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 (Michaelsen, 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 supressed 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

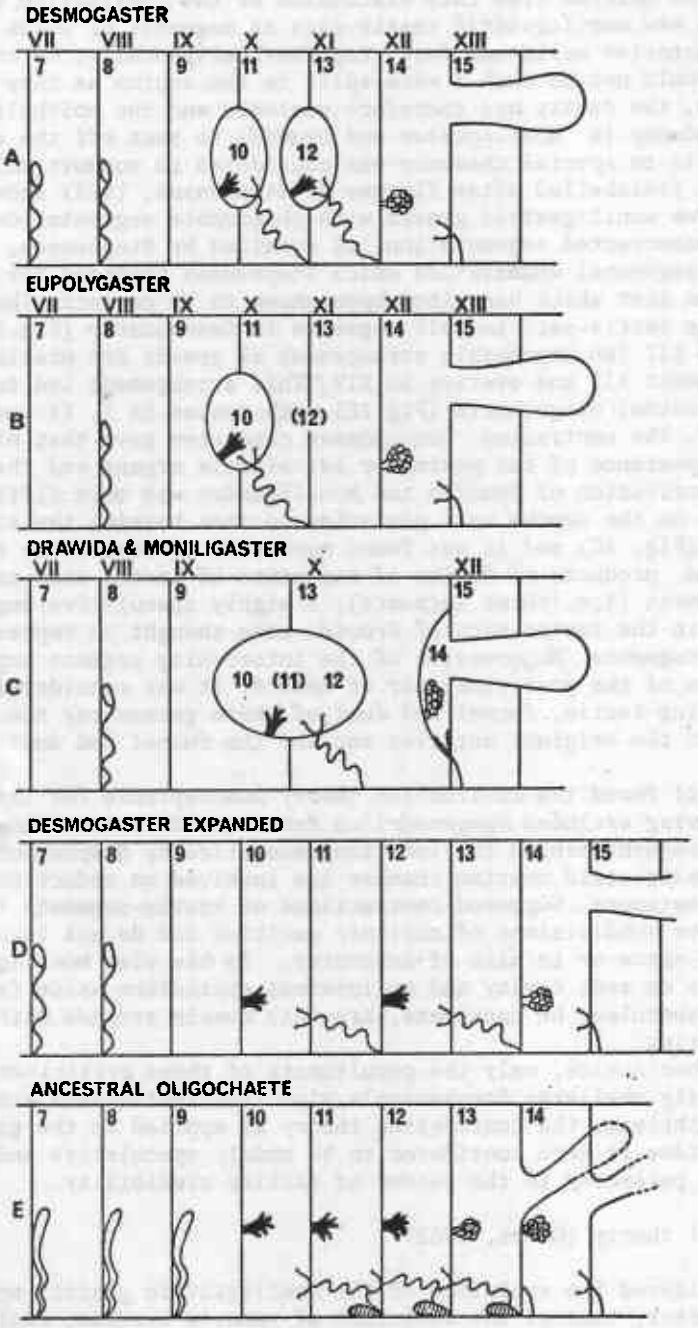

Fig.1. The contraction theory of Stephenson. Observed segmentation in roman numerals; supposed basic segmentation in arabic numerals. A, primitive condition as in *Desmogaster*. B, *Eupolygaster* derived by loss of the posterior testis-sacs and of segment 12. C,*Drawida* and *Moniligaster* derived by 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).

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-

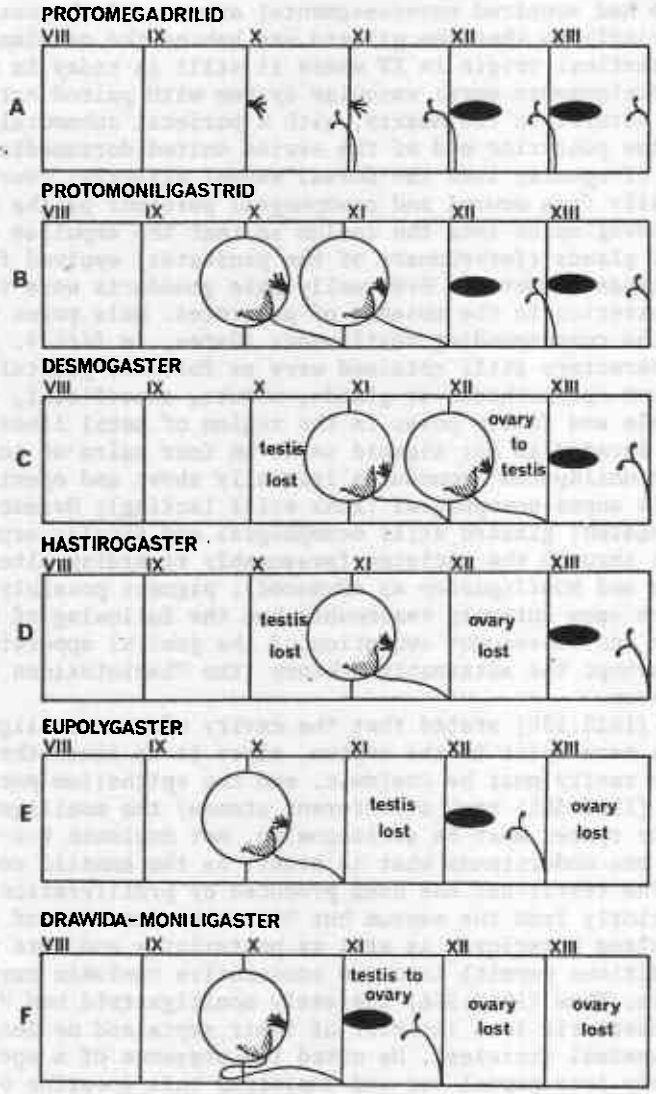

Fig.2. The sex-reversal theory of Gates. A, octogonadial, prosoporous protomegadrilid. B, protomoniligastrid derived from A by proliferation of the testes into their septa and incorporation of the sperm funnels in the testis-sacs thus produced. C, *Desmogaster* derived by loss of anterior testes and 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).