

ON THE PHYLOGENY OF THE MONILIGASTRIDAE, WITH DESCRIPTION OF  
A NEW SPECIES OF MONILIGASTER (OLIGOCHAETA, ANNELIDA)

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ABSTRACT: Previous theories of the origin and evolution of the family Moniligastridae and its constituent genera are examined. Evidence is presented that those based on interpretation of moniligastrid testis-sacs as contracted segments or as intraseptal cavities must be rejected. It is argued that each testis-sac, and enclosed testis and funnel, belongs to the segment anterior to the septum suspending the sac and that moniligastrids are opisthoporou oligochaetes derivable from octogonadial forms which had the condition of the genitalia seen in those haplotaxids in which the male ducts traverse only a single septum. The principles of Hennig are applied to obtain a phylogeny of the five genera of the Moniligastridae based on synapomorphies. The method of Camin and Sokal (1965) for deducing branching sequences in phylogeny gave identical results. The intra-generic homologies of the genitalia and their segments are discussed and represented graphically and zoogeography is briefly treated. Attention is drawn to the morphological and presumed morphogenetic similarities of the male and spermathecal systems. *Moniligaster troyi* n.sp. is described. It is diagnosed by the combination commencement of gizzards in segment XIII and bifid spermathecal gland.

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Introduction

The Moniligastridae is a family of earthworms indigenous to southeast and eastern Asia, from South India (and Ceylon?) to Manchuria, Korea, Japan, the Philippines, Borneo and Sumatra. This autochthonous range has been greatly exceeded by the genus *Drawida*, presumably as a result of transportation by man. The family contains five genera, *Moniligaster* Perrier, 1872, *Desmogaster* Rosa, 1890, *Drawida* Michaelsen, 1900, *Eupolygaster* Michaelsen, 1900, and *Hastirogaster* Gates, 1930. Of these, *Drawida*, with some 113 species, is by far the largest genus in the family and is one of the largest and most widely distributed oligochaete genera, both autochthonously and anthropochorously.

Moniligastridae are of special interest as, although they are earthworms (megadriles), sometimes of great size, they retain primitive features (the large-yolked eggs and single layered clitellum) typical of aquatic oligochaetes including the undoubtedly very primitive Lumbriculidae and Haplotaxidae. Furthermore, the most posterior location of the male genital pores in the family, in segment XIII, is anterior to and presumably more primitive than that in any other earthworms. The pores may occur in this or more anterior sites in morphs of the lumbricid *Eiseniella tetraedra* but there it appears to be a secondary condition. They are always located in XIII in the Alluroididae, an Ethiopian and Neotropical family transitional between freshwater and terrestrial Oligochaeta.

The observation by Gates (1972) that the number of unique diagnostic characters in the Moniligastridae is unparalleled in megadriles draws attention to the morphological distinctness and presumed phylogenetic discreteness of the family. Its phylogenetic position has been the subject of some debate (Beddard, 1895; Michaelsen, 1903, 1908, 1922, 1928; Stephenson, 1922, 1930; Gates, 1962, 1972; Pickford, 1948; Clark, 1969; Brinkhurst and Jamieson, 1971) and it is the purpose of this study to attempt some elucidation of these affinities.

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## Phylogeny of the Moniligastridae

## Preview

Theories of the origin of the Moniligastridae from a non-moniligastrid stock have to take into account and explain the existence in all members of the family of testis-sacs, containing testes and sperm funnels, which are unique in being each suspended by a septum. These sacs are considered by Gates (1962, 1972) to be intraseptal. Attempts to derive the Moniligastridae have also to explain the varied enumeration of the segments bounding these testis-sacs and containing other structures such as the ovaries and hearts. Thus the location of the testis-sacs varies from septum 9/10 to 11/12, that of the single pair of ovaries from XI to XIII and that of the last pair of hearts from IX to XI. It has been customary, and reasonable, to consider the Haplotaxidae, with paired testes in X and XI and paired ovaries in XII and XIII, as representing the ancestral stock from which the earthworms arose (Michaelson, 1903, 1917, 1922, 1928; Beddard, 1895; Brinkhurst and Jamieson, 1971). However, Stephenson (1922, 1930) and Gates (1962), exponents of the two major but conflicting theories of the origin of the Moniligastridae, both found it necessary to postulate the existence at some time in evolution of testes not only in X and XI but also in XII while agreeing with the other workers as to the presence of ovaries in XIII. Stephenson (1922) also envisaged an additional pair of ovaries in XIV in an ancestor which he saw as the precursor of all terrestrial oligochaetes. The requirement for testes in XII was occasioned by this location (actually at septum 11/12) in the moniligastrid genus *Desmogaster*. Elsewhere in the Oligochaeta, except in intraspecific variants (chiefly lumbriculids), XII contains no testes but it contains ovaries (in addition to ovaries in XIII) in haplotaxids and in three of the many species of earthworms.

Stephenson (1922) in his ingenious "contraction theory" regarded moniligastrid testis-sacs as the coelomic cavities of otherwise suppressed metameres and explained segmental variation in the location of the testes and other structures in terms of fusion of adjacent pairs of testis-sacs. Gates, on the other hand, in what may be termed his "sex-reversal theory", argued strongly for regarding the testis-sacs as intraseptal chambers formed when testes proliferated into the septum to which they were attached and not into the succeeding segment. Variation in location of testes from X to XII and of ovaries from XI to XIII was explained in terms of conversion of ovaries to testes or the opposite.

A third theory is advanced below which derives the moniligastrid arrangement from the octogonadial haplotaxid battery without the necessity for invoking sex-reversal, derivation of testis-sacs by contraction of metameres, fusion of segments, or intraseptal proliferation of testes. To anticipate, the crux of the theory is that the moniligastrid testis-sac belongs to the segment anterior to the septum in which it is suspended. Thus one of the most problematical aspects of moniligastrid anatomy, supposed location of testes in XII in *Desmogaster*, is considered illusory.

A further discussion of the theories of Stephenson and Gates will first be given.

## The contraction theory (Stephenson, 1922, 1930)

In advancing the contraction theory Stephenson made considerable use of the anatomy of *Syngenodrilus*, then referred to a monotypic subfamily of

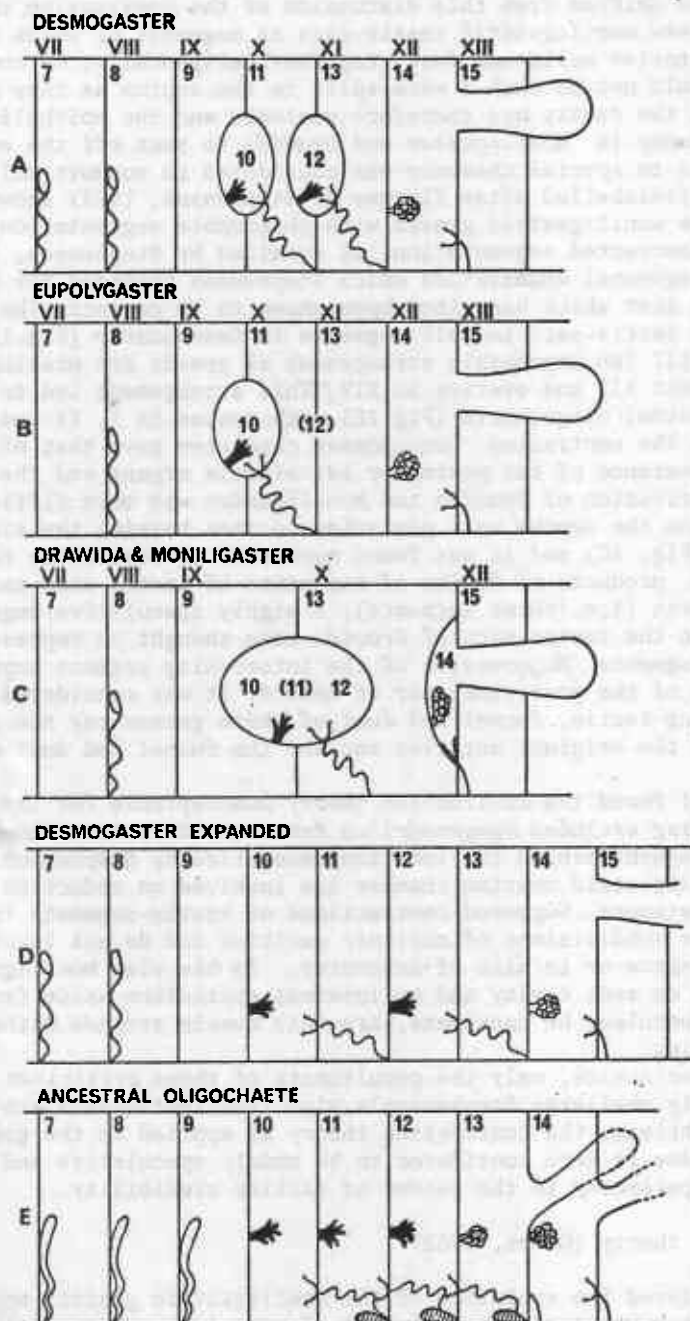


Fig.1. The contraction theory of Stephenson. Observed segmentation in roman numerals; supposed basic segmentation in arabic numerals. A, primitive condition as in *Desmogaster*. B, *Eupolygaster* derived by loss of the posterior testis-sacs and of segment 12. C, *Drawida* and *Moniligaster* derived by fusion of the coelomic cavities of 10, 11 and 12, to give a single pair of testis-sacs at IX/X. D, *Desmogaster* with its testis-sacs expanded as full segments. E, hypothetical ancestral oligochaete derived from the expanded *Desmogaster* condition by addition of spermathecae in segment 9, testes in 11, and ovaries in 13. (Based on diagrams of Stephenson, 1922).

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the Moniligastridae, the Syngenodrilidae. Gates (1945a) and Pickford (1945) have shown that Stephenson misinterpreted the anatomy of *Syngenodrilus* and Jamieson (1968), using taxonomic methods, confirmed Gates' view that *Syngenodrilus* has no close relationship with the Moniligastridae. *Syngenodrilus* will therefore be omitted from this discussion of the contraction theory.

Stephenson saw moniligastrid testis-sacs as segments of which the anterior and posterior walls had fused together peripherally. He considered that the sacs could not be each a mere split in the septum as they were lined with epithelium, the cavity was therefore coelomic and the epithelium peritoneal. The tendency in *Moniligaster* and *Drawida* to shut off the ovaries and their funnels in special chambers was considered to support this view.

Fig. 1 A-C (relabelled after figures of Stephenson, 1922) shows the genital segments of three moniligastrid genera with observable segmentation in roman numerals and uncontracted segmentation, as surmised by Stephenson, in arabic numerals. The segmental enumeration which Stephenson proposed for *Desmogaster* is one less than that which has since been shown to be correct. The result of expansion of the testis-sacs to full segments in *Desmogaster* (Fig. 1D) gave testes in X and XII (an improbable arrangement as gonads are missing from the intervening segment XI) and ovaries in XIV. This arrangement led to postulation of an ancestral oligochaete (Fig. 1E) with testes in X, XI and XII and ovaries in XIII and XIV. The contracted *Desmogaster* condition gave that of *Eupolygaster* by disappearance of the posterior set of male organs and the anterior spermathecae. Derivation of *Drawida* and *Moniligaster* was more difficult: in these the ovaries are on the septum next posterior to that bearing the single pair of testis-sacs (Fig. 1C) and it was found necessary to regard the testis-sacs (at 9/10) as the products of fusion of two pairs of testis-sacs and the intervening segment (i.e. three segments), a highly speculative suggestion. Trabeculae within the testis-sacs of *Drawida* were thought to represent the septa of fused segments. Suppression of the intervening segment supposedly resulted in loss of the posterior pair of hearts. It was considered that the "actually existing testis, funnel and duct of these genera may not improbably be the testis of the original anterior sac and the funnel and duct of the posterior".

Gates (1962) found the contraction theory unacceptable for the following reasons, having excluded *Syngenodrilus* from consideration. *Desmogaster* gonads are one segment behind the location recognized by Stephenson. Evolution of the moniligastrid ovarian chamber has involved no reduction in size of the ovarian metamere. Supposed contractions of testis-segments in megascolecids involve subdivisions of coelomic cavities and do not involve reduction in coelomic space or in size of metameres. In his view moniligastrid testis-sacs have no real cavity and no internal epithelium aside from the male funnel. Trabeculae, he considers, are only muscle strands without peritoneal covering.

In the author's view, only the penultimate of these criticisms would, if true, seriously challenge Stephenson's view that testis-sacs are reduced segments. Nevertheless, the contraction theory as applied to the genera of the Moniligastridae is here considered to be unduly speculative and to depart from reasonable parsimony to the extent of lacking credibility.

The sex-reversal theory (Gates, 1962)

Gates considered the evolution of the moniligastrid genital apparatus in a fuller context, that of the evolution of somatic systems, confining his discussion chiefly to the development of features peculiar to moniligastr-

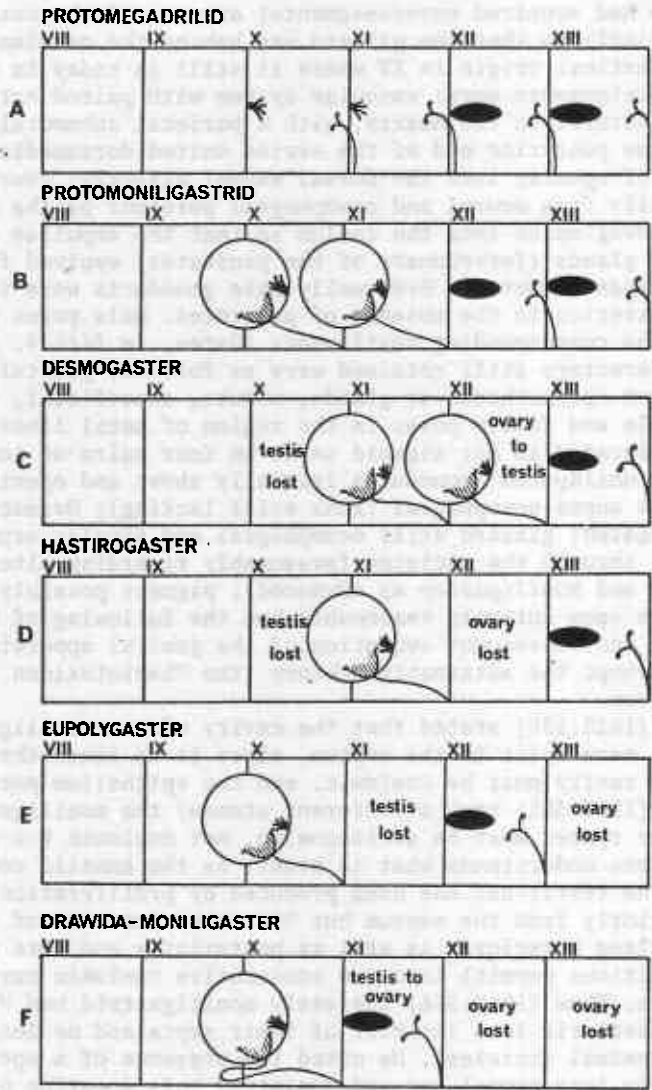


Fig.2. The sex-reversal theory of Gates. A, octogonadial, prosoporous proto-megadrilid. B, protomoniligastrid derived from A by proliferation of the testes into their septa and incorporation of the sperm funnels in the testis-sacs thus produced. C, *Desmogaster* derived by loss of anterior testes and conversion of ovaries of XII to testes. D, *Hastirogaster* derived by loss of anterior testes and of ovaries of XII. E, *Eupolygaster* derived by loss of posterior testes and posterior ovaries. F, *Drawida-Moniligaster* derived by conversion of the posterior testes to ovaries and loss of the ovaries of XII and XIII. (Constructed from the textual account of Gates, 1962).

rid anatomy. These are the synapomorphies (*sensu* Hennig, 1966) which jointly unify and distinguish the Moniligastridae. The following summary of Gates' views refers first to those which here appear acceptable. The more contentious subject of the evolution of the genital apparatus will be dealt with secondly.

Gates considers that unless peculiar characters, in identical combinations, evolved independently in the ancestry of each moniligastrid genus, an early moniligastrid should have differed from contemporaneous oligochaetes in the following respects: the prostomium had become independent of the peristomium and attached to the roof of the buccal cavity behind intersegment 1/2; the digestive system had acquired enterosegmental organs and the oesophagus had elongated posteriorly so that the gizzard was behind the ovarian segment, perhaps with intestinal origin in XV where it still is today in many megadriles. Other developments were: vascular system with paired extra-oesophageal trunks that are lateral to the hearts, with a parietal subneural trunk, one or two hearts at the posterior end of the series united dorsomedially in each segment instead of opening into the dorsal vessel directly; ovarian chamber closed off medially from neural and oesophageal portions of the coelom; spermathecae deeply invaginated into the coelom so that the ampullae are dorsal; capsular genital glands (forerunners of the prostates) evolved from ectodermal glands (the X glands of Gates). Eventually male gonoducts were to be unable to open to the exterior in the absence of prostates. Male pores were in the segment behind the corresponding testis-sacs (Gates, *in litt.*). Ancestral (plesiomorph) characters still retained were as follows: genital apertures, of all organs from spermathecae to glands, minute, superficial, ventral; spermathecal, male and female pores in the region of setal lines *ab*; gland pores variously located in *bb*; sigmoid setae in four pairs of longitudinal ranks; clitellum unilayered; gonoducts initially short and opening presetally; hearts lateral (a supra-oesophageal trunk still lacking); Ovisacs dorsal and posteriorly elongated; gizzard still oesophageal and single; nephridial ducts passing straight through the parietes (presumably regarding alternation of pores in *Drawida* and *Moniligaster* as advanced); pigment possibly absent. These suggestions seem entirely reasonable but the following of Gates' views as to the origin and subsequent evolution of the genital apparatus seem less acceptable and prompt the alternative theory (the "haplotaxidan theory") which will later be given.

Stephenson (1922:135) stated that the cavity of the moniligastrid testis-sac "cannot be a mere split in the septum, since it is lined throughout with epithelium...the cavity must be coelomic, and the epithelium peritoneal epithelium". Gates (1962:301) took a different stance: the moniligastrid testis-sac is solid, any spaces must be schizocoelic, not coelomic (a curious distinction, though one understands what is meant, as the annelid coelom is schizocoelic). The testis-sac has been produced by proliferation of the germ cells not posteriorly from the septum but "into the interior of a septum which becomes bulged anteriorly as well as posteriorly and more or less equally (if conditions permit) into two consecutive coelomic cavities" of the adjacent segments. Thus (1962:356) the early moniligastrid had "testes proliferating anteriorly into interior of their septa and no longer inducing development of seminal vesicles". He noted the presence of a sperm funnel in this supposedly intraseptal sac and explained this location of the funnel by the hypothesis that the testis induced the funnel on the nearest susceptible tissue.

The "apparently invariable passage (in *Drawida*, at least) of gonoducts from the funnel septum into the anterior segment" before turning posteriorly to pass to the prostate yielded no explanation. Having disposed of the testis-sacs of moniligastrids (as opposed to other oligochaetes) as intraseptal

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structures, derivation of the genera of the Moniligastridae from the protomoniligastrid was envisaged to have occurred by deletion and sex-reversal of gonads in the following ways (Fig.2, constructed from Gates' account and approved by him *in litt.*).

While the typical moniligastrid anatomy of the protomoniligastrid was being evolved "gonads of the ancestral battery may well have been eliminated in all but four segments", X-XIII. Reduction of the gonad battery was continued: in a line leading to *Desmogaster* gonads of X were aborted and those of XII, originally ovaries, became testes. In lines leading to *Hastirogaster* and *Euplygaster* gonads of X and XII and of X (clearly meaning XI) and XIII, respectively, were eliminated. In the main line leading to *Drawida-Moniligaster* gonads of XII-XIII disappeared (unless a segment was excalated anteriorly), those of XI being retained as ovaries (i.e. converted from testes to ovaries).

This "sex-reversal theory" has a number of shortcomings: there is no evidence that the moniligastrid testis-sac is produced by proliferation of the testis into the septum. While the true nature of the interior of the sac, whether coelomic as considered by Stephenson or intraseptal as Gates considers, still remains to be established, the view that it is coelomic cannot be considered to have been invalidated. The coelomic interpretation is, at least, more parsimonious in not requiring acceptance that the sperm funnel has migrated forward to the septum preceding its normal location so as to be enclosed in the testis-sac. The funnels have not done this in *Ocneroedrillus* in which testis-sacs are developed which Gates rightly deems to have non-coelomic cavities; the sacs are produced by capping of each testis by its own epithelium; sperm reaching the coelom by rupture of the sac. Gates' theory might, nevertheless, have been more credible had he allied the moniligastrid testis-sac to the ocneroedile type of sac.

Neither Gates' nor Stephenson's theory explains the passage of the sperm duct from the moniligastrid testis-sac into the anterior segment before passing to the male pore in the succeeding segment. Gates states that the testis proliferates anteriorly into its septum (and testis-sac) but Stephenson (1930: 338) appears correct in stating that the testis is usually on the anterior wall of the sac. The observation that moniligastrids have no seminal vesicles has not previously been questioned but it will be argued below that the moniligastrid testis-sac is a combined coelomic testis-sac, such as is common in earthworms, with persistent seminal vesicle, though the persistence of the seminal vesicle is not essential to the theory. Furthermore, while elimination of gonads required by Gates' theory is not unacceptable, the sequence of sex-reversals envisaged is less convincing. Thus one is asked to accept that testes at 10/11 became ovaries in *Drawida-Moniligaster* (Fig.2F), evidently with loss of their sacs and migration of the funnel back to the succeeding septum, while in *Desmogaster* (Fig.2C) not only did the ovaries of XII become testes but the latter organized surrounding sacs and enclosed funnels, from which, again, the ducts first passed into the preceding segment before turning posteriorly.

A theoretical advantage of Gates' theory is that it does not require postulation of excalation of segments to explain the more anterior position of the gonads in *Drawida-Moniligaster* compared with *Desmogaster*. Such elimination presents little difficulty, however. Gates (1962:365) states that the metamerism of the megascolecids *Tonoscolex* and *Nelloscolex* can be derived only by excalation of one metamere in front of the gonads. Gates' theory also ignores the presence of rudimentary prostates and pores in IX, in addition to those in X, in some specimens of *Drawida willsi* (a synonym of *D. japonica*) reported by Michaelsen (1909:144-5) and two pairs of well

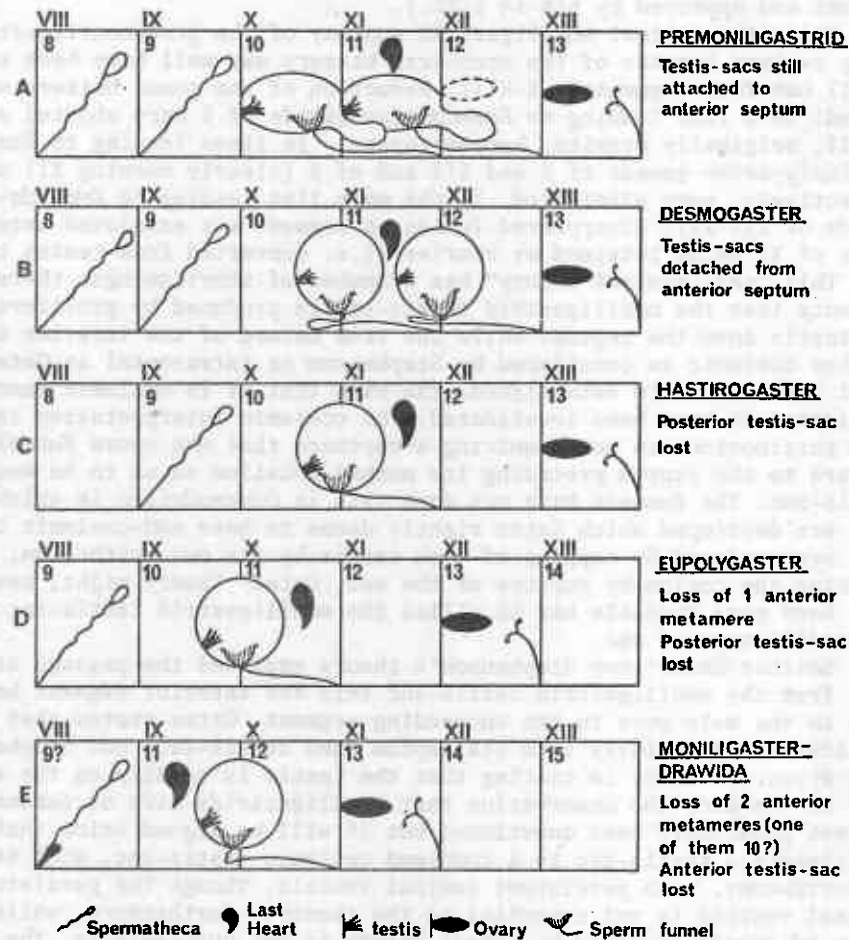


Fig.3. The Haplotoxidan theory of the author. Observed segmentation in roman numerals; inferred basic metamerism in arabic numerals; annotations indicate salient morphological changes. A, premoniligastroid. B, *Desmogaster* derived from premoniligastroid by separation of testis-sacs from the anterior septa of segments 10 and 11 and loss of the ovaries of 12. C and D, *Hastirogaster* and *Eupolygaster* derived from the *Desmogaster* condition by loss of the posterior pair of testis-sacs and, in *Eupolygaster*, the loss of an anterior segment. E, *Moniligaster-Drawida* arising from the *Desmogaster* condition by loss of anterior testes and independent loss of two anterior segments.



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developed prostates in *D. scandens* Rao, 1921. These specimens demand testes in IX in the protomoniligastrid, for which Gates makes no allowance.

## The haplotaxidan theory

The main tenet of the third theory is that in the Moniligastridae each testis-sac, suspended by a septum, belongs to the segment preceding the septum and not to that posterior to the septum. This hypothesis, derived independently by the author, was foreshadowed by Michaelsen (1922:19, footnote). Thus the sac at 11/12 in *Desmogaster* belongs to segment XI and its funnel belongs to the septum on which it is situated, 11/12. It is therefore unnecessary to postulate sex-reversal of a gonad in XII to give a testis in that segment, or to envisage migration of a sperm funnel from its normal septum or the anterior proliferation of the testis into this septum to produce the cavity of the suspended testis-sac.

The evidence indicates that the moniligastrid testis-sac differs little from the type of testis-sac, common in earthworms, which is formed by enclosure of the testis and funnel in a longitudinal compartment separated from the persistent coelom of the remainder of the segment by a wall which is apparently peritoneal. The testis is located on the anterior wall of such a testis-sac, at the anterior septum of the enclosing segment, and the seminal funnel is located ventrally near its posterior end, shortly in front of the posterior septum of the same segment. Usually, as in *Lumbricus* and *Pheretima*, the testis-sac is continuous with a seminal vesicle in the succeeding segment formed by posterior evagination of the septum. It is possible that the posterior, postseptal portion of the moniligastrid testis-sac is a persistent seminal vesicle. The moniligastrid sac therefore differs from the common type solely in separation of its anterior wall and attached testis from the anterior septum of the segment, though it is noteworthy that the anterior wall of the testis-sac may remain in contact with the anterior septum as in *Drawida assamensis* Gates (1945b:59). This separation of the anterior wall of the testis-sac, and its attached testis, from the anterior septum of the segment is not entirely hypothetical as a very similar condition has been reported in *Pheretima* by Bergh (1886) in a species of which the anterior testis-sac was found to be sessile on the anterior face of septum 10/11 with the testis attached to the inner surface of the anterior wall of the sac. The posterior sac was similarly situated on septum 11/12, connected with the posterior face of septum 10/11 by a strand of tissue, and hence did not stretch as a complete tube from septum to septum; the corresponding testis was again attached to the inner surface of the anterior wall of the sac.

The "solid" nature of the moniligastrid testis-sac, packed with developing sperm morulae among numerous trabeculae, which led Gates to deny its coelomic nature, conforms closely to that of an earthworm seminal vesicle the cavity of which, like that of the testis-sac, is a subdivision of the coelom. It will be shown that, just as in the normal earthworm testis-sac, the vas deferens leaves its funnel in the segment to which the testis-sac belongs and then passes posteriorly to penetrate the posterior septum. In all other earthworm families the vas passes through more than one complete segment so that the male pore is never more anterior than segment XIII (excepting some morphs of *Eiseniella tetraedra*). Passage through one or more complete segments is the opisthopore condition and moniligastrids, with the vas traversing only one segment posterior to that containing the seminal funnel agree with most Haplotaxidae, in which *H. violaceus* has testis-sacs. Gates' (1962, 1972) interpretation of the testis-sacs of Moniligastridae would necessitate regarding most members of the family (having male pores at the posterior

intersegment of the segment to which he presumes the corresponding testes to have belonged) as prosoporous, a condition otherwise limited to the Lumbriculidae.

Stephenson's contraction theory, although rejected here, agrees with the present theory in regarding the cavity of the moniligastrid testis-sac as coelomic and tacitly recognizing the opisthoporous nature of the family. Brinkhurst and Jamieson (1971) allowed the supposedly prosoporous condition of the Moniligastridae, with other peculiarities of the group, to merit placing the family in a separate order, the Moniligastrida, separate from the Lumbriculida on the one hand and the remainder of the Oligochaeta, the order Haplotaxida, on the other though derived from the lumbriculid (prosoporous) condition. The interpretation of the testis-sacs and segmentation of the Moniligastridae here proposed supports derivation of the family from opisthopores with the haplotaxid condition of the gonads. Consideration must be given to placing the family, in a suborder Moniligastrina, within the order Haplotaxida, hence the name "haplotaxidan theory" for the theory here advanced.

Having drawn a comparison between the moniligastrid testis-sac and that of other earthworms it will be appropriate to enlarge on the evidence for recognizing this similarity and in general support of the views presented above. As long ago as 1894, in what is still one of the most thorough examinations of a moniligastrid, Bourne stated that in *Drawida grandis* (with a single pair of testis-sacs, at 9/10) "the testes belong to segment IX. The sperm-duct joins the sperm-sac (testis-sac) just behind the testis, but still in front of the equatorial attachment of the septum - i.e. in Segment IX". Furthermore, the epitheliate nature of the internal wall of the testis-sac was recognized by his observation that the ciliated epithelium of the sperm funnel is directly continuous with the rest of the epithelium of the sperm-sac. Most important in indicating that the testis-sac belongs to the segment anterior to its septum is Bourne's statement that in sections of a juvenile worm the minute testis-sacs lay in front of, although in contact with, septum 9/10. The trabeculae were shown to consist of blood vessels with a minute amount of connective tissue and muscle.

The presence of a testis anteriorly in the sac (varying from anterior, to anteroventral, to ventral though preseptal) with the sperm duct emerging anteriorly to the suspending septum before posteriad penetration, is well documented. Examples are given by Chen (1933) for *Desmogaster sinensis*, *Drawida gisti*, *Dr. sinica* and *Dr. linhaiensis*. Michaelsen (1931:9) makes the following clear statement for *Dr. gisti*: "A broad tufted testis stretches from the ventral wall of the testis sac into the lumen of segment 9. Behind the testis, there is a large seminal funnel on the wall of the testis sac. Close in front of septum 9-10 there arises from the testis sac a narrow sperm duct (which) forms a large narrow coil in segment 9, enters segment 10, forms here a somewhat similar coil, and finally opens into the proximal end of the male atrium". Gates' (1962) reference to the apparently invariable passage in *Drawida* of the sperm ducts from the funnel septum into the anterior segment before turning posteriorly to pass to the prostate has already been mentioned. Numerous examples of such anterior origin (and of the opisthoporous condition here recognized) are to be found in addition to those already given. The vas, having left the portion of the testis-sac in IX, actually loops around the heart of that segment in *Drawida aculeata*, *Dr. coonoorensis*, *Dr. lennori* and *Dr. thurstoni* (vide Gates, 1945b) and in *Dr. japonica*, *Dr. gisti* and *Dr. sinica* (vide Chen, 1933) and is stated to be anterior to 9/10 entally in *Dr. ampullacea*, *Dr. bifida* (vide Gates, 1945b), *Dr. gisti* (vide Michaelsen, 1931), *Dr. linhaiensis* (vide Chen, 1933), *Dr. caerulea* (vide Gates, 1926, 1933) and *Dr. lacertosa* (vide Gates, 1933). The vas is said to be on the anterior and

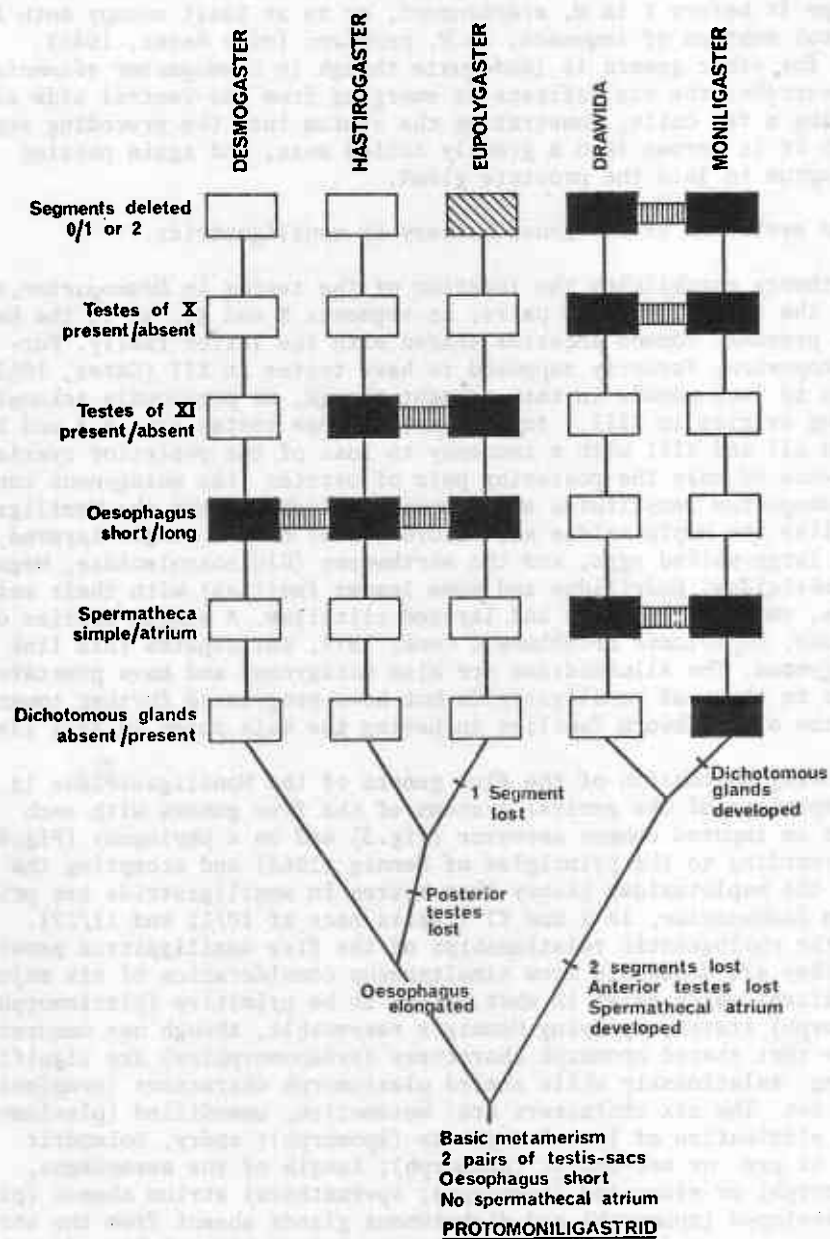


Fig.4. Phylogeny of the five moniligastrid genera utilizing only shared advanced characters (synapomorphies). The protomoniligastrid is envisaged as having the morphology of *Desmogaster* shown in Fig.3B but possessing a short oesophagus. Rectangles: blank = plesiomorph, black = apomorph, cross-hatched = non-congruent apomorphy (1 segment deleted as opposed to 2 in *Drawida-Moniligaster*).