk and/or the appendages were found in 209 out of 809 specimens examined (25.8 %). Of these specimens, 52 (6.4 %) have anomalous features in the trunk, 153 (18.9 %) have leg defects in trunk regions that are not affected by other anomalies, and 20 (2.5 %) have defects on the antennae. These figures do not include defects recognisable as scars resulting from post-embryonic life accidents (found in 47 % of the specimens).

Trunk anomalies include mispaired tergites, shrunk segments, variously deformed sclerites, bifurcated trunk, defect of spiracles and sternal pore areas, and one specimen with a perfect segmentally patterned trunk, but with an even number of leg-bearing segments. These anomalies are most probably congenital and are thus interpreted as the effects of perturbation of specific morphogenetic processes in trunk embryonic segmentation, as described and discussed in Leśniewska et al. (2009).

There are 217 cases of defective legs. These include anomalous size of the whole leg (from minor reduction to complete absence, or legs larger than expected), anomalous number of articles (either reduced or increased), article deformation, anarthrogenesis (i.e. incomplete division between articles), schistomely (i.e. bifurcation of articles or apical claws). There is no significant difference in the frequency of occurrence between the two body sides (χ^2 test, n = 217, d.f. = 1, $p > 0.10$), and the relative frequency of individuals with leg defects does not differ significantly between sexes (Z test, n = 153, $p > 0.50$). Most of the leg defects (56.6 %) occur within the first two-fifths of the series of trunk segments (distribution significantly different from equiprobability; χ^2 test, n = 217, d.f. = 9, $p < 0.001$, Fig. 4).

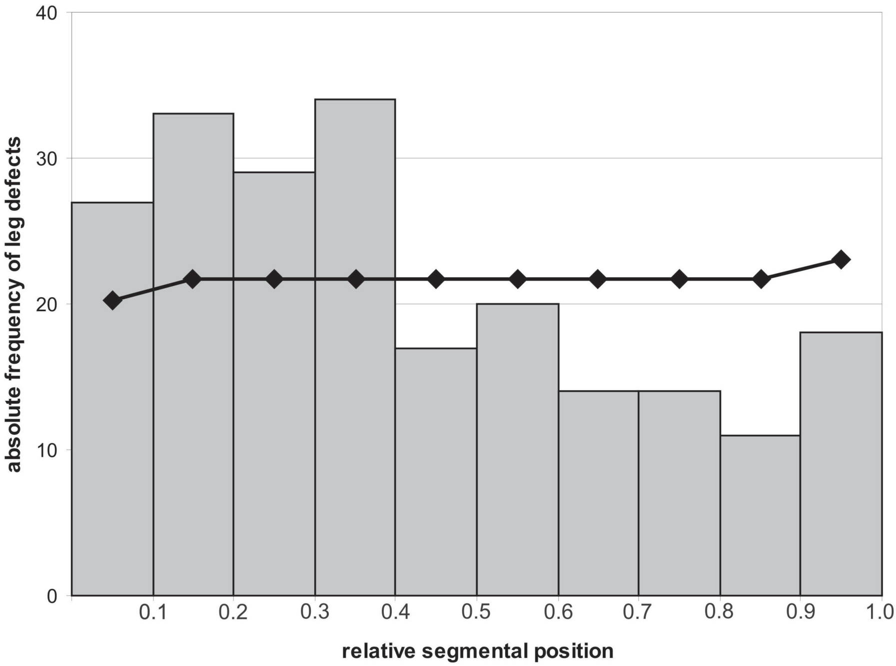

Fig. 4 Frequency distribution of the relative segmental position of leg defects along the trunk (217 cases in 153 specimens). The line shows the expected frequencies for each class of position in case of equiprobability. These are calculated considering that, for each number of leg pairs, a different number of absolute positional segmental values falls under each relative segmental position class (the number of leg pairs is never a multiple of the number of classes). The expected frequencies are weight-averages of the different expectations for each number of leg pairs, weighted on the basis of the actual number of leg pair frequency in the sample.

There are 21 cases of defective antennae. These include reduced number of articles (11 to 13 instead of 14), several kinds of article deformations, and schistomely (i.e. bifurcation). Usually only one antenna of the pair is anomalous, but in one case both antennae have 11 similarly deformed articles. There is no significant difference in the frequency of anomalies between left and right antennae (χ^2 test, n = 21, d.f. = 1, $p > 0.50$), and the relative frequency of individuals with antennal defects does not differ significantly between sexes (Z test, n = 20, $p > 0.20$).

We have scarce information on the modes of appendage healing and there is uncertainty on the possibility of appendage regeneration in Geophilomorpha (Minelli et al. 2000). At the present state of knowledge, this does not allow confidently to discriminate between congenital defects and defects resulting from imperfect regeneration (Maruzzo et al. 2005). For these reasons, our evaluation of appendage anomalies does not go beyond a descriptive analysis, and in any case frequency data should be taken with reserve.

No other centipede species found in the Citadel exhibits such a high incidence of anomalies. Out of 1075 specimens of the other nine centipede species, only 7 (0.7 %) present anomalies, and these are exclusively minor anomalies of legs and antennae (Tab. 2).

4. Discussion

The causes of the anomalies recorded in the Poznań population of *Stigmatogaster subterranea* are still to be identified. The high incidence and the extreme diversity of the morphological defects would suggest a local cause, for instance the presence of some environmental physico-chemical factor which would increase developmental instability, or a genetic constitution, derived by the recent colonisation and/or by the subsequent isolation, with high level of homozygosity for alleles with deleterious effect. However, preliminary data of different kinds invite considering alternative hypotheses.

Soil pollution: Our chemical analysis of the soil demonstrated very low presence of heavy metals – much lower than the permissible one, according to the strict standards established for soil in protected areas in Poland (Tab. 3). Specialist studies conducted in this area demonstrate that there has been no artificial exposure to radiation (Biernacka 2006). Additionally, there are no human activities in the vicinity which could have been the source of environmental contamination. In agreement with this data, no comparable frequency of morphological anomalies was found in any of the other nine species of centipedes living in the same site.

Non-optimal environmental conditions: Some environmental factors – especially humidity and temperature – may exert teratogenic influence on animals, as recorded in the beetle *Tenebrio molitor* Linnaeus, 1758 (Balazuc 1948), the millipede *Glomeris marginata* (Villers, 1789) (Juberthie-Jupeau 1969), and the tick *Hyalomma marginatum* Koch, 1844 (Buczek 2000). The Poznań population of *S. subterranea* lives far beyond the borders of the natural range of the species (see above) and is subject to environmental conditions that are possibly very different from the optimal ones. Barber & Keay (1988) provided most of the information concerning habitat selection in *S. subterranea*: this is a common woodland animal in the south part of the British Isles, but it is often found also in shore sites, gardens, arable, grassland, and disturbed areas. The experimental study by Keay & Forman (1987) showed that *S. subterranea* prefers high humidity and when it is exposed to low humidity it loses water (and bodyweight) quickly. The fact that in the north-eastern Europe the species occurs exclusively in synanthropic sites (and often in greenhouses) suggests that it may prefer high humidity combined with high temperature. In summer, when the majority of the specimens supposedly go through the early stages of development, the southern slope of the Citadel is exposed to very high temperature combined with low humidity. However, there is no direct evidence that such sub-optimal conditions for the species can explain the increased occurrence of anomalies.

Spread of anomalies: The optimal ranges of environmental parameters for *S. subterranea* are not known with adequate precision. For instance, the density of the Poznań population is very high in comparison with the densities of other geophilomorph species in Poland (Leśniewska 1997), although high densities seem not to be unusual for *S. subterranea* populations living in synanthropic sites (Lindner 2007, A. Keay pers. comm., H. Enghoff pers. comm.). Similarly, there are no available data on the genetic constitution of the population, and thus, for instance, we do not know the actual inbreeding coefficient. However, all these possible local causes cannot explain the fact that segmental anomalies of the same kinds occur with comparable high frequency also in other European populations of *S. subterranea*, from both natural and altered habitats, from within the natural range of the species, but also beyond it (Fig. 5). This suggests that a constitutionally high level of developmental instability could be a general feature of the species, or of a conspicuous fraction of populations. Further studies will be necessary to assess the geographic distribution and to identify the causes of these anomalies.

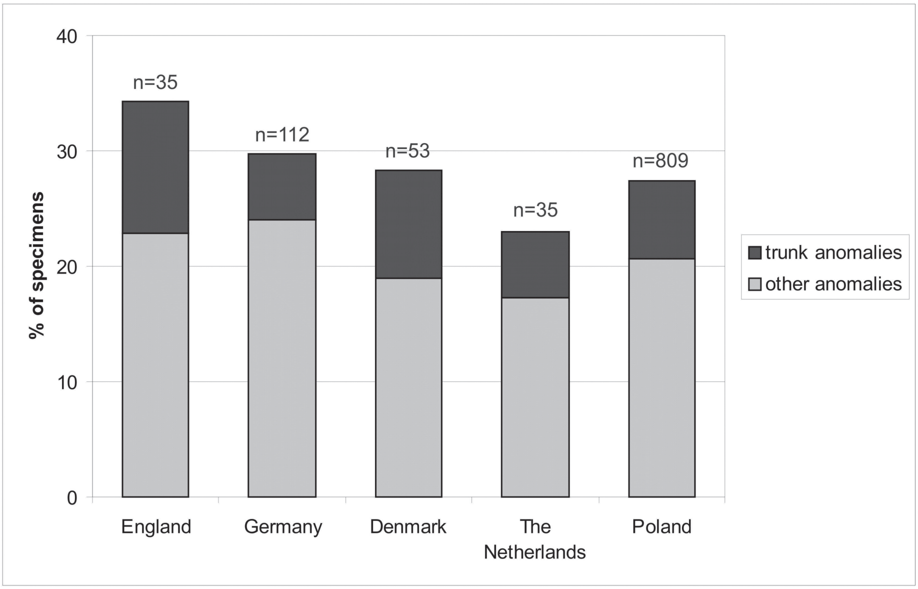

Fig. 5 Frequency of anomalous specimens in different groups of populations of *S. subterranea* (for more precise geographical provenance, see text).

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