

On the *sedgwicki* Complex of the Earthworm Genus *Pheretima* Kinberg, 1886¹

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A short series of earthworms secured by Dr. Y. Kondo enables correction of an important error in previous accounts of an unusual species, a better characterization of the taxon, as well as a preliminary contribution toward recognition of an unanticipated species group. The new data herein contained provide further proof of the etymological inappropriateness of certain terms long used by oligochaetologists. (Explanations of various terms and conventions may be found in Gates, 1956).

MEGASCOLECIDAE

PHERETIMA Kinberg, 1866

Pheretima sedgwicki (Benham, 1897)

Perichaeta Sedgwickii Benham, 1897, p. 201; Beddard, 1899, p. 183.

Amyntas Godefroyi Michaelsen, 1899, p. 17.

Pheretima sedgwicki Ude, 1905, p. 451, 455; Michaelsen, 1913, p. 265.

Pheretima (Metapheretima) sedgwicki Ude, 1932, p. 183, 184, 185.

SPECIMENS. Solomon Islands, Kiu, Malaita, middle south coast at ± 800 feet (± 244 m), in rotten log, April 20, 1966, 1-0-3. Y. Kondo.

EXTERNAL CHARACTERISTICS. Length, 87-90 mm. Diameter, 5-6 mm. Segments, 88 (juvenile, 52 by 3 mm), 90 (probably with a tail regenerate at 75/76), 99, 103. Color, in dorsum, reddish, lighter or seemingly lacking in slightly raised, equatorial ridges in postclitellar segments. Prostomium, epilobous, tongue open (4 specimens). Setae, circles seemingly not regularly interrupted ventrally or dorsally, so deeply retracted that tips often were not distinguishable. First dorsal pore, at 12/13 (4).

Clitellum, annular, extending from slightly behind 13/14 to slightly behind eq/xvi, dorsal pores occluded, intersegmental furrows obliterated, but setae present, at least ventrally in each segment. Spermathecal pores, small transverse slits, three pairs, about $\frac{1}{2}C$ or slightly more apart from each other ventrally, at 5/6-7/8. Distance between entrance of spermathecal ducts into body wall in each segment of a pinned-open specimen, about 5 mm. Female pores, rather closely paired (3), presetal, within an area lacking indications of double origin.

Male pores, superficial, small, transverse slits, seemingly of crescentic shape

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but probably because of presence of a tiny, nearly spheroidal, anterior protuberance from posterior lip, each at center of a transversely elliptical, glabrous, slightly protuberant area with a convex surface. Immediately anterior and posterior thereto in xviii, a transversely placed, crescentic marking probably only slightly depressed below general level but seemingly deeper because of protuberance of adjacent area bearing male porophore. Other genital markings, paired, subspheroidal to shortly and transversely elliptical, each with a circular central area of greyish translucence, and a peripherally indistinct band-like margin. Locations; presetal, near mV in xvii-xxi (3), postsetal, further laterally and about in line with the male porophores, in xiv-xvii (3), xix (1) xix-xx (1), xix-xxi (1).

INTERNAL ANATOMY. Septa, 8/9 complete but membranous (3, probably destroyed in pinning out the first dissected specimen), 9/10 somewhat muscularized (4), 10/11 still more so, thickness decreasing through 11/12-13/14, pregizzard septa not thickly muscular. Insertion on gut of septum 8/9, with reference to a postgizzard, irregularly interrupted collar (of blood glands?), not determined. Pigment, reddish, in circular muscle layer. Special longitudinal muscle band at mD, recognizable only behind 11/12. Lymph glands, present in intestinal segments. Brown bodies (immature) present only in posteriormost segments of several specimens. Diagonal muscle bands, small but numerous in region of xvii-xxiii.

Intestinal origin, in xv (4). Intestinal caecum, unpaired, ventral, arising in xxii (4), sometimes extending as far forward as into xix. Typhlosole, low, so small as possibly to be considered rudimentary but simply lamelliform, present from xxii and terminating in 66th (of 103), seemingly in the 50th (of 88, the juvenile), 66th (of 90), 64th (of 99 segments), respectively leaving 37, 38, 24, and 35 intestinal metameres atyphlosolate.

Dorsal blood vessel, unrecognizable in front of 5/6. Ventral trunk, complete, bifurcating above subpharyngeal ganglia. Supra-esophageal trunk, in ix-xiv. Extra-esophageals, passing off from gut in xiv. Subneural trunk, unrecognised. Hearts, of vii present, unaborted dorsal portions of those in viii passing into gizzard, in ix on left side (2), right side (2, ventral portion on the left side aborted), of x-xii latero-esophageal (4), of xiii lacking.

Testis sacs, paired, not in contact midventrally, vertical, in contact with the anterior septa of their segments only near their ventral ends, reaching to or almost to dorsal trunk, in xi-xii (4)! Seminal vesicles, two pairs, in xii, xiii. Prostates, compact, confined to xvii-xix or xviii-xix. Ducts, *ca.* 2 mm long, straight, with muscular sheen and rather spindle-shaped. Male gonoducts, passing to ental ends of prostatic ducts.

Ovaries, each along with its oviducal funnel, enclosed in a small, conical, posteriorly directed, subsophageal sac just underneath a seminal vesicle. Oviducal funnels, small. Ovaries, each curved around on itself into an annulus from the free margin of which hang short egg strings (with unusually small ova?). Pseudo-vesicles, in xiv, each only a small knob with a central depression, on posterior face of 14/15 just above level of emergence of oviduct.

Spermathecal ducts (including parietal portions), usually longer than ampullae. Diverticulum, shorter than duct, emerging from its anterior face at parietes or at various levels nearly to middle of coelomic length, comprising a spheroidal to pyriform seminal chamber as well as a slightly narrower and usually shorter stalk.

GM glands, none recognized in coelom or on parietes.

REPRODUCTION. Spermatozoal iridescence was not recognizable on any male funnel. However, flecks of such iridescence characterized content of each spermathecal seminal chamber (3). Anatomical degradation such as is often associated with parthenogenesis was not recognized. Nevertheless, some of the divergences from usual pheretima norms do sometimes appear after reproduction has become uniparental. Among such are presence of testes in xii, absence of those gonads in x, enclosure of testes by connective tissue sacs (when such are lacking in normal individuals of the species).

The question now requiring answer is: Are the Malaita specimens of an aberrant parthenogenetic morph or of an amphimictic population? If of an aberrant morph, information about the amphimictic parental population is needed for adequate characterization of the species.

INGESTA. Brownish organic matter with soil or rock particles. Whether the species feeds selectively or not, not determinable.

ABNORMALITY and REGENERATION. A metameric anomaly was found near the hind end of one individual without suspected tail regeneration. One instance of caudal regeneration is mentioned above.

REMARKS. Counts of follicle apertures were unsatisfactory. Accurate determination of setal numbers would have involved unwarranted damage to rare museum specimens.

Limitation of intestinal caeca to a single ventromedian pocket is unknown elsewhere in megadriles and the segmental location is unusually close to the intestinal origin.

Three pairs of seminal vesicles certainly do seem at first to be present in a pinned-out specimen. Dissection showed that the first two pairs of organs actually are vertical testis sacs. The first pair of testes was correctly placed in xi by most previous accounts. The first pair of seminal vesicles accordingly would have to be in xii. So the second pair of sacs formerly was thought to be seminal vesicles. Inclusion of seminal vesicles within testis sacs was unrecognized or misunderstood by classical specialists. At best, the prevailing condition was characterized as testis sacs and seminal vesicles "miteinander verwachsen". The same specialists failed to find the testes and male funnels of xii. Recognition of their presence may have been prevented by a strongly held classical belief that testes cannot be present behind the eleventh segment.

Presence of testes in xi-xii is uniquely diagnostic among megadriles and is approximated only in a moniligastrid genus *Desmogaster* Rosa in which testes, originally in coelomic cavities of xi and xii, now are within septa 10/11 and 11/12.

The ovarian sacs are not to be confused with most megadrile ovisacs (egg sacs

only) which are free-egg-containing bodies on the posterior face of the septum that bears on its anterior face the female funnels. The condition was erroneously characterized by previous writers as ovaries and oviducts "miteinander verwachsen". Actually gonads and ducts are discrete but are within a pair of chambers closed off from the rest of the coelomic cavity of xiii.

Accordingly *sedgwicki* ovarian sacs are the morphological equivalents of the paired testis sacs of many pheretimas. Such ovarian sacs are unknown elsewhere in megadriles.

SYSTEMATICS

Material referred in the past to *P. sedgwicki* has been characterized by considerable uniformity in characters often of systematic importance such as: 1) Location of first dorsal pore at 12/13. 2) A clitellum shorter than usual in the genus. 3) Superficial genital pores (not in parietal or coelomic invaginations). 4) Paired female pores. 5) Persistence into maturity of 8/9-9/10 as complete septa. 6) Intestinal origin in xv. 7) Absence of hearts in xiii. 8) Absence of GM glands. 9) Similarity of spermathecal shape. 10) Number of setae per segment (50-60) in postclitellar region. 11) Origin of a single ventromedian intestinal caecum in xxii. 12) Presence of paired ovarian sacs also containing the female funnels. A thirteenth character probably will have to be added—presence of paired testes in xii.

Characters 2-8 are regarded as primitive in the genus *Pheretima*. Caecal and ovarian sac characters of course are regarded as advanced specializations. The andry also would have been regarded as specialized inasmuch as it had to be derived from the classical ancestral gonadal battery by abortion of testes of x and conversion of ovaries of xii to testes. Evidence that such conversion can take place and has done so is available (Gates, 1962) even though the postulated octogonadal battery no longer is acceptable in the remote ancestry of the oligochaetes.

The *sedgwicki* uniqueness is paralleled consistently in the megadriles only by that of an entire family, the Moniligastridae (cf. Gates, 1962). Is then the classical *sedgwicki* a species in the modern sense of a single interbreeding population?

Inadequate and sometimes erroneous descriptions (of 37 and more years ago) provide the only clues. One such is the variation in characters usually distinguishing closely related species from each other. Examples: Location of paired spermathecal pores close to mV to 1/2 C or more apart from each other. Variation in number of spermathecae, sixthcal with pores at 5/6-7/8, quadrithcal with pores at 6/7-7/8, quadrithcal but with one pore each at 5/6, 6/7 and two at 7/8. Variation in distance between male pores. Differences in number and location of genital markings.

Single spermathecae if asymmetrically placed with reference to mV and not resulting from a midventral union of ducts, are among the numerous morphological degradations of the genitalia allowed to appear by parthenogenesis. Paired testis sacs, in one widely distributed lumbricid species, are present only in more or less

degraded parthenogenetic morphs. Whether homologous ovarian sacs also can result from parthenogenetic evolution remains to be learned. Very rarely parthenogenesis allows reversion. Accordingly reappearance of gonads in xii, even as testes, is possible.

Differences in longitudinal meridians of spermathecal and male pore locations and in location of genital markings are more likely to be associated with discrete amphimictic populations. Available data as to anatomical variation, though inadequate, does suggest that the classical *P. sedgwicki* may be a complex of species or subspecies along perhaps with some parthenogenetic morphs.

The rugged, mountain terrain of New Britain, with recently active volcanos, provides opportunities for the geographical isolation now thought to be so important in evolution of species.

The *sedgwicki* complex presumably evolved in New Britain from whence it was taken, probably by man, to Viti, St. Mathias, the Solomon, New Hebrides, Fiji, Samoa and Tonga islands, *i.e.*, mainly to the east and along the routes of past human migrations through Melanesia.

Material hitherto referred to *P. sedgwicki* has all been of a size 90–150 by 3.5–6.0 mm and with only 90–96 segments. A specimen unlikely to copulate with worms of that size accordingly is regarded as of a different (*cf.* below) but closely related species.

Pheretima mira n. sp.

SPECIMEN. New Britain Camp 12,700 feet (3872 m), Whiteman Range, December 18, 1958. 0–1–0. A.M.N.H. No. 3916.

EXTERNAL CHARACTERISTICS. Size, 164 by 12 mm. Segments, *ca.* 128, a posterior terminal region of 7–8 segments, where setae are few or lacking, almost conical. Secondary annulation, a presetal and a postsetal secondary furrow recognizable in ix–xiii and xvi–xx. Color, white (alcoholic preservation). Prostomium, epilobous, tongue open. Setae, size increasing slightly through ii–viii, smaller from x posteriorly, 26/ii, 33/iii, 43/iv, 44/v, 57/vi, 55/vii, 58/viii, 70/xii, vi/27, vii/27, xviii/29, xviii/22, xix/29, one or more possibly lost from ii–iii. Circles, without a regular gap midventrally, with a slight but irregular gap mid-dorsally. First dorsal pore, at 12/13.

Spermathecal pores, transversely slit-like at 5/6–7/8, ventrally more than $\frac{1}{2}$ C apart. Female pore, minute, presetal in xiv. Male pores, transversely slit-like, at eq/xviii, each in a slight elevation.

Genital markings, transversely elliptical, presetal and postsetal in xvi, xvii, xviii, xix, xx and presetal in xxi, in four longitudinal rows, all markings with an opaque, fairly wide rim and a greyish translucent central area.

Segments xiv–xv, with glabrous epidermis, follicle apertures unrecognizable. Intersegmental furrow 14/15, faintly recognizable but dorsal pores at 14/15 and 15/16 occluded.

INTERNAL ANATOMY. Septa, 4/5 and 8/9 membranous but complete, 5/6–7/8, 9/10 slightly muscularized, 10/11–12/13 thicker, 13/14 less muscularized. Pigment,

none recognized in longitudinal sections through the body wall, the circular muscle layer of a different shade than the longitudinal layer. Special longitudinal muscle band at mD, present. Diagonal muscles, numerous and large, from pharynx, esophagus and gizzard to the parietes, strictly parietal in xvi-xxiv. Lymph glands, present from xv, in some segments seemingly but probably not paired, sometimes distended by brown bodies. Brown bodies, of various sizes filling coelomic cavities of several segments in front of conical posterior end of body.

Gizzard, large, in viii. Intestinal origin, in xv. Caecum, large, narrowing anteriorly, horizontally flattened, extending through xxi-xxii but seemingly arising in xxiii. Typhlosole, lacking or very rudimentary, a slight elevation of gut roof at mD perhaps indicative only of a gorged, longitudinal blood channel. Supra-intestinal glands, none.

Dorsal blood vessel, single throughout and complete. Ventral trunk, also complete. Supra-esophageal, present. Extra-esophageals, median to the hearts. Subneural, not seen, (perhaps unrecognized because empty). Hearts, in v represented only by slender, transparent branches of dorsal vessel close to 5/6, in vi-vii lateral (not traced to the ventral vessel), in viii unaborted dorsal portions passing to gizzard, in ix lateral and both at first seemingly present but that on left side disappearing into the blood glands, in x-xii latero-esophageal, in xiii lacking. Blood glands, small and scattered in pharyngeal region, in a large but irregularly interrupted collar behind gizzard, in ix.

Testis sacs, two pairs, well apart from each other mesially, fairly large, vertical, in xi, xii. Seminal vesicles, not as large as testis sacs, in xiii. Prostates, confined to xviii, each with several long lobes. Prostatic duct, rather shortly spindle-shaped, 3 mm long, muscular, lumen small but rather stellate in transverse section, due to presence of low longitudinal ridges two of which have a fine longitudinal groove each.

Spermathecae, in vi-viii. Duct, shorter and narrower than the ampulla from which demarcation externally is not distinct. Diverticulum, small, sessile on anterior face of the duct near the parietes.

Ovaries and female funnels, probably in paired ovarian sacs as in *P. sedgwicki* but ovaries were not seen, perhaps because of postsexual regression. Pseudovesicles, rudimentary, thin, circular discs adherent to posterior face of 13/14 at usual sites.

REPRODUCTION. No iridescence was recognized on male funnels. Spermathecae were filled with a whitish coagulum. Diverticular content mostly is transparent and reddish as often in preserved postsexual individuals. At the center of two spheroidal masses there was some slight iridescence presumably from small aggregates of sperm that had not yet been lysed. Other indicators of postsexual regression were not recognized. As sperm had been exchanged in copulation, biparental reproduction can be expected.

PARASITES. Two large cysts on the dorsal face of the gut in a middle portion of the body were filled with nematode ova and with several nematodes. Nematodes

from a coelomic brown body were of *Miranema mirae* Timm. Pseudonavicellae cysts were found in several other places. A large cyst, without nematodes or their ova was on the dorsal face of the nerve cord in vii.

REMARKS. The surface of an anterior portion of the body was damaged but otherwise preservation was good. Insofar as could be determined, only segments xiv-xv are involved in the clitellum.

A knowledge of the internal anatomy is essential for generic definition. A specimen suspected of belonging to an undescribed species has been treated in various ways in the past: 1) Left unopened and unsectioned in accordance with museum regulations (in which case reference to a genus is pure guesswork). 2) The anterior end sectioned, either transversely, horizontally or sagittally. 3) The right or left half of the anterior end removed and sectioned. 4) The anterior end opened and dissected. None of those methods is satisfactory and each results in loss of some value as a type specimen. The New Britain worm was pinned open but dissection was restricted as far as possible to one side. Even so determination of some characteristics was impossible without further destruction of value as a type.

Seminal vesicles of xii, if present, will be within the testis sacs of that segment. Male gonoducts were not traced but on one side of the body a cord (vas deferens?) seemed to join the prostatic duct just ental to the epidermis. Such a junction would be very unusual in the genus *Pheretima* in which vasa deferentia often are traceable on the coelomic face of the parietes to an ental junction with prostatic ducts.

Diverticular content, of each spermathecae on left and right sides of vii, viii is in two masses of nearly spheroidal shape. That of diverticula on right and left spermathecae of viii is in one spheroid only. On the posterior face of the left spermatheca of vi is a second diverticulum, also with a single spheroid. The diverticulum on the right spermatheca of vii is almost completely separated into right and left halves.

A pseudovesicle of xiv was filled by a coagulum containing pseudonavicellae cysts.

TERMINOLOGY

The ancestral megadrile, if not also ancestral oligochaetes, according to one basic axiom of the classical system of the Oligochaeta (Michaelsen, 1900; Stephenson, 1930), was octogonadal. Paired testes were in x, xi. Paired ovaries were in xii, xiii. Gonadal sex, according to an unmentioned but associated corollary, was unalterable. During all subsequent evolution to date, the only changes made in that battery were deletions of one pair of testes and/or one pair of ovaries. Original conditions were termed holandry and hologyny. Subsequently, evolved, reduced states were termed proandric (not protandric) and metandric, progynous and metagynous.

Moniligastrid conditions did not fit the classical pattern. Stephenson's inge-

nious but needlessly complicated, compression- theory (cf. Gates, 1962) provided an ancestral decagonadal battery with testes in x-xii and ovaries in xiii-xiv. Nevertheless, previous andric and gynec characters were retained by Stephenson and all other oligochaetologists.

Gonadal conditions of *Tonoscolex* Gates and *Nelloscolex* Gates like those of the Moniligastridae, could not be explained because of the arbitrary limits classical oligochaetologists had imposed on themselves. Classical andric and gynec characters were shown (Gates, 1962) to be etymologically erroneous. The *sedgwicki* complex provides further proof. Nevertheless andric characters have been so commonly used for so long, in so much of the literature as well as in thought, that they should be retained. That is possible only by redefinition without etymological significance. Thus holandric can be defined as follows: Having two pairs of testes, in two consecutive segments that usually are x, xi, but that may be ix, x or xi, xii (if not also others?).

Megadrile parthenogenesis has shown that sex determination of gonads is not irreversible. Since such change is possible all gonadal conditions of the Oligochaeta can be easily derived from an ancestral gonadal battery extending through v-xxii. Irreversible only is location of testes anterior to ovaries.

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