Ann. Zool. Fennici 25:303–320. 1988

Morphological and morphometric variation of the parthenogenetic earthworm *Dendrobaena octaedra* (Sav.) (Oligochaeta, Lumbricidae) in eastern Fennoscandia

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Terhivuo, J. 1988: Morphological and morphometric variation of the parthenogenetic earthworm *Dendrobaena octaedra* (Sav.) (Oligochaeta, Lumbricidae) in eastern Fennoscandia. — Ann. Zool. Fennici 25:303–320.

The morphological and morphometric variability of the parthenogenetic earthworm *D. octaedra* was surveyed in relation to environmental and geographical variables by inspecting worms according to sets of biotopes in different parts of eastern Fennoscandia where the species lives at the northern edge of its range. The number of segments ranged widely (56–108) but populations were homogeneous as to mean and median numbers of segments in all biotopes and regions. Since adults and small juveniles (≤ 15mm) possess the same number of segments, the individuals grow by increase in size rather than in the number of segments. Characters related to body size, viz., circumference and size of post-clitellar segments, body length and weight increased northwards; this cline was also observed within each biotope. In southern adults the clitellum and tubercula pubertatis were more protruding than in northern ones.

The relative intersetal distances in the post-clitellar segments were constant in all age groups, biotopes and areas. In 38% of *D. octaedra* adults and in 40% of subadults male pores were lacking. Populations were homogeneous in this respect; no seasonal or geographical variation was observed.

D. octaedra adults representing common clones (= overall allozyme phenotypes) and clone groups (= overall allozyme phenotypes deviating with respect to one to four enzyme variants from those of the most abundant clone) were inspected to relate morphological and morphometric variability to genotypic differences between the worms. The genotypes did not correlate with the cline: post-clitellar segment size varied greatly but the northward increase was observable within the clones and clone groups irrespective of the biotope. The cline was thus interpreted as a probable general adaptation to the climate. The number of segments, presence of male pores and protuberance of the clitellum and tubercula pubertatis did not correlate with the genotype, either.

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1. Introduction

Dendrobaena octaedra is a circumpolaric earthworm that originates in the Palearctic region (Stephenson 1930, Stöp-Bowitz 1969). Though being obligatorily parthenogenetic (Omodeo 1955, Casellato & Rodighiero 1972) it occupies a wide range of habitats and shows great morphological and morphometric variability in different parts of its range (Bornebusch 1928, Backlund 1949, Julin 1949, Balzer 1956, Omodeo 1957, 1961, 1962, Stöp-Bowitz 1969, Bouché 1972, Gates 1972, 1974, Terhivuo & Valovirta 1978, Sims & Gerard 1985). Gates (1974) states that "Because of the parthenogenesis any *D. octaedra* colony theoretically may be monoclonal in origin. At one or two sites, such an origin at one time did seem possible. Often, the more the specimens that were secured at a site, the larger the number of anatomically distinct morphs that were recognized. So great indeed was the easily recognizable diversity that an attempt to keep records of individual morphs by locality names, even with the use of

subscripts, was abandoned". Parthenogenetic earthworms also show a common evolutionary trend towards the reduction of male reproductive organs (e.g., Stephenson 1930, Perel 1982, Sims & Gerard 1985). Gates (1974) implied that in *D. octaedra* and some other parthenogenetic megadrile earthworms "genital organization proceeds more rapidly than does that of the more conservative somatic anatomy".

The present paper examines morphological and morphometric variation in non-reproductive and genital organs of *D. octaedra* in eastern Fennoscandia, where the species occurs near the northern margin of its geographical distribution. Worms sampled between latitudes 60°–71°N were analyzed according to biotopes and areas to assess corresponding variations and to work out whether trends or other regularities can be observed. An attempt is also made to correlate morphological variability with genotypic differences between the worms.

2. Material and methods

2.1. Sample sets A–C

Sample set A

This material comprises *D. octaedra* individuals whose overall allozymic phenotypes (= clones in brief) were electrophoretically determined by Terhivuo & Saura (1989). They are now examined morphologically to assess within- and among-clone and clone group variations in an array of biotopes in different parts of eastern Fennoscandia.

The sample localities (locs. 1–85) form a north-south (N-S) and an east-west (E-W) transect (Fig. 1). The former consists of six (I–VI) and the latter of five (VII–XI) subareas. The subareas are grouped on the basis of the 100×100 km squares of the Finnish uniform grid (27°E) system (Heikinheimo & Raatikainen 1971). Subareas I–V are situated in the middle boreal and north boreal vegetation zones and when pooled they are called "the north". Correspondingly, "the south" refers to subareas VI–XI that are mainly located in the south boreal and hemiboreal vegetation zones. These groupings correspond to those in Terhivuo & Saura (1989). The biotopes sampled and the numbers of localities are indicated in Table 1.

The worms in sample set A were kept deeply frozen prior to subjecting them to electrophoresis (for details see Terhivuo & Saura 1989). After melting, that part of the worm not used was preserved in 70–80% ethanol for morphological and morphometric analysis.

Sample set B

This consists of *D. octaedra* samples deposited at the Zoological Museum, University of Helsinki. I only examined samples from southernmost and northernmost Finland to maximize geographic variability (Fig. 2). This data set was mainly studied because the individuals were killed by immersing them in 70–80% ethanol when alive, i.e. unlike those in sample set A. Surveying this material can thus be useful in checking the validity of the results based on sample set A.

Likewise in sample set A the samples of sample set B are grouped into those from the south (locs. 86–146) and those from the north (locs. 147–181). Table 1 shows the biotopes and the numbers of sample localities in them.

Table 1. Biotopes and numbers of sample localities in sample sets A–C.

Biotope	A	B	C
Deciduous forests	28	26	32
Coniferous forests	21	19	22
Shore alder thickets	–	6	18
Shores	15	14	18
Meadows	19	13	27
Arctic mountains	–	7	–
Waste soils	2	5	–
Others (bogs, islands, clear-cut forests)	–	6	–
Total	85	96	117

Sample set C

This consists of *D. octaedra* individuals sampled by me in 1977, 1979 and 1984 in three areas of southern Finland, viz., in subarea XI, coastal parts of subarea IX and southern parts of subareas VII–VIII (Fig. 1). This material totals 117 samples representing five kinds of biotopes (Table 1). For details see Terhivuo (1989).

2.2 Laboratory procedures

After some anterior segments were detached for electrophoresis, the number of segments of each worm in sample set A was counted and those detached were added to the count. Postclitellar segments between the 36th and the 42nd body segments were then removed and eventually opened to measure distances between the setae and the circumference and size of the segments. Cuticula and internal organs were removed and the edges of the body wall were spread out laterally in a few drops of water before microscopic examination. A glass cover clip was lowered on to the preparation without squeezing the latter (Fig. 3).

The contours of the segments and the position of the setae were drawn using a microscope with a Wild M5-Zeichentubus. All intersetal distances were measured on both sides of a randomly chosen segment in the drawings and converted to absolute distances. The length, as measured along the middorsal line between the dorsal pores, multiplied by the circumference (= maximum width of the same segment) equals the size of the segment.

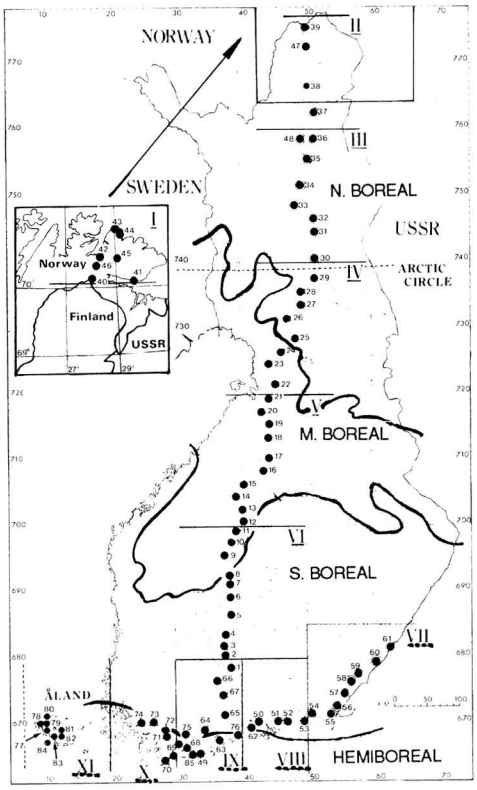


Fig. 1. Sample localities (1–85) and subareas (I–XI) for sample set A. Subareas I–VI (bold vertical bars) comprise the north-south (N-S) and those of VII–XI (broken lines) the east-west (E-W) transects. Vegetation zones are according to Ahti et al. (1968). For additional information see text.

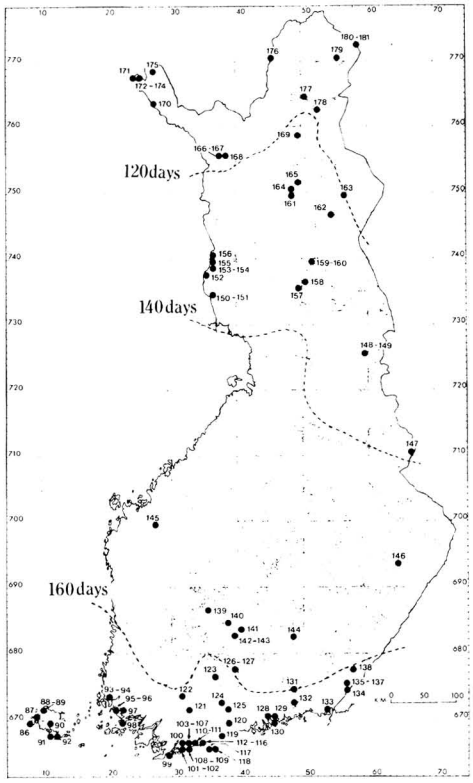
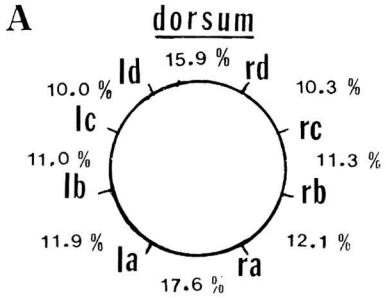


Fig. 2. Sample localities (86–181) for sample set B. Broken lines indicate the mean annual length of the vegetation period (daily mean temperature ≥6°C) (redrawn from Johannesen 1970). Locs. 86–146 comprise "the south" and locs. 147–181 "the north".



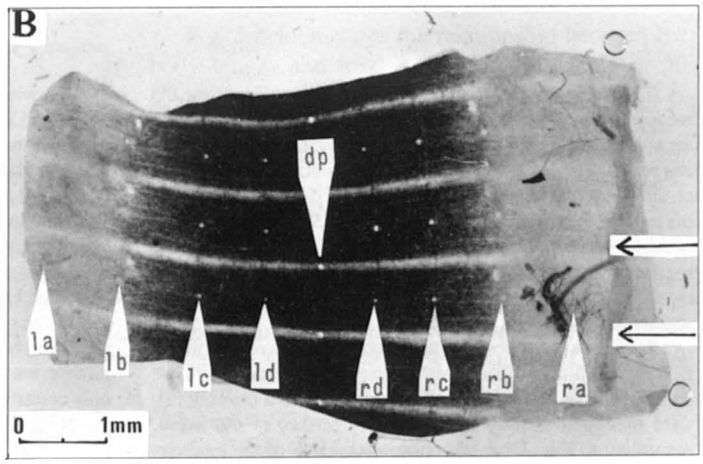


Fig. 3. Post-clitellar segments of adult *D. octaedra*. A. Relative setal pattern (% of total circumference) on the right (r) and left (l) side of the body based on the means counted for the 315 adults included in sample set A. B. Dorsal view of a preparation of midventrally opened post-clitellar segments. White tapering signs show the rows of the setae (symbols as in A) and dorsal pores (dp) and arrows indicate the intersegmental furrows.

Fig. 4. Examples of *D. octaedra* juveniles, subadults and adults: A. Small juvenile (length 12 mm, 73 segments) (loc. 178), B. Young subadult (29 mm, 88 segments) (loc. 98) having male pores but hardly any sign of tubercula pubertatis, C. Subadult (25 mm, 95 segments) (loc. 173) lacking male pores but having signs of developing tubercula pubertatis, D. Young adult (35 mm, 95 segments) (loc.173), E. Adult (37.5 mm, 108 segments) (loc. 99), F. Adult (51.5 mm, 94 segments) (loc. 171), G–H. Adult having a male pore on the right side of the body but lacking one on the left side (35.0 mm, 73 segments) (loc. 155), I. Big adult (71.5 mm, 100 segments) (loc. 155) and J. Small adult (18.0 mm, 90 segments) (loc. 119).

To check whether the nearby segments differ from the measured ones the circumference and size of two neighbouring segments were measured from a random sample of 50 *D. octaedra* adults. The circumference of the anterior member of the set of three successive segments was (mean ± *SD*) 6.97 ± 1.34, of the middle one (used in the final analysis) 6.96 ± 1.34 and of the posterior one 6.94 ± 1.34. Correspondingly, the size of the same segments was 4.57 ± 1.98, 4.61 ± 1.98 and 4.58 ± 1.98. These measurements indicate no significant differences between the segments.

Since it was not possible to dissect the adults of sample set B, the ventral post-clitellar setal distance la–ra (= aa), and the dorsal distance ld–rd (= dd) of the same segment (see Fig. 3), were measured directly from the body surface of the worm. According to Fig. 3A aa+dd constitutes >33% of the total circumference of the segment and the greater the sum of the two distances the greater the circumference of the segment. I also checked the relation of aa+dd to the size of the segment by calculating Spearman's rank correlation for adults in sample set A: in all the subareas of Fig. 1 the statistical significance was $P<0.05$, with the exception of subarea II where it was $P=0.24$. In sample set B aa+dd correlated highly significantly with the body length of the adult ($r_s = 0.374^{***}$, $n=125$).

The body lengths and weights of the adults without any observable segment amputees were also measured (sample set B). Body length was measured to the nearest 0.5 mm along the ventral body surface. 'Weight' refers to the wet weights of worms preserved in ethanol. Prior to weighing, each worm was placed on blotting paper for about two minutes to dry.

In sample set C all the intact *D. octaedra* adults in a sample were weighed together and the mean weight of worms in each biotope was calculated from this data. However, samples with only one adult were used together with sample set B.

In adults and subadults from sample sets A and B the presence of male pores was observed and the protrusion of male terminalia, clitellum and tubercula pubertatis was visually estimated by using a scale from zero to three (0 = absent, 1 = poorly developed and diffusely demarcated, 2 = rather prominent and well-demarcated and 3 = very protruded and sharply demarcated). For instance, in Fig. 4E the clitellum is

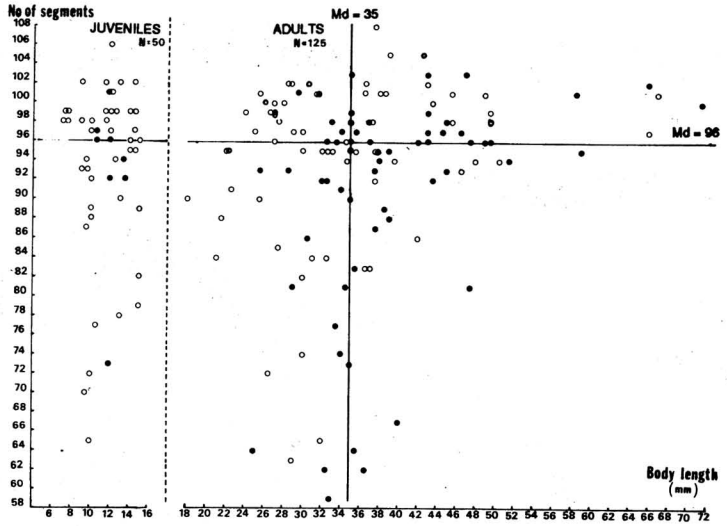


Fig. 5. Number of segments plotted against body length in small (≤ 15 mm) *D. octaedra* juveniles and adults (sample set B). Solid circles indicate the northern worms and open circles southern worms (see Fig. 2). Md = median. Note the skewness of the distributions. For additional information see the text.

diffusely demarcated, whereas in 4J it is very protruding and shaply demarcated. The location of the clitellum was concomitantly determined.

2.3. Age categories and statistics

The following criteria were adopted for grouping *D. octaedra* individuals into age categories. Small worms without a clitellum or tubercula pubertatis and without any change in the colour of the segments of these were considered juveniles (Fig. 4A). Those with signs of a developing clitellum and/or tubercula pubertatis are subadults (Fig. 4B–C), and those with complete tubercula pubertatis and clitellum are adults (Fig. 4D–J).

Statistical significances are indicated as follows; o = $0.10 \geq P > 0.05$, * = $0.05 \geq P > 0.01$, ** = $0.01 \geq P > 0.001$ and *** = $0.001 \geq P$, ns = not significant.

Since the frequency distributions for many characters and morphometric measurements, e.g., numbers of segments (e.g. Table 11), body lengths (Fig. 5) and circumferences and sizes of post-clitellar segments, are significantly skew (circumference: $t_1 = 2.731$**, $df = \infty$, segment size: $t_1 = 7.701$***, $df = \infty$) I have indicated both the means and the medians and applied only non-parametric statistical tests.

3. Results

3.1. Age and morphological traits

The development and function of many morphological characters correlate with the age of an earthworm. Depending upon the species an earthworm grows by adding new segments from a growth zone lying in front of the anus region, and/or its segments grow (Edwards & Lofty 1972). In regard to *D. octaedra*, there is no information on the role of the two aspects of growth.

The smallest *D. octaedra* juvenile in sample set B measured 7.0 mm and the longest adult 71.5 mm. The mean body length of adults is (mean ± *SD*) 36.7 ± 9.7 mm ($n = 125$, median 35.0 mm). Hence, a juvenile has to grow some 30 mm to become an adult.

Fig. 5 demonstrates the relationship between the body length and total number of segments in 50 *D. octaedra* juveniles measuring ≤ 15 mm, as well as in 125 adults of sample set B. The two age categories are similar in this respect; adults have 92.4 ± 10.3, (median = 95), and juveniles 92.9 ± 9.2, (median = 96), segments (Mann-Whitney test, $z = 0.230$, ns, $n = 125$). This is also the case in the north ($z = 0.118$, ns, $n = 58$) and in the south ($z = 0.535$, ns, $n = 67$).

In sample set A juveniles without any observable segment amputees have 89.1 ± 10.8 segments (median = 94, $n = 49$), the subadults 87.0 ± 12.9 (median = 92, $n = 55$), and the adults 90.2 ± 11.4 (median = 95, $n = 291$) segments. The three age groups thus widely overlap and no statistical difference between them exists (Kruskal-Wallis test, $H^* = 3.288$, ns, $df = 2$). I conclude that *D. octaedra* grows by increasing size rather than by increasing the number of segments.

Table 2. Mean relative intersetal distances (% of the total circumference) in post-clitellar segments of *D. octaedra* juveniles, subadults and adults sampled in the south (= subareas VI–XI in Fig. 1) and the north (= subareas I–V) (sample set A). For the setal distances see Fig. 3A.

Intersetal distance	South Juv.	South Subad.	South Adults	North Juv.	North Subad.	North Adults
la–lb	11.5	12.0	11.8	11.6	11.8	11.9
lb–lc	11.5	11.5	11.0	11.4	11.0	11.0
lc–ld	10.5	10.1	10.1	10.2	10.1	9.9
ld–rd	15.8	15.3	15.9	16.5	16.3	16.1
rc–rd	10.5	10.4	10.3	10.2	10.1	10.3
rb–rc	11.3	11.5	11.2	11.2	11.0	11.5
ra–rb	12.0	12.0	11.9	12.1	11.7	12.3
ra–la	16.9	17.1	17.8	16.9	17.9	17.1
n	14	25	210	41	33	105

Apart from the first segment the chitinous bristles in successive segments form four setal lines (a–d, Fig. 3) on both sides of the body. Table 2 shows that the mean relative intersetal distances are almost equal in southern and northern juveniles, subadults and adults, indicating that all parts of a post-clitellar segment grow at about the same rate.

As Fig. 4A demonstrates, secondary sexual organs (male pores, tubercula pubertatis and clitellum) are absent in *D. octaedra* juveniles. Subadults (B–C) and adults (D–J) may possess, but often lack, male pores situated laterally on the 15th body segment. Male pores, if present, seem to appear first and they are followed by the formation of the tubercula pubertatis (C) ventrolaterally across segments 31–33 just above setal line b. Assuming that in some worms male pores appear after the development of the clitellum, the relative proportion of individuals with male pores should be higher in adults than in subadults. This was not, however, observed here (section 3.2.6). A young adult (D) usually has the tubercula pubertatis and more or less protruding clitellum on segments 29–33. Senile adults loose their clitellum prior to death.

3.2. Geographical variability

3.2.1. Body weight

In Table 3 the samples of sample set C with only one intact *D. octaedra* adult are pooled with those of sample set B to indicate variation within and between biotopes. Despite great variation between the biotopes the adults in the north are highly significantly heavier than those in the south. In most biotopes *D. octaedra* adults are significantly heavier in the north than in the south, too.

In sample set C, referring to *D. octaedra* in the south, the mean weight of adults in deciduous forests was 0.110 g (n = 25), in coniferous forests 0.124 g (n = 61), in meadows 0.098 g (n = 44), in shores 0.134 g (n = 23) and in shore alder thickets 0.130 g (n = 36). In this material all adults in the same sample were weighed together, so no statistics on variation between most adults are available.

3.2.2. Body length

An earthworm maintains its form by the elasticity of the body wall and by the hydrostatic pressure of the coelomic fluid within. Contractions of the longitudinal and circular muscle layers of the body wall

Table 3. Mean and median body weights (g) for *D. octaedra* adults, preserved in ethanol, from different biotopes in the south (see Fig. 2) and the north, based on pooled sample sets B and C. For statistical significances see section 2.3.

Biotope	South Mean ± *SD*	South Median	South *n*	North Mean ± *SD*	North Median	North *n*	Mann-Whitney *z*
Deciduous forests	0.113 ± 0.040	0.104	30	0.187 ± 0.074	0.183	21	3.95***
Coniferous forests	0.145 ± 0.054	0.140	21	0.162 ± 0.089	0.142	5	ns
Meadows	0.087 ± 0.026	0.087	16	0.166 ± 0.051	0.162	10	3.53***
Shores	0.126 ± 0.049	0.130	17	0.205 ± 0.053	0.197	10	3.21**
Others	0.145 ± 0.055	0.130	30	0.193 ± 0.053	0.172	12	2.17*
Total	0.125 ± 0.050	0.118	114	0.186 ± 0.064	0.183	58	6.09***

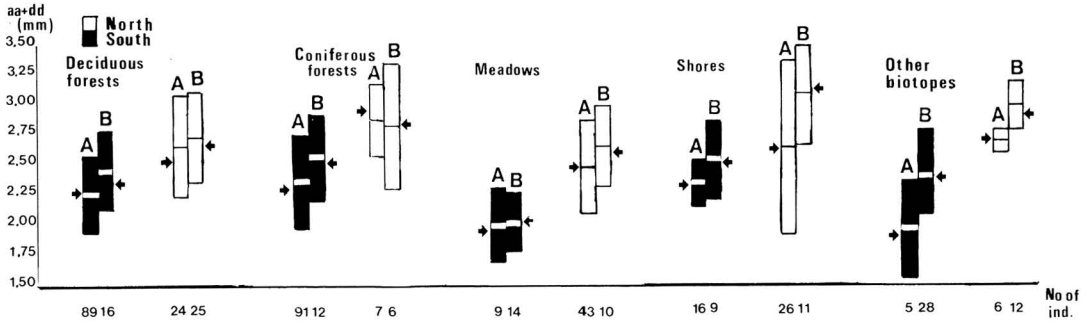


Fig. 6. Bar (mean ± *SD*) diagram of combined ventral post-clitellar setal distance la–ra (= aa) and dorsal distance ld–rd (= dd) (see Fig. 3) for *D. octaedra* adults from different biotopes of the south and the north. The sum aa + dd correlates significantly with body length as explained in section 2.2. Bar A refers to adults in sample set A and bar B to those in sample set B. Arrows indicate the median for each bar.

make the worm and its segments shorter or longer, respectively (Laverack 1963). In preserved material the state of muscle contraction in a worm is hard to assess.

In sample set A the complete loss of muscle tonus in worms killed by freezing did not warrant measuring their body lengths.

Sample set B consists of individuals preserved in ethanol when alive. I assumed that the state of muscle contraction varies equally among the groups of individuals compared. Southern adults are shorter than northern ones: the totals of the two groups differ significantly from each other, but there is also considerable variation within the biotopes (Table 4).

In sample set B the sum of the ventral setal distance la–ra and the dorsal distance ld–rd correlates highly significantly with the body length (section 2.2.). Assuming that the correlation is also relevant for the worms in sample set A, the two study materials can be compared in this respect. Fig. 6 demonstrates that irrespective of the study material, i.e. method of preservation, northern *D. octaedra* adults tend to be longer than southern ones in all biotopes.

3.2.3. Number of segments

It is not always easy to detect losses of posterior segments: at least 7.6% of the 315 adults, 5.2 % of the 58 subadults and 10.9% of the 55 juveniles in sample set A had such losses. In this data set the median number of segments in *D. octaedra* adults without observable amputees is 95. When the adults having fewer and those having more segments than the median are considered, no heterogeneity among subareas was observed ($\chi^2 = 10.758$, ns, $df = 9$, subareas I

Table 4. Mean and median body lengths (mm) of *D. octaedra* adults, preserved in ethanol, from different biotopes in the south (Fig. 2) and the north, according to sample set B. For statistical significances see section 2.3.

Biotope	South Mean ± *SD*	South Median	South *n*	North Mean ± *SD*	North Median	North *n*	Mann-Whitney *z*
Deciduous forests	28.8 ± 5.6	28.5	14	40.7 ± 12.5	36.5	21	3.33***
Coniferous forests	31.0 ± 7.1	31.0	11	33.5 ± 9.5	32.5	5	0.23 ns
Meadows	32.2 ± 8.2	28.0	10	38.8 ± 6.9	38.0	10	1.51 ns
Shores	36.2 ± 11.6	33.5	9	40.1 ± 5.9	39.5	10	1.92°
Others	39.8 ± 10.1	38.5	23	38.7 ± 6.1	38.0	12	0.19 ns
Total	34.4 ± 9.7	32.0	67	39.2 ± 9.2	36.8	58	3.11**

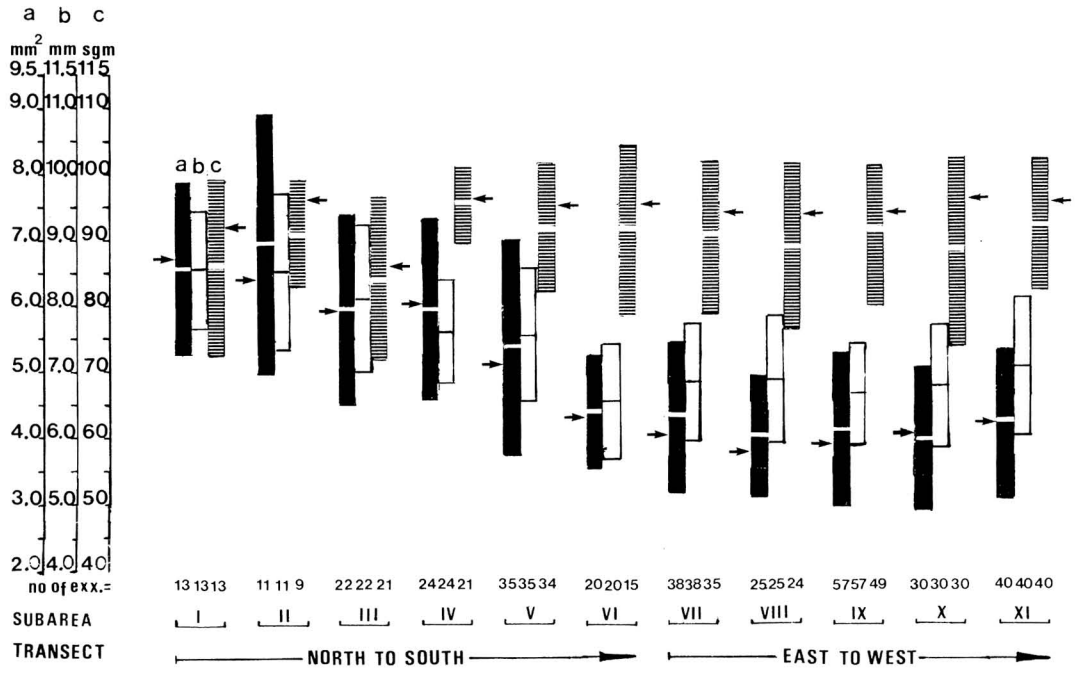


Fig. 7. Bar (mean ± SD) diagram of the size (bar a) and circumference (bar b) of post-clitellar segments, and the total number of segments (bar c) of *D. octaedra* adults from the eleven subareas indicated in Fig. 1. Arrows show the medians for a and c, respectively.

and II pooled and the worms having the median number of segments omitted, Fig. 7, bar c).

The two transects were also similar in this respect (Fig. 7, bar c) and the same applies to different biotopes in the north and the south (Table 5). As the age groups were also homogeneous in this respect (sample sets A and B, section 3.1.), I conclude that *D. octaedra* populations are homogeneous in respect of the number of segments in my study area.

3.2.4. Circumference and size of post-clitellar segments

In order to analyze more thoroughly the difference observed in body size between northern and southern *D. octaedra* adults (sections 3.2.1. and 3.2.2), I measured the circumference and size of the post-clitellar segments from the adults in sample set A, in which muscle tonus did not affect the measurements.

Table 5. Mean and median number of segments for *D. octaedra* adults sampled in different biotopes of the south and the north (see Figs. 2–3). (Sample sets A and B pooled), ns = not significant.

Biotope	South			North			Mann-Whitney
	Mean ± *SD*	Median	*n*	Mean ± *SD*	Median	*n*	*z*
Deciduous forests	89.9 ± 12.2	94	96	88.6 ± 12.3	93	43	ns
Coniferous forests	91.9 ± 10.5	94.5	96	86.5 ± 14.8	96.5	12	ns
Shore alder thickets	94.6 ± 6.6	96	8	– –	–	–	–
Shores	91.5 ± 8.8	95	24	90.1 ± 10.4	94.5	34	ns
Meadows	91.8 ± 11.4	95.5	16	91.6 ± 10.1	96	51	ns
Arctic mountains	– –	–	–	89.2 ± 8.6	92	11	–
Others	92.5 ± 12.9	97.5	20	97.6 ± 3.1	99	5	ns
Total	91.3 11.1		260	90.1 11.0		156	ns

The medians for the circumferences and sizes of post-clitellar segments in adults are 7.02 mm and 4.52 mm^2, respectively. The following tabulation shows the percentages of adults with values greater than these medians in subareas I–XI (sample size in parentheses):

	Circumf.	Size		Circumf.	Size
I	100 (13)	100 (13)	VII	37 (38)	34 (38)
II	91 (11)	100 (11)	VIII	44 (25)	28 (25)
III	77 (22)	82 (22)	IX	33 (57)	39 (57)
IV	71 (24)	79 (24)	X	27 (30)	30 (30)
V	63 (35)	71 (35)	XI	50 (40)	40 (40)
VI	30 (20)	45 (20)			

The variation among subareas is highly significant (circumference: $\chi^2 = 50.668$***, $df = 7$, subareas I–III pooled, size: $\chi^2 = 69.562$***, $df = 7$, subareas I–IV pooled). This heterogeneity is largely a result of a northward increase in these dimensions (Fig. 7). The increase in circumference and size of post-clitellar segments shows a clinal pattern: subareas III–V form a zone of intergradation.

3.2.5. *Intersetal distances*

Relative intersetal distances of post-clitellar segments in adults, subadults and juveniles in sample set A are indicated in Table 2. In all three age categories the individuals in the north seem to be similar to those in the south in this respect: aa (= ra–la) >dd>rab>lab>rbc>lbc>rcd>lcd. On both sides of the segment ab>bc>cd. The total of the relative distances between ab, bc and cd is a bit longer on the right than on the left side of the segment, suggesting that the setae are not quite symmetrically situated. The constant setal pattern in all stages of the life-cycle suggests its importance to the fitness of *D. octaedra*.

Table 6. Patterns of intersetal distances in post-clitellar segments of *D. octaedra* adults in the eleven subareas (see Fig. 1). The means of absolute distances a–b, b–c and c–d on the right (r), and on the left (l), side of the body, as well as those of ra–la and rd–ld (see Fig. 3), are replaced by serial numbers from one to eight according to the magnitude of the means within each subarea (1 = smallest, 8 = largest) (sample set A). For further explanation see the text.

Inter-setal distance	Subarea I	II	III	IV	V	VI	VII	VIII	IX	X	XI	mean
la–lb	6	6	4	5	5	5	6	5	5	6	5	4.8
lb–lc	3	3	3	3	3	3	3	3	3	4	4	3.2
lc–ld	1	1	1	1	1	1	1	1	1	1.5	1	1.0
ld–rd	8	7	7	8	7	8	7	8	7	7	7	7.4
rc–ld	2	2	2	2	2	2	2	2	2	1.5	2	2.0
rb–rc	4	4	5	4	4	4	4	4	4	3	3	3.9
ra–rb	5	5	6	6	6	6	5	6	6	5	6	5.6
ra–la	7	8	8	7	8	7	8	7	8	8	8	7.6
n	13	11	22	24	35	20	38	25	57	30	40	–

To work out variation in patterns of setal distances in the eleven subareas, the means of absolute intersetal distances were replaced with numbers from one to eight (1 = smallest, 8 = largest). As Table 6 shows, intersetal ratios do not vary much along the N-S or E-W transects, either.

Except in southern deciduous forests, the relative setal distances of adults were rather similar in the different biotopes of the south and the north (Table 7).

Table 7. Relative intersetal distances (% of total circumference) in post-clitellar segments of *D. octaedra* adults in different biotopes of the south and the north (sample set A). Symbols for biotopes: CF = coniferous forests, DF = deciduous forests, Sh = shores, Me = meadows and WS = waste soils close to human habitation. Diff. = largest difference.

Setal distance	South CF	DF	Sh	Me	WS	Diff.	North CF	DF	Sh	Me	WS	Diff.
la–lb	11.9	10.7	12.0	11.8	11.6	1.3	11.2	11.8	11.7	12.3	12.1	1.1
lb–lc	10.9	9.9	11.1	11.0	11.2	1.2	10.9	10.5	11.0	11.3	11.3	0.8
lc–ld	10.1	9.2	9.7	10.0	10.9	1.7	11.0	9.7	9.6	9.9	9.7	1.4
ld–rd	16.1	14.4	15.4	15.5	16.1	1.8	16.6	16.3	16.3	15.6	15.6	1.0
rd–rc	10.2	9.3	10.4	10.8	9.8	1.5	10.6	10.4	10.6	10.1	10.4	0.5
rc–rb	10.9	10.1	11.3	11.8	10.7	1.7	11.2	11.8	11.8	11.1	11.0	0.8
rb–ra	11.9	10.8	12.4	12.3	11.4	1.6	11.8	12.3	12.1	12.3	12.7	0.9
ra–la	18.0	25.8	17.7	16.8	18.2	9.0	16.7	17.3	16.8	17.2	17.2	0.5
Circumference (mm)	7.0	7.4	7.0	6.2	5.7		8.6	7.9	8.2	7.5	8.4	
n	91	89	16	9	5		7	24	46	43	5	

Absolute distances were, however, greater in the north than in the south because of the northward increase in body size.

3.2.6. Male pores and male terminalia

Of the 458 adults surveyed (sample sets A and B pooled) 172 (37.6%) had no male pores and 23 (39.7%) of the 58 subadults also lacked these. The two age-categories were similar in this respect (χ^2 = 0.097, ns, *df* = 1). The high proportion lacking male pores strongly suggests parthenogenesis as the mode of reproduction for the species in eastern Fennoscandia, too. Adults with and without male pores were often found in the same sample site.

Of the 286 *D. octaedra* adults with visible male terminalia 18 (6.3%) had only one pore either on the left or on the right side of the body. One adult had two male pores (on segments 14 and 15) on the left but only one (on segment 15) on the right size of the body.

The proportions of individuals with or without male pores were similar in the north and south (χ^2 = 0.062, ns, *df* = 1, adults and subadults of sample sets A and B pooled), nor was there any significant difference in these frequencies when the data were analysed according to the subareas (χ^2 = 15.079, ns, *df* = 10), the biotopes (χ^2 = 6.729, ns, *df* = 4) or two-month periods (June–July, August–September and October–November; χ^2 = 0.454, ns, *df* = 2).

In sample set A variation in the visually estimated prominence of the vertical cleft with the surrounding tumescences that make up the male pore terminalia was similar between northern and southern adults (χ^2 = 2.346, ns, *df* = 3). The northern and southern adults were also homogeneous when their frequencies in two biotope groups, viz. forests (incl. coniferous and deciduous forests and shore alder thickets) and open biotopes (incl. meadows, shores, and other types of open sites) were compared (χ^2 = 13.194, ns, *df* = 9). Adults in sample set A were also homogeneous in these respects. I conclude that the prominence of male terminalia varies similarly in *D. octaedra* populations in eastern Fennoscandia.

3.2.7. Clitellum and tubercula pubertatis

The clitellum begins from the 29th body segment in 98.4% of the adults in the north (*n* = 64) and in 98.7% in the south (*n* = 79) (sample set B). It terminates at the 34th segment in 78.1% in the north and in 82.3% in the south (the next prevalent is the 33th segment, 18.8% in the north and 17.7% in the south and in one northern adult (3.1%) it terminates at the 35th segment). The location of the clitellum thus varies to some extent but I found no considerable differences between southern and northern adults or between them in different biotopes.

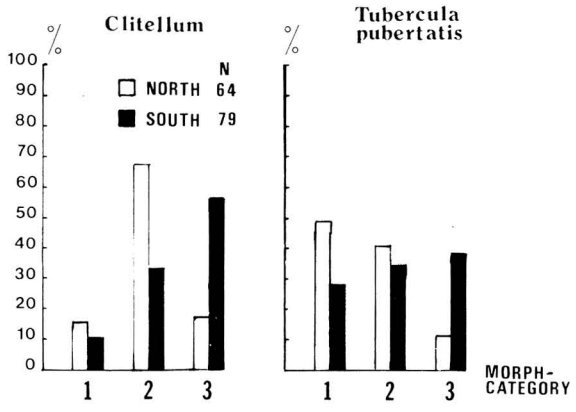


Fig. 8. Percent proportions of *D. octaedra* adults with 1 = poorly developed and diffusively demarcated, 2 = rather prominent and well-demarcated and 3 = very protuberant and shaply demarcated clitellum and tubercula pubertatis in the north and south (sample set A). See also the text.

The prominence of the clitellum and tubercula pubertatis was visually estimated for each adult and given an index value from one to three (section 2.2.). In sample set A the clitellum and tubercula pubertatis were more prominent in the south than in the north (clitellum: χ^2 = 4.815°, *df* = 2: tubercula pubertatis: χ^2 = 13.216**, *df* = 2, Fig. 8). In sample set B the corresponding differences were even more significant (clitellum: χ^2 = 23.741***, *df* = 2: tubercula pubertatis; χ^2 = 14.430***, *df* = 2). The difference between the north and the south thus seems to be independent of the method of preservation. On the other hand, most of the northern adults were sampled earlier (sample set A: 100% in July, B: 79.4% in August) than the southern adults (A: 91.4% in August or later, B: 86.3% in September or later) but this hardly explains the differences: my observations in N Norway indicate that *D. octaedra* adults are actively laying cocoons in July. There is no proof that September in the south is a more favourable period to lay cocoons than July or August in the north, either.

3.3. Variability within and between allozyme phenotypes

Based on six polymorphic enzyme systems Terhivuo & Saura (1989) demonstrated wide allozymic variability in north European *D. octaedra* populations. There was a high number of overall allozyme phenotypes (clones in brief) and four allozyme phenotype groups (clone groups in brief) deviating in one to four enzyme variants from those present in the most frequent clone. The clones and clone groups proved to be differently distributed in the study area and between the biotopes. This suggests dissimilar adaptation to specific environmental factor combinations and/or differences in their post-glacial dispersal history. On the other hand, the most abundant clones proved to be ecological generalists and they constitute a great proportion of the eastern Fennoscandian *D. octaedra* populations.

Below I examine morphological and morphometric variability in the common *D. octaedra* clones and the four clone groups distinguished by Terhivuo & Saura (1989). I assume that the worms of the same clone or clone group are genetically more similar to each other than to those of the other clones or clone groups. Attention is paid to within- and between-clone variation in two main types of biotopes (forests and open biotopes) in the north and the south.

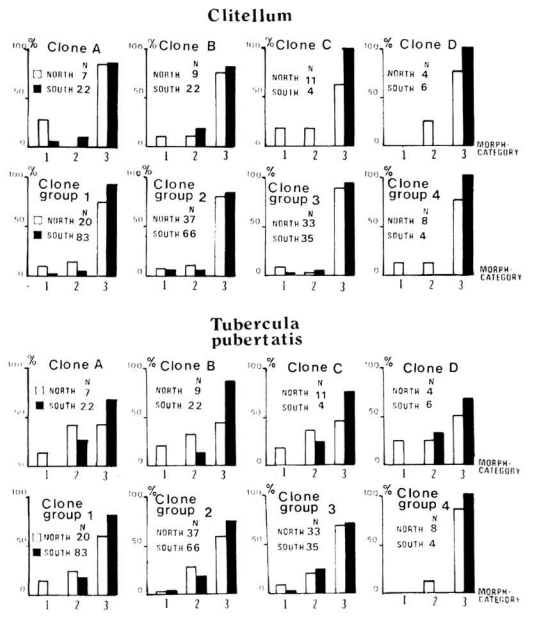


Fig. 9. Percent proportions of *D. octaedra* adults in different morph-categories referring to the protuberance and demarcation of the clitellum and tubercula pubertatis in the common clones (A–D) and clone groups (1–4) in the north and south (sample set A). For the definition of morph-categories see the legend to Fig. 8 and for the clones and clone groups see section 3.3.

3.3.1. Number of segments

The mean number of segments varies rather widely both between and within abundant clones (A–M) (Table 8). The latter variation suggests that environmental factors contribute greatly to the variability. This also holds true for the four clone groups (Table 9). Adults in northern forests tend to have a higher mean number of segments than those in southern forests but the corresponding ranges widely overlap. In open biotopes no clear-cut trend exists (Tables 8 and 9).

3.3.2. Size and intersetal distances of post-clitellar segments

The mean size of the post-clitellar segments within clones A–D is much greater in the north than in the south (Table 8). The trend is uniform within each clone despite considerable variation. With respect to the four clone groups (Table 9) the difference between the north and the south can be observed irrespective of the biotope.

Because the northward shift to greater body size for adults refers to clones and clone groups the trend does not seem to correlate with genotypic differences between the worms.

I also worked out absolute and relative intersetal distances for the adults of the common clones and clone groups: all the distances were longer in the north due to greater segment size, but the relative intersetal distances proved to be similar in the north and the south.

3.3.3. Clitellum, tubercula pubertatis and male pores

The differences in protuberance of the clitellum and tubercula pubertatis between southern and northern worms were also observed within the common clones and clone groups: in the south adults more often had a more protruding and well-demarcated clitellum and tubercula pubertatis compared to those in the north (Fig. 9). Again, the genotypic differences between adults did not correlate with the shift.

Table 8. Mean and median number of segments and size of post-clitellar segments in *D. octaedra* adults representing abundant overall allozyme phenotypes (= "clones" A–M) in sample set A. Identification of the clones is based on allozyme combinations of six polymorphic enzyme systems as explained in Terhivuo & Saura (1989). 'North' refers to subareas I–V and 'south' to subareas VI–XI (see Fig. 1). Forests comprise coniferous and deciduous forests. Shores, meadows and waste soils are included in open biotopes. See also the text.

Clone	Number of segments				Post-clitellar segment size (mm²)			
	mean ± *SD*	median	range	*n*	mean ± *SD*	median	range	*n*
A (total)	91.07 ± 9.20	94	70–103	27	4.33 ± 1.29	4.45	2.04–7.04	29
north	86.71 ± 11.83	87	70–102	7	5.84 ± 0.82	5.75	4.57–7.04	7
forests	78.50 ± 12.02	78.5	70–87	2	5.39 ± 1.16	5.39	4.57–6.21	2
open biotopes	90.00 ± 11.23	92	74–102	5	6.02 ± 0.72	5.75	5.31–7.04	5
south	92.60 ± 7.16	95	78–103	20	3.85 ± 0.99	3.70	2.04–5.84	22
forests	93.13 ± 8.23	95	78–103	17	4.01 ± 3.83	4.01	2.53–5.84	17
open biotopes	91.00 ± 8.81	95	81–99	5	3.32 ± 1.05	3.29	2.04–4.82	5
B (total)	87.53 ± 13.33	96	59–104	28	4.86 ± 1.45	4.52	2.65–8.10	31
north	82.55 ± 13.11	80	59–101	9	6.31 ± 1.32	6.72	3.97–8.10	9
forests	78.83 ± 13.47	78	59–101	6	6.29 ± 0.98	6.27	5.11–7.65	6
open biotopes	90.00 ± 10.39	96	78–96	3	6.35 ± 2.13	6.98	3.97–8.10	3
south	89.89 ± 13.12	96	59–104	19	4.30 ± 0.99	4.31	2.65–6s.84	22
forests	89.70 ± 13.73	96	59–104	17	4.37 ± 1.05	4.32	2.65–6.84	19
open biotopes	91.50 ± 11.26	91.5	78–96	3	3.90 ± 0.74	4.19	3.05–4.45	3
C (total)	87.53 ± 10.67	87	68–102	13	4.96 ± 1.51	4.68	2.95–8.17	15
north	88.30 ± 10.06	86.5	68–99	10	5.02 ± 1.53	4.68	3.41–8.17	11
south	85.00 ± 14.72	77	76–102	3	4.80 ± 1.64	4.95	2.95–6.32	4
D (total)	96.10 ± 4.24	97	89–101	10	4.33 ± 0.82	4.19	2.96–5.69	10
north	94.00 ± 5.30	93	89–101	4	4.52 ± 0.44	4.51	4.05–5.01	4
south	97.50 ± 3.09	98.5	92–100	6	4.20 ± 1.03	3.92	2.96–5.69	6
E (total)	93.35 ± 7.97	95	75–103	14	4.41 ± 1.24	4.61	1.80–6.38	15
F (total)	86.00 ± 14.85	93	57–101	9	4.35 ± 1.05	4.56	2.35–5.71	9
G (total)	96.75 ± 3.30	96.5	93–101	4	5.48 ± 1.84	5.85	3.17–7.83	6
H (total)	91.37 ± 12.56	97	63–99	8	4.58 ± 1.17	4.24	3.29–6.09	9
I (total)	94.20 ± 9.10	98	78–99	5	3.41 ± 0.72	3.60	2.29–4.27	5
J (total)	90.28 ± 14.42	96	58–98	7	4.53 ± 1.75	3.68	2.32–6.96	7
K (total)	86.16 ± 12.84	90.5	67–97	6	4.90 ± 1.49	4.87	3.18–6.41	6
M (total)	83.00 ± 13.77	84	62–98	6	4.79 ± 1.35	4.42	3.55–6.66	6

The occurrence of male pores in the common clones (A–F) and clone groups (1–4) comprising > 10 adults or subadults was also studied (Table 10). A slight statistical difference was indicated between clones ($\chi^2 = 13.680^*$, $df = 5$) but not between the four clone groups ($\chi^2 = 3.611$, ns, $df = 3$). In the south adults and subadults of clone A more often had male pores than they did in the north ($\chi^2 = 4.502^*$, $df = 2$). The other clones were homogeneous in this respect.

4. Discussion

4.1. Methods of surveying

Several sources of error are involved in measuring the body dimensions of earthworms, as demonstrated by e.g. Satchell (1971) and Nordström & Rundgren (1972). I have supposed that within each data set the sources of error involved have similarly affected the measurements made on *D. octaedra* in different biotopes and/or areas. Studying worms preserved by different methods warranted cross-checking of the results. The measurements obtained for soft-bodied worms are indices rather than absolute values. For instance, there is no definite body length for an earthworm. In this study three parameters, viz., body length, weight and size of post-clitellar segments were used as indices for body size.

In sample set B the worms were killed by submersing them in ethanol, causing them to withdraw. This explains why the combined setal distances aa+dd are in general greater in sample set B than in A (see Fig. 6). Both data sets, however, equally indicate that northern adults are longer than southern ones.

Table 9. Mean number of segments and size of post-clitellar segments in *D. octaedra* adults representing clone groups 1–4. The four clone groups comprise individuals deviating in one to four enzyme variants from those recorded in the most abundant clone A in sample set A. Identification of the clone groups are explained in Terhivuo & Saura (1988). 'North' refers to subareas I–V and 'south' to subareas VI–XI, respectively (see Fig. 1). Forests comprise deciduous and coniferous forests, whereas shores, meadows and waste soils are included in open biotopes.

Clone	Number of segments mean ± *SD*	median	range	*n*	Post-clitellar segment size (mm²) mean ± *SD*	median	range	*n*
Group 1 (total)	89.52 ± 11.94	95	57–104	99	4.55 ± 1.12	4.32	1.80–8.10	103
north	89.85 ± 11.23	95	59–102	20	5.78 ± 1.30	5.68	3.68–8.10	20
forests	87.00 ± 13.76	89	59–102	11	6.10 ± 1.19	5.85	4.05–8.01	11
open biotopes	93.33 ± 6.03	96	78–97	9	5.40 ± 0.90	5.53	3.68–8.10	9
south	89.44 ± 12.18	95	57–104	79	4.27 ± 0.91	4.08	1.80–6.96	83
forests	89.75 ± 12.05	95	57–104	70	4.36 ± 0.94	4.10	2.32–6.96	73
open biotopes	87.00 ± 13.44	88	58–100	9	3.63 ± 1.17	3.93	1.80–4.86	10
Group 2 (total)	89.57 ± 12.28	94.5	58–106	92	4.75 ± 1.01	4.48	2.26–8.66	103
north	89.05 ± 11.54	94	58–104	35	5.61 ± 1.03	5.25	3.28–8.66	37
forests	88.33 ± 10.65	87	68–99	9	5.97 ± 1.16	5.40	4.60–8.17	11
open biotopes	89.30 ± 12.03	94.5	58–104	26	5.46 ± 0.97	5.25	3.28–8.67	26
south	89.89 ± 12.83	95	62–106	57	4.27 ± 0.89	4.18	2.26–8.32	66
forests	89.72 ± 12.94	93	62–106	50	4.22 ± 0.90	4.10	2.26–8.32	56
open biotopes	91.14 ± 12.99	97	65–102	7	4.55 ± 0.73	3.97	3.10–6.33	10
Group 3 (total)	91.80 ± 10.23	95	59–103	61	5.08 ± 1.09	4.64	2.47–12.23	61
north	91.82 ± 9.84	96	59–102	28	6.38 ± 1.15	6.09	3.17–12.23	33
forests	84.80 ± 19.01	97	59–101	5	6.84 ± 1.27	5.69	3.48–11.67	5
open biotopes	93.34 ± 6.23	96	80–102	23	6.30 ± 1.11	6.22	3.17–12.23	28
south	91.87 ± 10.74	95	62–103	33	3.86 ± 0.77	6.58	5.20–8.07	35
forests	90.93 ± 11.15	94	62–103	29	3.85 ± 0.78	3.59	2.47–7.00	31
open biotopes	98.00 ± 3.56	97.5	95–102	4	3.93 ± 0.72	4.26	2.64–4.57	4
Group 4 (total)	89.50 ± 9.79	93.5	75–101	12	5.48 ± 1.25	5.47	1.72–7.89	12
north	90.62 ± 9.67	94.5	75–101	8	5.98 ± 0.96	6.32	3.30–7.89	8
forests	82.50 ± 6.36	82.5	78–87	2	6.11 ± 1.06	6.11	4.32–7.89	2
open biotopes	93.33 ± 9.36	96.5	75–101	6	5.94 ± 1.03	6.32	3.30–7.84	6
south	87.25 ± 10.90	86.5	77–99	4	4.48 ± 1.72	5.01	1.72–6.18	4
forests	90.66 ± 10.41	94	79–99	3	4.36 ± 2.03	5.18	1.72–6.18	3
open biotopes	77.00 –	–	–	1	4.83 –	–	–	1

Earthworms lose weight when preserved, the rate of loss being greater during the first few months of preservation (e.g. Satchell 1971). In sample set B worms from the north and the south were secured a few years to some decades ago. Such old worms probably lose weight at a much lower rate than newly preserved ones. Some weight loss due to evaporation of the preservative while weighing the worms was unavoidable. However, the worms were dried in a standard way. The gut content also influences the total weight: I have supposed that the worms of the north are similar to those of the south in this respect.

The method of preservation may influence the shape of the clitellum and tubercula pubertatis (see e.g. Sims & Gerard 1985). A difference between northern and southern worms was, however, observed within sample sets A and B.

Table 10. Occurrence of male pores in adult and subadult *D. octaedra* representing clones (A–F) and clone groups (1–4) in the north and in the south (sample set A). For the determination of the clones and clone groups see the legends to Tables 8 and 9 and Terhivuo & Saura (1989). For further explanation see the text.

Clone or clone group	Male pores present *n*	present %	absent *n*	absent %
A	23	69.7	10	30.3
B	19	55.9	15	44.1
C	18	90.0	2	10.0
D	10	76.9	3	23.1
E	6	40.0	9	60.0
F	5	45.5	6	54.5
Group 1	70	60.3	46	39.7
Group 2	70	57.9	51	42.1
Group 3	43	50.0	43	50.0
Group 4	7	41.2	10	58.8

Table 11. Frequency distributions of segment numbers for adult *D. octaedra* sampled in different parts of its geographical range. The data sources are as follows; eastern Fennoscandia (present study), Greenland (Omodeo 1957), England (Gates 1974), Central France (Omodeo 1961), eastern Alps (Omodeo 1957), The Pyrenees (Omodeo 1961), U.S.S.R (studied by the author) and northeastern U.S.A (Gates 1974). Skewness is according to Pearson's index, i.e., 3 (mean – median)/s.

No of segments	Eastern Fennoscandia				Greenland		England		Central France		Eastern Alps		The Pyrenees		U.S.S.R		Northeast U.S.A	
	*n**	%*	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
54–57	–	–	1	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
58–61	–	–	6	1	–	–	2	3	–	–	–	–	1	2	–	–	2	2
62–65	1	2	15	4	–	–	4	7	–	–	2	2	3	5	3	7	2	2
66–69	–	–	10	2	2	2	2	3	2	2	1	1	2	3	–	–	2	2
70–73	3	6	8	2	–	–	1	2	2	2	4	4	1	2	2	4	3	3
74–77	1	2	19	5	2	2	11	18	3	6	5	5	2	3	3	7	2	2
78–81	2	4	20	5	2	2	5	8	1	2	4	4	–	–	6	13	3	3
82–85	1	2	29	7	3	3	2	3	1	2	6	6	1	2	1	2	4	4
86–89	4	8	23	6	6	5	1	2	3	6	2	2	3	5	–	–	4	4
90–93	6	12	46	11	5	4	7	11	2	4	14	14	21	31	4	9	5	5
94–97	13	26	108	26	17	14	7	11	7	15	35	36	23	34	10	22	52	53
98–101	14	28	95	23	67	55	16	26	12	25	19	20	10	15	14	31	11	11
102–105	4	8	34	8	18	15	4	7	10	21	4	4	–	–	2	4	8	8
106–109	1	2	2	1	–	–	–	–	5	10	1	1	–	–	–	–	–	–
Total	50		416		122		62		48		97		67		45		98	
mean	92.9		90.8		96.9		86.7		94.4		91.5		89.6		92.2		92.1	
SD	12.7		10.2		6.6		13.4		11.1		9.8		9.8		11.4		10.9	
median	96		95		99		91		98		95		93		96		96	
skewness	–1.1		–1.1		–0.9		–1.0		–0.9		–1.1		–0.7		–1.7		–1.1	

*small juveniles (≤15 mm)

4.2. Number of segments

In my study area *D. octaedra* populations are homogeneous regarding the number of segments. There is a lot of data on the segment numbers of *D. octaedra* in widely separate parts of its range. Table 11 implies that no clear-cut between-area differences exist. All the frequency distributions are negatively skew and with a wide overlap.

Gates (1974) counted 95–98 segments in 15 North American *D. octeadra* juveniles but 48–103 segments in another sample from the same region (n = 11). Gates concluded that the skewness in the frequency distributions of segment numbers in juveniles may be due to segments lost from the posterior end. On the other hand, Omodeo & Magaldi (1951) indicated in amphigonic *Aporrectodea caliginosa* that the number of segments at the time of hatching correlates with the amount of nutritive fluid available to an embryo in the cocoon. They also hypothesize that some sort of genetic control may underlie the phenotypic reaction. In Table 11 the frequency distribution for small juveniles is as skew as that for the adults, implying that segment losses in different phases of the life-cycle have no profound impact on frequencies. While the present study could not correlate segment numbers with genotypic differences, factors influencing juveniles prenatally may be important in this respect.

According to Moment (1979), newly emerged *Eisenia fetida* juveniles and adults have the same mean number of segments and the rate of regeneration is positively dependent on temperature. In sample set A the proportions of worms with segment losses were similar in age categories ($\chi^2 = 0.014$, ns, $df = 1$, juveniles and subadults pooled). This implies that regeneration influences the frequency distributions, as one would otherwise expect an increased number of losses with age. Southern and northern adults ($\chi^2 = 0.202$, ns, $df = 1$), subadults (Fisher, P = 1.000) and juveniles (Fisher, P = 0.483) were homogeneous in this respect. Regeneration does not therefore seem, however, to affect the worms at any area specific rate.

Table 12. Intersetal distance ratios (cd = 1) of *D. octaedra* adults sampled in different parts of the range. In my material the measures for the left and the right side of the body are pooled (sample set A).

Locality	Relative intersetal distance aa	ab	bc	cd	dd	*n*	Data source
Greenland	1.53	1.18	1.13	1	1.33	7	Omodeo 1957
Dolomitic Alps	1.56	1.22	1.21	1	1.43	5	Omodeo 1957
Iceland	1.70	1.43	1.36	1	1.60	1	Omodeo 1957
E Fennoscandia							
north	1.69	1.20	1.11	1	1.59	105	Terhivuo 1988
south	1.75	1.17	1.09	1	1.56	210	Terhivuo 1988
total	1.73	1.18	1.10	1	1.57	315	Terhivuo 1988

4.3. Setal patterns

Udel (1929) and Wilcke (1960) report the following setal pattern for *D. octaedra* in West Germany dd>aa=ab=bc=cd and the same applies to Norway (Stöp-Bowitz 1969). In England the formula for post-clitellar setal arrangement is aa:ab:bc:cd:dd = 1:1:1.2:1.2:1.8 (Gerard & Sims 1985) and in the U.S.A "dd often slightly < aa but slightly > or = or even <cd" (Gates 1974). In Denmark *D. octaedra* has "aa=ab=bc=cd, dd a bit longer" (Bornebusch 1928) and in France aa:ab:bc:cd:dd = 4:4:5:5:7 (=1:1:1.3:1.3:1.8) (Bouché 1972). However, no precise measurements or sample sizes are indicated in any of these data sources.

Omodeo (1957) indexed the shortest setal distance cd= 1 and reported setal formulas for *D. octaedra*: aa>dd>ab>bc>cd (Table 12). This corresponds with the pattern observed in sample set A. In eastern Fennoscandian *D. octaedra* populations relative setal distances ab and bc are close to those worms found in Greenland and the Dolomitic Alps, but aa and dd are closer to the measurements of the single Icelandic worm.

4.4. Body dimensions in relation to regional and environmental variables

Omodeo (1957:13) demonstrated that *D. octaedra* adults in Greenland are somewhat longer than their counterparts in the eastern Alps, the means being 33.5 and 29.5 mm, respectively. The two frequency distributions widely overlap, suggesting no clear-cut difference between the populations.

In northern parts of my study area the body length, weight and size of post-clitellar segments of *D. octaedra* adults are greater than in the south. This seems to be a general morphometric adaptation to the more extreme climatic conditions in arctic and subarctic areas as supported by the clinal pattern of the shift and the uniform difference between northern and southern adults irrespective of the biotope and the genotype.

The between-biotope differences in the south and in the north (Tables 3, 4 and Fig. 6) may be attributable to dissimilarities in specific environmental factors such as the quantity and quality of food. For instance, Neuhauser et al. (1980) pointed out that the maximum weight attained by *E. fetida* depended on the food available.

The different phases of an earthworm's life cycle are highly sensitive to temperature (e.g., Michon 1954, Lakhani & Satchell 1970, Watanabe & Tsukamoto 1976, Phillipson & Bolton 1977 and Mazantseva 1982). The length of the incubation period of cocoons, growth of juveniles, attainment of sexual maturity and longevity correlate negatively with temperature. Tsukamoto & Watanabe (1977) calculated that the theoretical developmental zero point is +5.6°C for the eggs of *E. fetida*. This is close to the temperature used to estimate the annual mean length of the vegetation period (daily mean temperature ≥6°C) in the Nordic Countries. Alhough the developmental zero undoubtedly is lower for *D. octaedra* than for *E. fetida* living in manure heaps and leaf composts with elevated temperature, the former species is in any case exposed to large differences in the growth period in different parts of the study area (the range being approximately six weeks, Fig. 2). The curve indicating a vegetation period of about 140 days runs through subareas IV and V, where *D. octaedra* populations are intermediate. The different

phases of the life cycle of *D. octaedra* may require longer periods in the north than in the south, while northern worms probably live longer than southern ones in order to be able to complete their life cycle. Whether or not this correlates with the attainment of greater body size remains unanswered. Another alternative is that the individuals in the north represent higher levels of polyploidy than those in the south, which might be related to larger body size. There are *D. octaedra* individuals with 5*n*, 6*n*, 6*n* ± x and 8*n* chromosomes from different parts of the range, but the data are too meagre to make it possible to draw definite conclusions in this respect (Casellato 1987, Hongell & Terhivuo 1989).

4.5. Sexual organs and reproduction

In *D. octaedra* the characters related to the reproductive system vary more than those related to the soma (Gates 1974). "Reproductive systems of most if not all of the available material of *D. octaedra* were anatomically defective or divergent from lumbricid norms", Gates stated. He found 0, 1 or 3 pairs of testes in segments IX–XI instead of the normal two pairs in X and XI. He also reported worms with 2 pairs of ovaries in segments X–XIV, or even with six pairs in XII–XVII instead of the normal pattern, i.e. one pair in segment XIII. Asymmetrical location of the gonads is not uncommon among *D. octaedra* adults, either (Gates 1974).

Secondary sexual organs of the male reproductive system show a variety of reductions involving absence of male pores. Variability in female secondary reproductive organs refers to e.g., the location of the clitellum and tubercula pubertatis (Gates 1974). In my study area *D. octaedra* populations are rather homogeneous in these respects, but in the south adults have a more prominent clitellum and tubercula pubertatis than in northern ones. The difference does not correlate with the genotype of the worms, implying the role of extrinsic factors. On the other hand, the reproductive state and/or age distribution of adults, are unknown.

In my study area parthenogenesis in *D. octaedra* is evidenced by e.g., the absence of male pores in about 40% of adults and the fact that the distance between male pores and the clitellum often varies so greatly that amphimixis according to the "normal lumbricid manner" can hardly take place between adults with highly differing body lengths (see Fig. 4). For chromosomal and electrophoretic evidence on parthenogenesis of the species in the study area, see Hongell & Terhivuo (1989) and Terhivuo & Saura (1989), respectively.

Parthenogenesis seemingly allows great variability in reproductive organs of both obligatorily (e.g., *D. octaedra* and *Eiseniella tetraedra*, Gates 1974, 1977) and facultatively parthenogenetic earthworm species (e.g., *Dendrodrilus rubidus*, Gates 1979). In biparentally reproducing Lumbricidae species non-reproductive characters vary more than those related to reproduction (see e.g. Sims & Gates 1985).

4.6. Morphometric variation in *D. octaedra* clones and clone groups

The present study failed to correlate morphological and morphometric variability with differences in the genetic make-up of *D. octaedra* individuals. It is worth recalling that clonal differences were measured by the allozyme differences of six polymorphic enzyme systems and these, of course, comprised only a fraction of the total genotypic differences involved. Variants of enzyme systems related to intracellular metabolism need not correlate with environmental and morphological variables: some other enzyme systems, like those related to digestion, could have been more definitive in this respect. For instance, Christensen (1977, 1979) was able to correlate amylase genotypic differences with habitat differences in some isopods.

4.7. Central Finland as a zoogeographical transition zone

D. octaedra is widely distributed in the northern hemisphere (Stöp-Bowitz 1969). Gates (1974) proposed that its range may be mainly delimited by climatic factors, probably temperature. In Scandinavia it lives on the northern margins of its range and its occurrence and dispersal there is not dependent on human habitation (Ökland 1928, Backlund 1949, Julin 1949, Stöp-Bowitz 1969).

In my study, the central parts of Finland (subareas III, IV and V) constitute a transition zone for southern and northern *D. octaedra* populations. In this area the individuals of some species of the Lycosidae spiders are intermediate between those in southern and northern populations (Palmgren 1939). It is also an intraspecific transition zone for polymorphic bird species such as the yellow wagtail (*Motacilla flava*) (Sammalisto 1958, Vepsäläinen 1968), the caper-

caillie (*Tetrao urogallus*) (Lindén & Väisänen 1986) and for mammals such as the red squirrel (*Sciurus vulgaris*) (Voipio 1950, 1956 and 1957), and it coincides with the ornithogeographical transition zone for Finnish land birds (Järvinen & Väisänen 1980). It also differs in vegetation from the southern and northern parts of the study area (Fig. 1). Lindén & Väisänen (1986) stressed the importance of bioclimatic factors in determining this transition zone for Finnish capercaillie populations. Environmental factors, probably those related to climate, may also be involved in the case of *D. octaedra*. Hence, the cline observed did not correlate with differences in biotope or genotype.

The transition zone may play a role in separating genetically different *D. octaedra* populations. *D. octaedra* populations are, however, very diverse in different parts of both the N-S and E-W transects. Besides mutations areal differences between *D. octaedra* clone pools may also be due to some extent at least to a dissimilar post-glacial history of dispersal of the clones (Terhivuo & Saura 1989).

Acknowledgements. I am indebted to Olli Järvinen, Anssi Saura, Kari Vepsäläinen and an unknown referee for critically reading the manuscript and making many suggestions for improvement. I also like to express my appreciation to Pertti Saurola, Esa Ranta and Jari Kouki for the computerization of some parts of the study material. I am grateful to Teresa Perel for permission to study her D. oct*aedra* material originating from different parts of the U.S.S.R. Leigh Plester checked this article linguistically. Reino Tyynelä photographed the figures and my wife Mirja-Liisa Terhivuo assisted me in the field with collecting the worms of sample set A. I cordially thank these persons, too.

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Received 10.IV.1988, revised 10.X.1988
Printed 30.XII.1988