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First record of *Dendrobaena attemsi* (Michaelsen) (Oligochaeta, Lumbricidae) in Scandinavia, with a critical review of its morphological variation, taxonomic relationships and geographical range

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Specimens of *Dendrobaena attemsi* (Michaelsen, 1902) are reported from a relict natural forest habitat in 'Nationalstadsparken', an urban national park within the city of Stockholm, Sweden. They represent the northernmost record of the species and the first from Scandinavia. A morphological comparison of the new material with conspecific samples from Italy and Turkey, and with literature data, shows that the typical traits of the species (small body size, pigmentation pattern, long-stalked spermathecae, hooked nephridial bladders, lack of hearts in xi) remain virtually invariant throughout its geographic range. A constancy is also observed in the regular nephropore alternation between setal levels *b* and *d* as well as in several aspects of chaetotaxy, including the relative size distribution of the clitellar genital setae *b* and their 'grooviness' (mean length of grooves/mean total setal length). Other features, e.g., the relative intersetal distances, the location and number of genital setae in the spermathecal and male areas, show intraspecific variation. Based upon the apomorphic states of the nephridial features and the number of hearts, *D. attemsi* is tentatively regarded as an early branch of a clade comprising at least also the Balkan *D. mahnerti*, *D. epirotica*, *D. pindonensis* and *D. rhodopensis*. The superficially similar *D. octaedra* and *D. decipiens* do not belong to such a clade. Recent records of *D. attemsi* in natural habitats of the Czech Republic and Germany suggest the possibility that, as is hypothesized for the western part of its range, also in Central Europe the species re-expanded northwards in postglacial times. Alternatively, the species was introduced to Sweden by man, although a historical association with human settlements seems unlikely.

Fig. 1. Geographic distribution of *D. attemsi*.

1. Introduction

Dendrobaena attemsi was first described from Austria (Michaelsen 1902), as *Helodrilus* (*Dendrobaena*) *attemsi*, and has subsequently been reported from throughout central and southern Europe, the Slovak, Ukrainian and Rumanian Carpathians, the north of Turkey and Caucasus (Michaelsen 1902, 1910, Cernosvitov 1931, 1935, 1937, 1938, Pop 1938, Omodeo 1952a, Graff 1953, 1954, Benes 1961, Plisko 1963, Zicsi 1965a, 1981, 1994, Alvarez 1972, 1977, Bouché 1972, 1978, Karaman 1972, Kurceva 1972, Sapkarev 1972, Zicsi & Michalis 1981, Kvavadze 1985, Pizl 1986, Zicsi & Csuzdi 1986, Omodeo & Rota 1989, 1991, Mrsic 1991). Until the present, the northernmost findings of the species have been in England (Sims & Gerard 1985), Ireland (Cotton 1992) and Germany (Beylich 1995), whilst no records were known from Fennoscandia or any of the Baltic countries.

According to Bouché (1972), *D. attemsi* is a rare stenotopic species associated to acid, organic-rich, sandy soils. Some European records refer to greenhouses or gardens (e.g., Cernosvitov 1935, Graff 1953, 1954), and in such habitats the species has been found also in the western United States (Fender 1982, 1985). However, most records are from woodland habitats with small human influence. In 1995, specimens of *D. attemsi* were discovered in a forest habitat in 'Nationalstadsparken', an urban national park comprising the royal parks Södra and Norra Djurgården, Haga and Ulriksdal, in the northeastern part of Stockholm, Sweden. Such a discovery is of considerable faunistic interest: it is the first record for Scandinavia and the northernmost reported so far (Fig. 1).

In this paper, the Stockholm specimens are compared with material from other geographic areas. In view of the revived interest in the setal morphology for the taxonomy of western Palaearctic Lumbricoidea (*sensu* Jamieson 1988) (e.g., Kvavadze 1991, 1993, Rota 1994), and to add to the poor knowledge of the variability of the setae at individual and populational levels, a morphometric study of the setal complement of the species, based on adult worms from three countries, is presented. The morphological traits of *D. attemsi* are critically evaluated and an attempt is made to outline the taxonomic relationships of the species. The possibility that *D. attemsi* is a natural element of the Swedish fauna, and was not introduced accidentally by man, is explored on the basis of biogeographical considerations.

2. Material and methods

The Stockholm sample of *D. attemsi* (4 adults and 1 subadult) was collected on 15 May 1995 in an open wood of spruce, birch and alder on a slope along Vargstigen-path (south of Laduviken, Norra Djurgården). The ground was covered with grasses, anemones, *Oxalis*. This habitat may be regarded as a relict of a typical herb-rich forest formerly widely distributed in central Fennoscandia (Anderberg & Nordenstam, pers. communication). Worms were found by a rotting tree stump in dark, moist peat mixed with spruce needles (pH 4.6). They were relaxed in 10% alcohol and fixed in 80% alcohol.

New samples of *D. attemsi* from Italy (in Omodeo & Rota's Collection) were also studied: 2 specimens from loc. Santuario, 1 380 m a.s.l., and loc. Ponte Parasacco, 750 m a.s.l., Valmala (Cuneo, Piedmont), Cottian Alps, 4 May 1993, G. B. Del Mastro leg.; 2 specimens from loc. Colle Quazzo, 1 130 m a.s.l., Garessio (Cuneo, Piedmont), Maritime Alps, 15 June 1993, G. B. Del Mastro leg.; 5 specimens from along Rio Giulian, 1 260 m a.s.l., Oncino (Cuneo, Piedmont), Cottian Alps, 4 July 1993, G. B. Del Mastro leg.; 26 specimens from a chestnut wood at Piani di Praglia (Genoa, Liguria), Ligurian Apennine, 600 m a.s.l., 19 May 1982, P. Barenghi & P. Omodeo leg.

To obtain a more thorough comparison with Turkish worms described by Omodeo and Rota (1989, 1991), the following material (also in Omodeo & Rota's Collection) was reexamined: *D. attemsi* from the foot of Ulu Dag, northwestern Turkey (Omodeo & Rota 1991: Stn. 72) and from Çankurtaran Pass, Vilayet Artvin, northeastern Turkey (Omodeo & Rota 1989: Stn. 33 bis/ter); *D. decipiens* (Michaelsen, 1910) from Çankurtaran Pass, Vilayet Artvin, northeastern Turkey (Omodeo & Rota 1989: Stn. 33, 33 bis/ter).

The anterior 20 segments of two Swedish, one Italian (Ligurian) and one northwestern Turkish specimen of *D. attemsi* were detached, cleared of gut contents, embedded in paraffin, longitudinally sectioned and stained in ferric haematoxylin. Setae were removed from the inner wall of dissected adult worms from various populations of *D. attemsi* and other *Dendrobaena* spp., and placed on a slide in a drop of a 1:1 solution of glycerin and 25% acetic acid, or in Faure's fluid, for examination.

The total length of the ordinary and genital setae (L) was measured in a straight line from their ectal tip to the lowest point of their base. The length of the non-grooved ental portion of the genital setae (δ) was measured from the lowest point of their curved base to the proximal end of the longest longitudinal groove (grooves are in general unequally long in a seta); δ was not measured in setae in which the ental hook was not completely grown. Measurements of the length of the grooved portion (Lg) included the distal tip of setae ($Lg = L - \delta$). In *D. attemsi*, the lengths of the clitellar genital setae *b* of each worm mostly fell into two separate groups (see Table 2); as δ values were generally more constant than Lg values within each group, setae with intermediate total length (found in a Swedish specimen) were grouped according to their δ value, i.e., to the length of their ungrooved portion. For each type of clitellar setae, the ratio of the mean length of the grooved portion to the mean total length (G = mean Lg/mean L) is given as a measure of the 'grooviness' of the group.

The nephropore arrangements were ascertained from worms in alcohol and longitudinal serial sections.

The Swedish material is deposited in the Swedish Museum of Natural History (SMNH), Stockholm.

3. Results

3.1. Variation in body morphology and anatomy

The main aspects of morphological variation between the Swedish specimens, and one Turkish and two Italian populations of *D. attemsi* (the four lots from Piedmont, very consistent in their morphology, have been treated as one 'Alpine' sample) are shown in Table 1. All worms exhibit a small body size but their anterior region is somewhat variable in shape and width, partly depending on the glandular development of male porophores and other genital tumescences. The red pigmentation can be more or less intense, distributed all over the body or restricted to preclitellar and caudal segments, but segments ix–xii are constantly sharply depigmented below setae *d* (Fig. 2). Spermathecae always have their ampullae in ix and x, and long, slender, intraseptal ducts opening through inconspicuous pores at 9/10 and 10/11 on *d*. A pair of glandular cushions, corresponding to Gates' (1974) "blister organs", extend from *c* to *d* in 1/2ix–1/2xii, traversed by equatorial depressions in x and xi (Fig. 3). In all populations, from segment to segment, the nephropores alternate, with few exceptions, between setal lines *b* and *d*, their zig-zag arrangements being asymmetrical on the two sides of the body; nephropores of xv and xvi are always on line *b*. Nephropores on *b* are obvious, those on *d* much smaller, some-

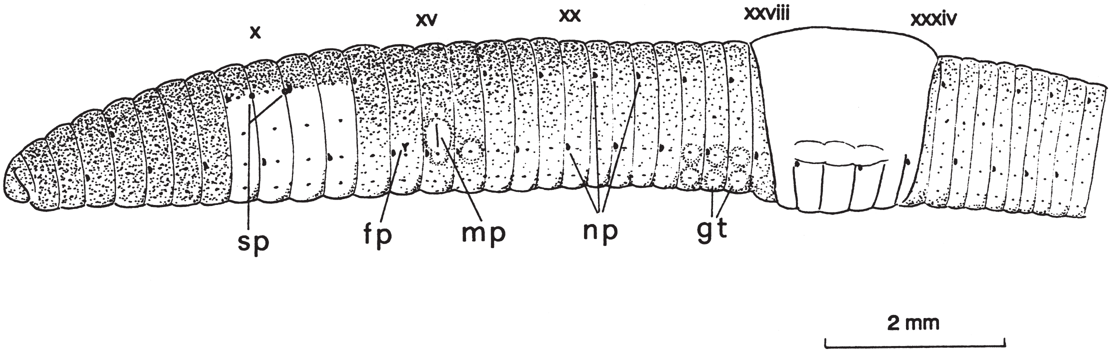

Fig. 2. Anterior part of the body of a Swedish specimen of *D. attemsi.* Note the peristomium, short, partly fused with segment ii, and the typical pattern of pigmentation, with segments ix–xii sharply depigmented below setae *d.* Abbreviations: fp, female pore; gt, glandular tumescences; mp, male pore; np, nephropores; sp, spermathecal pores.

times difficult to locate in whole worms. The nephridial bladders are slender, J-shaped (*sensu* Fender 1985, i.e., with distal, ventral end curving anterodorsally into the body wall); all terminal ducts enter the body wall near the anterior border of segments on *b*, but then they either open directly to the exterior or ascend through subepidermal canals (clearly visible externally in postclitellar and caudal segments) up to *d* level. Hearts are always missing in xi.

3.2. Chaetotaxy

The somatic setae (Fig. 4A) are unornamented, small and little protruding from the body surface

Table 1. Variation of body morphology in four populations of *Dendrobaena attemsi.*

	Stockholm (Sweden)	Piedmont (Italy)	Liguria (Italy)	Ulu Dag (W Turkey)
Body shape	Cylindrical	Cylindrical	Flattened at clitellum	Ventrally flattened from xv to clitellum
Size	27–42 by 1.5–2 mm	25–33 by 2 mm	35–60 by 2 mm	27–50 by 2.5–3 mm
Segment number	100–135 (*n* = 5) Mean = 121.2 ± 16.4	92–129 (*n* = 9) Mean = 114.6 ± 15.3	102–136 (*n* = 25) Mean = 123.8 ± 9 Modes = 118; 132	85–151 (*n* = 35) Mean = 126.4 ± 13.8 Mode = 131.5
Pigmentation	Faint reddish; only preclitellar and caudal	Purplish red; also on postclitellar region	Purplish red	Pale reddish
Mean relative intersetal distances				
at segment x	1.3 : 1 : 1.2 : 1.4 : 2.3	1.1 : 1 : 1.2 : 1.7 : 2.3	1.4 : 1 : 1.4 : 1.6 : 2.8	1.2 : 1 : 1.2 : 1.1 : 2.5
at segment l	1.2 : 1 : 1.3 : 1.1 : 2.4	1.2 : 1 : 1.4 : 1.3 : 2.4	1.5 : 1 : 1.4 : 1.1 : 2.9	1.4 : 1.1 : 1.2 : 1 : 2.4
(no. of specimens)	(3)	(6)	(3)	(3)
1st dorsal pore	5/6	7/8	5/6, 6/7	26/27
Male porophores	xv	xv or xv–xvi	xv–xvi	1/2xiv–1/2xvi
Glandular papillae				
a, *b*	ix–xi, xvi, xxv–xxvii, xxviii–xxxiv	ix, xv–xvi, xxiii–xxvii, xxviii–xxxiv	ix, xi, xiv–xvi, xxiv–xxv xxix–xxxiv	viii–xi, xiv–xvi, xxiii–xxvi, xxix–xxxiv
c	x		ix	
Hearts	vii–x	vi–x	vi–ix	vii–ix

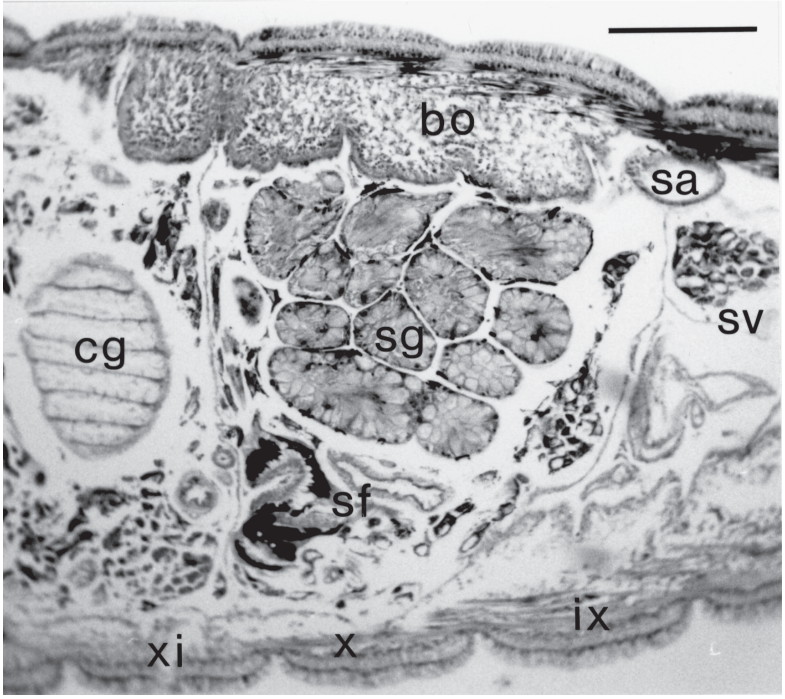

Fig. 3. Longitudinal parasagittal section of a Swedish specimen of *D. attemsi*, showing the internal anatomy of segments ix through xi. Note the conspicuous multilobular gland (sg), typically associated with the follicles of genital setae *b* and *c*, and the glandular cushion in 1/2ix–1/2xii corresponding to the blister organ described by Gates (1974). Abbreviations: bo, blister organ; cg, calciferous glands; sa, spermathecal ampulla; sf, sperm funnel; sg, multilobular setal gland; sv, seminal vesicle of ix. Scale, 250 µm.

in all material examined. Measurements of their lengths in anterior (vii, x), preclitellar (xvii, xxiii), midbody (lx) and caudal (cxv or cxxv) segments of adult specimens from Sweden, Liguria and northwestern Turkey (Table 2) show that such setae are on average shortest in the Swedish worms, longest in the Ligurian ones. The length of the ventral and dorsal setae does not change consistently along the body in animals of different geographic origins. This might be expected, given their different body shapes (Table 1). However, some common trends do exist: in all specimens examined, the shortest setae are situated dorsally in midbody (segment lx) and the longest ones ventrally in x.

Modified genital setae occur at *a* and *b* in all clitellar segments (Fig. 4B–G). The length of setae *a* is rather homogeneous throughout the clitellum and only a little greater than the mean length of the somatic setae; like the latter, clitellar setae *a* are shortest in the Swedish specimens, longest in the Italian ones. Their longest grooves are on average a little shorter than half the setal length in both the Swedish and the western Turkish material, equal to half the setal length in the Italian material (Table 2).

In the beginning of our study, the length of clitellar setae *b* of the Swedish specimens appeared very diverse (Fig. 4C–G). Variation dropped considerably by taking into account only the length of their smooth ental portions. By this expedient, setae simply fell into two length classes (named ‘short’ and ‘long’ types). Two such classes were also found in the worms from Italy and from Turkey (Table 2): here the classes are more clearcut, not only with regard to the length of the ungrooved portion (δ) but also to the total setal length (L). The long type is typical for the segments bearing the tubercula pubertatis (Fig. 5A) and is found there even in young adults, which still have their genital setae at early stages of development. The short type develops in the remaining clitellar segments and does not seem to be precursory of a longer type. The mean ‘grooviness’ (G) is virtually identical in the two classes, but changes a little in worms from different populations (Table 2). Thus, all clitellar setae *b* are on average less grooved in the northwestern Turkish material than they are in both the Swedish and the Ligurian populations (Table 2). It is worth noting that both classes of clitellar setae *b* are longer in the Swedish specimens than in the northwestern Turkish material;

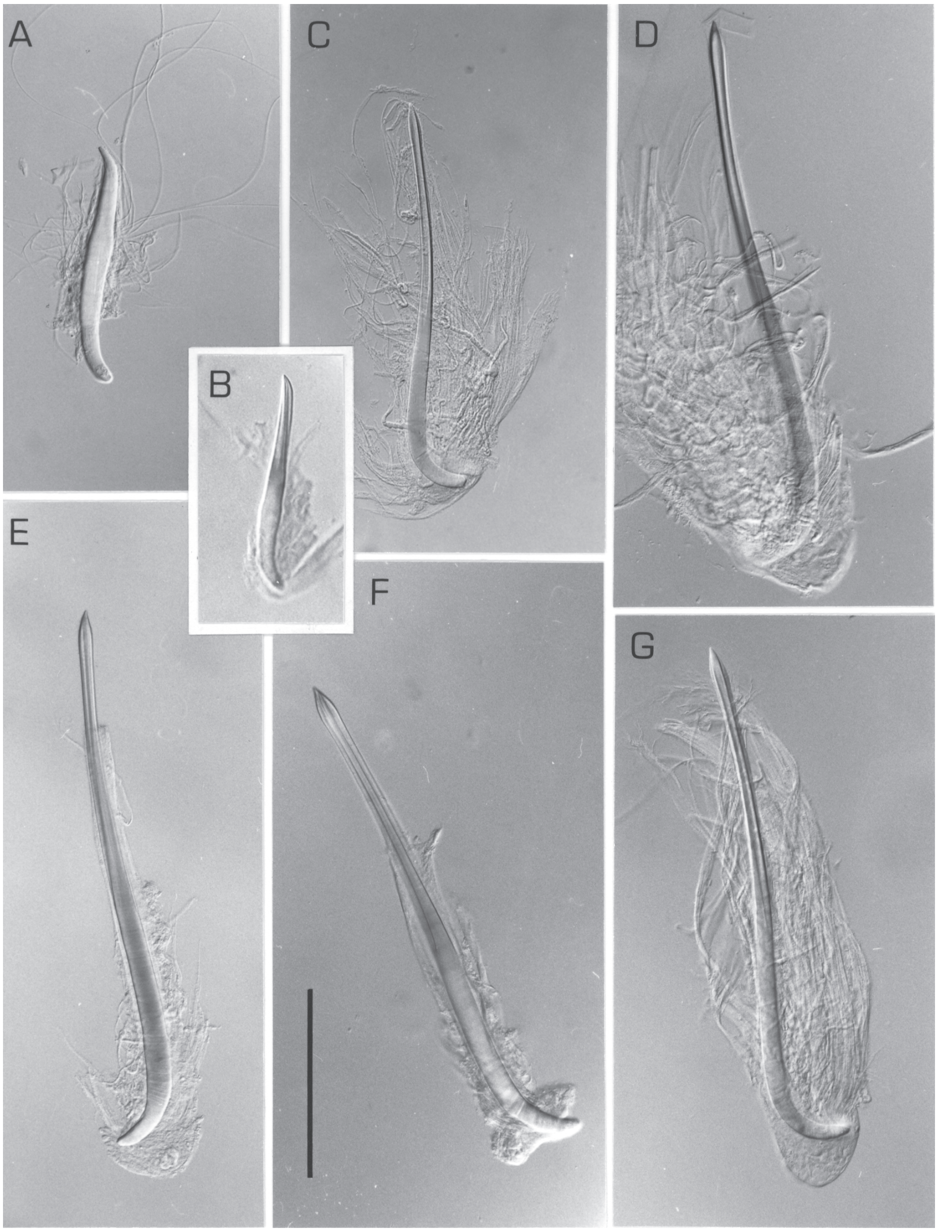

Fig. 4. Setae of Swedish specimens of *D. attemsi*. The ordinary setae are small and unornamented; the genital setae are pointed, slightly bent and with four (unequally long) longitudinal grooves running along their distal portion. (A) ordinary seta *b* of xxvii. (B) genital seta *a* of xxx. (C) genital seta *b* (short type) of xxviii. (D–G) genital setae *b* (long type) of xxx–xxxii. All setae to same scale, 200 µm.

this contrasts with the somatic setae and the genital setae *a*, which are shorter in the Swedish worms (Table 2).

The Swedish specimens differ from all other material examined in lacking genital setae ventrally in front of clitellum, although typical glandular tumescences occur there (xxv–xxvii) in both *a* and *b* positions (Fig. 2).

As to the genital setae associated with the spermathecal and male pore areas (involving segments ix–xi and xiv–xvi, respectively), all samples show a wide individual variation both in the setal size

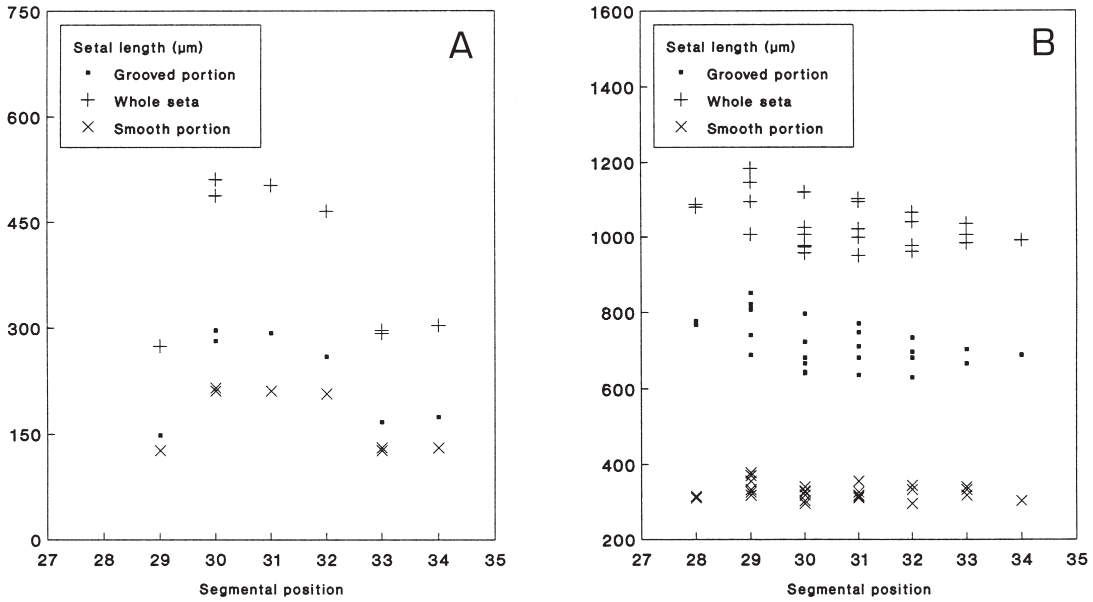

Fig. 5. Different variation in length of clitellar setae *b* according to segmental position in two sympatric populations of *Dendrobaena attemsi* (A) and *D. decipiens* (B) from Çankurtaran Pass (Artvin, NE Turkey). In *D. attemsi* (A), such setae show their maximal lengths in segments bearing the tubercula tubertatis (xxx–xxxii). In *D. decipiens* (B), the longest setae are found immediately in front (xxix) of the tubercula pubertatis (which in this species are also located in xxx–xxxii).

Table 2. Variation of setal length and 'grooviness' in three populations of *Dendrobaena attemsi*. For genital setae, L = total length of setae, Lg = length of the grooved distal portion, δ = length of the smooth ental portion, G = mean Lg/mean L. In brackets, mean ± standard deviation, n = no. of setae measured.

Setae	Stockholm (Sweden)	Liguria (Italy)	Ulu Dag (W Turkey)
Ordinary type*	133–233 µm [187 ± 25.6, n = 24]	170–289 µm [229 ± 23.3, n = 26]	155–259 µm [211 ± 28.4, n = 28]
Genital type			
ix–xi (*b*, *c*)	496 µm (δ = 200 µm) (*b* xi)	474 µm (δ = 215 µm) (*b* xi) 592 µm (δ = 207 µm) (*c* ix)	511–570 µm (δ = 240–244 µm) (*b* ix)
xiv–xvi (*b*)	195 µm (δ = 96 µm) 481 µm (δ = 200 µm)	374 µm (δ = 163 µm) 570–577 µm (δ = 215 µm)	289 µm (δ = 148 µm) 414–492 µm (δ = 174–196 µm)
xxiv–xxvii (*a*)	– •	311–322 µm (δ = 159–163 µm)	259–296 µm (δ = 133–137 µm)
(*b*)	– •	581–607 µm (δ = 229–244 µm)	503–555 µm (δ = 215–237 µm)
xxviii–xxxiv (clitellum)			
(*a*) L	211–231 µm [222 ± 6.34, n = 6]	289–311 µm [300 ± 7.8, n = 8]	240–274 µm [254 ± 10.4, n = 12]
δ	107–130 µm [118 ± 8.1, n = 6]	141–159 µm [150 ± 5.9, n = 8]	126–148 µm [138 ± 7.4, n = 12]
Lg	100–111 µm [103 ± 4, n = 6]	148–155 µm [150 ± 3.4, n = 8]	92–133 µm [116 ± 12.9, n = 12]
G	0.464	0.5	0.457
(*b*) L (short type)	407–533 µm [451 ± 47.3, n = 6]	400–518 µm [466 ± 36, n = 8]	303–348 µm [333 ± 25.6, n = 3]
δ	170–200 µm [184 ± 13.6, n = 6]	155–192 µm [181 ± 12.5, n =8]	141–155 µm [148 ± 7.4, n = 3]
Lg	237–333 µm [267 ± 18.2, n = 6]	244–326 µm [285 ± 25.3, n = 8]	163–200 µm [185 ± 19.6, n = 3]
G	0.592	0.611	0.55
L (long type)	533–599 µm [557 ± 18.2, n = 11]	596–651 µm [621 ± 16.4, n = 12]	459–518 µm [502 ± 16.3, n = 12]
δ	215–259 µm [235 ± 14.3, n = 11]	222–263 µm [243 ± 12.8, n = 12]	203–244 µm [223 ± 12, n = 12]
Lg	296–344 µm [322 ± 14.4, n = 11]	359–407 µm [378 ± 11.9, n = 12]	255–300 µm [279 ± 13.8, n = 12]
G	0.578	0.609	0.55

* Only based on setae *a*, *b*, *c*, *d* of segments vii, x, xi, xvii, xxiii, lx, cxv (or cxxv).

• In this region, all Swedish specimens examined have ordinary setae.

(Table 2) and in the location and number per individual. Furthermore, these setae are often asymmetrically developed on the two sides of the body.

4. Discussion

4.1. Intraspecific variation

The rare features (i.e., the small body size, the clearcut pigmentation pattern and glandular development of the spermathecal region, the long-stalked spermathecal ampullae, the hooked nephridial bladders, the lack of hearts in xi) which make *D. attemsi* readily distinguishable from its many congeners possessing a similar location and extent of the reproductive organs, remain virtually invariant throughout the geographic range of the species (cf. Michaelsen 1902, Cernosvitov 1931, 1935, Plisko 1963, Zicsi 1965b, Alvarez 1972, Bouché 1972, Perel 1979, Fender 1982, 1985, Sims & Gerard 1985, Zicsi & Csuzdi 1986). Also the nephropore distribution pattern observed in our material fits perfectly that described for American (Gates 1974, Fender 1982, 1985) and Bulgarian specimens (Zicsi & Csuzdi 1986); we agree here with Fender (1985) that any discrepancy in this respect (e.g., Bouché 1972, Sims & Gerard 1985) can probably be attributed to incorrect observations.

In contrast, much intraspecific variation (especially between populations) occurs in characters which are consistent within most other *Dendrobaena* species. Such variation does not appear to follow any geographic pattern; instead, differences are often found between relatively close populations. Four examples are discussed here:

(1) The relative intersetal distances in postclitellar segments of the Swedish and the Piedmont specimens (Table 1) resemble those of the type material from Austria (Michaelsen 1902) and of the Greek material described by Cernosvitov (1938): in all of them $ab < aa \leq cd < bc$, and $dd < 1/4$ of the body circumference. In the Ligurian material (Table 1), on the other hand, we found $aa > bc > cd$, and $dd > 1/4$ of the body circumference, as recorded by Cernosvitov (1935) in worms from Prague. The material from northwestern Turkey (Table 1), with $aa = bc$ and $ab = cd$, is reminiscent of samples from Caucasus (Michaelsen 1910, Kvavadze 1985), Bulgaria (Plisko 1963) and Spain (Alvarez 1972), whereas other Turkish samples (Omodeo & Rota 1989), possessing $bc = cd < aa$, are closer to those described from France by Bouché (1972). Intersetal distances similar to those reported for North American worms (Fender 1982, $ab = bc = cd$) are so far known only for English material (see Sims & Gerard 1985). Such a wide intraspecific variability is rare in *Dendrobaena*, even in those species where, as in *D. attemsi*, *a*, *b*, *c* and *d* approach equidistance (e.g., *D. octaedra* (Savigny, 1826), see Terhivuo 1988a).

(2) The different positions of the first dorsal pore in the four populations examined (Table 1) conform to the wide range of variation (even within one sample), from various pre- or postclitellar positions to the total loss of pores, recorded in the literature (Graff 1953, Fender 1982, 1985, Omodeo & Rota 1989).

(3) A shift of the spermathecal pores towards the middorsal line has been reported for some material from Greece (Zicsi & Michalis 1981). (Their displacement towards setal level *b* in specimens from northern Caucasus (Michaelsen 1910) should be taken with caution (perhaps a misprint?), as that would be an exceptional position among lumbricids.)

(4) Hearts, characteristically missing in xi, can be absent in x as well (Table 1). Ligurian worms conform in this respect not only to North American material (Gates 1974, Fender 1985) but also to samples from Ulu Dag and some western and eastern Turkish localities (Omodeo & Rota 1989, 1991). The Italian material proves that the location of the most anterior pair is also variable in this species: it is most frequently in vii, but we found it in vi in both Piedmont and Ligurian samples. The location of the first pair in viii described by Omodeo and Rota (1989) for some Turkish specimens proved incorrect upon re-examination: the first pair of hearts are in vii in all Turkish worms. The reduction of hearts from five to three pairs does not appear to be related to a diminished body size, as shown by the Ulu Dag population.

Our results show that in each population the genital setae are rather variable — depending especially on their intrasegmental position and location along the body, but that such variation can be resolved into a few discrete groups. Single data, as often recorded in the literature, are not reliable for the characterization of the setae. However, some features of the groups appear to be intraspecifically consistent and can have a practical application in questions of species discrimination (see 4.2.2 and 4.2.3).

4.2. Taxonomic relationships

4.2.1. Presumed nearest relatives

Dendrobaena Eisen, 1874, currently comprising over 60 species, exhibits little informative variation in the majority of the traditional taxonomic characters, e.g., locations of clitella, tubercula pubertatis, spermathecal pores, calciferous glands, seminal vesicles, etc. The species are defined by unique combinations and permutations of the states of an extended set of characters.

Various attributes have evidently appeared, reversed and reappeared several times, producing a high degree of homoplasy within the genus. Homoplasy is indeed common in the Lumbricidae as a whole, thus frustrating any attempt at reconstructing the history of the various lineages. However, some features, e.g., the location of nephropores or the shape of the nephridial bladders (unfortunately overlooked or inadequately described for several species) appear less homoplaseous and possess uncommon, unambiguously apomorphic states useful for phylogenetic reconstructions. Some of these rare attributes indicate that *D. attemsi* is a relatively advanced taxon within its genus (Table 3).

Most lumbricid genera have their own pattern of nephropore arrangement. Pores arranged at two or more levels along each side of the body are the

Table 3. Morphological comparisons between *Dendrobaena attemsi*, its presumed phylogenetic neighbours (*D. epirotica* through *D. rhodopensis*), other possibly close relatives (*D. olympica* through *D. illyrica*) and some similar but unrelated congeners (*D. alpina* through *D. vejdovskyi*). Putative apomorphic states of the characters are indicated in boldface.

	Nephropore pattern	Nephridial bladders	Clitellum	Tubercula pubertatis	Sptheca ducts	Sptheca pores	Blister organs	Gizzard	Seminal vesicles	Last hearts
D. epirotica	***b-d-b-d***	J-shaped	**xxxi–xxxviii**	**xxxiii–xxxv**	Short	*d*	–	**xvii–xix**	ix,xi,xii	**x**
D. pindonensis	***b-d-b-d***	J-shaped	**xxxiii–xl**	**xxxv–xxxvii**	Short	*d*	–	**xvii–xix**	ix,xi,xii	**x**
D. mahnerti	***b-d-b-d***	J-shaped	**xxxv–xlii**	**xxxviii–xl**	**Long**	*d*	**+ (Small)**	**xvii–xix**	ix,xi,xii	**x**
D. attemsi	***b-d-b-d***	J-shaped	xxviii–xxxiii	xxx–xxxii	**Long**	*d*	**+**	xvii–xviii	ix,xi,xii	**ix or x**
D. rhodopensis	***b-d-b-d***	**Biscuit-shaped**	1/2xxvii–xxxiii	xxix–xxxi	**Long**	m*d*	**+**	xvii–xviii	ix,xi,xii	**x**
D. olympica	?	?	xxvii–xxxvi	xxx–xxxii	**Long**	m*d*	**+**	xviii–xix	xi,xii	**x**
D. bosniaca	?	Sausage-shaped	1/2xxvi–xxxiii	xxix–xxxi	Short	*d*	?	xvii–xviii	xi,xii	**x**
D. vranicensis	?	?	xxviii–xxxiv	xxxi–xxxii	Short	*cd*	?	**xvii–xix**	xi,xii	**x**
D. illyrica	?	?	xxviii–xxxiv	xxxi–xxxiii	Sessile	*d*	?	xvii–xviii	ix,xi,xii	**x**
D. alpina	Irregular	Rod-shaped	xxvii–xxxiii	xxx–xxxii	Short	*d* or m*d*	**+**	xvii–xviii	ix,xi,xii	**x** or xi
D. decipiens	Irregular	Rod-shaped	xxvii–xxxiii	xxx–xxxii	**Long**	m*d*	**+**	xvii–xviii	ix,xi,xii	xi
D. octaedra	*b*	**Ocarine-shaped**	xxix–xxxiv	xxxi–xxxiii	Sessile	*d*	**+**	xvii–xviii	ix,xi,xii	**ix**
D. nicaensis	?	?	xxvii–xxxiii	xxx–xxxi	**Long**	m*d*	**+**	xvii–xviii	xi,xii	xi
D. vejdovskyi	*b*	?	xxviii–xxxiii	xxxi–xxxii	**Long**	*d*	**+**	xvii–xviii	xi,xii	?

rule in *Lumbricus*, *Allolobophora*, *Aporrectodea*, *Eisenia*, *Dendrodrilus* (see Sims & Gerard 1985) and *Scherotheca* (see Bouché 1972). In *Octodrilus* and in *Octolasion*, the nephropores are mostly on setal line *b*, but those of the first nephridiate segments (iii–vi) are invariably shifted towards a more dorsal level (Rota, pers. obs.).

In *Dendrobaena*, however, the situation is diverse (e.g., Gates 1974, Fender 1982, 1985, Zicsi 1985, Zicsi & Csuzdi 1986, Zicsi & Michalis 1993; own observations). Most frequently, all nephropores are aligned on *b* (e.g., *D. octaedra*, *D. byblica* (Rosa, 1893), *D. cognettii* Michaelsen, 1903, *D. vejdovskyi* (Cernosvitov, 1935), *D. ilievae* Kvavadze & Miloikova, 1993, *D. steineri* Zicsi, 1994), or they irregularly alternate between *b* and *d* (e.g., *D. alpina alpina* (Rosa, 1884), *D. veneta* (Rosa, 1886), *D. hortensis* (Michaelsen, 1890), *D. semitica* (Rosa, 1893), *D. decipiens* (Michaelsen, 1910), *D. balcanica* (Cernosvitov, 1937), *D. orientalis* Cernosvitov, 1940)). A regular alternation between *b* and *d* is exceptional, probably representing an advanced condition, and may thus be informative with regard to the closest relatives of *D. attemsi*.

The four *Dendrobaena* species known to have such a nephropore arrangement (Table 3) combine it, like *D. attemsi*, with another apomorphy, the lack of hearts in xi. They are the Greek *D. mahnerti* Zicsi, 1974 (see Zicsi & Michalis 1993), *D. epirotica* Zicsi & Michalis, 1993 and *D. pindonensis* Zicsi & Michalis, 1993 and the Bulgarian *D. rhodopensis* (Cernosvitov, 1937) (see Zicsi & Csuzdi 1986). The first three species also resemble *D. attemsi* in possessing rod-like, distally recurved, nephridial bladders (see Zicsi & Michalis 1981, 1993, for *D. mahnerti*). According to Perel (1976), however, this would be an ancestral shape compared with the biscuit- and ocarine-shaped bladders of most other *Dendrobaena* spp.; in the latter, the descending and ascending terminal tracts of the bladder have become fused together. *Dendrobaena mahnerti*, *D. epirotica* and *D. pindonensis* diverge from *D. attemsi* (and from all other congeners) by the posterior location of their clitella and tubercula pubertatis. This triad does also share a three-segment long gizzard (Table 3).

Most similarities between *D. rhodopensis* and *D. attemsi* (e.g., in the locations of the clitellum, calciferous glands and gizzard) appear symplesiomorphic; the majority of *Dendrobaena* spp. are similar in these respects. A putative synapomorphic feature for the two is the very long spermathecal ducts emerging through glandular thickenings of the body wall (blister organs), present also in *D. mahnerti* (but apparently reversed in *D. epirotica* and *D. pindonensis*). This feature, however, seems to have evolved more than once within the genus (Table 3). In *D. rhodopensis*, like in most *Dendrobaena* spp., the nephridial bladders are biscuit-shaped (Zicsi & Csuzdi 1986).

Only a few other species share the lack of hearts in xi with *D. attemsi* (Table 3). Three of them are again from the Balkan peninsula, i.e., *D. olympica* (Cernosvitov, 1938), *D. bosniaca* Mrsic, 1988 and *D. vranicensis* Mrsic, 1991. Like *D. attemsi*, *D. olympica* has long spermathecal ducts but of the gizzard in xviii–xix. Another species with the posteriormost hearts in x is *D. illyrica* Cognetti, 1906 from central Europe; the latter, however, has sessile spermathecal ampullae (Zicsi 1965b). The relationships between these four species and *D. attemsi* will certainly become clearer once their nephropore arrangements and the shapes of their nephridial bladders have been described.

Nephropore and other nephridial information is also needed to clarify the identity of the material from Waxenberg (Austria) identified by Pop (1947) as '*D. octaedra* f. *typica*', but exhibiting two traits very atypical for the latter (pp. 25–27): a tanylobous prostomium (as in *D. illyrica*), and a regular alternation of the nephropores between *b* and *d*, with asymmetry on the two sides of the body (as known for *D. attemsi*). (This was the first time that this particular arrangement was recorded.) Indeed, by that time Pop (1947) granted *D. octaedra* a very broad intraspecific variation (also in these two characters) and synonymized with it several species, including *D. attemsi* and *D. illyrica* (*ibid.*, p. 24).

To summarize, *D. attemsi* appears to belong to a group characterized by the lack of hearts in xi and a regular *b*-*d* nephropore alternation, both unique features within *Dendrobaena*. As long as the nephropore arrangement is unknown for *D. olympica*, *D. bosniaca*, *D. vranicensis* and *D. illyrica*, *D. attemsi* appears as an early branch of a clade comprising at least also *D. mahnerti*, *D. epirotica*, *D. pindonensis* and *D. rhodopensis*.

4.2.2. Relationship to D. octaedra

Pop's (1947) opinion that *D. octaedra* and *D. attemsi* were synonyms was certainly based on their remarkable correspondence in the location and extent of the clitellum, reduction of the hearts and inner glandular modification of the spermathecal area (Table 3). Pop merely regarded their discrepancies in the number of spermathecae (three pairs in *D. octaedra*), the location of the tubercula pubertatis and other reproductive characters, as part of the many alterations and rudimentational events frequently encountered in *D. octaedra*. This view was supported by Gates (1974: 43) who also noted the possibility that the differences between the two are determined by parthenogenetic alterations in *D. octaedra*. Fender (1982, 1985), however, rejected any close relationship between the two species, emphasizing their significant differences in the shape of the nephridial bladders, the arrangement of the nephropores (forming a straight series on *b*, except in the foremost segments, in *D. octaedra*), and the development of the calciferous glands (largely swollen, with no constriction at mid xi in *D. octaedra*). We point out that *D. octaedra* diverges from *D. attemsi* also in the (annular) shape of the clitellum, the intersetal distances ($aa \geq dd$ postclitellarly) and the size and grooviness of the genital setae. Measurements of the latter in material of *D. octaedra* from Italy are: clitellar setae *a* 540–550 µm long (grooved portion 318–333 µm long; G = 0.60), clitellar setae *b* 630–850 µm long (grooved portion 480–555 µm long; G = 0.70) and 30–37 µm wide at shaft midpoint. In conspecific material from Sweden: clitellar setae *a* 480–530 µm long (grooved portion 290–296 µm long; G = 0.59), clitellar setae *b* 700–733 µm long (grooved portion 466–503 µm long; G = 0.67) and 30 µm wide at shaft midpoint.

4.2.3. Relationship to D. decipiens

The relationship between *D. attemsi* and *D. decipiens* is somewhat controversial. The latter, endemic to western Caucasus and Lazistan (Omodeo & Rota 1989), was originally described as deceivingly similar to *D. attemsi* in body size, colour, location of the clitellum and tubercula pubertatis, relative intersetal distances and length of the spermathecal ducts (Michaelsen 1910). However, its different location of the spermathecal pores (near the middorsal line) and wider extent of the associated depigmentation and inner glandular pad (both reaching the middorsal line), induced Michaelsen (1910) to classify it as a variety of the polymorphic *D. alpina*, *Helodrilus (Dendrobaena) alpinus* var. *decipiens*. The affinity to *D. attemsi* was supported by Perel (1979), who regarded *attemsi* and *decipiens* as synonyms. Later, a study of new Caucasian material of both taxa led Kvavadze (1985) to resume *decipiens* as a subspecies of *D. attemsi*, a nomenclature maintained also in recent works (Kvavadze 1991, 1993). Omodeo and Rota (1989) recorded the two taxa as sympatric in northeastern Turkey and, on account of their different number of hearts (6 pairs in vi–xi in *decipiens*), size of the setae (Fig. 6), etc., ranked *D. decipiens* as a separate species, a view further substantiated by additional important differences found in the present study: (1) the arrangement of the nephropores (irregularly alternating between *b* and *d* in *D. decipiens*) (Table 3); (2) the morphology of the clitellar genital setae (in *D. decipiens* grooves are generally more extended but their length poorly correlated with the total setal length) (Fig. 7) and their size distribution (in *D. decipiens* the setae are longest in xxix, i.e., in front of the tubercula pubertatis) (Fig. 5B); (3) the shape of the clitellum (in *D. decipiens* uniformly developed on the lateral sides of all clitellar segments); (4) the morphology of the ordinary setae (in *D. decipiens* their distal end is conspicuously ornamented with transverse striations and minute tooth-like spines) (Fig. 6C). In this latter respect *D. decipiens* appears similar to *D. alpina* (see Cognetti 1903; Rota, pers. obs.).

4.3. Geographic distribution

The Swedish record gives an opportunity to reconsider some traits of the biogeography of *D. attemsi*, already treated by Omodeo (1952b) but now better understandable.

Following Michaelsen's (1910) view that many lumbricids originated in the Caucasian area, Omodeo (1952b) hypothesized that *D. attemsi* spread from that region, along the northern shores of the Black Sea, towards Romania and Czechoslova-

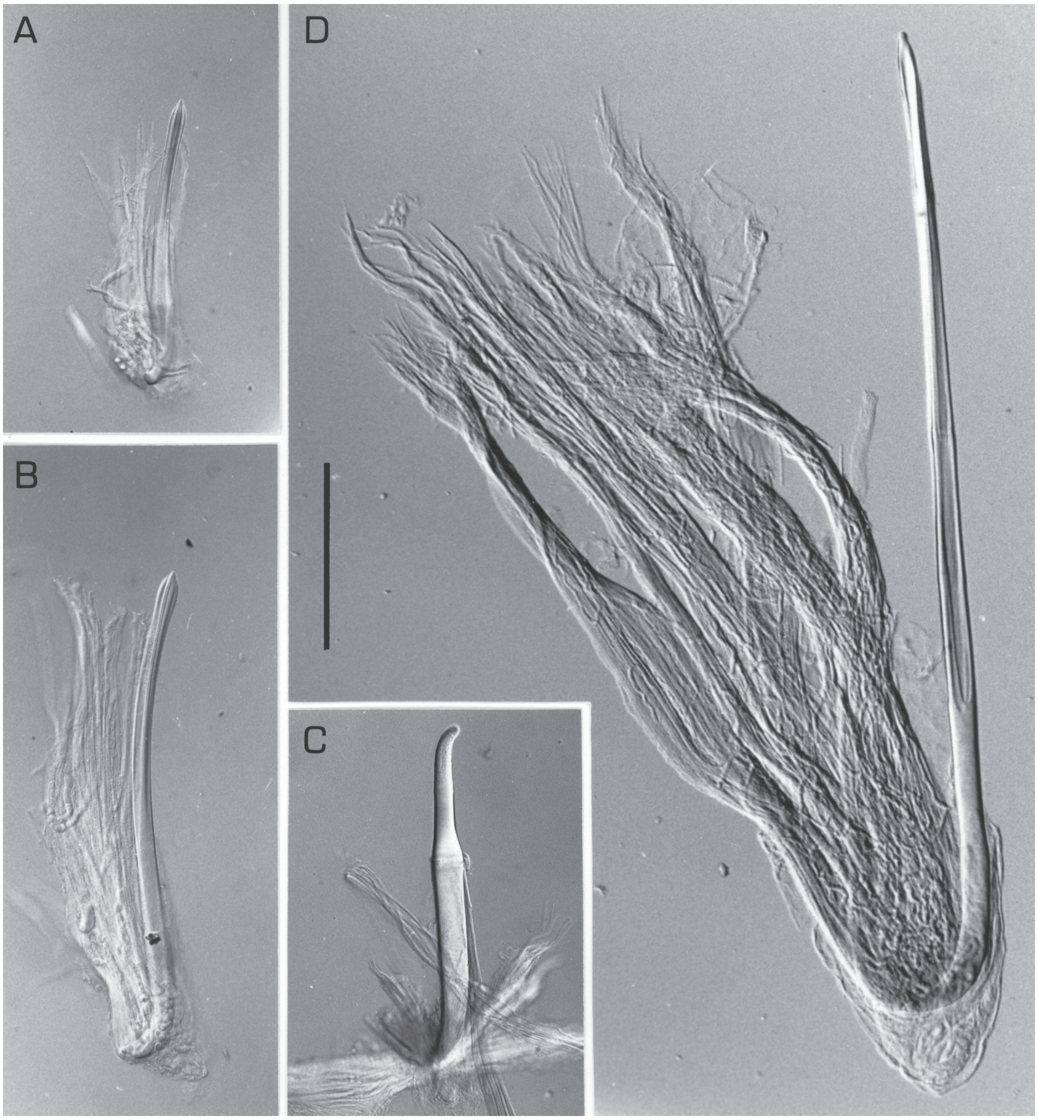

Fig. 6. Setae of two sympatric populations of *D. attemsi* (A–B) and *D. decipiens* (C–D) from northeastern Turkey. (A) genital seta *b* (short type) of xxxiii. (B) genital seta *b* (long type) of xxx. (C) ordinary seta *a* of lxxxv. (D) genital seta *b* of xxviii. All setae to same scale, 200 μm.

kia. From there it was assumed to have migrated southwards into the Balkan Peninsula and then again northwards, across the Dinaric range, to Austria.

Dendrobaena attemsi appears now to have a somewhat disjunct distribution (Fig. 1) comprising: (1) a western area centred in France, stretching southeastwards to Italy just across the Maritime Alps and southwestwards to Spain across the northeastern Pyrenees, and penetrating northwards into Great Britain and Ireland; and (2) an eastern area, much larger and perhaps more ancient (overlapping with the ranges of all presumed nearest relatives), gravitating around the Balkan-Anatolian-Caucasian region and sporadically reaching Central Europe (Czech Rep., Slovak Rep., Ukraine, Romania). The species has never been recorded in Hungary, Poland, and the Baltic republics.

According to Bouché (1972), *D. attemsi* is a mobile species which in France, after the ice age, re-expanded from a refugial area in the Loire basin following a migratory flux directed north-

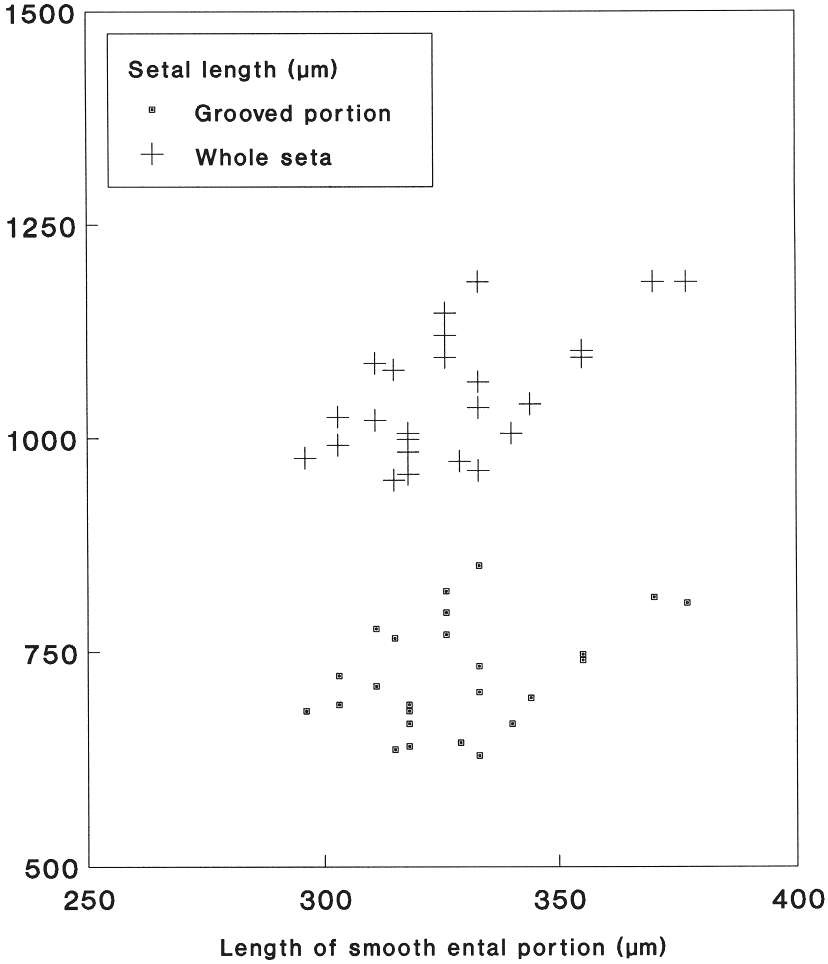

Fig. 7. Morphometry of clitellar setae *b* in *D. decipiens* from northeastern Turkey. The lengths of their smooth basal portion plotted against the total setal lengths (+) or the lengths of their grooved distal portion (■), show that there is a random variation in length of the different portions.

wards, as already suggested (Omodeo 1952b) for *Allolobophora icterica* (Savigny, 1826), *Lumbricus festivus* (Savigny, 1826) and *L. friendi* Cognetti, 1904. In the north it might have colonized new vast territories but, due to subsequent evolution of climate and soils, was partly replaced by termophilous species associated with neutral soils. As a result, it is now confined to the acid soils persisting in the Massif Central, Brittany and the Ardennes (Bouché 1972).

In Spain the species is reported only from Navarra and Huesca (Alvarez 1972, 1977, Diaz Cosin *et al.* 1980) and is possibly restricted to a Basque-Pyrenean vegetational zone characterized by a Central European fauna (Diaz Cosin *et al.* 1992). In Italy it only occurs in the northwestern regions (Zicsi 1981; present paper). The absence from the rest of the Italian Alps is puzzling, since suitable habitats would be available throughout the Alpine arc. Furthermore, the species has been extensively recorded in Slovenia as well as in the rest of former Yugoslavia (Mrsic 1991), and is abundant in Austria (Michaelsen 1902, Zicsi 1965a, 1994). It may be worth noting, however, that *D. alpina* too, like *D. attemsi*, is restricted in Italy to the western Alps, although it is spread throughout former Yugoslavia, Switzerland and Austria (Pop 1947, Zicsi 1965b, Mrsic 1991).

The findings of *D. attemsi* in the Czech Republic and Germany were first restricted to anthropogenic environments (Cernosvitov 1935, Graff 1954), but recent records in a nature reserve in Bohemia (Pizl 1986) and in forest habitats to the west of Hamburg (Beylich 1995) and in Baden-Württenberg (Römbke, pers. communication), demonstrate that the species also occurs in the wild and further to the north in Central Europe than it was previously thought. This suggests the possibility that at these longitudes too the range of the species has expanded northwards in post-glacial times. Thus, it would not be surprising to discover that there is a continuous distribution from the Carpathians across Bohemia and eastern Germany (or alternatively, from the French area through Belgium, Germany and Denmark?) up to Sweden. If so, the arrival in southern Scandinavia could date back to the Sub-Atlantic period during the expansion of conifers (Faegri 1963). A careful search for this species in Denmark and southern Sweden and a genetic comparison between the Swedish population and those of the neighbouring countries would be crucial to clarify the matter.

Alternatively, *D. attemsi* could have been accidentally introduced to Sweden by man. Like *Dendrodrilus rubidus* (Savigny, 1826), *Dendrobaena octaedra* and *D. hortensis*, it inhabits forest litter and decaying wood and is thus prone to be more subject to passive dispersal than are species living in deeper soil layers (see Terhivuo 1988b). In Fennoscandia, as well as in other parts of their ranges, *D. rubidus* and *D. octaedra* are widely distributed both in the wild and in anthropogenic habitats (Martinucci *et al.* 1983, Sims & Gerard 1985, Terhivuo 1988b), facilitated by ecological versatility and parthenogenetic reproduction (Terhivuo 1988b). The Norwegian, Swedish, Finnish, and even the German, records of (the amphigonic) *D. hortensis* are, instead, restricted to compost heaps or to other man-made habitats (Julin 1949, Terhivuo 1988b, Judas & Büchner 1989). *Dendrobaena attemsi* (which also is amphigonic), on the contrary, is very seldom associated with human activities (except gardening). Furthermore, it is highly stenotopic, often inhabiting habitats that are devoid of other lumbricids. Thus a historical association with human settlements seems unlikely. Rather the species could have arrived recently with imported plant material, as it did in the USA (Fender 1982, 1985). Whatever the time and mode of introduction, the Stockholm population, established in a proper natural site, testifies that *D. attemsi* is now a natural element of the Swedish fauna.

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References

Alvarez, J. 1972: Oligoquetos terricolas ibericos. 2. Lumbricidos (1. parte). — Bol. R. Soc. Espanola Hist. Nat. (Biol.) 70: 5–22.

Alvarez, J. 1977: La distribucion de las especies de oligoquetos terricolas en la Jacetania. — P. Cent. pir. Biol. exp. 9: 121–124.

Benes, J. 1961: K poznání zízal Vihorlatu. — Biológia, Bratislava 16: 195–201.

Beylich, A. 1995: Ein Versuch zur Bodenverbesserung an sauren Waldstandorten: Auswirkungen auf die Zersetzergesellschaft. — Newsletter on Enchytraeidae 4: 35–44.

Bouché, M. B. 1972: Lombriciens de France. Ecologie et Systématique. — INRA, Paris. 672 pp.

Bouché, M. B. 1978: Atlas provisoire des lombriciens de Belgique et des pays limitrophes. — In: Leclercq, J. & Gaspar, C. (eds.), Cartographie des Invertebrés européens, Fac. Sci. Agron. Etat — Zool. gén. et faun., Gembloux, 42 cartes. 12 pp.

Cernosvitov, L. 1931: Zur Kenntnis der Oligochaetenfauna des Balkans. III. Oligochaeten aus Montenegro und Südserbien. — Zool. Anz. 95: 312–327.

Cernosvitov, L. 1935: Monographie der tschechoslowakischen Lumbriciden. — Arch. Prir. Vyzk. Cech. 19: 1–86.

Cernosvitov, L. 1937: Die Oligochaetenfauna Bulgariens. — Mitt. k. Naturw. Inst. Sofia 10: 69–92.

Cernosvitov, L. 1938: Zur Kenntnis der Oligochätenfauna des Balkans. VI. Oligochäten aus Griechenland. — Zool. Anz. 123: 192–200.

Cernosvitov, L. 1940: On some Oligochaeta from Palestine. — Ann. Mag. nat. Hist. (11) 6: 438–447.

Cognetti, L. 1903: Res Italicae. VI. Lombrichi delle Alpi Marittime. — Boll. Mus. Zool. Anat. comp. R. Univ. Torino 18: 1–9.

Cognetti, L. 1904: Lombricidi dei Pirenei. — Boll. Mus. Zool. Anat. comp. R. Univ. Torino 19: 1–14.

Cognetti, L. 1906: Nuovi dati sui Lumbricidi dell'Europa orientale. — Boll. Mus. Zool. Anat. comp. R. Univ. Torino 21: 1–18.

Cotton, D. C. F. 1992: Dendrobaena attemsi (Michaelsen, 1902) and Microscolex phosphoreus (Dugès, 1837), two earthworms new to Ireland. — Irish Nat. J. 24: 74–75.

Diaz Cosin, D. J., Moreno, A. G. & Jesus, J. B. 1980:

Lombrices de tierra (Lumbricidos, Megascolecidos y Glossoscolecidos) de la Peninsula Iberica, Baleares y Canarias. Inventario y citas. — Bol. R. Soc. Espan. Hist. nat. (Biol.) 78: 77–95.

Diaz Cosin, D. J., Trigo, D. & Mascato, R. 1992: Earthworms of the Iberian Peninsula. Species list and some geographical considerations. — Soil Biol. Biochem. 24: 1351–1356.

Eisen, G. 1874: Om Skandinaviens Lumbricider. — Öfvers. K. Vet. Akad. Förh. Stockh. 30(1873): 43–56.

Faegri, K. 1963: Problems of immigration and dispersal of the Scandinavian flora. — In: Löve, A. & Löve, D. (eds.), North Atlantic biota and their history. Pergamon Press, Oxford: 221–232.

Fender, W. M. 1982: Dendrobaena attemsi in an American greenhouse, with notes on its morphology and systematic position. — Megadrilogica 4: 8–11.

Fender, W. M. 1985: Earthworms of the western United States. Part I. Lumbricidae. — Megadrilogica 4: 93–132.

Gates, G. E. 1974: Contributions on North American earthworms (Annelida) No. 10. Contributions to a revision of the Lumbricidae. X. Dendrobaena octaedra (Savigny, 1826) with special reference to the importance of its parthenogenetic polymorphism for the classification of earthworms. — Bull. Tall Timbers Res. Stn. 15: 15–57.

Graff, O. 1953: Die Regenwürmer Deutschlands. — Schriftenreihe der Forschungsanstalt Landwirtschaft Braunschweig-Völkenrode 7: 1–81.

Graff, O. 1954: Die Regenwurmfauna im östlichen Niedersachsen und in Schleswig-Holstein. — Beitr. Naturkd. Niedersachsens 7: 48–56.

Jamieson, B. G. M. 1988: On the phylogeny and higher classification of the Oligochaeta. — Cladistics 4: 367–410.

Judas, M. & Büchner, S. 1989: Dendrobaena hortensis (Michaelsen) (Annelida: Oligochaeta: Lumbricidae) inhabiting medieval sewers in Göttingen. — Göttinger Naturk. Schr. 1: 71–79.

Julin, E. 1949: De svenska daggmaskarterna. — Ark. Zool. 42(A): 1–58.

Karaman, S. 1972: Beitrag zur Kenntnis der Oligochaetenfauna Jugoslawiens. — Biol. Vestn. 20: 95–105.

Kurceva, G. F. 1972: Die wirbellose Tiere in dem Waldböden der Transkarfaten. — Pedobiologia 12: 381–400. (In Russian with German summary.)

Kvavadze, E. Sh. 1985: The earthworms (Lumbricidae) of the Caucasus. — Metsniereba, Tbilisi. 238 pp. (In Russian with English summary.)

Kvavadze, E. Sh. 1991: Structure of the genital setae, a clue for the taxonomy of the genus Eisenia (Oligochaeta, Lumbricidae). — Naucno-izdatel'skij Sovet an Gruzii, Institut Zoologii, Tbilisi, Preprint. 12 pp. (In Russian with English summary.)

Kvavadze, E. Sh. 1993: A new genus of earthworms Omodeoia gen. nov. (Oligochaeta: Lumbricidae). — Bull. Acad. Sci. Georgia 148: 129–134.

Kvavadze, E. Sh. & Miloikova, G. 1993: New species of earthworms (Oligochaeta, Lumbricidae) from Bulgaria. — Bull. Acad. Sci. Georgia 148: 125–128.

Martinucci, G. B., Crespi, P., Omodeo, P., Osella, G. & Traldi, G. 1983: Earthworms and TCDD (2,3,7,8-tetrachlorodibenzo-p-dioxin) in Seveso. — In: Satchell, J. E. (ed.), Earthworm ecology: 275–283. Chapman & Hall, London.

Michaelsen, W. 1890: Die Lumbriciden Norddeutschlands. — Jb. hamb. wiss. Anst. 7: 1–19.

Michaelsen, W. 1902: Neue Oligochäten und neue Fundorte altbekannter. — Mitt. Naturhist. Mus. Hamburg 19: 1–54.

Michaelsen, W. 1903: Die geographische Verbreitung der Oligochaeten. — Berlin. 186 pp.

Michaelsen, W. 1910: Zur Kenntnis der Lumbriciden und ihrer Verbreitung. — Ann. Mus. Zool. Acad. Sci. St. Pétersbourg 15: 1–74.

Mrsic, N. 1988: Description of five new species of earthworms of the genus Dendrobaena Eisen 1874 (Lumbricidae). — Biol. Vestn. 36: 13–24.

Mrsic, N. 1991: Monograph on earthworms (Lumbricidae) of the Balkans. — Academia scientiarum et artium Slovenica, Cl. IV: Historia naturalis, Opera 31, Ljubljana. 757 pp.

Omodeo, P. 1952a: Oligocheti della Turchia. — Ann. Ist. Mus. Zool. Univ. Napoli 4: 1–20.

Omodeo, P. 1952b: Particolarità della zoogeografia dei lombrichi. — Boll. Zool. 19: 349–369.

Omodeo, P. & Rota, E. 1989: Earthworms of Turkey. — Boll. Zool. 56: 167–199.

Omodeo, P. & Rota, E. 1991: Earthworms of Turkey. II. — Boll. Zool. 58: 171–181.

Perel, T. S. 1976: A critical analysis of the Lumbricidae genera system (with key to the USSR fauna genera). — Rev. Écol. Biol. Sol 13: 635–643.

Perel, T. S. 1979: Range and regularities in the distribution of earthworms of the USSR fauna (with keys to Lumbricidae and other Megadrili). — Nauka, Moskva. 272 pp. (In Russian with English summary.)

Pizl, V. 1986: Zízaly (Oligochaeta, Lumbricidae) rezervace Ruzák na Decínsku [Regenwürmer (Oligochaeta, Lumbricidae) des Naturschutzgebietes Ruzák in Nordböhmen]. — Sborn. Severoces. Muz. (Prír. Vedy) 15: 69–76.

Plisko, J. D. 1963: Materialien zur Kenntnis der Regenwürmer (Oligochaeta, Lumbricidae) Bulgariens. — Fragm. Faun. Pol. Akad. Nauk 10: 425–440.

Pop, V. 1938: Neue Lumbriciden aus Rumänien. — Bull. Soc. Sti. Cluj 9: 134–152.

Pop, V. 1947: Die Lumbriciden der Ostalpen. — An. Acad. Rom. Mem. Sect. Sti., Ser. III, 22: 1–49.

Rosa, D. 1884: I Lumbricidi del Piemonte. — Torino. 54 pp.

Rosa, D. 1886: Note sui lombrici del Veneto. — Boll. Mus. Zool. Anat. comp. R. Univ. Torino 1: 1.

Rosa, D. 1893: Viaggio del Dr. E. Festa in Palestina, nel Libano e regioni vicine. II. Lumbricidae. — Boll. Mus. Zool. Anat. comp. R. Univ. Torino 8: 1–14.

Rota, E. 1994: Contribution to the taxonomy of the Hormogastridae (Annelida: Oligochaeta) with description of two new species from southern France. — J. nat. Hist.

28: 27–36.

Sapkarev, J. A. 1972: Lumbricidna fauna na Makedonija. 3. Dozdovni glisti (Oligochaeta: Lumbricidae) od Pelagoniskata kotlina. — Fragm. balc. 9: 125–135.

Savigny, J. C. 1826: La multiplicité des espèces de ver de terre. — Mem. Acad. Sci. Inst. Fr. (Phys.) 5: 176–184.

Sims, R. W. & Gerard, B. M. 1985: Earthworms. — Synopses of the British Fauna (New Series) No. 31, The Linnean Society of London & The Estuarine and Brackish-Water Sciences Association, Brill/Backhuys, London. 171 pp.

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

Terhivuo, J. 1988b: The Finnish Lumbricidae (Oligochaeta) fauna and its formation. — Ann. Zool. Fennici 25: 229–247.

Vedovini, A. 1970: Lombricides nouveaux de la région provençale. — Bull. Soc. Zool. France 96: 45–48.

Zicsi, A. 1965a: Beiträge zur Kenntnis der Lumbricidenfauna Österreichs. — Opusc. Zool. Budapest 5: 247–265.

Zicsi, A. 1965b: Die Lumbriciden Oberösterreichs und Österreichs unter Zugrundlegung der Sammlung Karl Wesselys mit besonderer Berücksichtigung des Linzer Raumes. — Naturkdl. Jahrb. Stadt Linz 11: 125–201.

Zicsi, A. 1974: Eine neue Dendrobaena-Art (Oligochaeta: Lumbricidae) aus Griechenland. — Acta Zool. Acad. Sci. Hungar. 20: 449–451.

Zicsi, A. 1981: Weitere Angaben zur Lumbricidenfauna Italiens (Oligochaeta: Lumbricidae). — Opusc. Zool. Budapest 16–17: 157–180.

Zicsi, A. 1985: Regenwürmer (Oligochaeta: Lumbricidae) aus Israel und den benachbarten Ländern. — Revue suisse Zool. 92: 323–331.

Zicsi, A. 1994: Die Regenwürmer Österreichs (Oligochaeta: Lumbricidae) mit Bestimmungstabellen der Arten. — Verh. Zool.-Bot. Ges. Österr. 131: 37–74.

Zicsi, A. & Csuzdi, Cs. 1986: Regenwürmer aus Bulgarien (Oligochaeta: Lumbricidae). — Opusc. Zool. Budapest 22: 113–121.

Zicsi, A. & Michalis, K. 1981: Übersicht der Regenwurm-Fauna Griechenlands (Oligochaeta: Lumbricidae). — Acta Zool. Acad. Sci. Hungar. 27: 239–264.

Zicsi, A. & Michalis, K. 1993: Zwei neue Dendrobaena-Arten aus Griechenland (Oligochaeta, Lumbricidae). — Acta Zool. Hungar. 39: 301–310.