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CONTRIBUTIONS TO A REVISION OF THE LUMBRICIDAE. III. EISENIA HORTENSIS (MICHAELSEN) (1890).'

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ABSTRACT. The classical system of the Oligochaeta (Michaelsen, 1900-Stephenson, 1930) and proposed neoclassical revisions, did not permit definitive conclusions as to disposition of a taxon variously known as var. or *f. hortensis* which has been in each of five lumbricid genera. Characters less liable to rapid evolutionary modification than those of the genitalia, on which previous systematics primarily had been based, allow inclusion of the taxon, as a distinct species, in a genus recently redefined in terms of formerly neglected somatic anatomy. Parthenogenesis may be facultative in some lines. Evolutionary developments now under way in *hortensis* parallel some of the degradations in genital anatomy associated, in *D. rubida*, with parthenogenesis and male sterility. Characteristics of an undegraded amphimictic morph are predicted. Abnormalities are characterized. To the distribution, as previously known, are added Ireland and Greece.

Disagreements as to systematic status and generic affiliations of various species (one example provided by the synonymy below) indicate a need for revision of lumbricid classification. Even widely spread anthropochores, that usually, though mistakenly, are believed to be adequately characterized systematically, need a searching reinvestigation.

A single Irish specimen that arrived on St. Patrick's day provided a clue to a possible solution of some of the problems hitherto associated with "dendroidea."

LUMBRICIDAE EISENIA Malm, 1877 EISENIA HORTENSIS (Michaelsen, 1890)

Allolobophora subrubicunda f. hortensis Michaelsen, 1890, Jahrb. Hamburgischen Wiss. Anst., 7: 15. (Type locality, Hamburg. Types, originally in the Hamburg Museum.)

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- Dendrobaena veneta var. hibernica f. dendroidea + D. v. var. hortensis Gerard, 1964, Linnean Soc. London, Synopses of the British Fauna, No. 6 (2d ed.): 39.
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SPECIMENS EXAMINED

- Oregon. Yamhill County. McMinnville, kitchen drain, August 11, 1944, 0-0-6. Backyard, March 12, 1945, 0-1-1. Backyard, brought out by wash water, October 31, 1945, 0-0-1. Chicken yard, under cow manure, November 14, 1945, 0-1-0, November 23, 1945, 0-4-10. Under wet paper carton on back porch, January 10, 1946, several specimens. Backyard, December 1, 1947, 0-1-7. D. McKey-Fender.
- California. San Francisco County. Arboretum of Golden Gate Park, March 28, 1951, 0-0-2. H. B. Leech per D. McKey-Fender.
- Ohio. Trumbull County. Masury, greenhouse, 0-0-2. W. R. Murchie.
- Virginia. Giles County. Goldbond, sawdust, August 21, 1955, a number of specimens. W. A. Harman.
- Italy. Naples, November 23, 1925, 0-0-2. Posillipo, October 7, 1925, 0-0-7. G. E. Hutchinson per G. E. Pickford.
- India. Darjiling, Northpoint, at ca. 6250 feet, June 1945 0-1-38.

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EISENIA HORTENSIS MICHAELSEN

INTERCEPTIONS BY U.S. BUREAU OF PLANT QUARANTINE.

- Ireland. From 25 pounds of wood duff with seeds of Crataegus oxycanthus in mail arriving at Hoboken, November 1, 1963, (?)-1-0.
- Greece. From soil with 25 unidentified herbs in baggage on plane arriving at Boston, August 28, 1962, 6-0-0.

DESCRIPTION

External characteristics. Size, 26 by 11/2 mm (Ireland), 26-32 by $2-2\frac{1}{2}$ mm (Maine, New York), to 22 by $2\frac{1}{2}$ mm (Greece), to 37 by 2+ mm (Ohio), 42-54 by $2\frac{1}{2}-3$ mm (Naples), width measured in the clitellar region not always at maximal tumescence, thickness of adults near hind end 11/2 mm. The body is dorsoventrally compressed behind the clitellum and almost oblong in transverse section, ventral and lateral sides flat, the dorsum slightly convex. The b and d setae are at the four corners of the body. Segments, 42, 50, 55, 56, 60 (2), 64 (2), 69 (2), 70 (2), 74, 76, 77, 81, 82, 83, 84 (2), 85, 86 (2), 88, 90 (3), 92 (3), 94 (3), 95 (7), 96 (4), 97 (5), 98 (4), 99 (2), 100 (3), 101 (2), 102 (3), 103 (4), 104 (2), 105, 108, 115 (2), 124, 126, 130. The mean number of segments for 69 of the specimens is 90.7536, with a standard deviation of 17.4266 and a standard deviation of the mean of 2.0979. A large majority of unamputated worms have segments in a range of 90-105 which may be more useful systematically than the computerized figures. Worms with 115-130 segments were from Maine greenhouses in which they might almost be said to have been force-fed. Color, unrecognizable after alcohol preservation, otherwise light to bright red, reddish, restricted to dorsum and lacking below C except in front of xv and near the hind end where the ventrum may also be colored. In some Greek worms, color is in discontinuous unpatterned areas. Prostomium, epilobous, tongue open (all).

Setae, present from ii where none usually are lacking though sometimes hard to recognize, not closely paired, width of AB and CD somewhat variable but CD slightly < or > AB < BC < or >AA < DD which is of course $< \frac{1}{2}C$, the c setae often seeming to be about at mL. In some worms, AB is ca. $= \frac{1}{2}AA$ and slightly < BC. Nephropores, inconspicuous, in xv-xvi at or just above B (39 specimens), one pore of xv at D (1), one pore of xvi at D (1), both pores of xiv at D (4), at B (10), one of xiv at B the other at D (22), usually unrecognizable in iii-vi or vii. Nephropores, at B on left sides of 17th, 19th, 21st, 24th, 26th, 29th, 30th, 33d, 34th, and on the right sides of the 17th, 23d, 25th, 27th-29th, 31st-33d

segments (No. 1), on left sides of 14th-20th, right sides of 15th-17th, 19th, 20th segments (No. 2). On the left side of No. 3 the following locations were noted, at B, 35th-40th, 52d, 57th, 60th, 61st, 64th, 65th, at D in the 34th, 42d-51st, 53d-56th, 58th-59th, 62d-63d. Pores on the opposite sides of those same segments more often than not were in the alternate location. Both pores of vi were in CD, one Italian worm on which the right pores of 7th, 8th, and 11th segments were near B, of 12th at D, but those of 13th-17th in BC. Nephropores, just above B, on left sides of 7th, 8th, 11th, 14th-16th, 18th-22nd, 24th-32d, on the right side of 8th, 9th, 12th-15th, 17th-34th (Naples, No. 4), on the left of 7th-10th, 12th, 13th, 15th-22d, 24th, 27th, right sides of 7th-8th, 10th-12th, 15th-19th, 22d, 24th, 26th (Naples, No. 5). At present, about the only seemingly feasible characterization is: pores usually alternate irregularly and with asymmetry between two major locations along most of the anteroposterior axis. First dorsal pore, at 5/6 (22 specimens), at 7/8 (2).

Spermathecal pores, minute, superficial, at 9/10-10/11, close to mD in an area where color often is faint or quite unrecognizable. Female pores, minute, superficial, equatorial in xiv and just lateral to *B*. Male pores, minute, not superficial, within a cleft laterally and seemingly about at *mBC*. Male tumescences, almost confined to median half of *BC* but obliterating 14/15-15/16 and reaching well into xv and xvi.

Clitellum, saddle-shaped, at maximal tumescence reaching to or nearly to B, dorsal pores occluded, intersegmental furrows obliterated, setae unrecognizable, xxvii-xxxii (15 specimens), xxviixxxii (14), eq/xxvii-xxxiii/eq (2), eq/xxvii-xxxiii (2), xxviiixxxii (29), xxviii-xxxiii (3), eq/xxviii-xxxiv/eq (9). Tubercula pubertatis, usually longitudinal bands of greyish translucence just lateral to B, with straight median margins but with lateral margins slightly convex, in xxx-xxxi but occasionally extending slightly into xxxii, rarely reaching eq/xxxii. A deep groove occasionally demarcates a tuberculum laterally. Even when a red coloration (post-preservation artifact) of the clitellum is best developed, none is recognizable in the tubercula.

Genital tumescences, often rather indistinct and especially so in relaxed material, include setal couples as follows: a, b of xi (1 specimen), xii (4), xvi (2), xxii (1), xxiii (7), xxiv (7), xxv (1), xxvi (1), xxix (26), xxx (35), xxxi (35), xxxii (9), c,d of x (1), xi (22). Condition obviated recording locations on a number of worms but dissections indicate that ventral setae of xxx and xxxi always were associated with tumescences. Follicles opening

through tumescences are thickened and have slightly enlarged apertures. The b,c and d follicles project conspicuously into the coelomic cavities but a follicles obviously are shorter and protrude only slightly above the parietes.

Internal anatomy. Septa, 13/14-14/15 often thickest and quite muscular, 10/11 near the gut separated into two lamellae the anterior of which passes straight to the gut, the other inserted on it more posteriorly so as to leave a space filled by a watery fluid without corpuscles or other solid matter. This curious situation presumably arises as a result of an ontogenetically late elongation of a small section of the esophagus. The anterior lamella seems to be at the front end of the calciferous gland. Setal gaps in longitudinal musculature, obviously eight. Special longitudinal muscle band at mD, present from 5/6. Pigment, red, in circular muscle layer, lacking immediately under intersegmental furrows. Pigment also is visible on or in the coelomic face of the parietes, dorsally throughout but also ventrally in front of xv, in flecks, or spots or rarely even in larger patches. Location of the brain is variable, a section exactly along 3/4 sometimes left the brain anteriorly in iii, sometimes anteriorly in iv. Pharyngeal glands, through iv-v to 5/6.

Esophagus of x has the shape of a truncate cone, narrower anteriorly. The wall is dark (gorged with blood?) and unthickened (no sacs or lamellae). The calciferous gland, insofar as could be learned from dissection, is between 10/11 and 12/13, sometimes not reaching the latter, usually not constricted at 11/12 but of the same thickness through both segments. Rarely the portion in xi is moniliform. Intestinal origin, in xv (62). Gizzard, superficially appearing to extend through xvii-xix. Actually, the muscular layer becomes much thinner just behind apparent level of insertion on gut of 17/18. Gut often valvular in region of insertion of 19/20. Typhlosole, beginning rather abruptly in region of xxi-xxv, thickly lamelliform, height variable, when gut is empty sometimes reaching or nearly touching intestinal floor, ending abruptly, as shown in Table 1.

The typhlosole does not end abruptly in specimens 1-5, 8-9, and 33 (cf. Table 1) but becomes much lower or even vestigial in the indicated regions, i.e., in 1xi-1xv of No. 9. Posterior amputation had been involved in each of those cases. The typhlosole, in a very large majority of the unamputated individuals, ended in a region comprising lxxiv-xcv. The typhlosole of the abovementioned specimens, on the contrary, ends in a region comprising xxxix-xlv, leaving 1-10 intestinal segments atyphlosolate. Very

probably, the typhlosole had completely disappeared in some segments of each of those worms. In unamputated worms with abrupt typhlosolar termination, 10-15 segments were atyphlosolate, 10 (3), 11 (5), 12 (7), 13 (13), 14 (6), 15 (2). If, as some have thought, the atyphlosolate portion of the gut is of proctodeal origin, then that part of the gut extends through more segments than the embryologists indicated.

Extra-esophageal trunk, passing up to dorsal vessel in xii, but often unrecognizable (because empty) behind 10/11. In xii (one specimen) the trunk bifurcated, the larger branch joining the dorsal vessel, the other branch passing ventrally and shortly disappearing. A branch from the trunk occasionally passes up to the dorsal trunk in x. When that connective is distended with blood and the posterior portion of the trunk is empty the extra-esophageal could be thought to end in x. The ventral trunk is complete, bifurcating over the subpharyngeal ganglion. The dorsal trunk is also complete, having been traced forward to the brain when blood is present. The subneural trunk probably always is complete but usually is not traceable throughout because of lack of blood. Hearts, present only in vii-xi (62 specimens).

Nephridia, present from iii (presence or absence in ii not determined), vesiculate. Bladders, sausage-shaped (ellipsoidal), transversely placed, reaching to or nearly to C or even beyond C, joined laterally by the tubular portion of the nephridium, passing into parietes at or near B.

Testes, fan-shaped. Male funnels, plicate, size normal with reference to that of the body. Sperm ducts, without epididymis. Seminal vesicles, in ix, xi and xii. Atrial glands, large, deeply cleft at eq/xv, extending through xiv as well as xvi.

TP and atrial glands, acinous, supraparietal. GS glands, acinous, each lobe narrowing to a slender thread-like duct that passes straight down in the parietes, associated only with the a,b follicles of xii (once), the b follicles of xxx and xxi but usually lacking even in those two segments.

Spermathecae, not sessile, ducts slender, coelomic portions shorter than, to longer than, the ampullae. Spermathecae, in ix, x (56 specimens) but the following divergences were recorded; all in x (twice), one of the anterior pair in x (once), one of the posterior pair in xi (twice), in x-xi (once).

Ovaries, in xiii, each with one egg string which may contain 1-6 ova. Oviducts, passing into parietes lateral to *B*. Ovisacs, small, lobed, always present.

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The peritoneum frequently is blistered away from the musculature. Intervening spaces are occupied by a flocculent white material. The blistering seems not to be so rigidly localized as anteriorly in *D. octaedra*. Areas recorded (perhaps not the only ones) from median margin of TP glands to just median to *A* in xxxi-xxxii or xxxiii, the surface more or less deeply cross-hatched, in poor preservation not easily distinguishable from the TP glands. Blistering, continuous through AA from one side to the other (once, Italy), between *A* and *B* of each side through xxvi-xxxii (Naples), in *DD* through a region containing the spermathecal pores.

Reproduction. Iridescence on male funnels and in spermathecae, of some worms, was so brilliant as to suggest profuse maturation as well as massive copulatory transfer. Spermatophores, some of which contained sperm, also were noted, in AB/xxviii. As a result, until nearly at the end of the present study, laboratory records contained the following comment, "Reproduction presumably is biparental." Although copulation usually had taken place in worms of appropriate age and stage, there does now seem to be some reason for suspecting facultative parthenogenesis.

Number of choromosomes in *hortensis* is 36 (2n) according to Muldal (1952:59) as well as Omodeo (1952:188). The latter says spermatogenesis is normal. Neither author mentioned any evidence indicative of parthenogenesis. Nor was polyploidy detected.

Breeding, in favorable conditions, may be year round.

Biology. Feeding appears to be selective, as guts contained only humus. Shaking ingesta in water produced no turbidity.

Male tumescences and tubercula pubertatis are obvious before other epidermal modifications are recognizable in the clitellar region.

Many of the worms were posterior amputees. Tail regenerates of the usual epimorphic sort never were seen. Regeneration caudally appears to be restricted (at least usually) to reorganizing posterior segments so that external evidence of the amputation no longer is recognizable. In such cases, if lysis has not yet proceeded too far, the typhlosole sometimes can provide proof of the amputation.

Brown bodies, in No. 36, were present in segments xc-xciii, one to three on each side of each segment. Coelomic cavities of xcxcviii in No. 39 were also filled with similar structures, but in this worm there was only one brown body on each side in a segment, though the coelomic cavities were thereby almost completely filled.

Similar brown matter was not found in coelomic cavities anteriorly. The bodies may then have been formed *in situ*.

Distribution. E. hortensis had not been recorded previously from Ireland and Greece.

The single record for Ohio is of a specimen found in a toilet bowl of a city building.

Commenting on the Nearctic distribution of E. hortensis, Mrs. D. McKey-Fender wrote (*in litt.*) "the paucity of North American records of this species may be due to the filthy places it inhabits. It takes some fortitude to collect it. The Oregon specimens are from friable black soil saturated with septic tank effluvium. They seem to be between the wettest zone, where E. foetida is even more numerous, and the wet, relatively uncontaminated soil where E. rosea, A. chlorotica and the caliginosa complex predominate."

Abnormality. Metameric abnormality, just behind clitellum (once), further posteriorly (two specimens); other instances seen during counting of segments not recorded.

- No. 1. Right ovary, rudimentary (clitellate adult).
- No. 2. Left anterior spermatheca, bifid entally. One ampulla is in ix and the other is in x (Naples).
- No. 3. Left female pore, anterior to eq/xiv but not quite half way toward 13/14. Extra pair of male clefts, associated with small male tumescences, in xvi. No pores were found in the posterior clefts and no sperm ducts were found in their vicinity. Atrial glands of xvi, large, each with a deep equatorial cleft.
- No. 4. (Ireland). Tubercula pubertatis, markedly protuberant, subcircular, two pairs, those of a side completely separated from each other by an uninterrupted intersegmental furrow, 30/31. Testes, one pair, in vertical testis sacs that reach up to level of dorsal face of gut in xi. Seminal vesicles, one pair, medium-sized, not filling coelomic cavity of xii. Spermathecae, lacking. Iridescence on male funnels, none. The worm obviously is male sterile.

Abnormalities in metamerism are common and their frequency indicates the ease with which development of normal segmentation can be influenced, in a single small region, in a much larger axial portion, in several more or less widely separated areas, or, occasionally, even throughout nearly all of the axis. Divergences from normal of specimens 1-3 appear to have resulted from a rarer sort of interference with development. So rare, in fact, that exact repetition is unknown. The male sterility of No. 4, being known at the moment only from a single specimen of *hortensis*, can also be of fortuitous origin. However, the aberrations of that worm exactly parallel conditions characterizing some male sterile morphs of various other megadrile species. In such taxa, where reproduction necessarily is parthenogenetic, the associated anatomy is exactly repeated again and again, always without spermatogenesis or receipt from another individual of copulatory sperm. The male sterility is inherited. Knowledge of the evolutionary changes associated with male

Knowledge of the evolutionary changes associated with male sterility and parthenogenesis in other megadriles enables characterization not only of a probably amphimictic norm for *E. hortensis* but also of current evolutionary trends therein.

Polymorphism. The amphimictic norm now postulated for E. hortensis is as follows. Male tumescences, large, obliterating 14/15-15/16 and extending through xiv-xvi. Male cleft deep but confined to parietes. Seminal vesicles, three pairs, in ix, xi, xii, all functional. Atrial, TP and GS glands, large, supraparietal, acinous. The atrial glands reach 13/14 as well as 16/17 and are deeply cleft at eq/xv

The more common evolutionary trends now recognizable in sperm-maturing and sperm-exchanging individuals are as follows. Reduction in size of male tumescences, confinement to xv with furrows 14/15-15/16 no longer obliterated though one or the other or both may be slightly displaced, restriction to slight swellings of immediate margins of male pore clefts. Finally, there will be no tumescence at all and clefts will have disappeared leaving the male pores superficial as in certain species of *Lumbricus*. Correlated with that trend is decrease in size of the associated atrial glands, limitation to xv, representation only by a few filaments slightly protuberant into the coelom from gaps between bands of longitudinal musculature. Slight protuberances of body wall, without interruptions of the muscular layer, over sites of male pores, may indicate presence of last rudiments of the atrial glands. Similar trends involve the TP and GS glands, one or the other or both of which have disappeared in certain lines.

Seminal vesicles of ix and xi, but never of xii, seem to be disappearing, more especially in ix. There the vesicles no longer become as large as in xi, and may retain a juvenile texture through maturity or may even be unrecognizable on one side or the other.

Inclusion of testes in paired, vertical testis sacs is known today, in the Lumbricidae, only in association with male sterility. The metandric reduction (deletion of tests and gonoducts of x), on the contrary, has been acquired in various families by amphimictic

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taxa as well as by male sterile morphs. Associated therewith is loss of all vesicles in ix and xi. Many male sterile morphs, in various families, are athecal but spermathecae have been lost by individuals that still produce mature sperm.

Evolutionary trends in *hortensis* may parallel, in part, those of *D. rubida*. That species has male fertile morphs (usually called subspecies, variety or f. *subrubicunda*) as well as male sterile morphs with obligatory parthenogenesis. Degradation of genital structure may have progressed further in *hortensis* than in *rubida*. Even more drastically modified morphs than now known are anticipated for *hortensis*, especially if its parthenogenesis was acquired earlier.

Disappearance of atrial and TP glands results in a state that parallels conditions characterizing the genus *Lumbricus*.

Remarks. Relaxed material furnished by Mrs. McKey-Fender provided beautiful demonstrations of nephropore locations and of uncollapsed nephridial bladders. Such information often is unprocurable from contracted specimens. Nevertheless, on her worms, genital tumescences were unrecognizable and clitellar boundaries probably could have been determined accurately, if at all, only from microtome sections.

Generic relationships. The following characters were found to be invariant in all samples examined. Calciferous gland, without sacs, opening directly into esophageal lumen behind insertion of 10/11 through a circumferential circle of small pores. Intestinal origin, in xv. Gizzard, mostly in xvii. Hearts, in vii-xi. Excretory organs, holoic. Nephridial bladders, sausage-shaped (ellipsoidal), transversely placed. Nephropores, inconspicuous, alternating irregularly and with asymmetry between a level just above B and another above D. Setae, paired. Longitudinal musculature, pinnate (as seen in transverse section). Pigment, red. Ovaries, in xiii, each terminating distally in a single egg string. Ovisacs, present in xiv. Some of these characters are now expected to be definitive at the family level. Others require inclusion of Michaelsen's hortensis in the genus Eisenia (cf. Gates, in press).

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TABLE 1

Typhlosole termination and segment number in Eisenia hortensis

Serial Number	Typhlosole ends in Segments	Atyphlosol- ate Segments	Segment Numbers	Comments
1.	36-39	3	42	24 95 13
2.	46-47	3	50	
3.	47-48	7	55	
4.	52-54	10	64	
5.	57-59	1	60	
6.	58	6	64	
7.	59	10	69	
8.	61-62	8	70	
9.	61-65	9	74	
10.	62	7	69	
11.	64	13	77	Greece, juvenile
12.	65	5	60	Posterior amputee
13.	68	8	76	Greece, juvenile
14.	71	10	81	Posterior amputee? Greece, juvenile
15.	72	11	83	
16.	74	8	82	
17.	76	9	85	Posterior amputee
18.	77	11	86	And the second states in the Constant of the
19.	78	6	84	
20.	78	10	88	
21-22.	78	12	90	Ohio (1)
23.	80	14	94	
24.	80	15	95	
25.	81	13	94	Greece, juvenile
26.	82	14	96	
27.	83	12	95	
28.	83	13	96	
29.	83	14	97	

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12			No. 300		
30-31.	84	11	95	San Francisco (1)	
32.	84	12	96	Ohio	
33.	80-84	8	92		
34-35.	85	13	98		
36.	86	8	94		
37-38.	86	12	98	Ohio (1)	
39.40	86	13	99	Maine, Italy	
41.	87	12	99		
42.	88	13	101	Great Britain	
43.	88	14	102		
44.	89	11	100		
45.	89	13	102		
46-47.	89	14	103		
48.	89	15	104		
49-50.	90	13	103	Ohio (1)	
51.	91	13	104		
52.	92	10	102	Posterior amputee?	
53.	92	13	105		
54.	95	13	108	Naples	



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