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 opisthoporous 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 intrageneric 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 (Michael-
sen, 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 pre-
cursor 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 ov-
aries (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 monil-
igastrid testis-sacs as the coelomic cavities of otherwise supressed meta-
meres 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 arrange-
ment from the octogonadial haplotaxid battery without the necessity for in-
voking 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
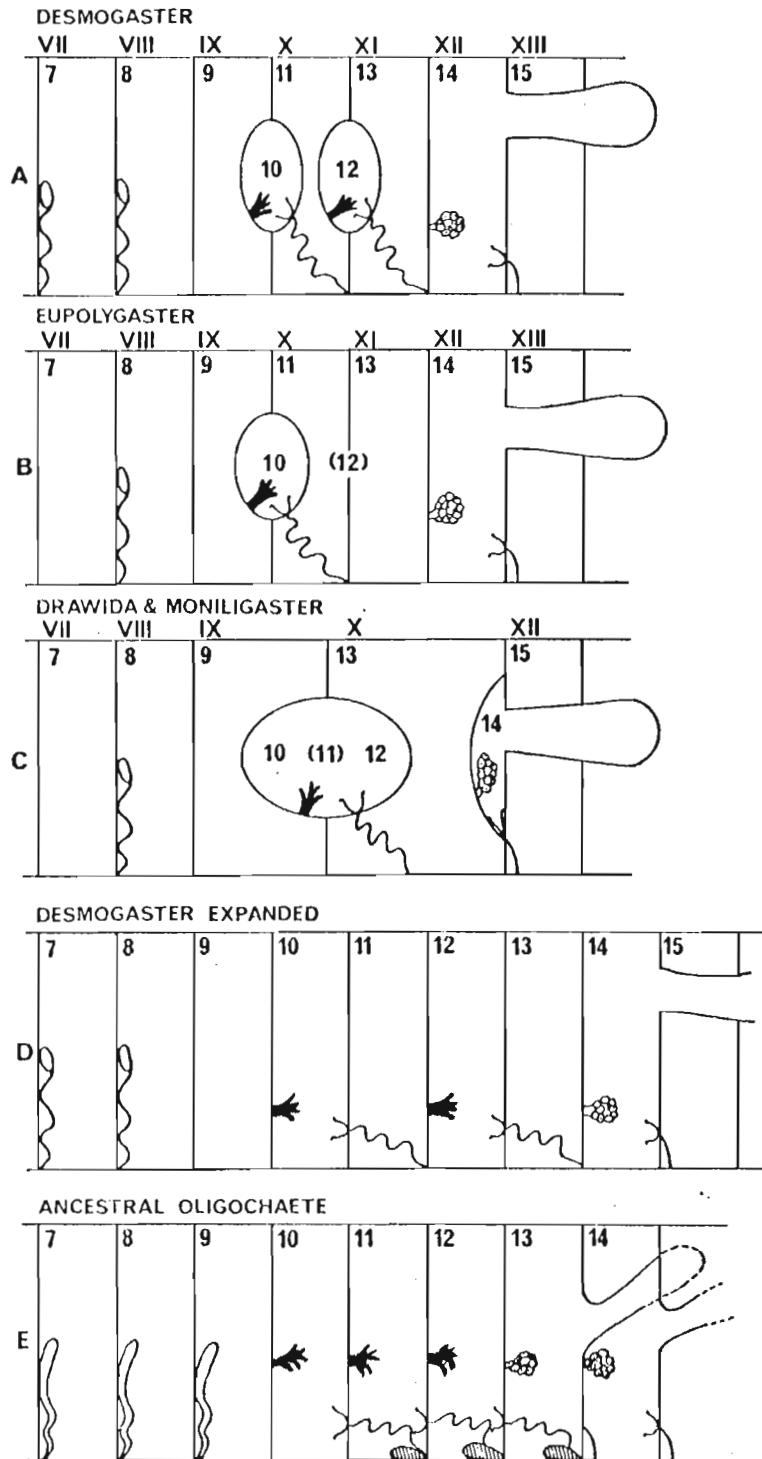of the anatomy of *Syngenodrilus*, then referred to a monotypic subfamily of

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).

the Moniligastridae, the Syngenodrilidae. Gates (1945a) and Pickford (1945) have shown that Stephenson misinterpreted the anatomy of *Syngenodrilus* and Jamieson (1968), using taxonometric 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 monilgastrid 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 moniligast-
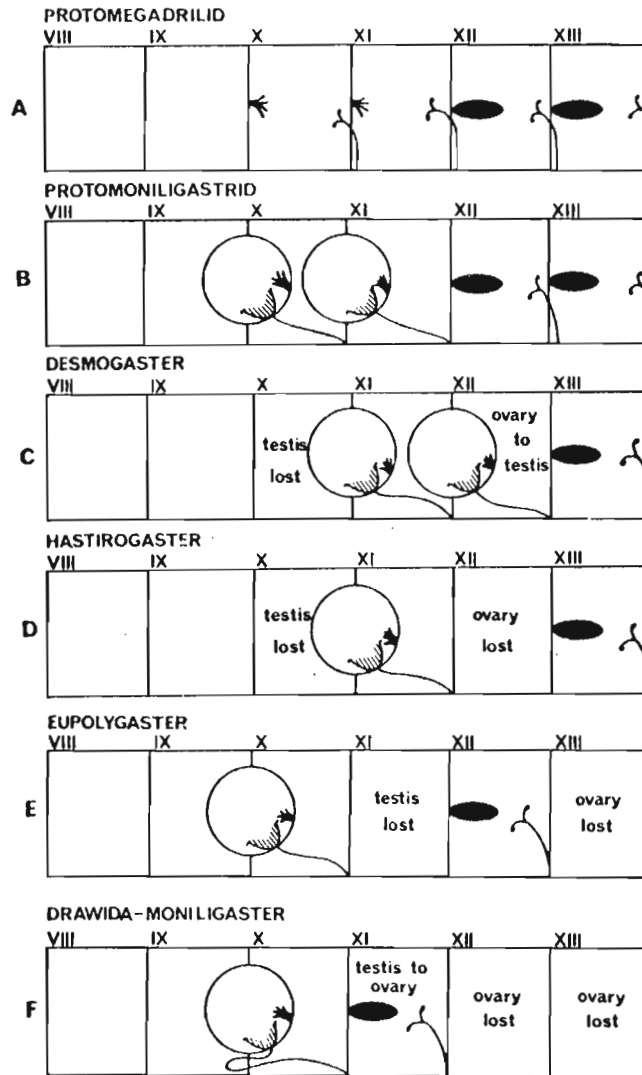
PROTOMEGADRILID
VIII IX X XI XII XIII

A

PROTOMONILIGASTRID
VIII IX X XI XII XIII

B

DESMOGASTER
VIII IX X XI XII XIII

C
testis
lost
ovary
to
testis

HASTIROGASTER
VIII IX X XI XII XIII

D
testis
lost
ovary
lost

EUPOLYGASTER
VIII IX X XI XII XIII

E
testis
lost
ovary
lost

DRAWIDA-MONILIGASTER
VIII IX X XI XII XIII

F
testis to
ovary
ovary
lost
ovary
lost

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 joint-
ly 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 mega-
driles. 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; sperm-
athecae 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 epi-
thelium". Gates (1962:301) took a different stance: the moniligastrid testis-
sac is solid, any spaces must be schizocoelic, not coelomic (a curious dist-
inction, 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 suscept-
ible 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

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 *Ocnerodrilus* 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 ocnerodile 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
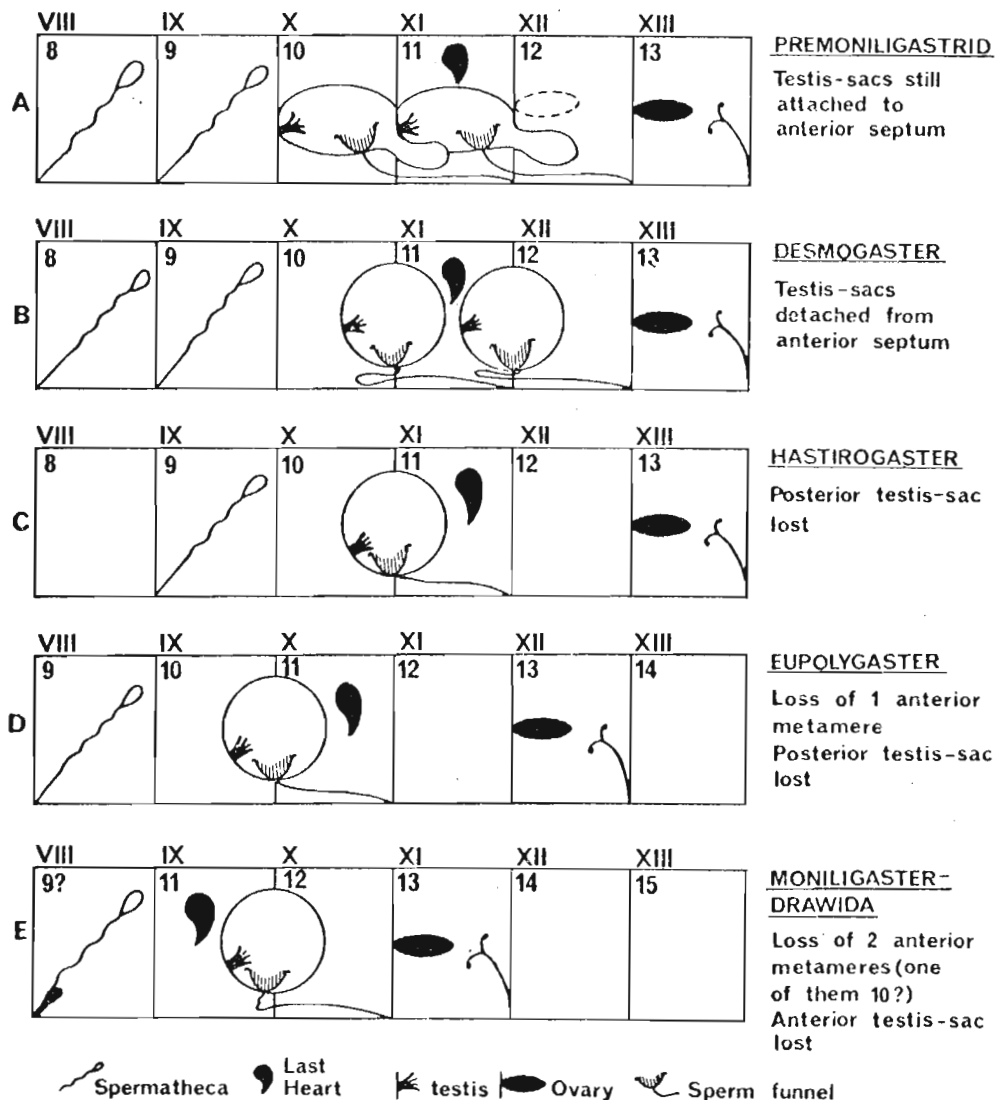
Fig.3. The Haplotaxidan theory of the author. Observed segmentation in roman numerals; inferred basic metamerism in arabic numerals; annotations indicate salient morphological changes. A, premoniligastrid. B, *Desmogaster* derived from premoniligastrid by separation of testis-sacs from the anterior septa 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
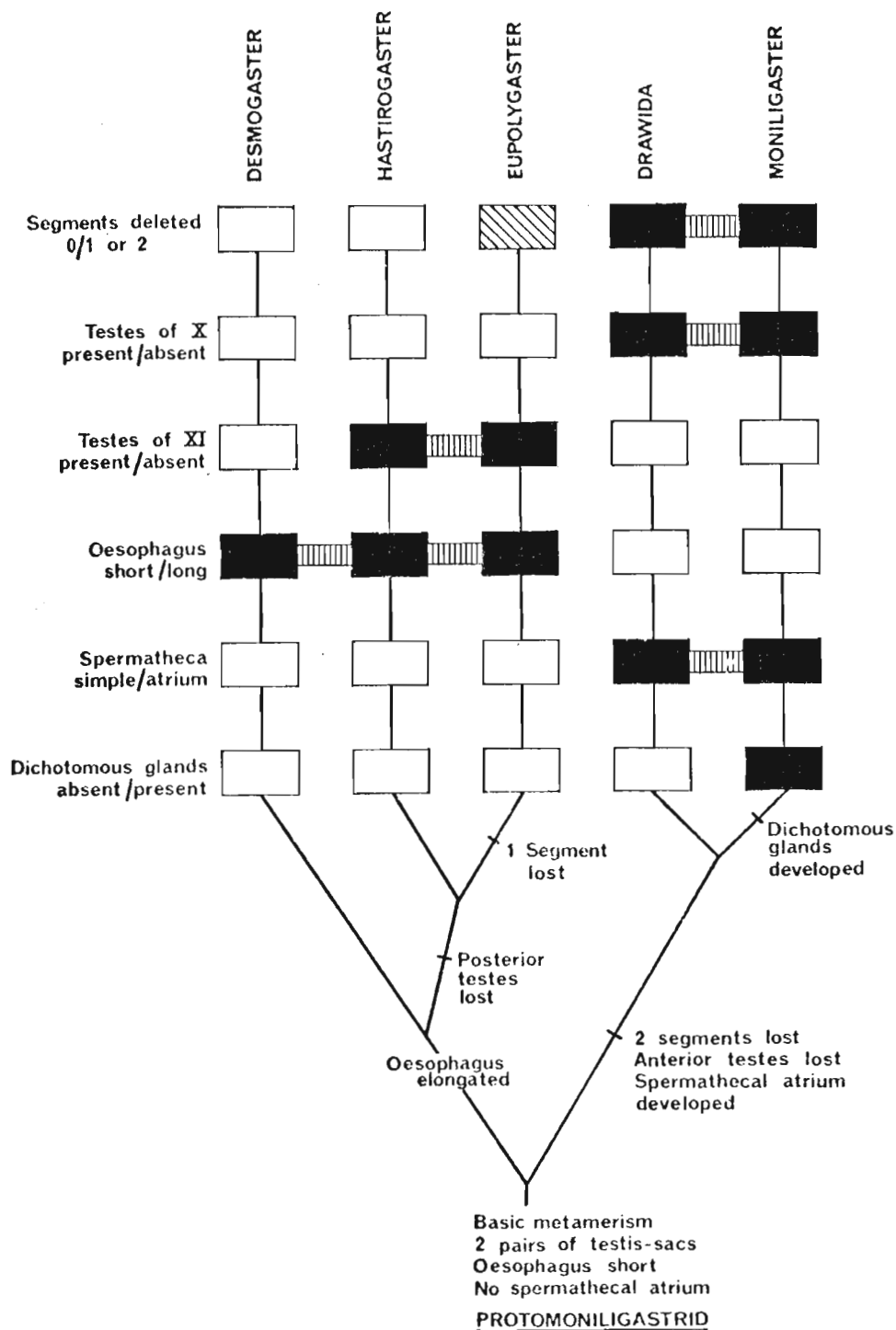
Fig.4. Phylogeny of the five moniligastrid genera utilizing only shared advanced characters (synapomorphies). The protomoniligastrid is envisaged as having the morphology of *Desmogaster* shown in Fig.3B but possessing a short oesophagus. Rectangles: blank = plesiomorph, black = apomorph, cross-hatched = non-congruent apomorphy (1 segment deleted as opposed to 2 in *Drawida-Moniligaster*).

posterior faces of septum 9/10, without mention of the sequence, in *Dr.flexa*, *Dr.constricta* and *Dr. gracilis* (*vide* Gates, 1933) and in *Dr. loricata, Dr. caenosa, Dr. exilis* and *Dr. fausta* (*vide* Gates, 1945b), to give some examples from this large genus.

In *Moniligaster* the vas appears to be invariably in IX before turning posteriorly to enter X and is known to loop around the hearts in IX in *M. aiyeri, M. cernosvitovi, M. deshayi, M. gravelyi, M. horsti* and *M. michael-seni*, to occupy IX before X in *M. stephensoni*, or to at least occupy both faces of 9/10, without mention of sequence, in *M. perrieri* (*vide* Gates, 1940).

Evidence for other genera is inadequate though in *Desmogaster sinensis* Chen (1933) describes the vas deferens as emerging from the ventral side of each sac, making a few coils, penetrating the septum into the preceding segment, in which it is thrown into a greatly coiled mass, and again passing through the septum to join the prostate gland.

Metamerism and evolution of the gonad battery in moniligastrids.

The new theory establishes the location of the testes in *Desmogaster*, the only genus of the family with two pairs, as segments X and XI, as in the Haplotaxidae and a presumed common ancestor shared with the latter family. Furthermore, *Desmogaster*, formerly supposed to have testes in XII (Gates, 1962, 1972) is shown to lack gonads in this segment though, as previously acknowledged, possessing ovaries in XIII. In the Haplotaxidae testes are in X and XI and ovaries in XII and XIII with a tendency to loss of the posterior ovaries, in XIII. Persistence of only the posterior pair of ovaries (the metagynous condition) in *Desmogaster* constitutes an interesting link between the Moniligastridae which (like the Haplotaxidae and Alluroididae) have a single layered clitellum and large-yolked eggs, and the earthworms (Glossoscolecidae, Megascolecidae, Lumbricidae, Eudrilidae and some lesser families) with their metagynous ovaries, small-yolked eggs and layered clitellum. A single species of the Haplotaxidae, *Haplotaxis brinkhursti* Cook, 1975, anticipates this link in being metagynous. The Alluroididae are also metagynous and have prostate glands similar to those of moniligastrids but have progressed further towards the organization of earthworm families in having the male pores in XIII (Jamieson, 1968, 1971a).

The following discussion of the five genera of the Moniligastridae is based on a comparison of the genital systems of the five genera with each other and with an imputed common ancestor (Fig.3) and on a phylogeny (Fig.4) constructed according to the principles of Hennig (1966) and accepting the main tenet of the haplotaxidan theory that testes in moniligastrids are primitively, as in *Desmogaster*, in X and XI (testis-sacs at 10/11 and 11/12). Fig.4 shows the phylogenetic relationships of the five moniligastrid genera in so far as they are deducible from simultaneous consideration of six major anatomical features which exist in what appear to be primitive (plesiomorph) or derived (apomorph) states, applying Hennig's reasonable, though not unquestionable principle that shared apomorph characters (synapomorphies) are significant in establishing relationship while shared plesiomorph characters (synplesiomorphies) are not. The six characters are: metamerism, unmodified (plesiomorph) or reduced by elimination of 1 or 2 segments (apomorph); andry, holandric (plesiomorph) or pro- or met-andric (apomorph); length of the oesophagus, short (plesiomorph) or elongated (apomorph); spermathecal atrium absent (plesiomorph) or developed (apomorph) and dichotomous glands absent from the atrium (plesiomorph) or present (apomorph - a consequential character which does not affect the phylogeny beyond establishing the greater apomorphy of *Moniligaster* over *Drawida*). Although the number of characters used is small, the phylogeny represents an advance over previous, intuitive, considerations based largely

on this same set of characters, selected because they are invariable, or nearly so, within each genus. Precisely the same phylogeny (cladogram) as shown in Fig.4 is obtained by applying the method for deducing branching sequences in phylogeny which was proposed by Camin and Sokal (1965). Before examining the phylogram it is necessary to return to Fig.3 which attempts to establish the homologies of the gonads batteries and testis-sacs in the five genera.

It must be stressed that, apart from the reconstruction of the organization of a precursor of the Moniligastridae (the "premoniligastrid"), all diagrams are of existing organization and that phylogenetic speculation is minimal. Evolution is deduced to have proceeded as follows. The premoniligastrid (Fig.3A) had testes on the anterior septa of X and XI with funnels on the posterior septa, each testis and corresponding funnel being enclosed in a longitudinal testis-sac. The pair of testis-sacs in each segment may have been in communication medianly as is usual in extant cleistorchous earthworms. At least one seminal vesicle would have been dependent from each testis-sac, notably into the succeeding segment. As already noted, the organization of *Desmogaster* suggests ovaries in XIII but a pair in XII, of the octogonadial set, may have temporarily persisted. Male pores were two pairs, as in *Desmogaster*, each in the segment behind the corresponding testis but not necessarily at the posterior border of the segment (i.e. the premoniligastrid may initially have been plesioporous). As spermathecal pores occur in 7/8 and/or 8/9 in *Desmogaster*, it is reasonable to envisage two pairs of spermathecae, in VIII and IX, corresponding with the two pairs of male pores. Last hearts would have been in XI as in *Desmogaster*, *Hastirogaster* and, when homologies here proposed are recognized, *Eupolygaster* (in X, originally XI) and *Drawida-Moniligaster* (in IX, originally XI).

A subsequent organization is envisaged (a "protomoniligastrid") in which the testis-sacs lost their connections with septa 9/10 and 10/11, giving typical moniligastrid testis-sacs suspended on the posterior septum and lacking separate seminal vesicles; ovaries in XII were lost. This protomoniligastrid organization agrees precisely with that of *Desmogaster* (Fig.3B) in which, however, there is a tendency to lose one or other of the pairs of spermathecae and in which the oesophagus has elongated.

Hastirogaster (Fig. 3C) is derived from a form with *Desmogaster* features by loss of the posterior testes and ducts (testis-sacs of 11/12) and, correspondingly, of the anterior spermathecae (of VIII).

Derivation of *Eupolygaster* Fig.3D) requires no change from the *Hastirogaster* condition other than elimination of an anterior segment. Occurrence of such a deletion is incontrovertible in *Tonoscolex* and *Nelloscolex* (*vide* Gates, 1962) and has occurred in *Digaster anomala* Jamieson, 1970, and *D. lumbricoides* (*vide* Jamieson, 1971b), apparently by loss of the division between the peristomium and first setigerous segment. That it is the anterior testis-sac which has persisted in *Hastirogaster* and *Eupolygaster* is indicated by the intervention of one free septum between the sac and the ovarian septum and by location of the last hearts in the segment behind the sac. In the phylogeny (Fig.4) it will be seen that *Hastirogaster-Eupolygaster* is the apomorph sister group of *Desmogaster*, the three genera sharing the apomorphic elongated oesophagus but *Hastirogaster-Eupolygaster* being advanced in loss of the posterior testes. *Eupolygaster* is the apomorph sister group of *Hastirogaster* owing to elimination of a metamere.

Moniligaster and *Drawida* (Fig.3E) have the ovarian septum next posterior to that suspending the single pair of testis-sacs, with the last hearts in the segment in front of the sacs. These facts indicate that they have lost the anterior testis-sacs. The ovaries and this posterior testis-sac are, however,

two segments in front of their primitive *Desmogaster* location. Two anterior
segments have therefore been deleted and, from Fig.4, both independently
of elimination of one segment in *Eupolygaster*. Whereas the observed ovarian
segment is XI, the homeotic equivalent of XIII, location of the spermathecae
in VIII would give an original segmentation of X. It is rare for the sperm-
athecae to occur behind IX in oligochaetes (exceptions are the highly modified
Eudrilidae, and Almidae and many Lumbriculidae) and it is therefore very likely
that the second segmental deletion in the origin of *Moniligaster-Drawida*
was loss of primitive segment X, bringing the last spermathecal segment (IX)
into conjunction with the segment containing the last hearts (XI).

In Fig.4 *Moniligaster* and *Drawida* are seen to comprise the apomorph
sister group of all other moniligastrids. None of their apomorph characters
is shared with the other three genera: deletion of two segments, loss of the
anterior testis-sacs or development of a spermathecal atrium. *Moniligaster*
is the apomorph sister group of *Drawida* by virtue of the development of
dichotomous glands on the atrium. Taxonomic implications of Fig.4 are that
Moniligaster and *Drawida* jointly are very distinct from *Desmogaster-Hastirogaster-*
Eupolygaster but that *Moniligaster* may be no more than a species-group of a
genus composed of the species currently placed in it and *Drawida*. (For an
excellent discussion of species groups within *Drawida* see Gates, 1962). Fig.4
also suggests that, even if *Hastirogaster* be considered generically distinct
from *Eupolygaster*, and this is questionable, *Desmogaster* is more distinct
than either is from the other.

Chorological progression in moniligastrid genera

The phylogeny presented in Fig.4 can be related generally to the spatial
distribution of the five moniligastrid genera though not in detail; that is,
chorological progression (*sensu* Hennig, 1966) is partially demonstrated. It
is possible that some of the lack of congruence is due to polyphyly or to
parallelism in at least *Hastirogaster* for the autoapomorphy, loss of posterior
testes, could have occurred independently in the Burmese and Sumatran branches
of this genus. Nevertheless, if the concept of chorological progression be
accepted (that the most apomorphous members of a group are furthest dispersed
from the focus of origin of the group) it must be inferred that the family
originated to the east of India and that peninsular India has been colonized
(by the highly apomorphous *Drawida*) from the north after the Cenozoic collision
of India with Asia. Restriction of the ultimate genus, *Moniligaster*, to
southern India would then indicate that this region was the last to be colonized,
Moniligaster being derivable from *Drawida*.

The fact that *Eupolygaster* occupies Borneo and Sumatra and is the apomorph
sister group of *Hastirogaster*, from Burma and Sumatra, and that the very
primitive *Desmogaster* occurs in Burma, China, Borneo and Sumatra, suggests that
the Indonesian (and Chinese?) distribution is secondary and that origin of the
moniligastrids may have been near Burma. It is noteworthy that Gates (1972)
suggests origin in the nearby Malay archipelago. Origin of protomoniligastrids
in south-east Asia may have occurred after the Triassic rifting of Laurasia from
Gondwanaland followed by entry of moniligastrids into India in the Tertiary.

Selective advantage of moniligastrid testis-sacs

No clear advantage is evident favouring selection for detachment of the
testis-sac from its anterior septum to give the moniligastrid type of sac. Its
development has certainly proved very effective in combination with other
characters, however, as *Drawida* has become one of the largest genera of the

Oligochaeta, with a range (Gates, 1972) exceeding that of *Pheretima s.lat.*
The remarkable similarity of the testis-sac and male ducts to the spermathecal
apparatus possibly offers a clue to the development of the moniligastrid
testis-sac. The spermathecae are almost unique in the Oligochaeta in the
extraordinary length of their ducts, a development paralleled by the great
length of the vasa deferentia which Bourne (1894) found to measure 9½ inches in
Drawida grandis, a length which is all the more remarkable as they traverse
only a single segment. A further similarity between the spermathecal and male
apparatus is that the spermathecae in *Drawida* and *Moniligaster* have atrial
enlargements at the ectal ends of their ducts which are reminiscent of the prostat-
es at the ends of the male ducts. Such virtual mimicry extends in *Drawida gisti
anchingiana* to replication of the accessory gland at the pore.

To reject the possibility of a common morphogenetic controlling mechanism
shared by the male and spermathecal apparatus as fanciful would seem premature
and the possibility of such a morphogenetic link is here proposed as worthy
of investigation. Spermathecae and prostates are considered to have originated
by specialization of ectodermal glands (the X glands of Gates, 1972) and although
the vasa deferentia and testis-sacs are presumably mesodermal while the sperm-
athecal ampulla and duct are regarded as ectodermal, these spermathecal com-
ponents clearly have mesodermal elements, including, unless it be myo-epithelial,
the musculature. Such a common morphogenetic control may account for the indep-
endence of the testis-sac from its anterior septum, paralleling the discrete-
ness of the spermathecal ampulla. It is noteworthy that, notwithstanding the
basic relationships of the sacs to particular septa demonstrated above, the
testis-sacs may develop a remarkable degree of autonomy, frequently being found
one to several segments anterior or posterior to the septum normally suspend-
ing them.

The functional significance of the very long, much coiled vasa defer-
entia may be, as Gates has suggested, storage of sperm in the absence of
discrete seminal vesicles, the ental portion of each vas being gorged with
sperm. It would not seem necessary,however, for the spermathecal duct to sub-
serve this function as, unlike the testis-sac, the lumen of the spermathecal
ampulla is not occluded by developing sperm morulae.

While this hypothesis of morphogenetic similarity of male and spermathecal
apparatus is advanced with much hesitation, it is felt that the haplotaxidan
theory and attendant phylogenetic discussion can be proposed with considerable
confidence.

Primitive oligochaetes, prosopores or plesiopores?

Derivation of the Moniligastridae from an ancestral stock which was not
only octogonadial but, like the haplotaxids, had reached the first stage of
opisthopory, implies that the Moniligastridae are further removed from the
supposedly prosoporous prehaplotaxid ancestral Oligochaeta than was suggested
by Brinkhurst and Jamieson (1971). Accepting Gates' interpretation of the
moniligastrid testis-sac, we implied a prosoporous condition for the Monili-
gastridae. The view that the prosoporous condition is primitive and ascribable
to the earliest precursors of all extant oligochaete groups is based on the
reasonable premise that gonoducts in oligochaetes are coelomoducts and that
primitively coelomoducts opened to the exterior in the segment the coelom of
which they drained.

Clark (1969) correctly observes that Goodrich (1946) envisaged coelomo-
ducts to penetrate a septum and to discharge in the segment behind, a sit-
uation which would necessitate regarding the plesioporous condition (in which
the vas deferens extends for only part of the segment posterior to the septum
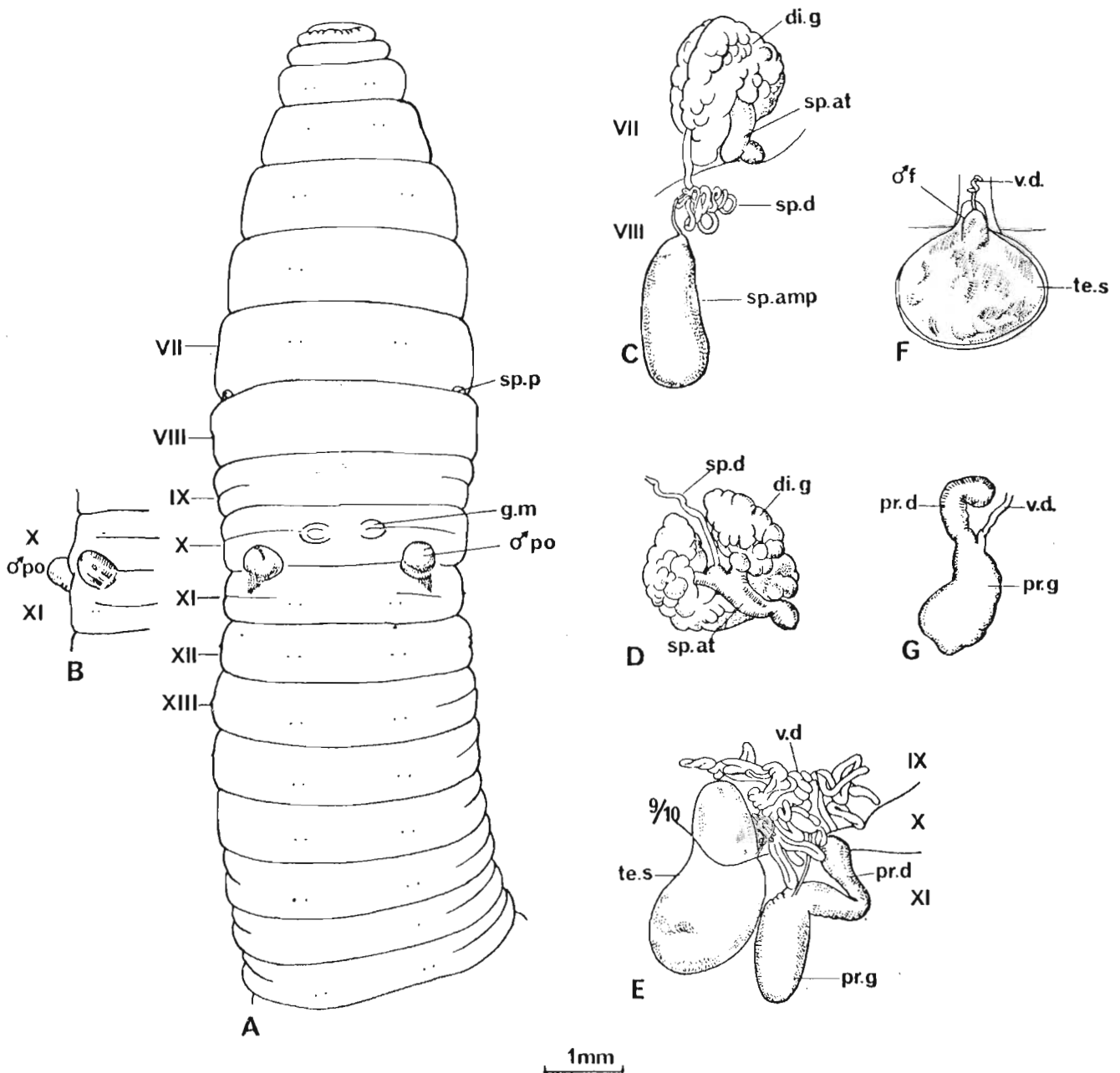bearing the corresponding sperm funnel) as primitive. The concepts of basically

Fig.5. *Moniligaster troyi* sp.n. Holotype. A, ventral view of anterior region. B, lateral view of male porophores. C, right spermatheca *in situ*. D,ventral view of spermathecal atrium showing Y-shaped branching with the two horns receiving the dichotomous glands and the intervening region receiving the slender spermathecal duct. E, left testis-sac (turned over to expose ventral surface) and atrium; the two are connected by the much-coiled vas deferens. F, right testis-sac viewed ventrally showing the sperm funnel seen through its semi-transparent wall.G, right atrium. di.g, dichotomous gland; g.m,genital marking; ♂po,male porophore; pr.d, prostate duct; pr.g,prostate gland;sp.amp, spermathecal ampulla; sp.at, spermathecal atrium; sp.d, spermathecal duct; sp.p, spermathecal pore; te.s, testis-sac; v.d, vas deferens. (All by camera lucida).

prosoporous coelomoducts and of a prosoporous ancestry of the oligochaetes are here maintained, however. It must be emphasized that, although it is considered sufficient to postulate an octogonadial (and plesioporous to opisthoporous) ancestry for the Moniligastridae, Gates' view (1962) that primitively oligochaetes may have had a longer series of gonads is not opposed.

Systematics

Moniligaster troyi sp. nov.

Fig. 5

Length 63, 60 mm, width (midclitellar) 3.5, 3.7 mm, segments 153, 123 (H,P; H with 2 helicometameres posteriorly). Body moderately slender; posterior extremity tapering to a point; segments I and II, especially the former, very short; anus a dorsoventral terminal slit; cross section circular; lateral lines and parietal thickening absent. Pigmentless in alcohol. Prostomium withdrawn; small, prolobous, but not attached to I. Dorsal pores absent. Setae 4 pairs per segment in regular longitudinal rows throughout; commencing in II (H) but minute and difficult to discern, especially in the first few segments (H,P); in XII $aa:ab:bc:cd:dd$ = 9.6:1.0:10.6:1.0:36.6; circumference 8.6 mm (H; obscured by the clitellum,P). Nephropores inconspicuous, anterior in their segments in d (including VII, VIII and X); visible externally from V to the caudal extremity (H,P); in XII and XIV in b (left) or d (right); in XVII lateral of b (left) or d (right); in XVIII in d (left) or b (right); behind this with only few, sporadic dislocations (H). Clitellum unrecognizable (H) or moderately protuberant owing to annular yellowish tumescence, though with deep intersegmental furrows retained, in X-XIII, and weaker in ½IX and all XIV. Male terminalia evaginated as a pair of long cylindrical pseudopenes in intersegment 10/11, at about one fourth bc lateral of b lines (H); pseudopenes and pores not visible in P. Female pores? A unilateral left pore anteriorly in XII in ab (visible in H only) may be a female pore but a similar pore in b in XIV is a nephropore (nephropores not discernible in d on this side in these segments. Spermathecal pores a pair of transverse slits (H) or externally visible on left only (P) with puckered lips forming an elliptical papilla, in 7/8, in c lines.

Internal anatomy (H): Septa: delicate or absent anterior to 6/7; 6/7 - 8/9 strongly thickened; the remainder thin; 10/11 not recognizable; 11/12 and 12/13 uniting dorsally above the gut at the level of the origin of the ovisacs but separating again further dorsally. Brain at the posterior limit of III(?); lateral nerves from ventral cord 2 anteriorly and 1 posteriorly on a side in each segment. Dorsal blood vessel single, traced as far anteriorly as IV: dorsoventral commissural vessels in VI - IX, subequal, heartlike; none further posteriorly. Supra-oesophageal vessel absent. Latero-oesophageal vessels a pair of large trunks in VI (slender more anteriorly?) to VIII in which they curve medially below the gut. Subneural vessel large, becoming slender anteriorly, in VII. Alimentary canal to IV enveloped in large (pharyngeal?) glandular masses. Oesophagus in V - XI not evidently modified; in XII with some muscularization giving a transitional stage towards development of a gizzard; in XIII forming a moderately muscular though still small gizzard; in each of XIV and XV with a large muscular gizzard (H,P); thinner walled canal commencing in XVI but (P) not thin walled until XXVII at the anterior septum of which there is a valve (oesophageal valve?); typhlosole absent. By XIX short vessels arising from the dorsal vessel anteriorly in each segment have become a pair of nodes or glomeruli sending vessels to the roof of the intestine, the enterosegmental

organs. Nephridia stomate exonephric holonephridia first certainly recogniz-
able in V in which they are enlarged; preseptal funnels demonstrated for ant-
erior intestinal region; these nephridia have a very long slender blind
diverticulum curving dorsad around the oesophagus, almost meeting that of
the other side, the caecum joining the ental end of a short fusiform bladder
but describing a short loop, with conjoined limbs, at the junction with the
bladder; the slender ectal duct of the nephridial body joining the bladder
alongside the junction of the latter with the caecum. Testes and funnels in
a pair of large diaphanous iridescent testis-sacs; the left sac suspended
by septum 9/10 so that its major portion is in X; the right sac suspended
by septum 11/12 (i.e. 2 septa behind the left sac) with its major part in
XII and only a small narrow protuberance into XI; the vas deferens from each
testis-sac joining the sac ventrally at the anterior face of the supporting
septum and passing into the anterior segment abutting on the septum; very
long and much coiled in this segment, numerous coils nearest the sac being
narrow and iridescent but by far the greater length wider and non-iridescent
with many hair pin bends and forming a cluster in IX intermediate in volume
between the smaller right and larger left testis-sac; the latter region
continuing, still much coiled, to join the glandular portion of the prostate
gland in XI, without penetrating the body wall musculature, nearer the ectal
end than the ental end of the prostate and about two thirds of the length of
the entire prostate glandular portion plus muscular duct from its ectal end.
The vas deferens immediately within the testis-sac, in IX, giving rise to
several iridescent (ciliated?) ribbons which pass posteriorly for the entire
length of the walls of the sac and appear to represent a backwardly directed
sperm funnel; the sac filled with a loose yet firm (testicular?) tissue containing
relatively few free spermatozoa. Each prostate extending from its pore at
10/11 to intersegment 13/14, with clavate superficially slightly lobulated
glandular portion and muscular duct poorly differentiated from the gland and
about one third the total length of gland plus duct; the gland sharply bent
near the ectal end of the glandular portion and the ental end of the duct;
the duct forming a round swelling at the pore. Elongate, folded (fanlike)
laminae on the anterior septum of XI (?) are apparently the ovaries; oviducal
funnels not recognizable; large elongate lobulate ovisacs extending into XIII;
but arising from septum 11/12 against which septum 13/14 is adpressed; some
lobules each containing a large-yolked egg with conspicuous nucleus. Sperm-
athecae 1 pair, each with a large elongate-ovoid ampulla in VIII, its duct
very long and much-coiled in this segment but almost straight after passing into
VII where it joins the apex of the wide muscular ectal spermathecal duct, the
latter duct with two branches or horns, one on each side of the apex, each of
which bears a large lobulated gland (dichotomous gland); the two glandular
masses adherent along a line which arises from the point of junction of the slender
ental spermathecal duct and continues to the apex of the combined glandular
mass; this spermathecal gland, with the ectal spermathecal duct discharging at
intersegment 7/8, constitutes the "spermathecal atrium".

Material examined

From 77°16'27" E.10°08'21"N,Vanderavu Range, Palni Hills, border between
Kerala State and Tamilnadu, hilly summit of a local dome. Soil type: montane
humic ferrallite (with highly organic upper horizons) constituting a typic
gibbsihumox (humic ferralsol); pH upper horizon 4.9; water 1/2.5, collector
Professor J.P. Troy - Holotype (H), British Museum (Natural History) Registration
Number 1978. 1.10; paratype (P) BM(NH) 1978.1.11 (sagittal half) and author's
collection (longitudinal serial sections of other half).

Remarks

Previously known species of *Moniligaster* differ from *M. troyi* in at least the following respects: *M. aiyeri* Gates, 1940; gizzards in XVI-XXIII; intestinal origin c. XXXI; prostatic capsule spheroidal; vas deferens passing under longitudinal parietal muscle. *M. cernosvitovi* Gates,1962: gizzards in XV-XXII; intestinal origin c. XXI. *M. deshayesi* Perrier, 1872;gizzards in XIV-XX; intestinal origin c. XXVII; prostates rodlike; thickened portion of vas deferens short; leaflet glands opening into the vas and prostate. *M. gravelyi* Stephenson, 1915: gizzards in XIII-XVIII; intestinal origin c. XXV; prostates straplike but capsule deeply incised; atrial gland of spermatheca single. *M. horsti* Gates, 1940: gizzards in XIV-XVIII; intestinal origin c. XXIX; vas deferens passing under parietal musculature. *M. michaelseni* Gates, 1940: gizzards in XVI-XXI; intestinal origin c. XXIX; prostate and duct bound to parietes in C-shaped figure. *M. perrieri* Michaelsen, 1907: gizzards in XIII-XIX; intestinal origin XXVIII; prostate capsule reniform. *M. stephensoni* Gates, 1940: gizzards in XIV-XXII; intestinal origin c. XXX-XXXIII; prostatic capsule flattened lateromesially, and not covered by glandular layer; vas deferens passing under parietal musculature.

The most distinctive feature of *M. troyi* is thus the extraordinarily anterior commencement of the gizzards, in XIII with a rudiment in XII. The gizzards commence in XIII in *M. gravelyi* (from Trichur, Cochin State) but there the spermathecal gland is not bifid.

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