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On a Hologynous Species of the Earthworm Genus *Diplocardia*, with Comments on Oligochaete Hologyny and "Consecutive Hermaphroditism"

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INTRODUCTION

A Texas species of *Diplocardia* has been known hitherto only from a specimen with ovaries in xii-xiii (hologyny), a condition that might have been expected to be an individual aberration. Topotypical material recently collected enables a more adequate characterization of the taxon and recognition of the hologyny as specific rather than sporadic.

To Mr. Ottys Sanders thanks are due for securing and preserving all the material that has been available for study. The Rockefeller Foundation is paying for the research from which the present contribution eventuated.

Diplocardia sandersi Gates

Diplocardia sandersi GATES, 1955, Bull. Mus. Comp. Zoöl. Harvard College, vol. 113, p. 247. Type locality, Dallas, Texas.

SPECIMENS EXAMINED: From laboratory grounds, Southwestern Biological Supply House, Dallas, Texas, March 11, 1957, 2-5-10 (relaxed, alcoholic preservation). April 1, 1957, 0-0-0-2 (contracted, formalin preservation). Ottys Sanders. (A.M.N.H. No. 3557).

EXTERNAL CHARACTERISTICS: Length, 142-150 (juveniles), 120-154 (contracted, formalin preservation), 140-263 mm. (relaxed, alcoholic

preservation). Diameter, in gizzard region, 3 mm. (relaxed juveniles), in clitellar region, 5–6 mm. (relaxed specimens), 6–7 mm. (contracted specimens). Segments, 139, 145 (posterior amputees), 133 (posterior amputee?), 148, 154, 155, 157, 162, 163, 164, 166, 167, 169, 172, 173, 174 (juvenile), 179 (juvenile), 188, 191. Body, in cross section, shortly and transversely elliptical to almost circular. Pigmentation brown, in part leached (?) or indistinguishable because of alcoholic browning but in formalin specimens dense in front of clitellum, circumferential in i–ii, lacking near mV in iii and thence posteriorly in areas of increasing width, present only in *DD* of xi–xii, from xx sparse and in discrete specks, increasingly restricted to region near mD. Prostomium epilobous, tongue closed (all). The peristomium around all its circumference is crossed by irregular longitudinal grooves which are continued on some specimens into ii, occasionally nearly to 2/3. One such groove near mD on each side sometimes is so nearly in line with that bounding side of prostomial tongue as to produce a resemblance to tanyloby. Secondary annulation; a deep furrow in the postequatorial portion of each of iv or v–xii, a similar furrow in the pre-equatorial portion of each of vi or vii–xii, two secondary furrows in formalin material (contracted) recognizable on each of the postclitellar segments until close to the hind end. Setae small, retracted, often (like follicle apertures) unrecognizable, just behind xx (formalin material),

$$AB < CD, AA < BC, DD \text{ ca. } = \frac{1}{2} C.$$

Nephropores, occasionally recognizable in some relaxed specimens, at or well above *D* on ii, posteriorly and whenever recognizable at *D*. Pigment is dense, in the last few segments, in a narrowly crescentic band just behind each nephropore. First dorsal pore at 10/11 (one specimen), 11/12 (six specimens), 12/13 (11 specimens).

Spermathecal pores minute, superficial, close to *A*, three pairs anteriorly on vii–ix. Although pores are close to the intersegmental furrows, a narrow strip of unmodified epidermis is visible between each furrow and the slightly tumescent margin of the pore.

Female pores, two pairs (19 specimens), on xiii–xiv, anteromedian to *a*, slightly closer to the setae than to each other or slightly nearer each other. Both pores of a segment sometimes are within a transversely spindle-shaped to elliptical area of epidermal thickening (in *BB*) that does not quite reach the anterior intersegmental furrow and that just includes the ventral setae posteriorly.

Seminal grooves between equators of xviii and xx (17 specimens), near *B* or in *AB*, deep, wide. Prostatic pores minute transverse slits, in

AB, at equators of xviii and xx, at ends of seminal grooves. Male pores have not been recognized on any of the specimens.

Clitellum annular, but thinner in *BB* (one specimen) or apparently saddle-shaped, epidermal tumescence possibly not maximal in any of the specimens, in xiii–xviii (all) but apparently reaching sometimes into xix or even (one specimen) to 19/20. Segments xiii–xviii of postsexual (April) specimens are yellow down to *A*.

Genital markings, apparently always present in adults, sometimes appear to be only areas of slight epidermal tumescence. Each marking, in best preservation, has a slightly depressed, circular, gray-translucent center and a wide, opaque margin where the epidermis is thicker. Paired markings are in, or with centers in, *AB* and are postsetal on xvii (16 specimens) and xx (16 specimens), in some of the specimens apparently dislocating but in others apparently crossing the posterior intersegmental furrows. Unpaired markings are in *AA*, on 10/11 (two specimens), 13/14 (one specimen), 14/15 (one specimen), 15/16 (one specimen), 16/17 (one specimen).

INTERNAL ANATOMY: Septum 5/6 membranous, 6/7–10/11 thickly muscular, 11/12–13/14 muscular. Pigment is lacking in the peritoneum, the longitudinal musculature, even at mD, and also in such portion of the circular muscle layer as can be peeled away from the epidermis after longitudinal musculature is stripped from the body wall. The pigment probably is in the epidermis or just beneath it.

Gizzards in v–vi (five specimens). Esophagus widened in x or xi–xv. Intestinal origin in xvii (six specimens). Typhlosole beginning in region of xxi–xxiii, ending in the sixty-ninth of 145 segments (posterior amputee) or of 172 segments, or in seventieth of 139 segments (posterior amputee). A rudimentary continuation is recognizable through several additional metameres or (145-segment amputee) even back to cix.

The dorsal blood vessel has been traced forward nearly to the brain and is single throughout (four specimens) or (one specimen) double in each of xiii–xiv, xvi, xviii. The trunk usually is completely covered, in the intestinal region, by thick chloragogue which must be scraped off for the simplex or duplex nature to be discovered. Chloragogue also is present in a thick layer on the long, looped, segmental connectives between dorsal and ventral trunks. The ventral trunk is continued anteriorly to the subpharyngeal ganglia where it bifurcates. A supraesophageal trunk is recognizable in two specimens in ix–xiv. Extraesophageal trunks are distended in three specimens, where they are looped in vi–ix but in other worms are indistinguishable. A subneural

trunk is unrecognizable throughout (five specimens) and presumably is lacking. Last hearts in xiii (six specimens). Hearts of x have been traced to the ventral trunk as also the slenderer lateral loops of ix-vi (but not of v).

Nephridia, not well preserved, appear to be avesculate, with long and slender ducts passing in clitellar segments (one specimen only) into parietes at *D*. Brain, circumpharyngeal connectives, and some portion of the subpharyngeal ganglia left by a transverse section exactly along $\frac{3}{4}$ in iii. The brain usually is slightly constricted in the median plane, but the shape varies considerably.

Holandric, testes fan-shaped. Male funnels plicate. Male gonoducts without looping, those of a side separate (one specimen) even as they pass into parietes in xix, apparently united (one juvenile). Prostatic ducts pass into parietes at *B* gaps. Penial and copulatory setae lacking (five specimens). Ovaries, each with several short egg strings, as well as oviducal funnels, are present in xii-xiii (six specimens). Ovisacs apparently are lacking (six specimens).

REPRODUCTION: The iridescence in each spermathecal diverticulum of clitellate specimens is brilliant. Iridescence on male funnels is less brilliant in clitellate and postsexual specimens. Sperm obviously had been matured and exchanged in copulation as in the holotype. Except for the hologyny, there would seem to be no reason for suspecting parthenogenesis. Reproduction is assumed to be sexual and biparental.

BREEDING SEASON: A short breeding season, in February-March, at Dallas is suggested by the available data.

LIFE-HISTORY STAGES: Sites of spermathecal, female, and prostatic pores are recognizable in the slender juveniles, but seminal grooves still are lacking. Ventral setae of xix still are present, but the *b* setae of xviii and xx are lacking. Reproductive organs are rudimentary, ental ends of spermathecae just protruding through the parietes, the prostates about 1 mm. long.

Iridescence still is recognizable in the coagulum within spermathecal seminal chambers of one postsexual worm. The chambers in the other postsexual individual are filled with a yellowish material, clumps of which are present in the ampullae. One clump of a similar aggregate is present in one of the seminal vesicles. Spermathecal ampullae of that worm probably are somewhat contracted, but other reproductive organs are of normal adult size.

INGESTA: Mainly plant material, in pieces up to 8 mm. long, but with some earth and fine sand.

REMARKS: The ratio *AA:BC* (intersetal intervals) varies considerably

from one region to another in a worm and in the same segment from one worm to another. Relaxation, contraction (local or general), or distention of gut (local) may be responsible for some of the differences.

The clitellar epidermis, probably at maximal tumescence, cracks under tension in one of the worms and comes away on slight pressure from the musculature. Pigment specks then appear to be on the circular muscle layer as well as on the inner face of the epidermis. Location of pigment, in the clitellar region at least, appears to be subepidermal. The information available as to the dorsal blood vessel (above and in Gates, 1955) in *Diplocardia*, though slight, is sufficient to show that the characters "single" and "double" do not always have the taxonomic value implied by previous use (cf. Gates, 1942, p. 92) in keys and in definitions. If the data now needed, for those and for other characters, are to be secured, long series of specimens that do not have to be retained in museum collections should be obtained.

The hologyny of *sandersi* now appears to be diagnostic.

PRECIS: Sexthecal, pores close to *A* and slightly behind intersegmental furrows on vii–ix. Prostatic pores on xviii and xx. Male pores on xix (?). Female pores, anteromedian to *a*, on xiii–xiv. Genital markings, paired and centered in *AB*, postsetal on xvii and xx (or crossing intersegmental furrows), occasionally unpaired and median on one or more of 10/11–16/17. Clitellum, annular (?), on xiii–xviii and part or all of xii and/or xix. First dorsal pore in region of 10/11–12/13. Nephropores, at or above *D* on ii, posteriorly at *D* (always?). Pigment brown. Segments, 148–191. 120–154 by 6–7 mm.

Gizzards in v–vi. Intestinal origin in xvii. Typhlosole, simply lamelliform, ending in region around sixty-ninth and seventieth segments. Dorsal blood vessel usually (?) single throughout. Hearts of x–xiii lateroesophageal. Holandric, seminal vesicles in ix and xii. Hologynous. Spermathecae medium-sized, each with several seminal chambers in a vertical, blade-like diverticulum opening into ental end of spermathecal duct. (GM glands, copulatory and penial setae lacking.)

DISTRIBUTION: Texas (Dallas).

DISCUSSION

Germinal tissues that had been diffuse in the polychaetes became localized, during evolution of the oligochaetes, in small ventral regions of the intersegmental septa near the nerve cord, one pair in each of several consecutive metameres. Four pairs of such gonads are required in the immediate ancestry of extant earthworms. The first two, in x–xi, were testes. The others, in xii–xiii, were ovaries.

Hologyny, as now known in earthworms, is of several sorts.

1. Transitory hologyny has been recorded for several lumbricid and megascolecid species (cf. Woodward, 1893; Beddard, 1892) in which the anterior ovaries are present in embryos but are lacking in later stages (adult metagyny). Abortion of an anterior pair of ovaries during development may well prove to be common; nothing is known about the embryology of most earthworms.

2. Sporadic adult hologyny has been found in several of the species in which it has been sought (cf. Woodward, 1892, 1893). It, too, may be much more common than the few published records indicate. Inhibition of embryonic abortion of the gonads in xii now can be anticipated with most assurance in strains in which reproduction is parthenogenetic. Unaborted ovaries in those strains produce mature and apparently normal ova. These gametes usually cannot be passed out of the body, as an anterior pair of oviducts is not developed. Functionally, then, because of morphological defects, the worms remain metagynous. Adult hologyny, to be "functional," requires oviducts that open into the coelomic cavities of segment xii. They have been found hitherto, in the megadrili (earthworms), only in a single species.

3. Functional hologyny, as in *Enantiodrillus borellii* Cognetti, 1902, always has been thought to be specific¹ rather than sporadic, and *Enantiodrillus* still is defined as hologynous, though the number of gonads in a second species² is unknown. Specific hologyny presumably can be either primitive or secondary. In the case of *borellii*, the first alternative was preferred by Michaelsen (1918) who placed *Enantiodrillus* along with other closely related glossoscolecid genera in a direct line of descent between a microdrile family³ and the less archaic glossoscolecid subfamilies.⁴ The hologyny of *Enantiodrillus* which had

¹ *Enantiodrillus borellii*, it must be noted, is known only from the original preserved material. Several specimens obviously were available, but the number was not stated.

² *Enantiodrillus cognettii* Michaelsen, 1933, is known only from the original description of juveniles in which reproductive organs were unrecognizable. The species is from Surinam and was referred to the same genus as the Argentine *borellii* because of similarity in the calciferous glands. The glands are also more or less like those of *Glossoscolex*.

³ The Haplotaxidae, the only other oligochaete family in which functional hologyny had been found. Here, too, the hologyny has been assumed to be specific rather than sporadic. Very little, however, is known about individual variation in any haplotaxid taxon.

⁴ The subfamilies Microchaetinae, Hormogastrinae, Criodrilineae, and Lumbricinae, each of which was subsequently raised by Michaelsen to family status.

seemed so important to Michaelsen was thought by Stephenson (1930) to be a "reversion." That requires inhibition of a long-established gonad abortion and, in the same segment, restoration of capacity to induce gonoducal development. One of those changes certainly has been made in parthenogenetic strains of at least three families. If the other reversionary change is possible, it is more likely to be found in parthenogenetic than in sexual populations, as the asexual method of reproduction permits more rapid accumulation of mutations. The macroscopic modifications of genital anatomy that result from such accumulations are now known sufficiently (cf. Gates, 1956) for reconsideration of the assumption that reproduction in *borellii* is sexual to be warranted.

The genital system in *borellii* diverges from the common hermaphroditic norm of sexual earthworms in several ways some of which are not mentioned above.

Absence of gonads in x Absence of testis sacs Absence of seminal vesicles Functional hologyny	Each of those characters has appeared in asexual strains after establishment of parthenogenesis. Pairs of those characters, and indeed the combination of all four, has been found in other asexual strains
Spermathecae, of mature individuals, provide no evidence of copulatory exchange of sperm	Spermathecae never have sperm in some parthenogenetic strains where male gametes still are matured
A few sperm, probably abnormal, are present in several small clusters within gonads of xi (no sperm in coelomic cavities)	Intragonadal maturation of sperm has been found in some parthenogenetic strains (sperm probably not released, in a functional state, from gonads)
The gonads of xi, which should be testes, contain ova	Any testis, or all of them, after establishment of parthenogenesis, may become hermaphroditic or even completely ovarian

Reproduction in *borellii* accordingly is more likely to be asexual than otherwise and, pending evidence to the contrary, is assumed to be parthenogenetic.¹ As that kind of reproduction permits reversionary morphological changes, there now seems to be little reason for attributing to the hologyny of *borellii* the antiquity that was involved in

¹ The taxon *borellii*, then, is not a species and the status of *Enantiodrilus*, known only from a few morphologically defective or juvenile individuals, is dubious.

Michaelsen's phylogeny. In *D. sandersi*, hologyny is associated with no anomalies of genital anatomy, and reproduction presumably is biparental. The *sandersi* hologyny may then prove to be older than that of *borellii*.

The "*ermafroditismo successivo*" of *Enantiodrillus borellii* (Cognetti, 1906) was thought to be second to that of another glossoscolecoid, *Pontoscolex corethrurus* (Müller, 1857). Gonads in that case (Beddard, 1889) were but two pairs,¹ all of which were supposed to be testes² in one specimen or, in two others, ovaries. Absence of testes and of seminal vesicles (also mentioned by Beddard and subsequently confirmed) now provides sufficient cause for suspecting parthenogenesis, and further justification was found in recently examined mature specimens in which spermathecae contained no sperm. If normal male gametes are not matured in *corethrurus* (which may be the case at least in certain lineages), there will be no consecutive hermaphroditism. If two sorts of gametes are matured consecutively in the anterior gonads of *borellii*, the sperm, even though normal, will have no function. Their presence seems to show that conversion of testes to ovaries is gradual rather than of the "all or none" sort.³

SUMMARY

The hologyny of *D. sandersi* is specific rather than sporadic, diagnostic in the genus, possibly unique among earthworms with biparental reproduction and older than in the parthenogenetic *Enantiodrillus borellii*. Postparthenogenetic evolutionary changes are responsible in *E. borellii* and *Pontoscolex corethrurus* for conditions previously regarded as evidence for consecutive hermaphroditism. Postparthenogenetic sterilization of male gonads and conversion of testes to ovaries probably is gradual.

¹ The gonads were said to be in segments xii-xiii. The last thickly muscular septum in *corethrurus* is attached to the body wall (as if inserted there; Gates, 1942, p. 93) one whole segment behind its real insertion, a modification that was for long unrecognized. Insertions of the very delicate septa of the gonad region likewise are aberrant. There also still is some doubt as to the number of segments in front of the gizzard metamere. Hence gonad locations recorded by Beddard probably are, at least in part, erroneous.

² Absence of ovaries, except when destroyed by parasites, now seems unlikely.

³ Postparthenogenetic sterilization of testes now appears also to be gradual.

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