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Trunk anomalies in the centipede *Stigmatogaster subterranea* provide insight into late-embryonic segmentation

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ABSTRACT

We describe and analyze naturally occurring anomalies in the segmental structures of the trunk in an isolated population of the geophilomorph centipede *Stigmatogaster subterranea*. Recorded anomalies include mispaired tergites, shrunk segments, variously deformed sclerites, bifurcated trunk, and defects of spiracles and sternal pore areas. One specimen has a perfect segmentally patterned trunk, but with an even number of leg-bearing segments, representing the first record of such a phenotype in adult centipedes. We interpret these anomalies as the effects of perturbation of specific morphogenetic processes in trunk segmentation, occurring at different embryonic stages. The variety of segmental anomalies found in this population provides insights into the developmental process of segmentation and its evolution in geophilomorph centipedes. Variation in dorsal mispairing anomalies demonstrates that segments, as traditionally defined in arthropod morphology, are not the effective developmental units throughout embryogenesis.

1. Introduction

Through a detailed analysis of naturally occurring morphological defects in a population of the geophilomorph centipede *Stigmatogaster subterranea* (Shaw, 1794), this study aims at contributing to the understanding of development and evolution of segmentation in this arthropod lineage.

The trunk of geophilomorphs consists of a first postcephalic segment (the forcipular segment) bearing a pair of poisonous maxillipedes (the forcipules), followed by a variable number of leg-bearing segments and a terminal genito-anal region of problematic segmental composition (Minelli, 1993). In the whole clade Geophilomorpha the number of leg-bearing segments varies between 27 and 191. In each leg-bearing segment we can distinguish (Supplementary material 1) two dorsal tergites, including a short anterior pretergite and a longer posterior metatergite, a ventral sternite accompanied by a couple of less conspicuous intercalary sternites, and a few lateral pleurites. Spiracles, i.e. the openings of the tracheal system, are placed on a distinct pleurite (the stigmatopleurite) from the second leg-bearing segment to the penultimate one.

The development of geophilomorph centipedes is confidently regarded as epimorphic (Lewis, 1981), i.e. juveniles hatch with the full complement of trunk segments. Rare reports on a possible anamorphic phase, of limited duration and effect (e.g., Misioch, 1978), have not been confirmed (see Horneland and Meidell, 1986). Epimorphic development is an apomorphy of the centipede clade Epimorpha, comprising Scolopendromorpha plus Geophilomorpha, while in the more basal centipede clades the number of trunk segments increases post-embryonically (anamorphic development). In epimorphic centipedes and in the adults of the anamorphic ones, the number of leg-bearing segments is invariably odd (Minelli and Bortoletto, 1988; Fusco, 2005).

Embryology of Epimorpha has been studied since the late nineteenth century with different approaches. Descriptive embryology is the subject of old papers (Metschnikoff, 1875; Sograff, 1882, 1883; Heymons, 1901; Verhoeff, 1902–1925; reviewed by Johannsen and Butt, 1941) dealing with half a dozen species. This first set of studies has been recently joined by investigations on trunk neurogenesis and the expression patterns of segmentation genes in the geophilomorph *Strigamia maritima* (Kettle et al., 2003; Chipman et al., 2004a,b; Chipman and Stollewerk, 2006; Chipman and Akam, 2008) and trunk neurogenesis in the scolopendromorph *Ethmostigmus rubripes* (Whitington et al., 1991). Gene expression patterns in the early phases of segmentation are thus well documented (Chipman and Akam, 2008), but later embryonic segmentation and morphogenesis are largely unexplored.

The study of morphological defects can provide useful insight into hitherto only vaguely described morphogenetic processes in

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normal development. These ‘naturally occurring experiments’ are particularly valuable for taxa which are not easily amenable to direct experimental manipulation, as geophilomorphs are.

Within the Epimorpha, no case of trunk segmental anomalies has been documented for the Scolopendromorpha to date, and only 13 cases have been reported for the Geophilomorpha (Supplementary material 2). To this short list of often incomplete and sometimes inaccurate descriptions we add here 68 cases of trunk anomalies (relative to 52 specimens) occurring in a single population of the geophilomorph species *S. subterranea*. We describe and analyze these anomalies, and try, as far as possible, to interpret them as specific perturbations of morphogenetic processes in trunk segmentation. Finally, we discuss our results in relation to development and evolution of arthropod segmentation.

2. Materials and methods

2.1. The species and the population

S. subterranea (Shaw, 1794) is distributed in the North-western part of Europe, occurring in natural sites from Great Britain to the Pyrenean region and western Germany. Isolated populations, most probably due to recent introduction, are scattered close to human settlements in the remaining part of Central and Northern Europe (Lindner, 2007).

The number of leg-bearing segments varies between 69 and 89 in most of the geographic range of the species, but reaches higher values, up to 101, in the Pyrenean region (Brölemann, 1908, 1930; Attems, 1929). Within a given population, the modal number of leg-bearing segments in females is two segments higher than in males, as common among geophilomorphs (Berto et al., 1997). Like most geophilomorph centipedes, *S. subterranea* has segmental clusters of exocrine glands whose opening pores are arranged in well-defined sternal pore areas. In this species, the areas, roughly transversally elliptical in shape, are present on all sternites from the second leg-bearing segment to about the mid-length of the trunk.

The material used in this study derives from a single, isolated population of *S. subterranea* in Poznań (Poland). This population is found in the ‘Citadel’ park, situated on a hill in the city centre, in a restricted area of 3400 m^2 on the bank of a deep moat, covered by a ruderal plant community. Anthropogenically transformed brown soil is found in the slope, and colluvial soil forms in some places of the slope.

As the population of *S. subterranea* in Poznań occurs far beyond the border of the species’ natural range, one may assume that it has been introduced in this site, most probably with garden soil. The population was discovered in 1991 (Leśniewska and Wojciechowski, 1992) and since then it has been monitored almost yearly.

For further details on the population and site biocenosis see Leśniewska et al. (in press).

2.2. Specimen sampling and scrutiny

A total of 809 specimens of *S. subterranea* were collected in 1991–2007 (Leśniewska et al., in press). In specimen examination, special attention was paid to size, shape and relative position of all sclerites along the trunk, to the arrangement of sternal pore areas and spiracles, and to size, shape and segmentation of antennae and legs. All specimens are preserved in M. Leśniewska’s collection.

Our analysis focuses on the segmental architecture of the trunk, thus disregarding anomalous features of the appendages, since, at the present state of knowledge, the scarce information on modes of appendage healing and uncertainty on the possibility of appendage regeneration in Geophilomorpha do not allow discriminating between congenital defects and defects resulting from accidents during post-embryonic life (Maruzzo et al., 2005). The 68 cases of trunk anomalies analyzed here are all almost certainly of developmental origin. As illustrated in the Result section, the regular geometry or, in other cases, the morphological complexity of these anomalies makes them hard to explain as the result of healing or regeneration. Of all the trunk anomalies recorded in the sample, we prudentially excluded from the analysis all the malformations possibly resulting from accidents during free-living stages or suspiciously deriving from collecting procedures. The possibility that a few cases among the less dramatic reported deformations are not congenital cannot be entirely ruled out, but this certainly does not apply to the most significant classes of trunk defects.

Sex was identified on the basis of the shape of the gonopods, to the exclusion of four early juveniles without emerging gonopods. As common practice in centipede morphometrics, the width of the cephalic shield was taken as a proxy for body size and, secondarily, for the individual’s age. In the anomalous specimens in which different serially homologous elements, either hemi-sclerites or legs, presented different cardinality, a value representative of the ‘total number of leg-bearing segments’ was computed as the maximal cardinality of serially homologous elements.

Examination of the specimens was limited to external morphology, postponing to a future study the destructive dissection of the specimens.

2.3. Methodological caveats

2.3.1. Biased defect diversity

The sample of anomalous specimens we have examined includes only specimens affected by developmental defects that were not embryonic-lethal, and did not prevent an individual from surviving until it was collected. Therefore, our sample might represent only a subset of the full diversity of developmental disturbances that can occur in the population, with a possible bias towards specific types of anomalies.

2.3.2. Somatic accommodation effects

An observed morphological alteration results from a developmental defect in its own, combined with some form of accommodation involving the flanking body tissues and structures. We have no general criteria for discriminating the relative contributions of these two processes to the final appearance of a given morphological anomaly.

3. Results

3.1. Basic statistics of trunk anomalies

Morphological anomalies were found in 206 out of the 809 examined specimens (25.5%). Most of these specimens (154 specimens, 19.0%) are affected by appendage defects exclusively (legs and/or antennae), and are not considered in the present study.

Anomalous features in the trunk putatively produced by developmental disturbances were found in 52 specimens (6.4%), some of which with more than one anomaly. Thus, a total of 68 distinct cases of perturbed trunk regions were recorded and analysed. The relative frequency of individuals with trunk anomalies does not differ significantly between sexes (Z test, $p > 0.24$). Anomalies were found in specimens from juveniles to full grown adults.

The number of leg-bearing segments in the specimens without trunk anomalies varies in the range 75–83 for the males ($n = 418$) and 77–85 for the females ($n = 335$), whereas the range in the anomalous specimens is 77–81 for the males ($n = 24$), and 79–87 for the females ($n = 27$). The frequency distribution of segment numbers in the anomalous specimens is not significantly different from that observed in all other specimens sampled from the same population, although with different statistical confidence in the two sexes (Kolmogorov–Smirnov test, males $p > 0.08$, females $p > 0.99$). However, it is perhaps worth noting that in the females the maximum segment number found in anomalous specimens is higher than in the normal ones (87 vs. 85), and the modal number of leg pairs in anomalous males is higher than in normal males (81 vs. 79).

On the basis of the morphological features of the perturbed trunk regions, seven recurrent structural patterns were identified, as described in the following.

3.2. Pure dorsal mispairing

3.2.1. Definition

The series of alternating pre- and metatergites of one side of the body (hemi-pretergites and hemi-metatergites) matches the contralateral series 'out of frame', thus some tergites present discordant left/right serial position and/or identity (pretergite or metatergite) (Figs. 1A and 2A; Supplementary material 3 and Movie 1). This type of anomaly occurs in regions with substantially undisturbed ventral and pleural structures.

From anterior to posterior, the salient elements of this anomalous segmental pattern are the following: one or more hemi-tergites of one side do not match with any tergite of the other side, their length shortening medialward to disappear approximately at the mid-longitudinal line ('anterior unpaired motif'); some following hemi-tergites of the same side match with more anterior hemi-tergites of the opposite side, forming 'oblique tergites'; the anomalous matching 'propagates' posteriorly until one or more hemi-tergites of the opposite side (the number being equal to that of the anterior unmatched set) fail to match with contralateral hemi-tergites ('posterior unpaired motif'), thereby re-establishing the regular segmental pattern. More complex unpaired motifs are possible (Section 3.2.3).

3.2.2. Occurrence and segmental position

Of this type of anomaly we recorded 10 cases in 8 specimens, both males and females, with different number of segments and of different body size (Fig. 3).

Pure dorsal mispairing always occurs in the posterior half of the trunk, most often among the eight most posterior leg-bearing segments. However, no preferred segmental positions are recognizable for either the anterior or the posterior ends of the perturbed region, or for its mid-point, and between-individual variation in these values is not significantly different when scored by counting segments from either the anterior or the posterior end of the trunk (F test, $p > 0.10$).

3.2.3. Structural features

The observed perturbed region encompasses 4–15 tergal units, counting pretergites and metatergites separately (Fig. 4). The pattern of tergites in the perturbed region is either palindromic (the unpaired motif at one end being a mirror-like copy of that at the other end) or not. The unpaired motif consists in either a single tergite (either pretergite or metatergite), or a pair of contiguous tergites (either pretergite–metatergite or metatergite–pretergite) or even in a pair of tergites of the same type (both of them pretergites or metatergites) separated by an oblique tergite composed of mispaired hemi-tergites from the two sides. Oblique tergites are composed of two hemi-tergites of either the same type (both hemi-pretergites or both hemi-metatergites) or of different types (a hemi-pretergite and a hemi-metatergite). Both alternative orientations of the oblique tergites are observed. Variation in structural features is not evidently affected by sex, body size or position along the body axis.

3.3. Trunk shrinking

3.3.1. Definition

Some contiguous trunk segments are asymmetrically reduced in length, seemingly as a result of local defective growth (Figs. 1B and 2B; Supplementary material 3 and Movie 2). Shrinking never extends uniformly to a complete transversal section of the trunk, and always presents left-right asymmetry. This defect affects number, shape and size of the serially arranged sclerites, appendages, spiracles and pore areas of the region.

3.3.2. Occurrence and segmental position

Of this type of anomaly we recorded 20 cases in as many specimens, including both males and females, with different number of segments and of different body size (Fig. 3).

Cases of trunk shrinking limited to ventral or pleural regions, i.e. not extending to the dorsal region (7 cases), occur in positions scattered along the trunk, from leg-bearing segment 5 to 79. Conversely, trunk shrinking involving the dorsal region, either when ventral (or pleural) shrinking on one side extends to the corresponding tergites (12 cases), or when only tergites are involved (1 case), are limited to two restricted regions of the trunk, one close to the anterior end (roughly from 10% to 15% of the series of leg-bearing segments) and the other close to the posterior end (roughly within the most posterior 9% of the series of leg-bearing segments). Within these regions, however, no special positions are recognizable for either the anterior or the posterior ends of the perturbed region, as well as for its mid-point. The position is not evidently affected by sex or body size.

3.3.3. Structural features

Shrinking usually involves a single segment, but it may extend to up to three contiguous segments. There is no significant difference in the frequency of occurrence between the two body sides (χ^2 test, $n = 20$, $p > 0.52$). Within the perturbed segmental units, the zone of maximum shrinking is most often localized in the pleuro-ventral or pleuro-dorsal region, on either the left or the right side; only in one case it is localized close to the dorsal midline. The effect of shrinking on size and shape of the sclerites is highly variable, from cases in which only one sclerite is reduced in size to cases in which the sclerites of about a half of the entire segmental unit are lacking. In 3 females, pleuro-ventral shrinking is associated with dorsal mispairing in the same region (Fig. 2C; Movie 3).

Localization of maximum shrinking (ranked in four zones, from dorsal to ventral) and magnitude of the shrinking (ranked in six degrees of magnitude) are not evidently affected by sex or body size, and the two variables are not correlated (Spearman correlation, $r = 0.10$, $n = 19$). The most severe cases of shrinking, involving the lack of an extended set of sclerites, are all close to the posterior end of the trunk.

3.4. Even number of leg-bearing segments

3.4.1. Definition

An apparently regular, or almost regular, trunk segmental pattern comprising, however, an even number of recognizable leg-bearing segments (Figs. 1C, D and 5).

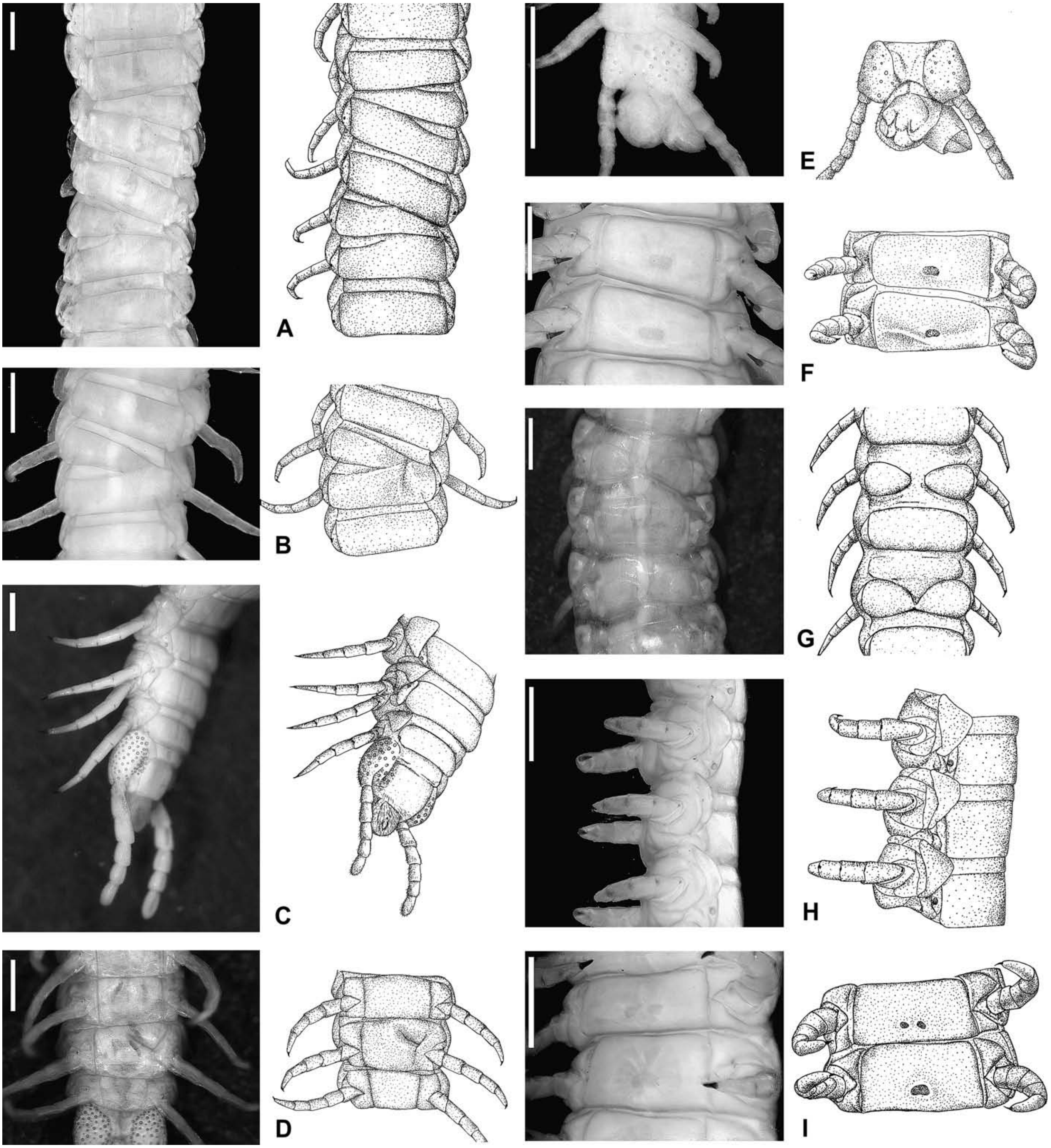

Fig. 1. Representative cases of the main types of trunk anomalies in *S. subterranea* from Poznań: A, pure dorsal mispairing; B, trunk shrinking; C, D, even number of leg-bearing segments; E, trunk bifurcation; F, G, sclerite deformation; H, defects of spiracles; I, defects of sternal pore areas. Bar 0.5 mm. Codes of trunk anomalies (see Supplementary material 3): A, 300a; B, 749; C, 164; D, 216a; E, 757; F, 719; G, 117b,c; H, 726; I, 561e. Anterior is towards the top.

3.4.2. Occurrence, segmental position and structural features

This type of anomaly was recorded in 3 specimens, all adult males with 80 unambiguously recognizable leg-bearing segments.

In one specimen with an apparently perfect segmental pattern (Fig. 5) it is not possible to identify the position of the defect responsible for the anomalous segment number, if the defect is actually localized. In the other two specimens, instead, leg-bearing segment 78 has anomalous features. In one of them (Fig. 1C), two legs, rather than one, emerge on the left side, from adjacent points within a regularly patterned pleural region, both legs being regular and similar in structure and size. In the other specimen (Fig. 1D), a transversal furrow on the left side of the sternite can be

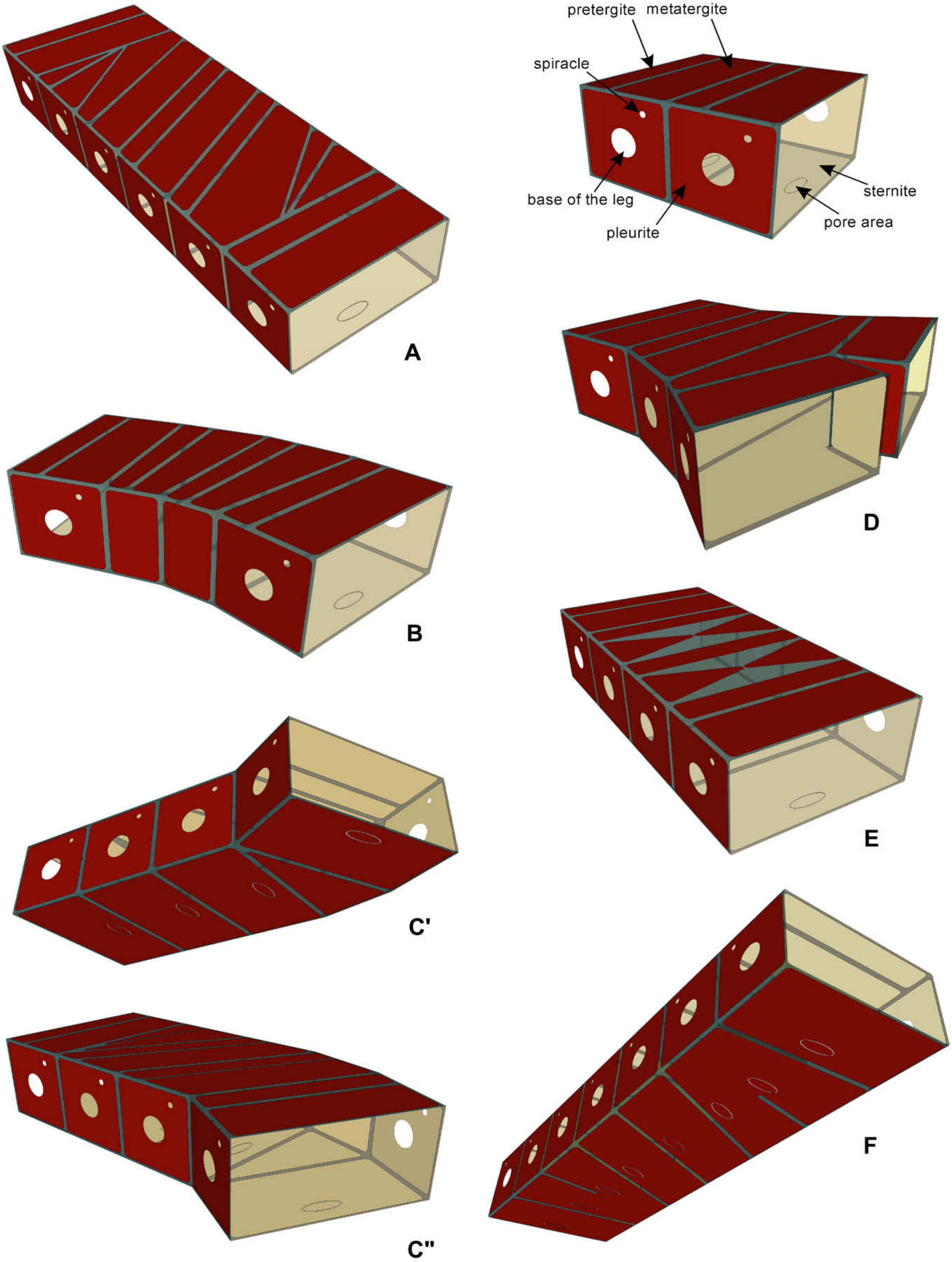

Fig. 2. Schematic drawings of the main types of trunk anomalies in geophilomorph centipedes. A, pure dorsal mispairing; B, trunk shrinking; C, trunk shrinking producing dorsal mispairing, in ventral (C′) and dorsal (C″) view; D, trunk bifurcation; E, sclerite deformation; F, ventral mispairing. Anterior is towards the left. (Animation movies of the models are available as supplementary online materials).

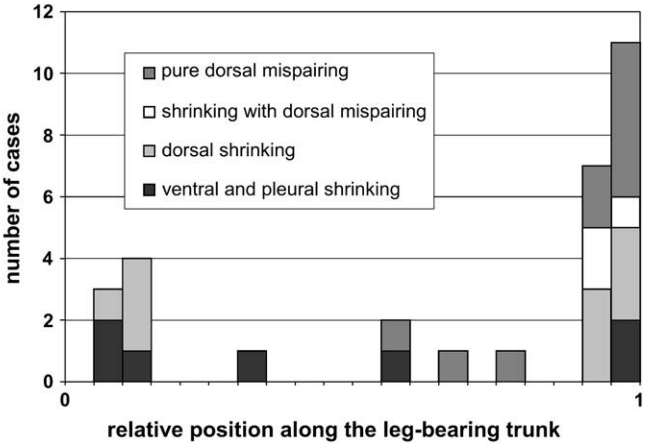

Fig. 3. Relative position along the leg-bearing trunk of the anomalies observed in *S. subterranea* from Poznań. Cases of anomalies affecting more than one segment are represented in a position corresponding to the mid-point of the perturbed region. Relative position is calculated as the ratio between segmental absolute position and the total number of leg-bearing segments in the specimen. The class indicated as 'dorsal shrinking' includes both cases of trunk shrinking exclusively involving the dorsal region (1 case), and cases where ventral (or pleural) shrinking on one side extends to the corresponding hemi-tergites (9 cases).

interpreted as imperfectly separating an additional, anterior, reduced hemi-sternite, which is not accompanied by a recognizable corresponding pleural region.

3.5. *Trunk bifurcation*

3.5.1. *Definition*

The posterior part of the trunk is split into two diverging terminal branches (Figs. 1E and 2D; Supplementary material 3 and Movie 4).

3.5.2. *Occurrence, segmental position and structural features*

A single case was recorded, in a juvenile male. No other anomalies affect the specimen. The branching point is within the terminal part of the trunk, posterior to the last leg-bearing segment. A well-formed posterior trunk region is connected on the dorsal-left side to a duplicated equivalent with unconventional morphology. The latter presents a pair of putatively ventral projections, possibly homologous to the anal valves, but no structure typical for the genital region is recognizable.

3.6. *Sclerite deformation*

3.6.1. *Definition*

One or a few sclerites are altered in size and/or shape, but, at variance with trunk shrinking, these malformations do not change the spatial relationships between segmental structures (Figs. 1F, G and 2E; Supplementary material 3 and Movie 5). This class of anomalies does not include sclerite malformations accompanying the more severe types of anomalies described above (Sections 3.2–3.5).

3.6.2. *Occurrence and segmental position*

Sclerite deformation was recorded 26 times, from 22 specimens, both males and females, with different number of segments and of different body size. In some specimens, deformed sclerites co-occur with other defects localized in different regions of the trunk. Sclerite deformations are scattered throughout the whole trunk, from the most anterior segments, with a case affecting the forcipular segment, to the penultimate leg-bearing segment. No region or position is evidently affected at higher frequency.

3.6.3. *Structural features*

Deformation usually involves single sclerites or pairs of contiguous sclerites, either tergites or sternites. More rarely deformation involves three contiguous segments, or affects the pleural region. In four cases (Fig. 1F), two contiguous sclerites, either tergites or sternites, have mirror-like trapezoidal shape, while the other sclerites of the same segments have regular shape. In another single case, however, sclerite shape irregularity can be described as a non-perfectly transversal plane separating all the sclerites (tergites, pleurites and sternites) of two contiguous segments, producing the effect of two wedge-shape segments with opposite left-right orientation. In a frequent deformation of a different kind, observed in 9 cases, two contralateral hemi-tergites, either pretergites or metatergites, do not match with a uniform length and straight margin, instead they either match with sinuous or angled margins or taper medially, eventually vanishing at about mid-line (Fig. 1G). Variation in structural features is not evidently affected by sex, body size or position along the body axis.

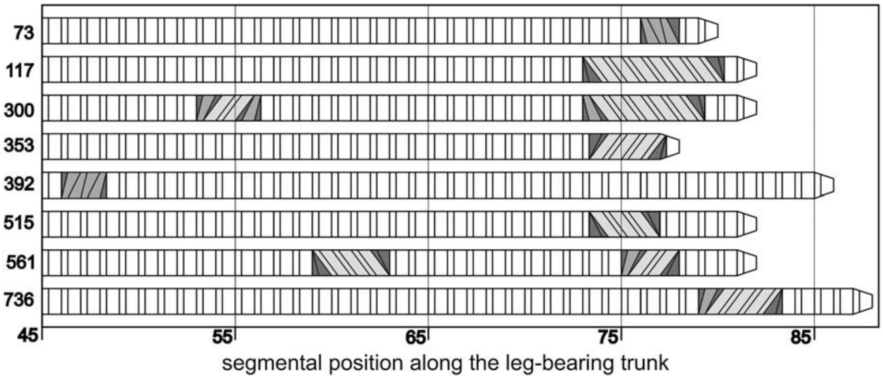

Fig. 4. Schematic representation of the segmental pattern of the cases of pure dorsal mispairing. Specimens are aligned referring to the anterior end of the leg-bearing trunk, even though only the most posterior part of the trunk is illustrated. Short and long empty rectangles represent pretergites and metatergites respectively, dark-gray triangles are unpaired hemi-tergites, light-gray parallelograms are mispaired hemi-tergites of the same kind (pretergite–pretergite or metatergite–metatergite), mid-gray trapeziums are mispaired hemi-tergites of different kind (pretergite–metatergite); the subterminal short trapeziums represent the anteriormost of the terminal segmental units of the genital region, which is involved in the mispairing in one specimen. Specimen identification code is reported on the left (see Supplementary material 3).

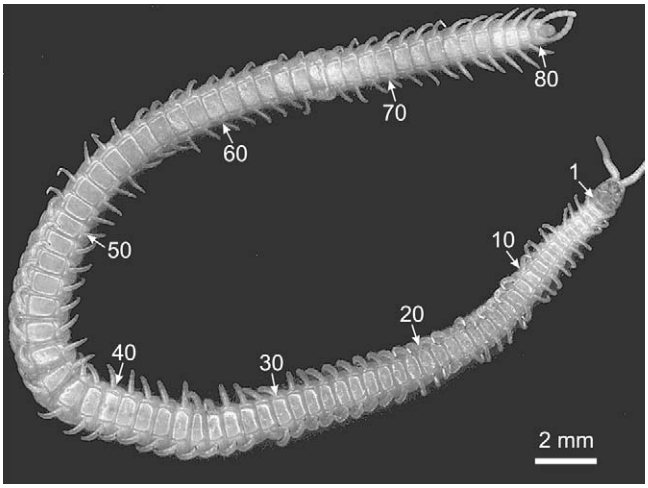

Fig. 5. Specimen of *S. subterranea* from Poznań with a regularly patterned trunk, but with an anomalous even number (80) of leg-bearing segments (specimen code 799, 25.4.2007, M. Leśniewska legit).

3.7. Defects of spiracles

3.7.1. Definition

The bilateral series of tracheal spiracles is locally perturbed (Fig. 1H; Supplementary material 3). This class of anomalies does not include spiracle defects accompanying the more severe anomalies described above (Sections 3.2–3.5).

3.7.2. Occurrence, segmental position and structural features

Apart from the cases where defective spiracles were found in association with other anomalies, usually with trunk shrinking (Section 3.3) that involves reduction or absence of the pleural region of a segment (9 cases in 9 specimens), this defect occurred in 3 other cases in 3 specimens.

Defective spiracles are recorded at different positions along the trunk. In two cases, a single spiracle is lacking. In the third case, the spiracle is replaced by two spiracles of normal size, opening on the same stigmatopleurite.

3.8. Defects of sternal pore areas

3.8.1. Definition

On some sternites of the trunk region with ventral pore areas, the pore area is deformed or absent (Fig. 1I; Supplementary material 3). This class of anomalies does not include pore area defects accompanying the more severe anomalies described above (Sections 3.2–3.5).

3.8.2. Occurrence, segmental position and structural features

This defect was recorded in 5 cases in 5 specimens, including both males and females, with different number of segments and of different body size. In 2 additional cases, defective sternal pore areas are associated with shape irregularity of the relevant sternite (Section 3.6).

Defects occur at different positions along the anterior part of the trunk where pore areas are normally present, without any evident positional prevalence. In all cases recorded, the defect is limited to a single segment.

Whenever deformed, the pore area can either extend into a small lateral projection or resolve into a pair of separate areas, of similar or different size. When the pore area is absent, no scattered pores are detectable on the whole surface of the sternite.

4. Discussion

4.1. Causes of developmental instability

The frequency of occurrence of segmental anomalies in the Poznań population of *S. subterranea* is unprecedented in centipede literature. On the basis of this high incidence of morphological defects, one would expect the involvement of some environmental causal factor (either chemical or physical) increasing developmental instability. However, this does not seem to be the case here, because: (a) physico-chemical parameters of the soil, including heavy metal content and radioactivity are within standard values; (b) no comparable frequency of morphological anomalies of any kind was found in any of the other nine species of centipedes living in the same site, including other four geophilomorph species; (c) preliminary data show that segmental anomalies of the same kind occur with comparable high frequency also in other European populations of *S. subterranea*, both within and outside its natural range (Leśniewska et al., in press). Specifically targeted investigations are necessary to identify the causes of this developmental instability.

4.2. Comparison with cases in the literature

The 13 published cases of anomalies affecting the trunk segmental pattern in epimorphic centipedes (all in the Geophilomorpha; Supplementary material 2), all refer to single specimens from different populations of eight species. Most of the cases are in the polypodous Himantariidae (6 cases in *Himantarium gabrielis* and two cases in *Stigmatogaster* species, including *S. subterranea*); other cases are mainly in the relatively oligopodous Schendylidae. Of these cases, only eight are recognizable as corresponding to any of the different kinds of anomalies described here (mostly, trunk shrinking), while the other five cases (four in *H. gabrielis* and one in *Geophilus procerus*) do not fit into any of our morphological categories.

These five anomalous specimens exhibit a sort of 'ventral mispairing'. At one end of the perturbed region, more than one hemisternite of one side match with a single contralateral hemi-sternite. This produces an 'out of frame' hemi-sternite pairing that extends for a number of segments until a complementary one-to-many hemi-sternite matching at the other end of the perturbed region re-establishes the normal segmental pattern (Fig. 2F; Movie 6).

This anomalous segmental pattern is known as 'helicomery' (variously referred to also as "helicomerism" and "spiral segmentation" in English, and "hélicomérie", "hélicométamérie", and "segmentation hélicine" in French; Balazuc and Schubart, 1962; Demange and Pereira, 1980; Minelli and Pasqual, 1986).

Helicomery has been reported for all major arthropod clades (insects, Cockayne, 1929, 1934; Ramsay, 1959; notostracan crustaceans, Linder, 1947; myriapods, Balazuc and Schubart, 1962; Demange and Pereira, 1980; Minelli and Pasqual, 1986; and chelicerates, Ćurčić et al., 1983), and annelids as well (Morgan, 1892).

Arthropod helicomery is defined as the condition of a region of a segmented structure (generally the trunk) where the sclerites are not in such a connection as to produce close belts around the axis (thus, identifying discrete axial units, or segments), but form instead one or more helical turns around the axis.

From our observations on *S. subterranea*, complemented by the five cases of 'helicomery' reported in literature, it is evident that a helicomeric pattern can result from different types of developmental defects. These are pure dorsal mispairing, trunk shrinking producing dorsal mispairing, and 'ventral mispairing'. Thus, helicomery being a pattern of sclerite arrangement that can result from more than one type of defect, of possibly different developmental origin (Sections 4.3.2–4.3.3), it should not be considered a class of anomalies in its own.

4.3. A developmental interpretation of anomalies

A guide to associating the observed anomalies with specific developmental processes is provided by what is currently known about trunk segmentation in the Epimorpha, namely (a) the sequential appearance of ventral segmental units in the germ-band, (b) the ventral to dorsal differentiation of trunk sclerites, and (c) the dorsal closure of the embryo after blastokinesis (i.e. after the bending of the germ-band at about mid-trunk and its 'sinking' into the egg yolk) (Chipman et al., 2004b).

The anomalies described above can be interpreted as due to perturbation of different morphogenetic processes occurring at different developmental stages. These are illustrated below, approximately from an early embryonic to an early post-embryonic stage. However, as segmental structure development in the germ-band proceeds from anterior to posterior, at any given time during this part of embryogenesis different segmental units can be considered as being at different developmental stage. Thus, in the following discussion 'developmental stage/phase' is more precisely referred to a phase of development of the segments in a given trunk region, rather than to the whole span of embryonic life.

4.3.1. Defective segmentation of the germ-band

In the early phases of embryogenesis of the geophilomorph model species *S. maritima*, stripes of expression of segmentation genes appear sequentially, from anterior to posterior, emerging from a subterminal region of the elongating germ-band (Chipman et al., 2004a; Chipman and Akam, 2008). This process goes on in parallel with germ-band elongation. Disturbance to this developmental process is expected to produce a significant alteration of the number of trunk segments. Reminding that the recorded anomalies possibly represent only a subset of the occurring defects (Section 2.3), these were evidently not so early in segmental patterning as to produce a substantial alteration of the final number of trunk segments, as there is no significant difference in the frequency distribution of this character between normal and anomalous specimens.

Although the genetic basis of the segmentation mechanism is not completely understood in geophilomorphs, there is some evidence of an early embryonic phase when segmental units are established in pairs, to be split into the final segmental units immediately thereafter. This is supported by developmental genetics and comparative morphology data as well (Chipman et al., 2004a; review in Fusco, 2005). This segmentation phase would provide scope for defects that break the general rule of the odd number of leg pairs in centipedes, through the failure of the split of one of these early bisegmental units. The three cases of perfectly or almost perfectly patterned trunks with an even number of leg-bearing segments (Section 3.4) could be the result of developmental disturbances at this specific phase of the segmentation process.

The perfectly patterned specimen with an even number of leg-bearing segments (Fig. 5) is the first ever reliably recorded in epimorphic centipedes. In the only superficially similar case, reported so far for a male of *S. maritima* (Kettle et al., 1999), one extra leg pair was produced by the homeotic transformation of an apodous segment of the genital region, thus affecting the identity of a single segment, rather than total number of the whole set of trunk segments. Actually, records of even numbers of segments in Geophilomorpha are quite frequent in the taxonomic and faunistic literature up to the first decades of the XX century. Both even and odd values for the number of leg pairs were frequently given, without comments, due to different causes: a) different criteria adopted for counting leg pairs (often excluding the last pair of legs because of their frequently peculiar shape, having sensorial function and not being used for walking); b) misprint; c) author's inaccuracy in counting. The most recent examples are one specimen of *Orya panousei* credited with 98 leg-bearing segments (Demange, 1961), and another 20 specimens of nine different species and subspecies, also credited – without any comment or discussion – with even numbers of leg-bearing segments (Demange, 1963).

4.3.2. Defective growth at germ-band stage

As the differentiation of segmental structures progresses, during germ-band stage, from the presumptive ventral region towards the pleural and dorsal regions of both sides (Chipman et al., 2004b), local defects in growth and/or differentiation of segmental structures on one side are expected to 'propagate' towards the anlagen of more dorsal regions, eventually affecting all the structures localized between the point of origin of the defect and the dorsal medial area of the same side.

These early developmental disturbances are thus expected to produce trunk shrinking (Section 3.3), although not all cases of trunk shrinking have this developmental origin. Actually, trunk shrinking can also originate from local defective growth at later developmental stages, i.e. after the complete formation of sclerites and the dorsal closure of the embryo (Section 4.3.4). Morphology does not provide criteria to distinguish between the two alternatives in all cases, however, when trunk shrinking is (a) bilaterally dorsal, or (b) affects ventral or pleural structures leaving the dorsal structures undisturbed, we have arguments for rejecting the hypothesis of an early (germ-band) defect (8 cases out of 20). In the three cases where the defective development of ventral structures produced dorsal mispairing, we can be confident about the early origin of the defect, since it must have arisen before the dorsal closure of the embryo.

Two other anomalies were perhaps produced during germ-band formation: the case of trunk bifurcation (Section 3.5) (interestingly, the only other case recorded in the literature was found in the same species; Selbie, 1913; Supplementary material 2), and the case of sclerite deformation resulting in two contiguous wedge-shape segments (Section 3.6).

4.3.3. Sclerite mismatch at dorsal closure

During the dorsal closure of the embryo, the leading edges of the opposing epidermal sheets may contact incorrectly across the mid-dorsal seam, failing to produce a regular pairing of the two sides. Once two hemi-tergites match incorrectly, this defect can propagate anteriorly or posteriorly, or in both directions, until the tergites already formed by a correct match cause the mismatch to stop and impose a form of accommodation to one or more residual anterior and posterior unpaired hemi-tergites. The ten cases of pure dorsal mispairing recorded in our sample can be interpreted as caused by this kind of developmental failure. In all cases examined, within the perturbed region there is no morphological evidence for a precise segmental localization of the origin of the mismatch.

In embryos of *Drosophila melanogaster*, this kind of defective embryo closure has been well documented, and its mechanics has been elucidated at cell and tissue levels (e.g., Jacinto et al., 2000, 2002; Liu et al., 2008). In *Drosophila*, during dorsal closure, epithelial sweeping and zippering progress from both the anterior and the posterior end of the dorsal hole (Jacinto et al., 2002).

Apparently, in *S. subterranea* the dorsal closure does not proceed in strictly sequential order, one segment after the other, as this mode would produce a preferred end point for the anomaly, irrespective of the localization of the starting point of the mismatch. This does not exclude the possibility of a main (long-range) direction for the dorsal closure of the embryo, perhaps centripetal, from the trunk ends towards a point in between. In this respect, our data provide no evidence about the main direction of the dorsal closure. The distribution of pure dorsal mispairing along the trunk (Fig. 3) suggests that erroneous matching between the edges of the two epidermal sheets may occur with the highest probability within a posterior subterminal part of the trunk, where dorsal closure is perhaps characterized by a higher level of developmental instability. However, alternative explanations cannot be excluded, as for instance that mispairing in other trunk regions seriously affects viability.

The high variation in the pattern of hemi-tergite matching in the perturbed region and the fact that no assortative matching has been found between pre- and metatergites suggest that these two morphologically recognizable sclerite types are equivalent with regard to embryonic morphogenetic processes, at dorsal closure at least.

The mechanism generating pure dorsal mispairing contrasts with the one producing dorsal mispairing as a consequence of ventral or pleural shrinking (Section 4.3.2). Here the origin of the defect is at one side of the perturbed region, where the defective development of one or more hemi-tergites of one side imposes a wrong matching to the tergites that follow in the direction of the closure. The unmatching tergites of the opposite side have instead the same ‘recovery role’ as in the case of pure dorsal mispairing. In two of the three cases recorded, the origin of the defect is posterior. In the other one, the region is too short (one segment) to be informative in this respect.

4.3.4. *Late local defective growth*

Developmental disturbances occurring at a stage later than those considered above, after blastokinesis and the dorsal closure of the embryo, can affect an already definitely patterned series of sclerites and appendage anlagen. These disturbances could be for instance a defective growth or a tissue necrosis limited to a small set of segmental structures. Anomalous trunk morphologies described above as sclerite deformation (26 cases, Section 3.6) and cases of trunk shrinking not originated at the level of germ-band (8 cases; Section 4.3.2) are probably the outcome of this kind of developmental accidents.

4.3.5. *Anomalous patterning of late structures*

In the few geophilomorph species studied up to now, spiracles and sternal pores open after hatching, apparently with the moult to the third post-embryonic stage (adolescents I) (Lewis, 1981). Local defects in the serial pattern of tracheal spiracles and sternal pore areas (Sections 3.7–3.8), when not associated with other defects, can be regarded as due to developmental disturbances in growth and differentiation occurring later in morphogenesis, after most of the segmental patterning of the trunk has been attained. These defects may even have a post-embryonic origin.

5. Conclusions

The variety of segmental defects exhibited by the Poznań population of *S. subterranea* contributes information on the developmental process of segmentation and its evolution in geophilomorph centipedes, with implications for segmentation in arthropods at large. Insight provided by these ‘monsters’ can be summarized in four points.

5.1. *The rule of odd leg-bearing segment numbers is not unexceptionable*

In geophilomorphs the number of leg-bearing segments varies between 27 and 191, but, as a rule, only odd numbers occur. The discontinuous occupancy of this wide range of variation has long been known to centipede specialists, but was first brought to the attention of evolutionary biologists as a case of developmental constraint by Minelli and Bortoletto (1988). Since then, it has become a classical example of developmental constraint (e.g., Arthur and Farrow, 1999), as it is difficult to explain this pattern of variation in terms of adaptation. The finding of one individual with a single perfectly patterned trunk with 80 leg-bearing segments obviously does not challenge the variation in geophilomorph segment numbers as a case of developmental constraint. It simply moves it from the class of ‘forbidden phenotypes’ to that of ‘highly improbable phenotypes’ that can be produced by the current developmental system (Fusco, 2001). On the contrary, it possibly reinforces the argument for an explanation in terms of developmental constraints, because it demonstrates that an animal with an even number of leg pairs can survive until adulthood. However, the developmental process, or processes, responsible for the rule of odd segment numbers in centipedes (Chipman et al., 2004a) is evidently not so rigorously canalized as thought, since it can apparently be overtaken in a proper genetic or developmental setting.

5.2. *Helicomery is not the result of a single type of developmental defect*

We found that in geophilomorphs helicomery is a pattern of sclerite arrangement that can result from more than one type of developmental defects. This raises the question of which developmental mechanisms are at the origin of similar aberrant segmental patterns in other segmented animals (Section 4.2). Among them are both short- and long-germ-band insects, anamorphic and epimorphic myriapods, crustaceans whose posterior segmentation is based on ectoteloblast proliferation and annelids whose terminal growth and segmentation are produced through mesoteloblast activity.

5.3. *Segmentation applies to specific structural components of a body axis*

Helicomery obviously questions the concept of segment as a body unit, as the ‘segmental identity’ of repetitive structures cannot be univocally determined, suggesting that segmentation applies to specific structural components of a body axis (sternites, tergites, leg pairs, etc.), rather than to the axis itself (see Minelli and Fusco, 2004). The diversity within the class of pure dorsal mispairing defects supports this ‘non-modular’ concept of segmentation even more strongly. Variation within these anomalous segmental patterns demonstrates that the traditional descriptive segmental units are not necessarily developmental units. Hemi-tergites behave independently at dorsal closure, disregarding their ‘belonging to a given segment’. The divide between pretergite and metatergite is not a subordinate division with respect to the putative ‘true segmental division’ between the metatergite of ‘one segment’ and the pretergite of the ‘following segment’. At some point in development, the two boundaries are perfectly equivalent.

5.4. *A process of ‘ventral closure’ recurs in the embryogenesis of the Epimorpha*

During embryogenesis of the geophilomorph model species *S. maritima*, just before the beginning of blastokinesis, the lateral (pleuro-dorsal) territories of the germ-band separate longitudinally from the presumptive ventral neuroectoderm, to which they remain connected by a membranous tissue (Chipman et al., 2004b; Chipman and Stollewerk, 2006). Apparently, the ventral tissues do not separate along the mid-line (as described in *Scolopendra*; Heymons, 1901), however gene expression is less marked (or null) and cell density is lower along the ventral neuroectoderm mid-line. Later in embryogenesis, the contact between the pleuro-dorsal and ventral parts of the body wall is restored (Chipman et al., 2004b).

The anomalous segmental pattern we call ventral mispairing, described for a pair of distantly related geophilomorph species (a himantariid and a geophilid), supports the possible existence in these species of a phase of interruption of the ventral continuity between the tissues of the two body sides (as observed in *Strigamia* and *Scolopendra*), or a gap at the level of the molecular markers involved in the subsequent ventral sealing. The subsequent retraction of this space, whatever its actual histological or molecular constitution, would provide scope for a wrong ventral pairing between the segmental anlagen of the two sides. Were these data on abnormal specimens confirmed by observation in normal development, in analogy to the corresponding dorsal process, this late-embryonic process could be termed 'ventral closure'.

Further studies and a larger taxon sampling will be necessary to assess whether this developmental character is an apomorphy of the Epimorpha.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.asd.2009.05.001.

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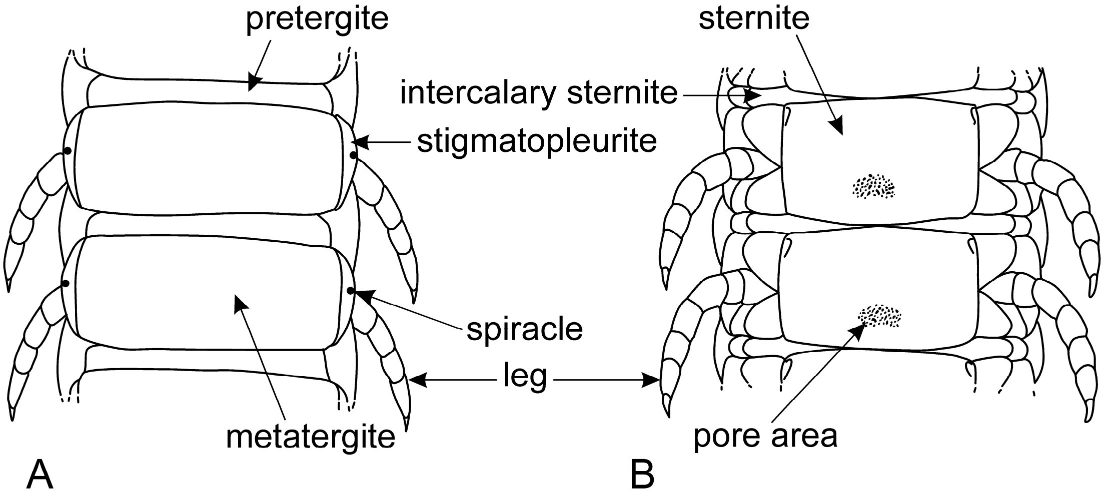
Supplementary material 1

Main morphological features of the trunk segments of Stigmatogaster subterranea

Simplified line-drawings of two contiguous leg-bearing segments: A, dorsal view; B, ventral view. Anterior is towards the top.



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Supplementary material 2

Published records of anomalies in the segmental pattern along the body trunk in Geophilomorpha, putatively due to early developmental defects

Current names of species are from ChiloBase (Minelli, 2006). The number of leg-bearing segments has been estimated as described in the Material and methods. Segmental position refers to the progressive number of leg-bearing segments from the most anterior one.
*For the case originally described by Shinohara (1949), data are not from the original source, which is unavailable to us, but as secondarily reported and emendated by Balazuc & Schubart (1962).

Reference	Current name of the species	Species cited as	Locality	Number of leg-bearing segments	Segmental position of the defect	Type of anomaly as described in the present paper
Brölemann, 1894	*Himantarium gabrielis* (Linnaeus, 1767)	*Himantarium gabrielis*	Lyon (France)	151	134-139, 143-144	Ventral mispairing
Léger & Duboscq, 1903	*Schendyla vizzavonae* Léger & Duboscq, 1903	*Schendyla vizzavonae*	Vizzavona (France)	49	40	Trunk shrinking
Brölemann, 1904	*Himantarium gabrielis* (Linnaeus, 1767)	*Himantarium gabrielis*	Principauté de Monaco	163	67-83	Ventral mispairing
Selbie, 1913	*Stigmatogaster subterranea* (Shaw, 1794)	*Stigmatogaster subterraneus*	Kilfinane, near Limerick (Ireland)	unknown	N-6 to N	Trunk bifurcation
Brolemann, 1920	*Stigmatogaster dimidiata* (Meinert, 1870)	*Haplophilus dimidiatus* forma *angusta*	Spain?	109	81	Trunk shrinking
Shinohara, 1949*	*Geophilus procerus* Koch, 1878	*Pleurogeophilus takakuwai*	unknown	unknown	56-60	Ventral mispairing
Demange & Pereira, 1980	*Schendylops pallidus* (Kraus, 1955)	*Schendylurus pallidus*	La Viuda (Peru)	65	31-33	Trunk shrinking
Demange & Pereira, 1980	*Schendylops titicacaensis* (Kraus, 1954)	*Schendylurus titicacaensis*	Choquechacra, Caraca, Lac Titicaca (Peru)	53	41	Trunk shrinking
Minelli & Pasqual, 1986	*Himantarium gabrielis* (Linnaeus, 1767)	*Himantarium gabrielis*	Monte Mufara (Italy)	unknown	36-39, 53-58	Trunk shrinking with dorsal mispairing. Sclerite deformation
Minelli & Pasqual, 1986	*Himantarium gabrielis* (Linnaeus, 1767)	*Himantarium gabrielis*	Arenzano (Italy)	unknown	141-150	Dorsal mispairing plus other irregularities
Pereira & Minelli, 1995	*Schendylops attemsi* (Verhoeff, 1900)	*Schendylurus attemsi*	Béni-Snassen (Morocco)	57	52-54	Trunk shrinking
Simaiakis et al., 2007	*Himantarium gabrielis* (Linnaeus, 1767)	*Himantarium gabrielis*	Bosnia-Erzegovina?	unknown	unknown	Ventral mispairing
Simaiakis et al., 2007	*Himantarium gabrielis* (Linnaeus, 1767)	*Himantarium gabrielis*	Bitola (Republic of Macedonia)	unknown	unknown	Ventral mispairing (?)

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Supplementary material 3

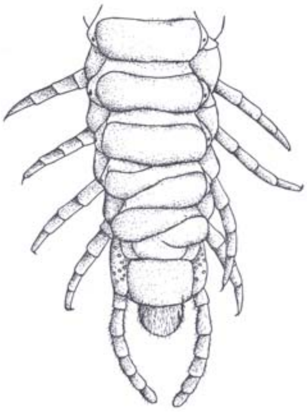
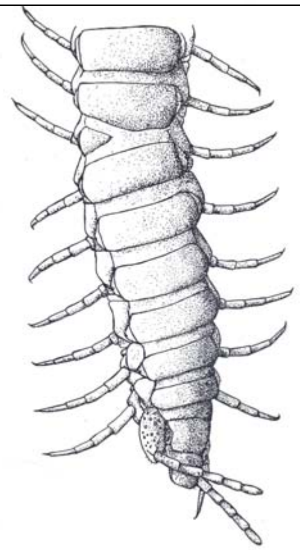
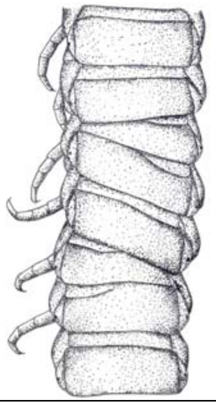
Frequency of the main types of trunk anomalies recorded in the Poznań population of *Stigmatogaster subterranea*

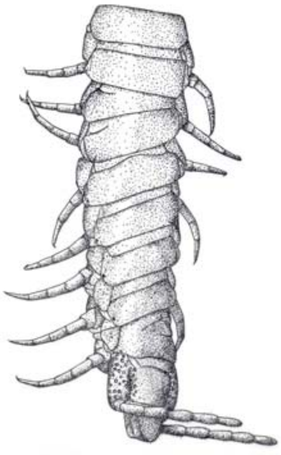
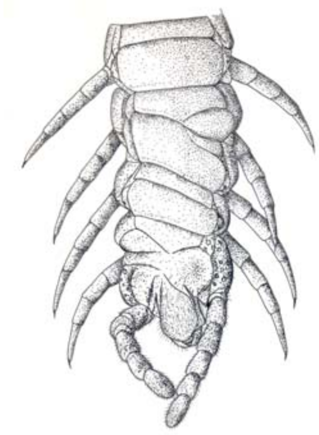
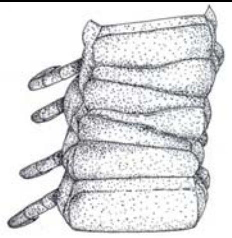
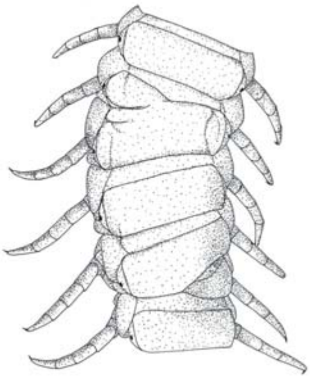
The number of leg-bearing segments has been counted as described in the text (Section 2.2). Total number of examined specimens = 809.

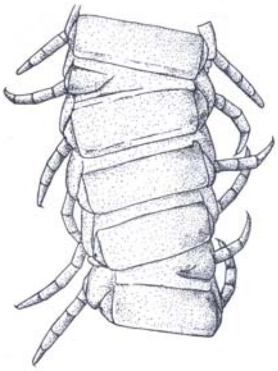
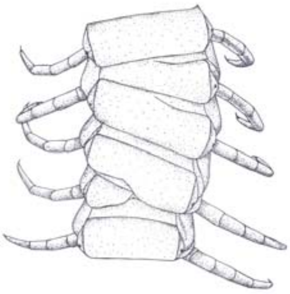
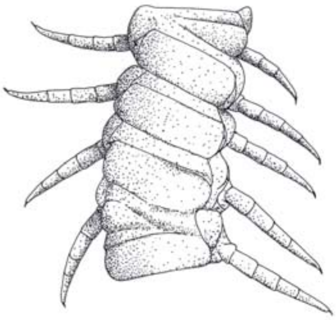
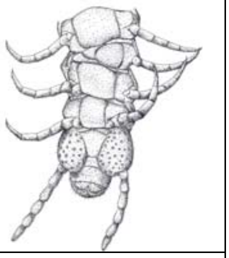
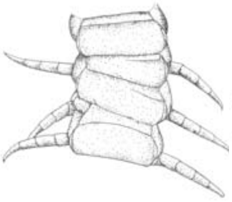
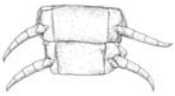
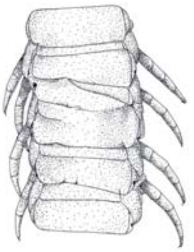
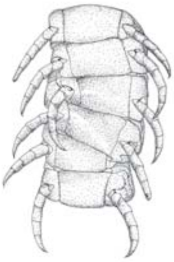
Type of anomaly	**Number of cases**	**Number of specimens**	**Number of leg-bearing segments**	**Cephalic width (mm)**
Pure dorsal mispairing	10	8 (5 ♀♀, 3 ♂♂)	♀ 81-87, ♂ 77-81	0.47-0.98
Trunk shrinking	20	20 (14 ♀♀, 6 ♂♂)	♀ 79-85, ♂ 79-81	0.40-1.01
Even number of leg-bearing segments	3	3 (3 ♂♂)	♂ 80	0.78-0.98
Trunk bifurcation	1	1 (♂)	♂ 79	0.49
Sclerite deformation	26	22 (10 ♀♀, 12 ♂♂)	♀ 79-83, ♂ 79-81	0.53-0.97
Defects of spiracles	3	3 (1 ♀, 2 ♂♂)	♀ 81, ♂ 77-81	0.80-0.86
Defects of sternal pore areas	5	5 (2 ♀♀, 3 ♂♂)	♀ 81, ♂ 77-81	0.75-1.01

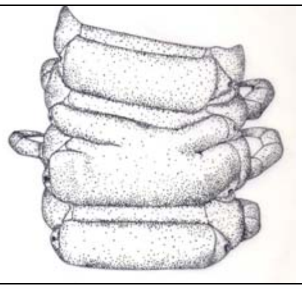
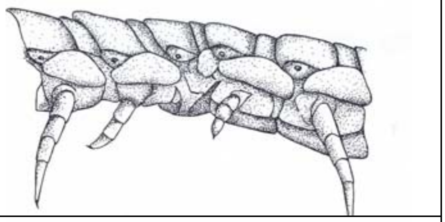
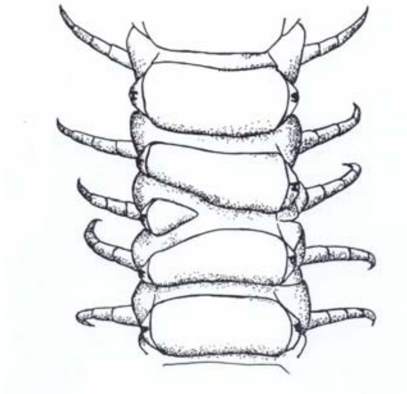
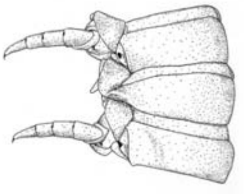
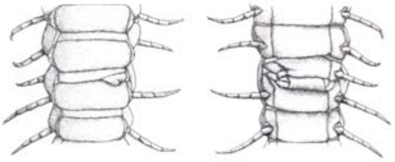
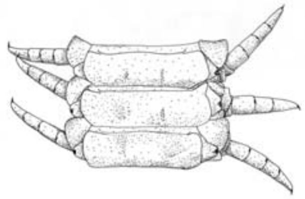
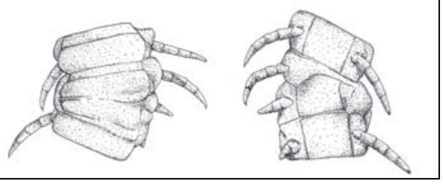
Synoptic table of the 68 trunk anomalies recorded in the Poznań population of *Stigmatogaster subterranea*

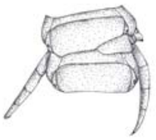
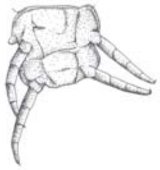
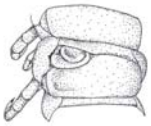
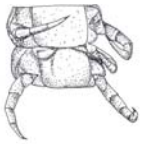
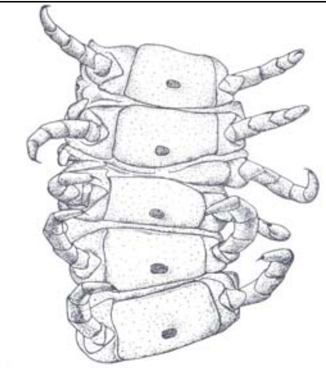
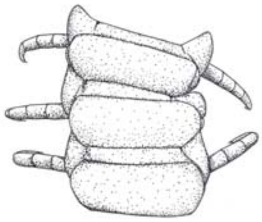
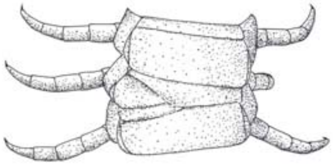
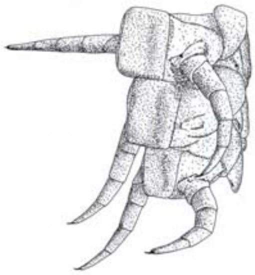
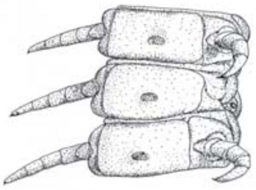
Anomalies are ordered by type. Each individual case is identified by a specimen identification number, followed by a letter when more than one anomaly has been recorded in the same specimen. The number of tergites refers to the number of couples pretergite-metatergite. A drawing of the anomalous trunk region is provided for most of the cases.
*N = unknown number of leg-bearing segments.

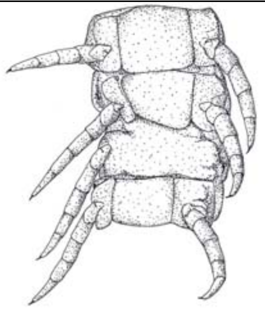
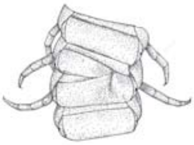
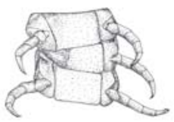
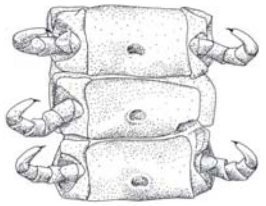
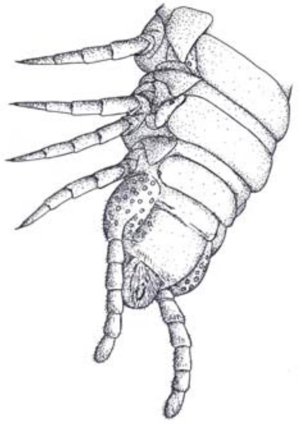
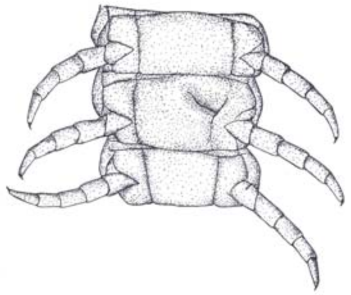
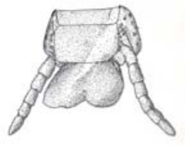
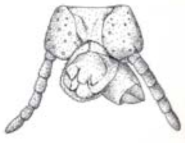
code	body length (mm)	sex	number of sternites (l/r)	number of legs (l/r)	number of tergites (l/r)	segmental position of the anomaly	type of anomaly	
73a	43	♂	79/79	79/79	79/79	77-78	pure dorsal mispairing	
117a	45	♀	81/81	81/81	81/81	74-81	pure dorsal mispairing	
300a	58	♀	81/81	81/81	81/81	54-57	pure dorsal mispairing	

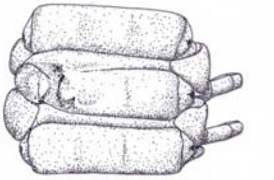
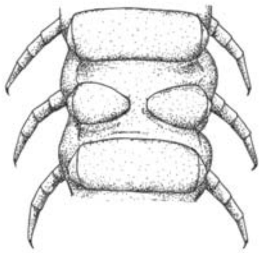
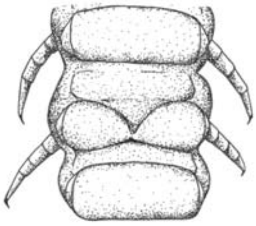
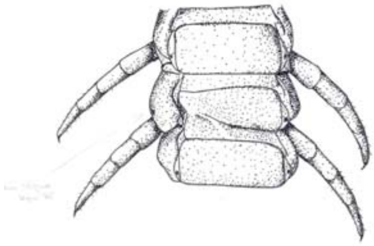
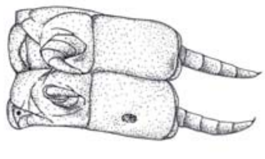
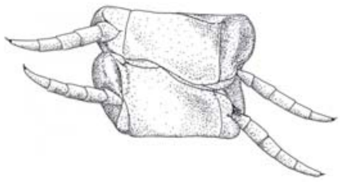
300b	58	♀	81/81	81/81	81/81	74-80	pure dorsal mispairing	
353	46	♂	77/77	77/77	77/77	74-77	pure dorsal mispairing	
392	21	♀	85/85	85/85	85/85	47-49	pure dorsal mispairing	
515b	47	♀	81/81	81/81	81/81	74-77	pure dorsal mispairing	

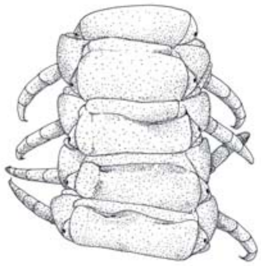
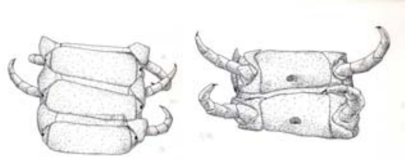
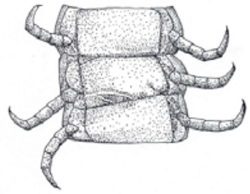
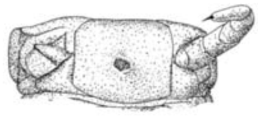
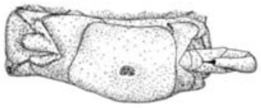
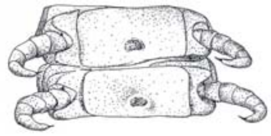
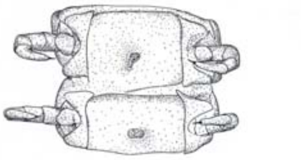
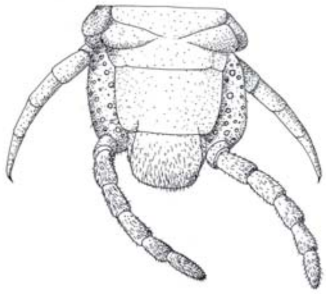
561b	39	♂	81/81	81/80	81/81	60-63	pure dorsal mispairing	
561c	39	♂	81/81	81/80	81/81	76-78	pure dorsal mispairing	
736	20	♀	87/87	87/87	87/87	80-84	pure dorsal mispairing	
307	49	♀	85/84	85/84	85/84	82-83	trunk shrinking with dorsal mispairing	 
333	51	♀	81/81	81/81	81/81	74-75	trunk shrinking with dorsal mispairing	 
644	56	♀	83/83	82/83	83/83	76-77	trunk shrinking with dorsal mispairing	 

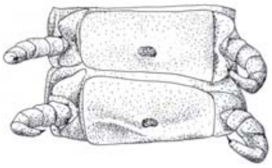
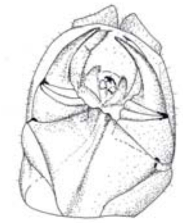
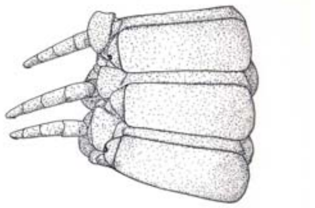
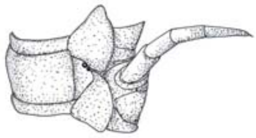
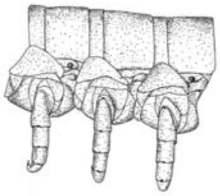
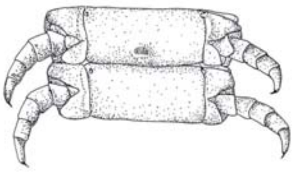
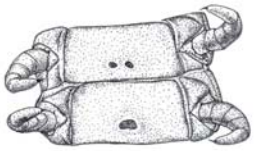
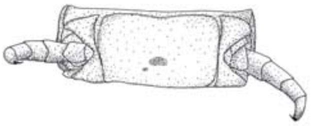
17a	40	♀	79/79	79/79	79/79	9-10	trunk shrinking	
109	44	♀	81/81	81/80	81/81	46	trunk shrinking	
122	42	♀	81/81	81/81	81/80	7	trunk shrinking	
194a	28	♀	83/83	82/83	83/83	9	trunk shrinking	
210	60	♀	83/83	82/81	81/~82	77-78	trunk shrinking	
297a	50	♂	79/79	79/79	79/79	11	trunk shrinking	
381	17	♂	81/81	79/81	81/81	75-76	trunk shrinking	

438	30	♀	80/81	80/80	80/81	78-79	trunk shrinking	 
491	?	♀	?	?	?	N-3*	trunk shrinking	 
561a	39	♂	81/81	81/80	81/81	4-5	trunk shrinking	
573	54	♀	81/81	81/80	81/81	7	trunk shrinking	
632	29	♂	81/81	81/81	81/80	78-79	trunk shrinking	
638	58	♀	81/81	80/81	81/81	79	trunk shrinking	
675	60	♀	81/81	80/81	81/81	11	trunk shrinking	

714	53	♂	81/81	80/81	81/81	77-78	trunk shrinking	
749	57	♀	83/83	83/82	83/82	77-79	trunk shrinking	 
803	46	♀	79/79	78/79	79/79	25	trunk shrinking	
164	51	♂	80/80	81/80	80/80	78	even number of leg-bearing segments	
216a	45	♂	80/80	80/80	80/80	78-79	even number of leg-bearing segments	
799	50	♂	80/80	80/80	80/80	–	even number of leg-bearing segments	
757	18	♂	79/79	79/79	79/79	terminal segments	trunk bifurcation	 

17b	40	♀	79/79	79/79	79/79	21	sclerite deformation	
53	56	♀	81/81	81/81	81/81	12	sclerite deformation	
73b	43	♂	79/79	79/79	79/79	69	sclerite deformation	
73c	43	♂	79/79	79/79	79/79	71	sclerite deformation	
73d	43	♂	79/79	79/79	79/79	73	sclerite deformation	
117b	45	♀	81/81	81/81	81/81	42	sclerite deformation	
117c	45	♀	81/81	81/81	81/81	44	sclerite deformation	
194b	28	♀	83/83	82/83	83/83	7-8	sclerite deformation	
216b	45	♂	81/80	80/80	80/80	58	sclerite deformation	
234	55	♂	81/81	81/81	81/81	78-79	sclerite deformation	
236	49	♂	79/79	79/79	79/79	35	sclerite deformation	
297b	50	♂	79/79	79/79	79/79	7	sclerite deformation	
362	52	♀	81/81	81/81	81/81	20	sclerite deformation	
387	17	♂	79/79	79/79	79/79	62-63	sclerite deformation	

515a	47	♀	81/81	81/81	81/81	32-34	sclerite deformation	
561d	39	♂	81/81	81/80	81/81	21-22	sclerite deformation	
575	49	♀	79/79	79/79	79/79	19-22	sclerite deformation	
576	47	♂	79/79	79/79	79/79	21-22	sclerite deformation	
577	39	♂	79/79	79/79	79/79	56	sclerite deformation	
600a	38	♀	83/83	83/83	83/83	3	sclerite deformation	
600b	38	♀	83/83	83/83	83/83	5	sclerite deformation	
637	56	♀	81/81	81/81	81/81	23	sclerite deformation	
660	47	♂	81/81	81/80	81/81	8	sclerite deformation	
667	62	♀	81/81	81/81	81/81	80	sclerite deformation	

719	48	♂	79/79	79/79	79/79	21-22	sclerite deformation	
801	50	♂	79/79	79/79	79/79	forcipular segment	sclerite deformation	
430	34	♂	81/81	81/81	81/81	44	defects of spiracles	
603	55	♀	81/81	81/81	81/81	79	defects of spiracles	
726	51	♂	77/77	77/77	77/77	23	defects of spiracles	
337	61	♀	81/81	81/81	81/81	44	defects of sternal pore areas	
561e	39	♂	81/81	81/80	81/81	25	defects of sternal pore areas	
571	51	♀	81/81	81/81	81/81	19	defects of sternal pore areas	
628	56	♂	77/77	77/77	77/77	15	defects of sternal pore areas	
784	50	♂	81/81	81/81	81/81	4	defects of sternal pore areas	