# THE EARTHWORMS OF BURMA. VII[1]

## THE GENUS *EUTYPHOEUS*, WITH NOTES ON SEVERAL INDIAN SPECIES.

*By* G. E. GATES.

CONTENTS



### Alphabetical list of species



[1]For the earlier parts I to VI of the series *vide* Gates, G. E., *Rec. Indian Mus.* XXXII, pp. 257-356 (1930); XXXIII, pp. 327-442 (1931); XXXIV, pp. 357-549 (1932); XXXV, pp. 413-606 (1933); XXXVIII, pp. 377-468 (1936); LII, pp. 55—93 (1954).

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Alphabetical list of species—*contd.*



## INTRODUCTION

The material with which this contribution is concerned was collected in Burma during the period from 1932 to the end of 1941, at which time the author's survey of the earthworms of that country was terminated by the Japanese invasion, and in India during the war. The Indian material comprised nearly ten thousand specimens, mostly from the Gangetic valley, all of which were identified. Locality records have been published elsewhere but a study of variation in the Gangetic forms had not been completed when return to Burma, as hostilities ceased, compelled abandonment of the project.

In this genus it was formerly thought (Stephenson, 1923, p. 428) that species are so much alike morphologically that their discrimination depended almost wholly on genital markings, penial setae and spermathecal diverticula, structures already known to be "extraordinarily variable" Many of the characteristics on which reliance had been placed were found, on examination of previous Indian material (Gates, 1938), to be of little or no taxonomic value. Even the dozen odd characteristics provided by the author's Burmese studies were inadequate for determining the status of several species. These, all still doubtful today, were represented in museum collections by a single worm, or several specimens and then usually from one locality, sometimes poorly preserved or even too immature to permit recognition of important specific characteristics. Short series of better preserved adult worms already had been found to be insufficient in Burma. Because of difficulties occasioned by absence of good criteria for specific distinction and by variation in the characteristics that had to be used—some of it of a nature regarded as "reversionary"—the genus *Eutyphoeus* was omitted from annual reports of progress on the survey of the earthworms of Burma after 1932. Meanwhile efforts were made to secure as much material from as many localities as possible. Abnormal or monstrous individuals, as well as juveniles that could be identified with some degree

of certainty, were also studied for any light they might throw on some of the problems that were involved. Finally, types and most of the previous material of Burmese species were re-examined.

Gradually it became clear that species from widely separated portions of the generic range could not be as closely related as the similarity in their morphology might suggest. Independent attainment of a similar grade of morphological organization then required that ancestry be taken into consideration. Recognition of evolution now under way or recently completed led back through earlier stages of intrageneric developments to an examination of phylogenetic relationships in the oriental section of the subfamily to which *Eutyphoeus* belongs. Determination of the changes that had taken place in the evolution of that group then provided a basis for a preliminary consideration of the mechanism by which those changes had been brought about.

Certain modifications of long established conventions have become advisable in the interest of more concise topographical characterization. These, and additional abbreviations, as well as several of the less familiar special terms are explained in the next section.

*Conventions and terminology.*—The letters *a*, *b*, *c*, *d*, as in the past, designate the setae of a segment in order from the midventral level laterally. The same letters are now capitalized to indicate meridians of longitude passing across the follicle apertures of those setae. Combinations such as *AA*, *BC*, *CD*, etc., designate the interval between two meridians, usually on the ventral side, though *DD*, like *dd* previously, refers to the dorsum unless the context requires the contrary.

D, V, L, are abbreviations for dorsal, ventral, lateral, and mD, mL, mV, indicate mid-dorsal, mid-lateral, mid-ventral points, sites, or segmental meridians. C( =U in German publications), as in the past, stands for circumference.

Equatorial, in this genus, coincides with an arc or circle across apertures of setal follicles of a segment and aq or pq indicate in front of or behind the equator, *i.e.*, presetal or postsetal.

Battery, when not used in connection with spermathecae or prostates, includes all of the setae adjacent to a prostatic duct. In *Eutyphoeus* a battery comprises the *a* and *b* setae of a side with each of which there is often associated a rank of reserves of gradually decreasing size.

Vestibulum, an invagination restricted to the parietes or protuberant into the coelom, containing the portion of the body wall bearing the fissure. Not to be confused with fissure, as sometimes in the past.

Vestibulate, having a definite vestibulum. Avestibulate, without a vestibulum.

Fissure, a shallow, transversely slit-like depression in an outer portion of the parietes, usually in region of *AB*, containing apertures of the penisetal follicles, male deferent and prostatic ducts.

Arsenosomphic, with male genital terminalia.

Anarsenosomphic, without male genital terminalia *i.e.*, male pores, and associated structures such as porophores, prostates, prostatic ducts, other glands, penes, fissures, vestibula, copulatory chambers, etc.

Holonephric, with one pair of funnelled (stomate) nephridia per segment, each nephridium with a parietal nephropore.

Meronephric, with more than two nephridia per segment.

Exonephric, with parietal nephropores.

Enteronephric, opening into the gut.

Stomate, with a funnel (nephrostome), with reference to nephridia. Astomate, without a funnel.

Thecal, provided with spermathecae.

Athecal, without spermathecae.

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## Systematics

The classification herein followed is that of Stephenson (1930). This has been obsolete for some time, so far as the Megascolecidae is concerned, but the only alternative available, that of Michaelsen (1928), gives even greater taxonomic value to a character now known to be acquired independently in different evolutionary lines (cf. p. 221).

### Family Megascolecidae

### Subfamily *Octochaetinae*

### Genus **Eutyphoeus** Michaelsen 1900

Certain characteristics no longer need mention in specific descriptions though they were recorded in the laboratory during dissection to prove this very statement. Among them is an intestinal origin in (xv) (some data in, Gates, 1933, p. 561). Deviation has been found only in association with metameric anomaly and each case is recorded below in the appropriate section on abnormality. A pair of hearts is almost always present in xiii (*loc. cit.* p. 561) and any deviation therefrom likewise has been mentioned below. No variation was found, in any of the numerous dissections that were made during some twenty odd years, as to presence or absence of: gizzard, calciferous glands (or in their basic structure), ventral intestinal caeca, typhlosole, supra-intestinal glands, or pharyngeal nephridia. Nor was any variation found as to number of gizzards, calciferous glands and bands of pharyngeal nephridia. The location of those organs always was the same, except in rare monstrosities. Variation as to absence of septa 6/7-7/8, and as to posterior displacement of subsequent septa, again was associated only with metameric anomaires.

The typhlosole always seems to be folded in a regularly zigzagged manner, with ventral margins of folds united. The folding is less obvious in small species and gradually disappears in all of them as the ridge becomes more translucent posteriorly. The typhlosole always terminates with supra-intestinal glands, supposedly hepatopancreatic in function. These glands are two pairs per segment with slight antero-posterior increase in size recognizable in each individual. Occasionally only two glands are present in the first gland segment (posterior half) and they may be so small as to be concealed from view beneath the distended dorsal blood vessel. Openings from gut lumen into the glands rarely were seen. When recognizable they were quite obvious and in a single longitudinal row at mD (ten noted in several specimens of *bifovis*).

The medianmost nephridium on each side in posterior segments of the body always appears to be stomate. The number of segments in which such funnels are present seems to be variable. All nephridia of the anterior segments and the lateral ones posteriorly always appear to be astomate. The pharyngeal nephridia usually have been said to be in an annular or horse-shoe-shaped parietal band. With relaxation a shortly and closely zigzagged arrangement of the cord (duct) to which the tubules are attached becomes recognizable. Although so noted only in a few species below this arrangement may be generically characteristic. The material available usually has not been in satisfactory condition for study of these minute organs and especially those in the region of *BC* where tubules usually are closely crowded together in strongly contracted specimens. Reference to number of longitudinal ranks in the posterior portion of the body accordingly has been omitted in the specific accounts. Several sample determinations are as follows: six ranks, one at *A*, *C*, and lateral to *C* on each side (*pusillulus*); three (?) in *BC*, one at *D*, two laterally (*compositus*); three (?) in *BC*, one at *D*, five laterally (*cochlearis*); several in *BC*, six lateral to *D*, with an occasional seventh tubule (*foveatus*), but only three to six ranks in mutant forms (Thanbula and Laboo); twenty ranks (*rarus*); 24 ranks, 12 on each side, several closely crowded in *BC* (*gigas*). Variation in the excretory system now appears to be of a minor nature and limited to inter-and intra-specific differences in number of times paired embryonic anlage are transversely split.

Data as to variation that is, or promises to be, of some taxonomic value has been included in accounts of the various species. Segment number, however, had not yet been studied when the work was ended.

A bulbus ejaculatorius always is present but variation as to size, muscularity and extent of concealment in the parietes appears to be about the same in a number of species. Similar variation may be shown in length of the prostatic ducts (8-21 mm in *rarus*). Number of seminal chambers in a spermathecal diverticulum may vary from one to twelve differences noted on opposite sides of the same spermatheca as well as between spermathecae of the same individual. When chambers are numerous they may be in a single row or in a some or less compact and berry-shaped mass

Additional general observations are as follows. Pigmentation refers hereinafter to a dark deposit responsible for a characteristic velvety brown appearance of the dorsum in certain species. A green color has been noted in *bifovis* (living and preserved ) and *gammiei* (after preservation). No corresponding deposit in the ventrum has been found and the color disappears regardless of preservative. A blueish grey coloration in several batches of unpigmented worms also disappeared after preservation. Pigment is only slowly bleached out in formalin but does disappear, in certain conditions, after some years.

The cuticle turns in at the anterior end of the body and is continued through the buccal cavity, pharynx and gizzard where it is thickened and much tougher. Behind the gizzard the cuticle usually is unrecognizable but in macerated specimens (*annulatus*, *compositus*, etc.) a complete layer has been recognized back into xi.

Calcareous material between the lamellae of the calciferous gland always has been finely granular though larger aggregates have been found just dorsal to the lamellae.

Species are arranged below in groups for the first time but for easy reference an alphabetical list is provided on pp. 93, 94.

Frequent reference is made hereinafter to a hypothetical ancestral form from which all species of the genus can be derived. As certain structural details irrelevant to the particular discussions were omitted therein, a more complete characterization of this form, as it is now visualized, is subjoined.

## The proto-eutyphoeus stage

Biprostatic, ducts of tubular glands opening to exterior in or close to *AB* (probably aq), on segment xvii. Male pores, external apertures of united male deferent ducts of a side, in *AB*/pq, on xvii. Bithecal, each spermatheca with a simple median and lateral diverticulum and opening to the exterior in the region of *AB* on intersegmental furrow 7/8. Female pores on xiv/aq at or near A, each pore at ectal end of a short oviduct with funnel in xiii. Setae four pairs per segment, in eight regular longitudinal ranks all within the ventrum. Septa between vi-vii and vii-viii aborated during embryonic development. Digestive system with one large gizzard formed by thickening of the muscular layer of that portion of the oesophagus belonging to vi, one pair of intramural calciferous glands in xii, intestinal origin in xv, a medium typhlosole ending with a short series of doubly paired supra-intestinal (hepatopancreatic?) glands, short lateral typhlosoles anteriorly, a midventral rank of small anteriorly directed, intestinal caeca one in each of several consecutive segments. Circulatory system with a single dorsal vessel, paired lateroparietal trunks instead of one subneural, paired latero-oesophageal hearts in x-xiii. Excretory system meronephric, nephridia all small, exonephric except in iii, astomate except for the medianmost on each side in posterior segments, nephridia of iii opening into the

pharynx. Reproductive system with testes in x and xi, seminal vesicles in ix and xii, ovaries in xiii.

The soma may well have comprised 150 or more segments, for all spcies of *Eutyphoeus*, as well as those of the two most closely related genera, do have that number.

## THE *hastatus* GROUP

### **Eutyphoeus hastatus** Gates 1929

1

Thayetmyo, August, 0-2-37. K. John.

Magwe, August, 0-1-21. K. John.

*External characteristics.*—Length, 80-180 mm. Diameter, 3-5½ mm. Unpigmented, as also in case of all material considered below. The *b* setae of xix, ornamented with transverse rows of fine teeth, are 0·35 mm long, 30μ thick (Magwe), 33μ (Thayetmyo). First dorsal pore on 10/11 or 11/12 and then often with a pore-like but apparently imperforate marking on 10/11. Clitellum reddish but not protuberant.

Spermathecal pores small slits in lateral half of *BC* or with centers at or just median to *C* (half of the Thayetmyo worms). Female pores both present (50), on or very slightly median to *A* and in a single, transversely placed, whitened area of rather indistinct outline that reaches into *AB*.

Male porophores distinctly demarcated, elliptical areas of slight parietal thickening and convex surface, extending from about *mBC* into a lateral portion of *AA*, transverse or slightly diagonal and then convergent anteriorly. A lateral portion may be widened and slightly more protuberant. The transversely slit-like fissure containing male and penisetal follicle pores is just lateral to *B* and is so small as to be practically filled by the thickened tip of one penial seta. Margin of the slit very rarely whitened and slightly protuberant but the tumescence scarcely deserves characterization as an annulus.

Genital markings primarily presetal but may include ventral setae, extending laterally to *A*, into *AB*, to or very rarely slightly beyond *B*, separated midventrally by a narrow median strip of unmodified epidermis, in contact but not united midventrally, margins united but greyish translucent central portions discrete, or central areas also united when only evidence of union (occasionally lacking) is provided by slight incisions at mV of anterior and posterior margins. An extra marking on xix (7 Thayetmyo, in 3 of which marking is rudimentary). Extra markings on xix and xx (2 Thayetmyo).

*Internal anatomy.*—Typhlosole begins in xxvii (1), xxvii (13), xxix 25) or xxx (4). Lateral typhlosoles always present (60), in caecal segment and that next behind. Caecal aperture only slightly smaller than caecal lumen. Ventral caeca in xxxii-lvi (1 Magwe), xxxii-lviii (1 Thayetmyo), xxxiii-lvii (2 Magwe), xxxiii-lviii (1 Magwe).

*Location of supra-intestinal glands*

| Segments | Number of specimens from Thayetmyo | Magwe |
|---|---|---|
| 76—80 | .. | 2 |
| 77—80 | 1 | |
| 77—81 | 7 | 7 |
| 78—81 | 5 | 1 |
| 78—82 | 8 | 5 |
| 79—82 | 5 | .. |
| 79—83 | 6 | 2 |
| 80—84 | .. | 2 |
| 81—85 | 2 | .. |

Circulatory system as in *gigas*, as also in case of all material considered below, except that the extraoesophageals are connected by a transverse vessel just behind 5/6, and the dorsal trunk is uninterrupted (60). Commissures of v almost always large and filled with blood.

Holandric, male funnels of x iridescent, testis sac annular (60) and when much distended by testicular coagulum often opened even by a cautious mid-dorsal incision. Seminal vesicles of ix, always present, reach up to or nearly to dorsal trunk and often bulge 8/9 anteriorly, especially ventrally. Vasa deferentia of a side usually come into contact in xii but do not unite until xvii. Bulbus ejaculatorius white, firm, elongate, coelomic, occasionally with slight sheen.

Spermathecal duct short, soft, white, lumen irregularly slit-like in cross section due to presence of vertical ridges, one on posterior wall often higher than the others and with a vertical groove, a similar ridge occasionally also on anterior wall. Diverticula median and lateral (119 spermathecae), elongate, widened entally, sperm marked off (especially entally) by fine greyish lines into spheroidal to shortly ellipsoidal masses. Each diverticulum of one worm has a slender stalk with several small, ellipsoidal seminal chambers entally. Median diverticulum of left spermatheca lacking (1 Magwe). An extra diverticulum on posterior or anterior face of duct of one spermatheca (2 Magwe). Lateral diverticulum in two discrete portions (1 Magwe).

Soft (glandular?) material in white cords somewhat similar in appearance to nephridial tubules passes downwards between strands of longitudinal musculature over sites of lateral portions of genital markings.

Penial setae (36 Thayetmyo and Magwe) 2·40-3·55 mm long, 45-75$\mu$ thick at base, 30-48 at neck, 42-75 at blade, 25-40 at tip. Shaft straight except for a slight curve at ectal end, yellow to neck, red ectally. Tip with widened blade tapering to a point. Ornamentation of transverse rows, of three or more fine spines, closely crowded ectally, more widely spaced entally and with more variation in size and shape of spines, in two worms in regular circles. Number 8-11 (36 batteries).

*Abnormality.*—(No. 1) Left spermatheca lacking (Magwe). (No. 2) An extra normal spermatheca on right side, opening to exterior on 6/7(1).

*Remarks.*—Genital markings, male porophores and locations of spermathecal pores are, in this material, as in the types for which the species was erected.

This species is rare at Prome, only one specimen having been obtained there since 1927.

2

Spermathecal pores, in types of *hamatus* (Kalewa), center about at *B.*

Male porophores transversely elliptical areas of greyish translucence and convex surface, extending from *A* nearly to *mBC.* The fissure approximately central, immediate margin whitened and very slightly tumescent.

Typhlosole begins in xxvi. Lateral typhlosoles in xxvi-xxvii. Supra-intestinal glands in lxxiii-lxxvi.

*Remarks.*—*E. hamatus* was erected for worms with a more median location of spermathecal pores, with genital markings in *A* to *mBC* on xx that crossed whole length of the segment, with male porophores having centrally located fissures, and with penial setae having a terminal spine recurved into a hook shape (Gates, 1930, p. 330, fig. 19*b*). The hooked tip of the penial setae seemed especially characteristic as such a conformation had not previously been recorded from the genus. Prostates were looped in a regularly zigzagged manner that had not previously been seen.

3

Typhlosole, of the types of *montanus* (Pegu yomas east of Letpadan), begins posteriorly in xxvii or in xxviii. Lateral typhlosoles low lamellae in xxviii. Supra-intestinal glands in lxxxiii-lxxxvi (1).

Spermathecal duct about one mm long, slightly bulbous, with muscular sheen, lumen irregularly slit-like in cross section due to presence of several low vertical ridges on anterior and posterior walls.

Body wall thickened in region of male porophores and slightly protuberant into coelomic cavity, penisetal follicle passing into apex of protuberance.

*Remarks.*—*E. montanus* was erected for holandric worms with spermathecal pores in the *hastatus* location but with circular male porophores and centrally located fissures, with genital markings in *A* to *mBC* of intersegmental and more posterior location, and having unusually large seminal vesicles penetrating through several septa. Such posterior extension of seminal vesicles has been even used in generic definition (Glossoscolecidae).

Three worms with foreshortened dorsal blood vessel indicate that abortion of an anterior part of that trunk in ontogenetic development can be accomplished as a result of a single mutation, and possibly for the first seven (1 specimen) as well as for the first six (2) segments.

4

Taungdwingyi (Magwe), August, 0-5-76. K. John.
Taungdwingyi, hills to the east, August, 0-0-2. K. John.

*External characteristics.*—Length, 55-110 mm. Diameter, 3-5 mm. Clitellum reddish, not or only very slightly protuberant. Seta *a* of xx ornamented by short transverse rows of fine spines. First dorsal pore on 11/12 (37), 11/12 but with a pore-like though apparently imperforate marking on 10/11 (32), 12/13 (3, of which two have a pore-like but apparently imperforate marking on 11/12).

Spermathecal pores usually centered at or median to *B*, occasionally just lateral to B. Female pores both present (82) and within a single, transverse white area in *AA*.

Male porophores greyish translucent, usually indistinctly delimited, occasionally with rather indefinite but opaque, white rim, slightly concave, extending from just median to *A* to or nearly to m*BC* and anteroposteriorly to or nearly to 16/17 and 17/18. A portion about in *AB* of the posteromedian quadrant containing the fissure is slightly raised and bears, around the fissure, an annulus that is delimited from the protuberance by a slight furrow and that is slightly notched mesially and laterally. The posterior lip thus indicated is often slightly enlarged and occasionally bilobed.

Genital markings circular, extending from just median to *A* to slightly lateral to *B* and anteroposteriorly to intersegmental furrows, symmetrical with reference to equator of segment, occasionally displacing *a* mesially and *b* laterally: on xx (77), on xx and right side of xix (3), or left side (2), on right side of xix and left side of xx (1). A small white transversely elliptical to spindle-shaped marking with convex surface present in *AB* on postsetal portion of xvi. Male porophores may be depressed so that these markings are on anterior walls of the concavity.

*Internal anatomy.*—Typhlosole begins in xxvii (23), xxviii (9). Lateral typhlosoles, always present, in xxvii-xxviii or xxviii-xxix, usually blade-like, occasionally thickened and then with rounded ventral margins or flattened and band-like, rarely divided into two portions separated from each other by an interval of nearly equal length, dark red (6) or white. Ventral caeca in xxxi-xxxvi (1), xxxi-xxxvii (2), xxxi-xxxviii (4), xxxi-xxxix (2), xxxii-xxxix (1), xxxii-xl (1). These caeca are large, with patent apertures into gut lumen, often containing soil. Several rudimentary caeca, apparently without apertures into gut lumen, were noted in one specimen and may have been present but unrecognized in others.

*Location of supra-intestinal glands*

| Segments | Number of specimens |
|---|---|
| 69-72 | 1 |
| 69-73 | 1 |
| 69-74 | 1 |
| 70-73 | 1 |
| 70-74 | 7 |
| 71-74 | 5 |
| 71-75 | 12 |
| 72-75 | 2 |
| 72-76 | 7 |
| 73-76 | 1 |

Dorsal blood vessel uninterrupted (72). Commissures of vi and v always present and filled with blood.

Seminal vesicles of ix fairly large (11), medium-sized (11), medium-sized on one side and small on the other (5), small on both sides (36). Small vesicles are acinous, rather translucent, with numerous flecks of black pigment. Medium-sized and large vesicles soft, opaque, with only slight traces of marginal lobulation. Male funnels always present in x (72), iridescent in 19. Iridescent funnels usually associated with medium-sized or large seminal vesicles in ix, but in one case with almost rudimentary vesicles (soft, opaque, no black flecks). Testis sac annular (72), distended with coagulum and in contact or almost so with parietes both dorsally and laterally. Vasa deferentia of a side come into contact in xii but unite only in xvii (22). Bulbus ejaculatorius small, soft, white, coelomic. Prostatic duct 1-2 mm long.

Spermathecal duct short, soft, thin-walled, no sheen, lumen irregularly crescentic in cross section due to presence of a high ridge with vertical groove on posterior wall and several lower ridges. Diverticula median and lateral (144 spermathecae), usually elongate and slightly widened entally. Spermatozoal iridescence confined to a shortly ellipsoidal and terminal seminal chamber or visible clear to duct. In the latter case sperm mass spirally coiled like a corkscrew, looped in a regularly zigzagged fashion with all loops short and in the same plane, or otherwise twisted.

Longitudinal musculature uninterrupted over genital markings.

Penial setae (37) 1·85-2·62 mm long, 40-65μ thick at base, 29-40 at neck, 40-70 at blade, 25-45 at tip. Shaft straight except for ectal curve. Tip widened, slightly flattened on one side, narrowing to a spine which is recurved as in types of *hamatus*. Ornamentation of fine spines in irregularly broken circles on blade, in short transverse rows further ectally and entally. Number, 6-9 (19 batteries), 12 (2 batteries of 1 worm). Tips, in two of the 70 functional setae examined in this connection, concave as in a spoon bowl, and in four other setae ending in a straight spine. Only one functional seta was present in one battery.

*Abnormality.*—Left spermatheca with no ampulla, duct spheroidal and distended by the sort of material usually present in ampulla, on dorsomedian and dorsolateral margins a small spheroidal diverticulum.

5

Pyinmana (Yamethin), October, 0-0-2. K. John.

*External characteristics.*—Length, 80-90 mm. Diameter, 3-4 mm. Clitellum yellowish.

Spermathecal pores in *AB*.

Margin of fissure of male porophores slightly tumescent but not definitely marked off by a groove as in the Taungdwingyi worms.

Genital markings present only on xvi, extending from *MBC* into *AA*, larger and more protuberant than on Taungdwingyi worms.

*Internal anatomy.*—Ventral intestinal caeca in xxxii-liii (1). Supra-intestinal glands in lxxvi-lxxix and lxxvi-lxxx.

Seminal vesicles of ix large and bulging 8/9 anteriorly, most markedly ventrally.

Penial setae (4) 2·6-2·74 mm long, 34-40μ thick at base, 40-44 at midshaft, 39-40 at neck, 58-59 at blade. Blade slightly flattened on both convex and concave sides of curve, ectal margin rounded and without spine or hook. Number, 6-9 (4 batteries). Color changes gradually from yellow to red as length decreases in a battery. Short reserve setae thicker near base than the functional setae.

6

*Remarks.*—Except as noted above these worms are like those from Taungdwingyi.

Magwe, vicinity of, August, 0-2-16. K. John.

*External characteristics.*—Length, 80-130 mm. Diameter, 4-6 mm. Clitellum reddish. Seta *b* of xix 0·37 mm long, 30μ thick at nodulus, an associated reserve seta 0·335 mm. and 28μ thick, tips of both ornamented with short transverse ridges of very fine teeth. First dorsal pore on 11/12 (16) but with a pore-like though apparently functionless marking on 10/11 (8).

Spermathecal pores in median portion of *BC* (8), with centers on or just lateral to *B* (8). Female pores both present (16). Male porophores circular areas of slight parietal thickening, extending from or slightly median to *A* to or nearly to *C*. A small lateral portion of each porophore grey translucent, depressed, the remainder white and markedly convex. Fissure, with protuberant setae, at center of convexity. Margin soft, tumscent, usually flattened but with an appearance of an indistinctly marked off annulus. Male pore on a small spheroidal protuberance from the anterior face of the posterior lip.

Genital markings of about the same size as the male porophores, in *AC*, on xxi (9), with an additional marking on right (2) or left side of xxii (2), right marking of xxi lacking (2), left lacking (2), paired on xxii (1).

*Internal anatomy.*—Typhlosole begins in xxviii (2), xxix (3), xxx (1). Lateral typhlosoles in first two typhlosolar segments (12, not found in 2). No lateral intestinal caeca (14). First ventral caecum in xxxii (1), xxxiii (6), xxxiv (3), caeca in xxxii-li (1), xxxiv-lv (1), xxxiv-lx (1).

*Location of supra-intestinal glands*

| Segments | Number of specimens |
|---|---|
| 95-101 | 2 |
| 96-101 | 4 |
| 96-102 | 1 |
| 97-101 | 2 |
| 97-102 | 2 |
| 98-103 | 1 |

Dorsal blood vessel uninterrupted (14), but commissures of v may have been functionless in three of the worms.

Testis sac annular (13, including 1 aclitellate), above dorsal blood vessel. Seminal vesicles of ix white, soft, anteroposteriorly flattened, reaching up to or nearly to dorsal blood vessel (14), but not as large as the posterior vesicles. Male funnels of x always large, crenellated (14), usually (12, including one aclitellate) iridescent. Fan-shaped or button-shaped testes recognizable in x (9). Vassa deferentia of a side unite only in xvii. Bulbus ejaculatorius soft, white, covered by transparent tissue. Prostatic duct 2-4 mm long.

Spermathecal diverticula median and lateral (28 spermathecae).

Longitudinal musculature uninterrupted over genital markings.

Penial setae (20) 1·0-1·7 mm long, 20-60μ thick at base, 25-45 at neck, 28-60 at blade, 12-20 at tip. Shaft practically straight. Tip red, widened, slightly flattened, tapering to a point. Ornamentation of thorn-like spines in short transverse rows ectally, in circles entally. Number, 6-9 (10 batteries).

7

*Eutyphoeus* sp., Gates, 1933, *Rec. Indian Mus.* 35, p. 601.

*External characteristics.*—An annular tumescence around the fissure containing the penisetal follicle pores is slightly more protuberant posteriorly. A vertical opaque line on the anterior face of that protuberance is associated with the male pore.

*Internal anatomy.*—Typhlosole begins in xxix. Lateral typhlosoles low, simple lamellae reaching slightly into xxviii and xxx. Supra-intestinal glands in lxxxii-lxxxiv.

Spermathecal diverticula median and lateral.

*Remarks.*—This Tiddim specimen differs from all others that have been assigned to *hastatus* in the dislocation of *d* setae in posteriormost segments to a position dorsal to mL, and the smaller number of supra-intestinal glands, in three segments. Penial setae lack a terminal hook and have no blade-like widening of the tip. Absence of genital markings is also noteworthy as these structures have been present in all clitellate individuals of *hastatus*.

The worm cannot be referred to any holandric species now known from the Arakan Yomas. Identification as *hastatus*, because of the differences just mentioned, must be tentative.

### VARIATION IN *E. hastatus*

Genital markings, in that portion of the *hastatus* range closely bordering the Irrawaddy and Chindwin rivers, do not vary with respect to presetal origin and postclitellar location. Always present on xviii, an occasional worm may have an extra pair, or more rarely two extra pairs, on the next one or two segments. Intrasegmental location apparently is restricted to *AA*. Increase in size of the markings would then be possible only by anteroposterior extension, approximation or even union at mV, all of which seem to be indicated by the material that has been available. Union midventrally of originally paired embyonic anlage may explain those cases in which no indication of double origin is recognizable in adults.

Passing up from the river bank to the eastern boundary of the range in the Pegu Yomas, as well as in a more northern portion of the Chindwin valley, the markings show no tendency to become united midventrally but rather one for greater midventral separation and lateral expansion. Only in one locality at the southern border of the range have markings become intersegmental, or more accurately bisegmental, and of symmetrical location with reference to the intersegmental furrow between the two segments concerned. Markings still are postclitellar except in the vicinity of Pyinmana where they are on a clitellar segment (xvi) as are the markings of *constrictus* from the same locality. A similar parallelism in location of markings, though on a different segment (xxi), is demonstrated by worms of the two species collected in a region extending from Natmauk down towards Magwe.

The rank of ventral intestinal caeca extends through xxxi-lx but the number, in the vicinity of Taungdwingyi, may be restricted to 6-9. Supra-intestinal glands are in lxix-lxxxvi and xcv-ciii, the discontinuity of eight segments due to the location of the glands of certain Magwe district worms in the same segments as in *constrictus* from the same area. The number of segments involved in an individual is 5-7, in those Magwe specimens of *hastatus*, rather than 4-5 or occasionally 6 as in the rest of the range.

Lateral intestinal caeca may be present or absent in a local population. An annular thickening of the gut wall such as may be present around the aperture into a definite caecum has been noted, in a number of specimens which, prior to opening and cleaning out gut contents had been tallied as acaecal. The opening through the annulus in these cases apparently leads only into a slight pocket without any constriction which is scarcely distinguishable, except for the annulus at an appropriate site for a caecum, from fortuitous bulges and sacculations in other intestinal regions.

Penial setae always have a blade-like local thickening near the ectal end but only in the populations from two widely separated areas has the blade narrowed to a terminal and recurved spine. Reserve penial setae always have been present in each battery.

Spermathecae have shown little variation as to number of diverticula. Of the 308 that were examined this time, one did lack a median diverticulum, two had an extra discrete diverticulum, and one diverticulum was completely bifid. The aberration, in each of these cases, characterized only one of a pair of lateral organs, and four individuals were involved.

The testis sac is annular throughout the range. A sort of penis, in the form of an annulus, seems to be developing, in some populations, around the fissure containing the male, prostatic and penisetal follicle pores. Whether this delicate structure is a permanent organ or temporary and then resulting from outrolling of the lining of the fissure or from tumescence of the margin of the fissure aperture is not yet clear.

Variation in *hastatus*, in general, does not appear to be continuous, in a north-south direction, throughout the eastern portion of the range. Evolutionary processes that now appear to be under way presumably

would result eventually in a number of small-range species in the Pegu Yomas.

*E. hastatus* is now defined as holandric. Any individual that varied in the number of testes, regardless of similarity in other characteristics would be referred to another species.

Holandry, *i.e.*, presence of a pair of testes in each of segments x-xi is basic throughout families of the megadrilous oligochaeta. Equally archaic are: arrangement of setae in eight regular longitudinal ranks within the ventrum, absence of interruption in the single dorsal blood vessel and presence of paired female pores. One-seventh of the species of *Eutyphoeus* share all of these primitive characteristics and are collectively designated for the first time, as above, by the name of the least specialized.

In young juveniles of these as well as of other species, somatic generic characteristics were already established in digestive and excretory systems but reproductive organs always were unrecognizable under the binocular. Presumably only microscopic anlage of gonads, and possibly of deferent duct funnels, are present in this early period of post-hatching existence. From the female funnel rudiments, which are on the anterior face of septum 13/14, deferent ducts later grow back through the septum down towards and then deep into the musculature of the body wall but usually not until maturity are patent external openings, the female pores, recognizable in the epidermis. After the breeding season and as the clitellum regresses, these pores, according to the evidence now available, are occluded and the epidermal section (at least) of the oviduct aborted. The male deferent ducts likewise grow back, from funnel rudiments on anterior faces of 10/11-11/12 but on reaching the parietes instead of penetrating deeply into the musculature continue to grow posteriorly. The ducts of a side, normally come into contact shortly and grow back together through six or seven segments but in xvii, after passing by, on the lateral side, sites of emergence of prostates into the coelom, unite, abruptly turn mesially and then bore down through the body wall. A portion of the united duct usually becomes more or less thickened to form an ejaculatory bulb that seems to be characteristic of this genus. Long before maturity the ducts acquire externally recognizable openings through the epidermis in *AB* and *behind the* equator of xvii. The apertures of the *a* and *b* follicles of that segment gradually become more closely approximated than in other segments, mostly it seems, by lateral migration of the *a* pore. The region immediately surrounding the follicle apertures then becomes depressed so as to be on the roof of a shallow fissure with a transversely slit-like superficial opening. These "fissures", to which frequent reference is necessary throughout this contribution, are developed in most species and now appear to be one of the basic innovations in the genus. Meanwhile the male pores have migrated forward to a site on the posterior wall of the fissure, and the sigmoid setae of the ventral follicles of xvii have been replaced by specialized shafts called penial. The prostatic pore rarely is recognizable even in adults but is located on the lateral or anterior wall of the fissure. The body wall adjacent to each fissure is

thickened and demarcated more or less definitely to form a male "porophore" presumably with some function at time of copulation. The roof of the fissure around the follicle apertures may acquire, in some species, the appearance of a tough glistening transverse tubercle or of two circular tubercles. Prior to maturity genital markings, areas of parietal modification, and the spermathecae begin to develop but the period in which the coelomic cavity of xi is reduced to the lumen of a testis sac cannot now be mentioned.

In aberrant individuals without prostates the male deferent ducts ceased to grow before reaching xvii, or in xvii or occasionally not until several segments behind, and always failed to penetrate deeply into the parietes. When, however, prostates developed in a wrong segment, whether anteriorly (xv or xvi) or posteriorly (xviii), the male ducts acquired external openings in the prostatic metamere and in normal topographical relationships to the prostatic and follicle apertures. Presence of but one prostate resulted in normal development only on its own side of the body, the male ducts of the other side ending blindly as in aprostatic individuals. Male porophores and penial setae were not developed in absence of prostates but did develop in wrong segments where prostates were present. In worms with prostates in different segments on opposite sides of the body, penial setae and porophores developed normally but in association with each prostate.

An extra prostate (very rare) was associated, in each case, with penial setae and an imperfectly developed male porophore without a male pore. These relationships permit an assumption that prostate anlage induce a series of changes that includes approximation of ventral follicles of xvii, development of the fissures, male porophores and penial setae, an abrupt change in direction of growth and then penetration of male deferent ducts into the parietes, as well as subsequent migration of the male pore into the fissure. The induction apparently becomes effective on male deferent ducts just as they are growing beyond level of the prostate anlage. When, however, the inducing influence is not exerted a duct may continue to grow straight posteriorly for ten segments more. In vestibulate species a vestibular invagination is induced also.

Male funnels had not developed in the usual segments, in certain aberrant individuals, when testes were lacking there but were present in wrong segments with testes. A similar relationship, also unilateral as in case of male funnels and male pores, was shown by the seminal vesicles. Here also an induction effect, this time by the testis anlage is assumed.

The prostate induction, in *hastatus*, so affects the associated setal follicles as to result in production of a battery of 6-12 shafts. Two of these assume the characteristics of functional setae and can be protruded through follicle apertures long before sexual maturity. Most of the "reserve" setae never will have any use in the way penial setae are supposed to function. Whether their production is one way of getting rid of certain wastes or whether they have some sort of a skeletal function, as suggested by Miss Chapman, the battery does represent one important specialization in a primitive species. Bends and wrinklings of ectal

portions of reserve setae occasionally noted in worms that had not copulated may have resulted from violent muscular contractions at preservation.

**Eutyphoeus manipurensis** Stephenson 1921

*External characteristics.*—Clitellum extends on specimens from Tiddim and Falam to 16/17 or just onto xvii. Spermathecal pores centered at or close to m*BC*.

Male pore in a circular area of opacity in, or on a spheroidal tubercle on, the tumescence at posterior margin of fissure. Prostatic pore anterolateral to male pore and between the two tumescences.

One genital marking on each side in lateral portion of *BC*, presetal, close to margin of male porophore (3 Tiddim). A median area of greyish translucence in presetal portion of xii (3) may be only a region of epidermal thinness but on two of the worms looks like a genital marking though no gland was found internally.

*Internal anatomy.*—Typhlosole begins in xxvi but has a low protuberance into posterior portion of xxv. Lateral typhlosoles well developed, in xxvi (5). Lateral caeca in xxvi (5). Ventral caeca in xxxi-xxxiv (1), xxxi-xxxvi (1). Supra-intestinal glands in lxv-lxviii (2), but rudimentary in lxv in (1), lxv-lxix (1 Falam), lxviii-lxxi (1 Falam).

Circulatory system as in *gigas* except that extraoesophageals are connected by a transverse vessel just behind 5/6 and the dorsal vessel is uninterrupted and with commissures in v and vi.

Testis sac annular, dorsal trunk not included. Male funnels of x with spermatozoal iridescence (5). Testes of x, when recognizable, fan-shaped. Seminal vesicles of ix large (5). Bulbus ejaculatorius small, whitish, in parietes.

Spermathecal duct about one mm. long, with muscular sheen, not bulbous, lumen irregularly slit-like in section due to presence of several low ridges, one on the posterior wall often slightly larger.

Genital marking glands small, acinous, sessile on parietes, covered dorsally by a very delicate, transparent membrane which may be peritoneal. Parietal portion of gland tougher, narrower and of slightly different colour.

Penial setae (12) 1·04-2·0 mm. long, 33-62μ thick at base, 26-41 at midshaft. Ornamentation variable, clearly visible or almost unrecognizable under low power of microscope, scattered single triangular teeth, or smaller spines in transverse rows of seven to eleven or in irregular circles rarely or frequently broken. Number, 2 (6 batteries), 2 functional and 1 reserve (2 batteries), 2 functional and three reserve (1).

*Remarks.*—The tag-like tumescences on the male porophores are regarded as equivalents of separated anterior and posterior halves of "annular" penes. Constant presence of the four tags indicates they may be permanent structures rather than temporary eversions or outrollings from the fissure. Slight depression of male porophores obviates protuberance beyond general level of body surface. However, tags of similar appearance in a species of *Toroscolex* appear to be independently retractile.

Sufficient material for estimation of extent and significance of variation with regard to taxonomically important structures has not been available in this species. The samples that have been studied are thought to indicate that the Burmese populations have become stable with reference to development and location of the lateral intestinal caeca but not with regard to number and location of genital markings. Apertures of the spermathecae have migrated laterally in the Burmese population but apparently have been retained, in the Manipur population, in a site that must be regarded as primitive. The Indian worms seem to have become more specialized with reference to the capsule around the genital marking glands but all are primitive in so far as modification and number of penial setae are concerned. Distribution presumably is continuous in a north-south direction through the Arakan mountain arc.

The difference in segmental location of the lateral intestinal caeca, in view of the evidence provided by various species (below), is thought to have resulted from independent evolution of those structures in different portions of the range rather than by a transfer of organ developing capacity from one segment to another. To call attention taxonomically to the differences while at the same time indicating a very close relationship, two subspecies are erected, *manipurensis* (n. subsp.) for the northern worms of India, *chinensis* (n. subsp.) for the Burmese worms in a southern part of the range.

By cancelling out obvious specializations, such as the fissure tags in *manipurensis*, modifications in penial setae and battery as well of course as the penial annulus in *hastatus*, together with genital markings and associated glands, lateral intestinal caeca, and parietal modifications around the fissures on xvii of both of those species, a stage of organization is obtained that may well have characterized a form ancestral to both of those species. This hypothetical form is referred to hereinafter as proto-eutyphoeus for from it there can be derived additionally not only all species of *Eutyphoeus* but even a closely related genus.

The most important morphological difference between *hastatus* and *manipurensis* is the absence in the latter of a median spermathecal diverticulum. This condition, in the genus *Eutyphoeus*, now appears not to be primitive and so proto-eutyphoeus is credited with bidiverticulate spermathecae. The unidiverticulate condition with which we are here concerned occasionally appears in individuals of species with bidiverticulate spermathecae. A single step, abrupt change of this sort suggests intervention of a mutation for inhibition of development of the median diverticulum. Establishment of this particular mutation, "unidiverticulate", is proposed as an important stage in the evolution of *manipurensis* from the proto-eutyphoeus.

### **Eutyphoeus marmoreus** Gates 1933

*Internal anatomy.*—Typhlosole begins, in the types, in xxix. Lateral typhlosoles low simple lamellae in xxix, reaching slightly into xxx. Lateral intestinal caeca in xxviii (2). Ventral caeca in xii—lx(1). Supra intestinal glands in lxxxv-lxxxviii (1), lxxxvi-lxxxviii (1).

Circulatory system as in *gigas* except that the extra-oesophageals are connected by a transverse vessel behind 5/6 and the dorsal trunk is uninterrupted.

Left posterior seminal vesicle of one worm passes back into xxiii. Vestibulum, when completely retracted, conspicuously protuberant into coelomic cavity and with a more or less pointed apex about two mm. above level of ventral parietes. Penisetal follicle and prostatic duct pass into apex of vestibular bulb, the bulbus ejaculatorius into the posterior wall and more ventrally. With partial eversion vestibular bulb is dorso-ventrally flattened and the externally protuberant portion is elongate and with a soft, wrinkled, greyish translucent surface.

Spermathecal duct slightly more than two mm. long and nearly two mm. thick. Lumen irregularly slit-like in cross section ectally, becoming rather crescentic entally, due to presence of several ridges ectally and of a high and thick posterior ridge ectally.

Penial setae 1·8-1·95 mm. long, 40-45μ thick at base, 23-40 at neck, 29-45 at blade. Tip flattened and slightly widened, narrowed to a spine. Ornamentation of fine thornlike teeth in regular circles, continued to 0·9 mm. level down the shaft. Number, 2-4. Reserve setae pink, tip with terminal hook.

*Remarks.*—Three worms from the type locality of *marmoreus* and *bullatus*, with a complete dorsal trunk and no genital markings, have been difficult to place. Because of apparent absence of testes in x and lack of any iridescence on male funnels indicating those gonads had been present, the specimens, in spite of the presence of seminal vesicles in ix, were regarded as metandric and referred to *bullatus*. Conditions since found in other species apparently indicate that testes of x may mature or at least cease functioning earlier than those of xi, and that discharged testes may regress so as to become macroscopically unrecognizable. The seminal vesicles of ix may then be expected to regress earlier than those of xii thus explaining the flattening against the anterior face of 9/10 (not 8/9). Accordingly, the three trouble ome worms are now considered to be *marmoreus*. If, however, as was firs thought, the three worms were unable to produce sperm in x, the condition would now be attributable to a mutation for metandry (p.128) unless of course, a third species closely related to the other two is present in the same locality.

*E. marmoreus* has penial setae of a more advanced type than does *manipurensis* and a battery that is more primitive than that of *hastatus*, but like the latter is distinguished from *manipurensis* by the primitive bidiverticulate spermathecae. Intestinal caeca, as in case of *manipurensis*, indicate a more advanced stage of evolutionary development and stability than has been attained by *hastatus*. Morphological specializations and geographical distribution rule out close relationship with all other holandric species. All that is needed, however, to derive *marmoreus* from the proto-eutyphoeus is to bring about the invagination into the coelomic cavity of that same portion of the body wall that become modified in the rest of the holandric species into a tough and sometimes

thickened, disc-like male porophore. The slightly concave depression in the male porophore of *manipurensis*, that seems to be necessary to prevent erosion of the delicate fissure tags, is suggestive of a very early stage of such an invagination.

The tag which bears the male pore (as in *manipurensis*) is now removed far away from the surface and at the same time a structure is obtained which can function as a temporary intromittent organ for direct transfer of sperm into a spermathecal duct. This eversible vestibulum with its muscular bulb is certainly an advanced sort of specialization and one that is lacking in many species of the derived groups that are next to be considered.

**Eutyphoeus bullatus** Gates 1933

Penial setae (6 from Tiddim types) are 1·62-2·58 mm. long, 33-50μ thick at base, 27-36 at midshaft, 10-15 at tip. Shaft straight except for ectal curvature. Tip flattened and tapering to a point. Ornamentation of thorn-like spines scattered single or in short transverse rows. Number, 2-4 (3 batteries). Reserve setae red, 0·45-0·52 mm. long, 55-59μ thick at midshaft. Tip more markedly flattened than in functional setae which are yellow.

*Remarks.*—Three of the types having been transferred to another species *bullatus* is now defined as metandric and with a foreshortened dorsal blood vessel. These two characteristics distinguish the species from those of the *hastatus* group. Absence of the testes of x (metandry), in organisms that have no more than two pairs of these gonads, long has been considered taxonomically important, often requiring generic distinction. Absence of an anterior portion of the dorsal blood vessel together with associated portions of the circulatory system, in animals of a relatively simple sort, has been thought to have taxonomic value at the species level. However, these two characteristics, in the case of *bullatus*, would indicate relationships to species that are geographically distant and isolated from it. The specialized and presumably eversible vestibula, on the contrary, suggest relationship to *marmoreus* which is present in the same area. The latter species, except for the intestinal caeca, is primitive enough to serve as an ancestor for *bullatus*.

Whether phyletic derivation is to be direct or from a common ancestor with *marmoreus*, or from an ancestor common to morphologically similar but geographically isolated species, it does require the two drastic modifications in reproductive and circulatory systems. Foreshortening of the dorsal trunk may have taken place earlier as presence of anterior seminal vesicles, structures usually eliminated long before the anterior male funnels and their deferent ducts, indicates quite recent acquisition of metandry. Phyletic origin from a common ancestor with *marmoreus* now seems to be the one required. This derivation justifies appending an otherwise isolated species to a fairly homogenous group of such different morphological organization.

## THE *constrictus* GROUP

### **Eutyphoeus constrictus** Gates 1929

1

Meiktila (the type locality), September, 1-0-22. K. John.

*External characteristics.*—Length, 110-150 mm. Diameter, 5-7 mm. Setae small, often recognizable only with difficulty: one *b* seta of xix 0·32 mm. long and 30μ thick at nodulus, ventral setae at least of viii-x ornamented with short transverse ridges of very fine teeth. First dorsal pore on 10/11 (4), ?11/12 (8), 11/12 (11). Clitellum reddish.

Spermathecal pores with centers at or median to *B*, often reaching to or nearly to *A*. Female pores both present (22). Male porophores areas of slight parietal thickening, nearly circular extending from or slightly median to *A* (rarely just lateral to mV) to or nearly to *C*.

The external male aperture represented by the transversely slit-like opening in the parietes through which penial setae may project, in *AB* and on the median half of a male porophore, occasionally close to the median margin. The portion of the porophore immediately adjacent to the slit is soft, whitish and often slightly tumescent, usually especially marked anteriorly and posteriorly but never with an appearance of a complete annulus. The primary male pore is minute and on the posterior wall of the shallow fissure into which the external aperture leads, occasionally on a hemispheroidal tubercle. On the anterior wall of the fissure is the prostatic pore. Two pits on the roof of the fissure apparently represent apertures of two discrete penisetal follicles. (No genital markings.)

*Internal anatomy.*—Typhlosole begins in xxvii (2), xxviii (7) or xxix (5). Lateral typhlosoles present in the first two typhlosolar segments (22). Lateral intestinal caeca lacking (6), or when present in xxvii (3), xxviii (10), xxix (1), two pairs, one each in xxviii-xxix (1). Caeca are slightly protuberant anteroposteriorly flattened flaps, definitely constricted off only dorsally (8). First ventral caecum in xxxiii (1) or xxxiv (5).

Location of supra-intestinal glands

| Segments | Specimens |
|---|---|
| 96-102 | 1 |
| 97-101 | 2 |
| 97-102 | 1 |
| 97-103 | 1 |
| 98-103 | 4* |
| 99-144 | 3 |
| 99-105 | 1 |
| 100-104 | 1 |

* Including the juvenile.

Circulatory system as in *gigas* except as follows: Dorsal blood vessel uninterrupted (22), commissures unrecognizable in v (5) or present but slender, translucent or opaque and then white and without blood (possibly functionless ? 5), with blood (12). Extra-oesophageal trunks connected by a transverse commissure just behind 5/6.

Testis sac ventral (1), annular (21) and above dorsal vessel. Male funnels present in x (22), usually only small and rounded knobs, larger and crenellated (3). Vasa deferentia of a side separate to xvii. Bulbus ejaculatorius small, soft, whitish, coelomic but covered by delicate tissues.

Spermathecal duct short, lumen rather large, irregularly slit-like in cross section due to presence of several low vertical ridges. Diverticula elongate, always paired (44 spermathecae), sperm mass usually twisted in a slightly spiral or shortly zigzag fashion.

*Abnormality.*—Right prostate unusually short, 2 mm. long, but of normal thickness.

*Remarks.*—Locations of supra-intestinal glands in the other eight worms were indeterminable because of condition. Location of these glands enables identification of the juvenile even though male porophores had not yet developed as there is no other unpigmented metandric species with uninterrupted dorsal vessel in the Meiktila area.

The lumen of the fissure in the male porophore now appears to be the equivalent of that within a penis and so should not be considered a rudimentary vestibular invagination. Location of the male pore on the tumescence at posterior margin of fissure aperture, when that tumescence is most pronounced, apparently indicates that the lining of the fissure can be pulled outwards.

2

*E. constrictus* has been found to the north of Meiktila only at Mansum presumably in Myitkyina district, 12 to 14 miles from Gora, at *ca.* 3,200 feet, in dense, rain-forest bamboo.

The single specimen secured has no genital markings, spermathecal pores slightly lateral to *B*, rudimentary lateral intestinal caeca in region of xxv, ventral caeca in xxxv-xxxvi (+?), and supra-intestinal glands in lxxxi-lxxxiv. The typhlosole begins in region of xxv-xxvii and there are rudiments of lateral typholosoles in xxv.

3

Myingyan, September 0-0-1. K. John.

Length, 83 mm. Diameter, 3½ mm.

Lateral intestinal caeca lacking. First ventral caecum in xxxii. Supra-intestinal glands in lxxxv-lxxxix.

Worms from other Myingyan localities, Chappea and Kyaukpadaung, also hadno genital markings.

Penial setae (25, Myingyan district localities) 1·4-1·77 mm. long, 40-55μ thick at base, 30-50 at neck, 60-82 through blade. Shaft nearly straight occasionally with circular constrictions in neck or blade regions,

Tip thickened, flattened on one side, red, tapering to a point. Ornamentation of scattered rows of four or more thorn-like teeth. Number, 5-8 (13 batteries), 14 (1 battery). Functional setae, the two longest of a battery, yellow except for tip which is red. Three functional, *i.e.*, yellow setae, present in the 14-shaft battery. Reserve setae thicker than functional setae and with entire shaft red. One functional seta only in each battery of several juveniles (75×2 mm.), all setae of other juvenile batteries entirely red. The largest setae of these juvenile batteries 0·4-0·41 mm. long.

4

South of Meiktila *E. constrictus* was found at Ywadaw and Pyinmana (Yamethin). Paired, triangular genital markings in *AC* are present on xvi of each of the 46 specimens from those two localities.

5

Further south in the Sittang valley *E. constrictus* was obtained at two different localities so near the town of Toungoo that no other information was recorded.

Genital markings were lacking in eight specimens from one of those colonies. Reproductive organs were juvenile in spite of marked clitellar tumescence and retardation in development may have been due to parasites present in huge numbers.

6

Spermathecal pores were centered at *C* in worms from the other Toungoo colony. Genital markings present on each of the five specimens were in *BC* on xiii. Markings were rather large and depressed so as to have a somewhat sucker-like appearance.

7

Daylo stream, Karen Hills (Toungoo,) 0-0-1.

*External characteristics.*—Length, 125 mm. Diameter, 4 mm. First dorsal pore on 11/12. Spermathecal pores with centers at or slightly lateral to *C*. Male porophores small, circular, indistinctly demarcated, slightly concave. Fissure containing male pore at center of porophore. Genital markings larger than porophores, in *AB*, on xv, between sites of 14/15 and 15/16.

*Internal anatomy.*—Typhlosole begins in xxvii. Lateral typhlosoles in xxvii. Lateral intestinal caeca in xxviii. Ventral caeca in xxxii-l, the first much larger and the only one with a recognizable aperture into intestinal lumen. Supra-intestinal glands in lxxix-lxxxii. Dorsal trunk uninterrupted, commissures of v blood-filled.

Testis sac annular. Male funnels present in x. Right anterior deferent duct comes into contact with posterior duct in xii, separates, in contact again from xv.

Over site of each genital marking there is a conspicuous protuberance into coelomic cavity with smooth, white, firm surface, probably with a thin but transparent layer of muscle continued across it.

8

Pa Taw Lo, between Sat Der and Chaung Na Kwa, Karen Hills (Toungoo), September, 0-0-1 (in poor condition). Dr. H. I. Marshall.

Male porophores raised in a rather mound-like manner. Spermathecal pores lateral to m*BC*. Genital markings extending slightly beyond *A* and *B*, on xix.

Lateral intestinal caeca in xxviii, but retracted into intestinal lumen. Supra-intestinal glands in lxxxii-lxxxvi. Male funnels of x small but slightly crenellated.

9

Pegu Yomas (Toungoo), September. Site No. 1, 0-15-14. Site No. 2, 0-0-1. Site No. 3, 0-0-1. Site No. 4, 0-1-5. Site No. 5, 0-0-1. G. E. Blackwell.

*External characteristics.*—Length, 120-230 mm. Diameter, 4-6 mm. Unpigmented, clitellum reddish but not protuberant. Setae begin on ii, fairly large, readily visible; a *b* seta of xix 0·43 mm. long and 37μ thick at nodulus, tip ornamented with transverse rows of very fine teeth. First dorsal pore on 11/12 but with an obviously imperforate, dark, greyish translucent marking on 10/11 (2), marking on 10/11 more pore-like but probably non-functional (5), no marking on 10/11 (30), on 12/13 (1).

Spermathecal pores small, in lateral portion of *BC* and usually nearer *C* than m*BC*, or with centers at or just lateral to *C* or more rarely with the whole pore lateral to *C*. Female pores both present (24). Male porophores small, unprotuberant, transversely elliptical to spindle-shaped, greyish translucent, with centers at or just median to *B*. Porophores on several specimens have a narrow, opaque, whitish, slightly raised rim, sharply demarcated both peripherally and from the grey portion by slight though definite grooves. The fissure is central, completely filled by tips of penial setae, margin of fissure aperture quite without tumescence or protuberance. A longitudinal crescentic area of grey translucence, concave on lateral side, is median to each male porophore and may have a clearly demarcated opaque rim. These areas may be slightly separate from, in contact with, or united with the male porophores; in latter case the grey portions of the areas and of the porophores continuous.

Genital markings reach to or nearly to intersegmental furrows, slightly beyond *B*, and mesially are in contact (8), or with rims united at mV (1), or with rims separated midventrally by a strip of unmodified epidermis of variable width (29). Locations: on xv (10, 9 from site 1), xviii (16, 9 from site 1), xix (12, 7 from site 1), left side only (1, site 5).

*Internal anatomy.*—Typhlosole begins in xxvii (1), xxviii (11), or xxix (10). Lateral typhlosoles always present (38), in first two typhlosolar segments Lateral intestinal caeca small, occasionally clearly constricted from gut all around the periphery but usually so marked off only dorsally, laterally, or anteriorly: in xxviii (24), left side only and retracted into intestinal lumen (1), xxix (3), left side of xxviii and right side of xxix (1), lacking (1). Ventral caeca in xxxii-xl (1), xxxiii-lx (1); first caecum in xxx (1), xxxii (2), xxxiii (14), xxxiv (1), in worms in which entire range was not determinable.

Location of supra-intestinal glands

| Segments | Number of specimens from site | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| 83-87 | — | — | — | — | 1 |
| 84-88 | 1 | — | — | — | — |
| 85-88 | — | — | — | 1 | — |
| 85-89 | — | — | — | 1 | — |
| 86-89 | 5 | — | — | 2 | — |
| 86-90 | 1 | — | — | — | — |
| 87-90 | 3 | — | — | — | — |
| 87-91 | 1 | 1 | — | 1 | — |
| 88-98 | 2 | — | 1 | 1 | — |
| 88-92 | 1 | — | — | — | — |
| 89-92 | 1 | — | — | — | — |

Dorsal blood vessel uninterrupted (38), commissures of v usually large and red. Lateroparietal trunks may be clearly visible as far back as lxxxv.

Testis sac annular (38). Seminal vesicles extend into xiii (2), xiv (3), xv (9), xvi (2), xxii and constricted by septa (1, from site 5). Male funnels of x small (38), usually rounded rather than crenellated. Anterior male ducts always smaller, usually much smaller. Bulbus ejaculatorius fairly large, whitish, and in a worm from site 5 two mm. long.

Spermathecal duct short, lumen crescentic in cross section due to presence of a vertical ridge (with vertical groove) on posterior wall. Diverticula median and lateral (76 spermathecae), usually elongate.

Penial setae (34, various localities) 1·45-2·88 mm. long, 30-50μ thick at base, 28-50 (58-65, worm from site 5), at neck, 50-85 (100-125, worm from site 5) at blade. Shaft straight. Tip pink, slightly flattened on one side, tapering rapidly. Ornamentation of fine thorn-like teeth. Number, 8-11 (17 batteries). Reserve setae entirely red.

*Abnormality.*—(No. 1) Right male funnel of xi herniated through 10/11 into x. (No. 2) An extra diverticulum on anterior face of one spermathecal duct. (No. 3) An extra diverticulum on posterior face of one spermathecal duct. (No. 4) One diverticulum almost completely bifid.

10

Twante (Hanthawaddy), September, 0-0-64. K. John.
Hlegu (Insein), September, 0-0-2. K. John.

*External characteristics.*—Length, 150-230 mm. Diameter, 5-6 mm. Unpigmented, clitellum yellowish, yellowish brown or brownish. Setae usually begin on ii but may be wholly or in part lacking on that segment: on xx, $AB<CD<BC<AA$, $DD$ *ca.*$=\frac{1}{2}$C. First dorsal pore on

9/10 (1), 10/11 (86, a small pore-like but imperforate marking on 9/10 on several), 11/12 (1).

Spermathecal apertures small, in lateral half of *BC* or with centers at or very close to *C*. Female pores both present (67, sites not determinable on others), usually at or just median to *A*, occasionally one or both just lateral to *A*.

Male porophores shortly elliptical (and then transverse) to circular, from a lateral portion of *AA* to or nearly to m*BC* and anteroposteriorly to or almost to 16/17 and 17/18, each with a slightly protuberant, white, narrow rim quite distinct from remaining portion in which epidermis is greish translucent. A completely circumferential annulus, at or just lateral to *B* around aperture of the fissure on each specimen except several from Twante (and then collapsed or retracted?). Two discrete penisetal pits present on roof of fissure which is very slightly dorsal to level of porophore surface. Male pore minute and on a rounded tubercle on posterior wall of fissure.

Genital markings shortly and transversely elliptical, with a narrow, raised,white marginal rim and a greyish translucent central portion, usually slightly smaller than the male porophores with which they are in line, on xx right side only (15), left side (13), both sides (8 Twante and 1 Hlegu), lacking (23 Twante and 1 Hlegu).

*Internal anatomy*.—Typhlosole begins abruptly in xxviii-xxix. Small lateral typhlosoles always present in first two or three typhosolar segments (85). Lateral intestinal caeca usually lacking or represented only by slight bulges without distinct demarcation, definitely constricted off and ventrally directed caeca in xxviii (9), xxix (2, in one retracted into gut lumen). Ventral caeca in xxxiv-lix (2), xxxiv-lx (1), xxxiv-lvii (1), xxxvii-lix (1).

Location of supra-intestinal glands

| Segments | Twante | | Hlegu |
|---|---|---|---|
| | without genital markings | with genital markings | |
| 85-88 | 4 | 2 | — |
| 85-89 | 2 | 1 | 1 |
| 86-89 | 3 | 2 | — |
| 86-90 | — | 2 | — |
| 87-90 | — | 2 | — |
| 87-91 | 2 | 3 | — |
| 88-91 | 1 | 3 | — |
| 88-93 | — | — | |
| 89-92 | — | 1 | — |

Dorsal blood vessel uninterrupted (85), commissures of v large and red 82).

Testis sac annular (80), U-shaped (3), or ventral (2). Male funnels present in x, usually crenellated, rarely (5) more rudimentary and knob-like. Anterior deferent ducts lacking on both sides (4 Twante and 1 Hlegu), present on one side only (2 Twante), present on both sides (48 Twante), occasionally recognizably smaller than the posterior ducts.

Spermathecal duct short, lumen rather crescentic in cross section due to presence of a high vertical ridge with vertical groove on posterior wall (lower and less definite ridges laterally and anteriorly). Diverticula median and lateral (165 spermathecae), short and thick, bilobed, trilobed or multilobed distally, occasionally digitiform.

Penial setae (4 Hlegu and 16 Twante) 2·4-3·06 mm. long, 40-65μ thick at base, 42-56 at neck, 65-90 at widest part of blade-like ectal portion. Major portion of shaft nearly straight, a terminal portion beginning just ental to blade curved to one side. Blade thickened and flattened on inner and outer sides of curve, narrowing gradually to an apparent point as viewed from side as seta lies on slide but when rolled over end is rounded or truncate. Ornamentation, ental to blade, of short, transverse rows of a few fine spines. Number, 10-14 (10 batteries).

*Abnormality.*—(No. 1) Right spermatheca adiverticulate (Twante). No. 2-3) Athecal, even rudiments of pores lacking.

*Remarks.*—Parietal protuberances into coelomic cavity of xvii such as are present in Bassein worms, are either lacking here or so indefinite as not to be certainly recognizable.

11

Padaukchaung (Bassein), jungle, October, 0-0-36. K. John.

*External characteristics.*—Length, 96-135 mm. Diameter, 3-4 mm Setae may be wholly or in part lacking on iii or iii-iv as well as on ii.

On each male porophore of each specimen there are two slightly raised and fairly distinctly delimited areas, one median and the other lateral to the penial annulus. These areas may be circular or triangular and then with apices towards annulus and bases at rim of porophore.

Genital markings on xviii (1), xix (10), xx (26), lacking on none.

*Internal anatomy.*—

Location of supra-intestinal glands

| Segments | In worms with genital markings | |
|---|---|---|
| | on ix | on xx |
| 81-84 | — | 1 |
| 82-85 | 2 | 3 |
| 83-86 | 2 | 6 |
| 83-87 | 1 | — |
| 84-87 | 4 | 1 |

Male funnels and anterior deferent ducts lacking on both sides (30). Bulbus ejaculatorius rather small, with no muscular sheen, concealed from view and bound to parietes by delicate tissues. The body wall is protuberant into coelomic cavity of xvii on each side, the protuberance of a rather hemispheroidal shape and soft. The prostatic duct passes into the anterior face, the penisetal follicle into the dorsal face, and the bulbus into the posterior face.

Penial setae (6) 2·48-2·76 mm. long, 42-50μ thick at base, 42-48 at neck, 70-76 at widest part of blade-like ectal portion. Number, 6-9 (3 batteries).

*Remarks.*—The organization of these worms, except as otherwise indicated above, is as in those from Twante and Hlegu.

12

Labu (Prome), August, 9-0-7, K. John.

*External characteristics.*—Length, to 195 mm. Diameter, 5-6 mm. Clitellum reddish. Setae large, one *b* of xix 0·5 mm. long, 50μ thick at nodulus. First dorsal pore on 10/11 (15, including 9 juveniles), 11/12 (1).

Spermathecal pores with centers at or lateral to *C*, in latter case pores entirely in *CD*. Female pores both present (6). Male porophores small, protuberant, shortly elliptical opaque areas, transversely or antero-laterally directed. Median half of porophore occupied by a small but definite annulus usually centered at *B*. A fairly clearly demarcated area of grey translucence just anteromedian to each porophore and with a narrow, opaque marginal band.

Genital markings lacking (5), paired but with margins united at mV, primarily presetal, in *BB* on xvi (1). A single marking on right side of a presetal portion of xviii of the other worm extends from m*BC* to *A*. An indistinct area of grey translucence on left side of xviii may represent a rudiment of the other marking of a pair.

*Internal anatomy.*—Typhlosole begins in xxix (3). Lateral typhlosoles present in xxviii-xxix (5). Lateral intestinal caeca rudimentary and marked off dorsally, in xxviii (4), marked off ventrally, in xxix (3). Ventral caeca in xxxv-liii (1), first ventral caecum in xxxiii (1), xxxiv (2), xxxv (5).

Location of supra-intestinal glands

| Segments | Number of juveniles | Number of adults |
|---|---|---|
| 81-86 | 1 | |
| 82-86 | 1 | |
| 82-87 | .. | 1 |
| 83-87 | .. | 1 |
| 83-88 | 1 | ... |
| 84-88 | 1 | .. |
| 84-90 | .. | 1 |
| 85-89 | 2 | 1 |
| 85-90 | .. | . |
| 86-89 | 1 | .. |
| 86-90 | | 2 |
| 86-91 | 1 | .. |

Dorsal vessel uninterrupted, segmental commissures present in v (5). Testis sac annular (5). Male funnels present in x (5), deferent ducts of a side unite in xvii. Bulbus ejaculatorius more than one mm. long, coelomic.

Spermathecal duct short, lumen irregularly crescentic in cross section, due to presence of several small and one large vertical ridges, latter with a vertical groove at least ventrally. Diverticula median and lateral (10 spermathecae), usually elongate, sperm occasionally in a zigzag looped or spirally coiled mass.

*Remarks.*—These worms were collected near a cluster of several houses that is too unimportant to be on any of the maps but which is located not far from the river bank, across the Irrawaddy from the town of Prome.

13

Prome, August, 4-17-14. K. John.
Paukkaung (Prome), August 0-0-14. K. John.
Thanbula (Thayetmyo), August, 0-1-14. K. John.

*External characteristics.*—Length, 80-160 mm. Diameter, 3-5 mm. Clitellum reddish. First dorsal pore on 10/11 but with an imperforate marking on 9/10 (Thanbula a-b), on 11/12, occasionally with a pore-like but imperforate marking on 10/11 (Thanbula c and several others).

Measurements of b setae of xix

| Length in mm | Thickness in micra at nodulus* | |
|---|---|---|
| 0·43 | 40 | Prome |
| 0·47 | 40 | .. |
| 0·39 | 40 | Paukkaung |
| 0·31 | 33 | Thanbula |
| 0·31 | 25 | .. |
| 0·32 | 30 | .. |
| 0·25 | 20 | Thanbula a |
| 0·26 | 26 | b |
| 0·48 | 38 | c |

Spermathecal pores in lateral portion of *BC*. Female pores both present (53). Male porophores circular or nearly so, or transversely elliptical and then occasionally approximating to size and shape of porophores of *hastatus*. The fissure, at or close to *B*, usually central, occasionally slightly lateral.

General markings in contact mesially or nearly so, on xiv (2 Paukkaung), xv (1 Thanbula), xviii (11), xix (5), xx (1), xxi (4).

*Ornamentation of transverse rows of fine teeth near tip.

*Internal anatomy.*—Typhlosole begins in xxviii-xxix. Lateral typhlosoles present in first one or two typhlosolar segments (63). Lateral intestinal caeca unrecognizable in some but present though rudimentary in others, in xxviii. Ventral caeca in xxxi-xliv (1 Prome), xxxii-li (1 Prome), xxxii-liv (1 Prome), xxxii-lv (1 Prome), xxxiii-l (Thanbula b) xxxiv-lvii (Thanbula c).

Location of supra-intestinal glands

| Segments | Number of specimens from | | |
|---|---|---|---|
| | Prome | Paukkaung | Thanbula |
| 73-76 | .. | 1 | .. |
| 75-77 | .. | 1 | .. |
| 75-78 | .. | 1 | |
| 76-80 | .. | 1 | .. |
| 77-80 | .. | 6 | . |
| 77-81 | 2 | 1 | 2 |
| 78-81 | 1 | 1 | .. |
| 78-82 | 3 | 1 | 1 |
| 79-82 | 1 | 1 | .. |
| 79-83 | 2 | .. | 3 (including a) |
| 80-83 | 1 | .. | .. |
| 80-84 | 5 | .. | 5 |
| 80-85 | 1 | .. | .. |
| 81-84 | 2 | .. | .. |
| 81-85 | 4 | .. | 1 |
| 81-86 | 1 | .. | 1 |
| 82-86 | 4 | .. | .. |
| 82-87 | 3 | .. | .. |
| 83-87 | 3 | .. | .. |
| 84-88 | 1 | .. | .. |
| 84-89 | 1 | .. | .. |
| 85-89 | 1 | .. | 1 (b) |
| 89-93 | .. | .. | 1 (c) |

Dorsal vessel uninterrupted (63), segmental commissures of vi and v always present (63), usually large and blood filled.

Testis sac annular (63). Male funnels of x present (63), usually small, with no ducts (6 Prome), ducts present but slenderer than the posterior ducts (57).

Spermathecal diverticua median and lateral (126 spermathecae). Occasionally with a double widening distally to produce a rathercruciform shape (8 diverticula).

Penial setae (20 from Prome) 1·49-2·51 mm· long, 42-70μ thick at base 35-50 at neck (just ental to blade), 51-75 at widened blade. Shaft nearly straight except for curvature ectal to neck. Ornamentation, from neck entally, of transverse rows of 3-12 spine-like teeth, or occasionally teeth in somewhat irregular circles. Number, 7-9 (10 batteries), 10-11 (2 batteries), 7-13 (8 batteries of aprostatic juveniles). All setae usually yellow, functional setae of a deeper color, or functional setae with pink tips, or reserve setae pink and functional yellow (3 batteries from Thanbula a-b-c).

*Remarks.*—Aprostatic juveniles, in which prostates are not yet recognizable internally, are 53-62 mm. long and 3 mm. thick. Rudiments of seminal vesicles are recognizable and ental ends of spermathecae just protrude through the parietes. Rudiments of genital markings are recognizable on a slightly larger juvenile, 87 ×3·8 mm.

Spermathecal pores of Thanbula a and b are in median half of *BC*. Genital markings are on xi in *BC* (Thanbula a), on xii-xiii in *BC* (Thanbula b), and those of Thanbula c are in *AB*, on xix, postsetal with *a* and *b* in anterior margin.

14

Natmauk (Magwe), on the road from Magwe, August, 5-0-5. K. John.

*External characteristics.*—Length, to 110 mm. Diameter, to 5 mm. Clitellum yellowish. Setae small, one *b* of xix 0·32 mm. long and 32μ thick at nodulus, a reserve associated therewith being 0·25 mm. and 25μ. First dorsal pore on 11/12 (5).

Spermathecal pores with centers at or slightly lateral to *B* and reaching m*BC*. Female pores both present (5). Male porophores as on topotypical material (1), or slightly elongated so as to dislocate 16/17 and 17/18 (3), larger and circular and extending from *A* to *C* (worm with markings on xix). Fissure just lateral to *B*, margin of fissure aperture usually slightly tumescent, annular (1) and distinctly marked off by a completely circumferential furrow.

Genital markings, of about the size of porophores (3) or slightly smaller, in *BC* or *AC*, on xv, right side (1), both sides (3), xix (1).

*Internal anatomy.*—Typhlosole begins in xxvii (1) or xxviii (4). Lateral typhlosoles always present in first two typhlosolar segments. Lateral intestinal caeca lacking (1), represented by small trilobed flaps in xxvii(1), or by slightly protuberant, anteroposteriorly or lateromesially flattened flaps, definitely constricted off only dorsally, in xxviii (3). First ventral caecum in xxxiii (1), xxxiv (1) or xxxv (3).

Location of supra-intestinal glands

| Segments | Number of specimens | |
|---|---|---|
| 101-105 | 1 | Markings+on xix |
| 102-106 | 2 | Including 1 juvenile |
| 103-109 | 1 | Juvenile |
| 104-109 | 2 | |

Dorsal blood vessel uninterrupted, commissures of v present and red (7, including 2 juveniles).

Testis sac annular (5), above dorsal vessel. Male funnels of x larger than in topotypical worms and crenellated. Bulbus ejaculatorius small, soft, whitish, covered by delicate tissues.

Spermathecal duct so short as to be almost unrecognizable in coelomic cavity. Diverticula median and lateral (14 spermathecae).

15

Magwe, vicinity of, August, 0-0-9. K. John.

Male porophores and genital markings (on xxi) appear to be the same as in *hastatus* from the same locality. Supra-intestinal glands are in xcv-ciii, the same segments as are involved in *hastatus* from the same locality.

*Remarks.*—Other portions of the records and the specimens were destroyed during the war.

16

Pegu Yomas, opposite Letpadan (Tharrawaddy), August, 0-0-2. G. R. Anderson.

Genital markings on 21/22. Markings and male porophores as in *hastatus* from the same locality. Seminal vesicles of xii reach into xvii.

*Remarks.*—Other records as well as the specimens were destroyed during the war.

Intersegmental markings have not been found, in this species, at any other locality. Similarly, such markings have been found, in *hastatus*, only at this locality. Both holandric and metandric individuals were characterized by unusually long seminal vesicles. Accordingly it appears that worms which must be referred to *constrictus* have arisen, *in situ*, from *hastatus* by the metandric mutation.

17

Mt. Victoria (Pakokku), at 3,000 feet, in teak forest and grass land on east side near path from Kanpetlet to summit, July, 7-0-0. Dr. G. Heinrich.

*External characteristics.*—Length, 70-100 mm. Diameter, 3-5 mm. Setae begin on ii on which all are present though almost unrecognizable except with brilliant illumination because of small size and deep retraction ; on xx, $AB<CD<BC<AA$, $BC$ quite definitely $< AA$ throughout the rest of the axis. A *b* seta of xix of the most mature specimen is 0·32 mm. long and 22μ thick and without recognizable ornamentation. A reserve seta from same follicle 0·085 mm. long and 25μ thick at base. First dorsal pore on 11/12 (3) or 12/13 (1).

Spermathecal pores in median half of *BC*. Female pores both present. A penial annulus centered about at *B* in a slight convacity extending from *A* to m*BC* and no deeper than that of the genital markings. Posterior part of the annulus slightly thickened.

Genital markings paired, depressed, greyish translucent, from *A* to m*BC*, on xx (3).

*Internal anatomy.*—Typhlosole begins in xxix (6). Lateral typhlosoles in first one or two typhlosolar segments (6). Lateral intestinal caeca represented by small, vertical protuberances without definite demarcation, in xxviii (6), apertures into gut lumen in anteriormost portion of xxix clearly marked off on inner wall of intestine. Ventral caeca present. Supraintestinal glands in lxxv-lxxviii (2), lxxvi-lxxix (2), lxxvii-lxxix (1), lxxvii-lxxx (1), lxxviii-lxxxi (1).

Dorsal blood vessel uninterrupted (7), segmental commissures of v blood filled (7). A transverse vessel connects the extra-oesophageals just behind 5/6.

Testis sac annular (3). Seminal vesicles restricted to xii (6), including most mature worm extending into xiv (1), a slender posterior lobe directed dorsally (6), posteriorly directed and in a rather closely zigzagged series of loops (1). Male funnels of x only slightly smaller than the posterior funnels.

Spermathecal diverticula median and lateral (2 spermathecae).

Penial setae (12) 0·36-1·23 mm long, 13-28μ thick at base, 15-47 at midshaft, 5-15 at tip. Shaft slightly bowed, gradually widened to a blade-like region ectally and then tapering to a blunt point, tip slightly curved in opposite direction to that of the other part of the shaft. Ornamentation of fine teeth in broken circles. Number, 9-15 (6 batteries). Two longest setae in each follicle, otherwise indistinguishable, from the reserves were measured. Reserve setae are thicker than the others.

*Remarks.*—Most mature worm is only 85 mm long. The penial annulus seems to be unusually well developed in comparison with other sex organs.

Gut of several worms is filled with a black "vegetable mould"

Identification of small juveniles of *Eutyphoeus* from a region of unknown fauna at present can be only tentative. In their present stage the worms are indistinguishable from *constrictus*. If the penial annulus represents an early rudiment of an elongate penis, development of some sort of an invagination to contain it is to be expected. Unpigmented worms with elongate penes and uninterrupted dorsal blood vessel, whether uni- or bi-vestibulate, cannot be referred to any species now known.

18

Mt. Victoria (Pakokku), in pine forest and evergreen jungle on east side near path from Kanpetlet to summit, at 7,800 feet, May 10 to June 10, 27-0-0. Dr. G. Heinrich.

*External characteristics.*—Length, 47,90 mm, Diameter, 3-4 mm. Setae begin on ii on which all are present ; on xx, $AB<CD<BC$, $BC$ *ca.*- or slightly<or slightly<$AA$. A *b* seta from xx of the most mature specimen 0·43 mm long and 36μ thick at nodules, 0·34μ and 32μ from opposite side of same segment, an ectal portion lacking in both cases, ornamented with transverse rows of fine teeth. A reserve setae 0·04 mm long and nearly 20μ thick at base (ental end). First dorsal pore on 11/12 but with a pore-like though imperforate marking on 10/11 (9), 12/13 (1).

Spermathecal pores just lateral to *B*. Punctate depressions mark sites of both female pores. The male porophore is represented by an area of slight epidermal thickening, extending from just median to *A* to a slightly greater distance lateral to *B*, on which are two minute apertures. The anterior is a (combined ?) opening of penisetal follicles, the posterior a male pore. The margin of the male pore is very slightly turnescent on one of the worms.

Genital markings on xviii and xix, with centers about on *A* and reaching laterally to *B* (1, the largest specimen).

*Internal anatomy.*—The typhlosole begins in xxix (10). Lateral typhlosoles present in first one or two typhlosolar segments. Lateral intestinal caeca small, clearly marked off from gut, usually directed ventrally, in xxviii (10) but opening into gut in anteriormost portion of xxix. Ventral caeca in xxxi-lii (1), first caecum in xxxiii (3). Supra-intestinal glands in lxvii-lxix (1), lxviii-lxx (4), lxix-lxxi (2), lxx-lxxii (2), lxxi-lxxiii (1).

Dorsal blood vessel uninterrupted (10), commissures of v filled with blood (10).

Testis sac annular (10). Seminal vesicles reach posteriorly into xvii or even further back (1), xv (1), confined to xii (8). Each vesicle, in the latter case, in two distinct portions, an anterior which reaches only part way up the gut, and a posterior that is longer, usually narrower, reaching up to dorsal vessel or even across it to opposite side. Male funnels of x rudimentary, posterior funnels much larger but still button-shaped and of course without spermatozoal iridescence.

Spermathecal diverticula median and lateral (20 spermathecae).

Penial setae (18) 0·78-1·92 mm long, 16-27μ thick at base, 23-35 at midshaft, 9-15 at tip. Shaft straight except for a slight curve at ectal end and there widened but not flattened. Tip rather pointed or ending in a slight spine (4 setae). Ornamentation of fine spines in closely crowded, broken circles. Number, 10-15 (19 batteries). (The longest seta of each follicle considered as "functional" and measured. Other setae, reserves, thicker and yellower.)

*Remarks.*—Some of these worms were found crawling around on the ground after only two days of rain, according to Dr. Heinrich, though earthworms had not been found prior to that time. Others were found on trees, under bark and in holes made by beetles at about five feet from the ground. Intestines of such worms were filled with a black "vegetable mould" while the guts of others were filled with a yellowish or brownish soil.

These worms are distinguished from those of the 3,000 foot level by the smaller number of supra-intestinal glands (in 3 instead of 4 segments), the more anterior location of those glands (a slight discontinuity in segments involved in the two localities), better development of lateral intestinal caeca, larger setae, more anterior location of the genital markings, and absence of a penial annulus. In their present stage of development these worms, like those from the lower level, cannot be specifically distinguished from *constrictus*.

### VARIATION IN *E. constrictus*

A functional dorsal pore on 10/11, presumably primitive, characterizes worms from the extreme southern part of the range (Hanthawaddy, Insein and Bassein districts), and from the west bank of the Irrawaddy in Prome but is occasionally still found in other localities (as Prome, Myitkyina). Location of spermathecal pores at or close to *B*, also primitive, characterizes worms from a central part of the range (Meiktila, Myingyan, Yamethin districts) and occasional individuals from Toungoo. Pores are in a median portion of *BC* in material from Natmauk (also in the dry zone), Mt. Victoria and Myitkyina but elsewhere have been shifted still further, to lateral part of *BC* or even into *CD*.

Genital markings have been lacking in all material from Myingyan, Meiktila and Myitkyina districts, in nearly a half of the worms from Hanthawaddy and Insein districts, as well as on occasional individuals elsewhere. Markings are segmental, paired, present only in clitellar and postclitellar (xviii-xxi) regions but vary in size, shape, intrasegmental location and number. Intraclitellar locations have been found only in worms from a middle portion of the southern half of the range (Magwe, Yamethin, Toungoo, Prome districts). Male porophores also vary as to size, shape and appearance. A distinct annulus around aperture into the fissure of the male porophore is generally present only in southern material (Hanthawaddy, Insein, Bassein, Labu), but even here it is not yet certain whether this annulus is a permanent structure or formed perhaps by rolling outwards of the wall of the fissure.

Variation as to segment in which the typhlosole begins is slight and there was none as to presence or absence of lateral typhlosoles. Lateral intestinal caeca are frequently lacking, often quite rudimentary, and at most not constricted off from gut all around the circumference. Caeca are usually in xxviii rarely in xxv (Myitkyina), xxvii (Meiktila) or xxix (several localities).

Number of segments with supra-intestinal glands, in an individual, varies, 3-7 ; 3-5 at Paukkaung, 4-5 at Padaukchaung and Pegu Yomas, 4-6 at Thanbula, Prome, Twante, 4-7 at Labu, 5-7 at Natmauk and Meiktila. Number of segments in which glands have been found, in a local population, is greater ; 7 at Mt. Victoria (7 and 10 specimen samples), Bassein (20) ; 9 at Natmauk (6), Hanthawaddy (53), Insein (2), Pegu Yomas (15), and Meiktila (14) ; 10 at Paukkaung (14) ; 11 at Labu (15) ; 13 at Prome (36) ; 17 at Thanbula (15). The number for the species is still larger, 37, the segments lxxiii-cix. The most anterior locations were in Prome material and the most posterior in that from Natmauk, the former locality well within and the other near the dry zone.

Male funnels usually are present in x most everywhere but apparently have disappeared in the Bassein population. There is no variation in termination of the dorsal vessel, any specimen with a foreshortened trunk would be identified as another species. Variation in taxonomically significant characteristics of the spermathecae is almost nil. Of the 406 (+)

spermathecae of 302 + specimens of *constrictus* that were examined in this connection, 603 were bidiverticulate. One lacked both diverticula. Several worms have had an extra diverticulum on anterior or posterior face of the duct. Only two athecal individuals of this species were ever found.

The range of *constrictus* includes all of the Pegu Yomas and their northern continuation between the Chindwin and Irrawaddy rivers as well as the western lowlands down to the latter between the bend and Prome. In recent alluvium the species has been found across the river from Prome once, at one locality in Bassein district, and near the yomas in Insein district but probably is present in older alluvium of the Sittang Valley north of Toungoo as it has been found occasionally in the Toungoo hills at the western margin of the Shan plateau. Included is all of the *hastatus* range that is east of the Chindwin and the Irrawaddy.

Morphologically about all that seems to be needed to derive *constrictus* directly from *hastatus* is elimination of the testes in x. The similarity of male porophores, identical location of similar genital markings in worms of the two species from each of several localities, in particular the very unusual intersegmental locations found at one Yoma site, seem to indicate that such a change may even now be taking place. The location of supra-intestinal glands in the same segments of both species through the Magwe-Natmauk section, in view of the marked discontinuity from the rest of *hastatus*, is also of interest in this connection.

The change required for the local phyletic derivation suggests appearance of a mutation, "metandric", for abortion of the anterior testes. Indeed, the lessened importance of the gonads of x in reproduction apparently evidenced by many specimens of *hastatus*, especially in an eastern portion of the range, may indicate that the mutation is already fairly well established in various populations of that species though its expression is masked or delayed until late in life of the individual. Persistence of functionless male funnels in x throughout most of the *constrictus* range has been regarded as evidence of recent origin. Occasional presence of rudimentary seminal vesicles in certain Yoma localities should then require a still more recent origin as vesicles certainly have disappeared in most metandric species long before the funnels of x. Retention of these useless organs, the funnels and vesicles, in *bullatus* as well as *constrictus*, and their eventual disappearance pose a problem with Lamarckian implications. The solution proposed is delay in penetrance till after gonads have induced development of the other organs, the delay greater in individuals with vesicles. Disappearance of the male funnels of x in certain isolated populations of *constrictus* would then indicate a fourth and still earlier stage of penetrance.

No geographically feasible alternative to phyletic derivation of *constrictus* from *hastatus* is available. The name of the former is now given to a group of species with ranges contiguous to or overlapping that *of constrictus*.

Two specimens of *constrictus* without spermathecae are to be explained as the result of appearance of a mutation, for inhibition of development of spermathecae. This mutation, "athecal", appears very much more rarely in *Eutyphoeus*, where only these two cases are known, than in various Burmese species of *Pheretima*. Athecal mutants cannot receive sperm in copulation. In absence of parthenogenetic capacity, as apparently in *Eutyphoeus*, there will be no offspring to perpetuate the mutation at least insofar as the female side of the hermaphroditic animal is concerned.

**Eutyphoeus peguanus** Gates 1925

1

Rangoon and immediate vicinity maHthawaddy), July-August, 0-0-69. K John.

Syriam (Hanthawaddy), August, 0-10-50. K. John.

Kyauktan (Hanthawaddy). August, 0-12-22. K. John.

Hmawbi (Insein), September, 0-0-34. K. John.

Taukkyan (Insein), September, 0-11-54. K. John.

Wanetchaung (Insein), September, 0-3-54. K. John.

Wakema (Myaungmya), October, 0-0-1. Maung Ohn Maung.

Pantenaw (Maubin), October, 3-0-0. Maung Ohn Maung.

*External characteristics.*—Unpigmented, as all material considered below. Clitellum reddish, at most only slightly tumescent. Ventral setae of viii-x ornamented as in *constrictus*, a *b* seta of xix from an aclitellate Rangoon worm 0·5 mm long and 44μ thick at nodulus. First dorsal pore on ?11/12 (2), 11/12 (52, of which 15 have an imperforate marking on 10/11).

Spermathecal pores large, in *BC*, occasionally reaching both *B* and *C*, usually centered at or near m*BC*, occasionally just median to *C*, rarely median to m*BC*. Female pores both present (63).

Male porophores large, circular or slightly extended longitudinally (never transversely), on large worms about 2 mm wide or 2 + 2½ mm, extending from or just median to *A* to m*BC*, often less distinctly demarcated mesially, body wall often slightly raised just beyond lateral margins. The small, shallow transverse fissure just lateral to *B*, usually on posterolateral quadrant, or near middle of posterior half (Kyauktan, Hlegu, Taukkyan). Two distinct penisetal follicle apertures present on roof of fissure but definite tubercles have not been recognized. Male pore on a small protuberance from posterior portion of fissure and may be nearly spheroidal, or depressed centrally so as to have a ring shape or in addition narrowed proximally so as to have more or less of a funnel-shape. Prostatic pore on anterior wall of fissure.

Genital markings lacking or paired and segmental, extending from just median to *A* to m*BC* or even further laterally, slightly dislocating intersegmental furrows both anteriorly and posteriorly, nearly circular or slightly extended longitudinally (never transversely), and of about the same size as the porophores. Markings may be slightly or markedly concave, level or nearly so, or a lateral portion may be elevated.

*Location of genital markings*

| Locality | Number of specimens with markings on | | | | No markings |
|---|---|---|---|---|---|
| | xix | xx | xxi | xxii | |
| Rangoon | 7 | .. | 50 | .. | 12 |
| Syriam | .. | 3 | .. | 51 | 1 |
| Kyauktan | 6 | 19 | 1 | 4 | 2 |
| Hlegu | .. | 32 | .. | .. | .. |
| Hmawbi | 24 | 10 | .. | .. | .. |
| Taukkyan | .. | 32 | .. | .. | 2 |
| Wanetchaung | 1 | 17 | .. | 3 | 28 |
| Wakema | .. | .. | 1 | .. | .. |

Syriam : Rxx and xxii (1), Lxxi and Rxxii (2), Rxxi (1), xx and Rxxii (1).
Kyauktan : Rxx and Lxxi (1).
Hlegu : Rxx (1).
Taukkyan : Rxx and Lxxi (1), Lxx (1).
Wanetchaung: Lxx (7), Lxix and Rxx (1).

Genital markings present on three consecutive segments, xx, xxi and xxii (1 Kyauktan) are smaller than the male porophores.

*Internal anatomy.*—Typhlosole begins in xxviii or xxix (as in other material below). Lateral typhlosoles present in xxviii-xxix (247 unrecognized in 3 worms), just median to caecal apertures. Lateral intestinal caeca are usually present. They may be slight lateral protuberances not clearly marked off from gut. When more distinctly constricted they may be bluntly rounded or pointed and then anteriorly, posteriorly, dorsally or ventrally directed. Occasionally they are completely retracted into gut lumen (4). In xxvii (2), xxviii (65), xxix but opening into gut at 28/29 or in xxviii (2).

Circulatory system, as in material considered below, as in *gigas* except that extra-oesophageal trunks are connected just behind 5/6 by a transverse vessel. Dorsal blood vessel ends with segmental commissures of vii (2), continued anteriorly (all others), usually ending with commissures of vi but at 5/6 (many Wanetchaung, some Syriam, several from other localities), at 4/5 (3 Syriam, several Wanetchaung). The portion anterior to commissures of vi may be white and slender (functionless?) or nearly as thick as posteriorly and then red but transparent even to 4/5 and with a pair of slender (functionless?) commissures just anterior to 5/6 (3).

*Location of supra-intestinal glands and ventral caeca*

| Segments | Number of specimens from | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 3—95 | .. | 1 | .. | .. | .. | .. | .. | .. |
| 94—98 | .. | 1 | 1 | 3 | .. | .. | .. | .. |
| 94—99 | .. | 2 | 1 | 1 | .. | .. | .. | .. |
| 95—99 | 4 | 2 | 6 | 4 | .. | .. | .. | |
| 95—100 | .. | 2 | .. | 4 | .. | .. | .. | .. |

*Location of supra-intestinal glands and ventral caeca*—contd.

| | Number of specimens from | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 96—99 | 1 | .. | .. | .. | .. | .. | .. | .. |
| 96—100 | 4 | .. | 1 | 3 | .. | .. | .. | .. |
| 96—101 | 1 | 2 | .. | 1 | .. | .. | .. | .. |
| 97—101 | 2 | .. | 3 | 2 | .. | .. | .. | .. |
| 97—102 | 3 | 1 | .. | .. | .. | .. | 1 | .. |
| 98—102 | 5 | 1 | .. | .. | .. | .. | .. | .. |
| 98—103 | .. | .. | .. | .. | 1 | .. | 1 | .. |
| 99—103 | 1 | .. | .. | .. | .. | .. | 2 | .. |
| 99—104 | .. | .. | .. | .. | .. | 1 | 7 | .. |
| 99—106 | .. | .. | .. | .. | .. | .. | 1 | .. |
| 100—104 | .. | .. | .. | .. | .. | 1 | 2 | .. |
| 100—105 | .. | .. | .. | .. | 1 | .. | 9 | .. |
| 100—106 | .. | .. | .. | .. | .. | .. | 2 | .. |
| 101—105 | .. | .. | .. | .. | 1 | .. | 4 | .. |
| 101—106 | .. | .. | .. | .. | .. | .. | 13 | .. |
| 101—107 | .. | .. | .. | .. | .. | .. | 2 | .. |
| 102—106 | .. | .. | .. | .. | .. | 2 | 2 | 1 |
| 102—107 | .. | .. | .. | .. | 1 | .. | 8 | .. |
| 103—106 | .. | .. | .. | .. | 2 | .. | .. | .. |
| 103—107 | .. | .. | .. | .. | 1 | .. | .. | .. |
| 103—108 | .. | .. | .. | .. | 2 | 2 | 7 | |
| 104—108 | .. | .. | .. | .. | .. | 3 | .. | .. |
| 104—109 | .. | .. | .. | .. | 1 | 1 | 4 | .. |
| 104—111 | .. | .. | .. | .. | .. | .. | 1 | .. |
| 105—109 | .. | .. | .. | .. | .. | 1 | .. | .. |
| 105—110 | .. | .. | .. | .. | .. | .. | 1 | . |
| 106—110 | .. | .. | .. | .. | .. | .. | | .. |
| 107—112 | .. | .. | .. | .. | .. | .. | 1 | .. |
| 34—66 | | | | | | | 1 | .. |
| 34—67 | | | | | | | 2 | .. |
| 34—68 | | | | | | | .. | 1 |
| 34—72 | | | | | | | 1 | .. |

Left column worms with genital markings on xxi, right column those with markings on xix.

*Location of supra-intestinal glands and ventral caeca*—contd.

| Segments | Number of specimens from 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | Left column worms with genital marking on xxi, right column those with marking on xix. |
|---|---|---|---|---|---|---|---|---|---|
| 34—73 . . . . | | | | | | | .. | 1 | |
| 35—70 . . | | | | | | | .. | 1 | |

1 Syriam. 2 Kyauktan. 3 Hmawbi.
4 Wanetchaung. 5 Hlegu. 6 Taukkyan.
7 Rangoon. 8 Wakema.

The first supra-intestinal gland is at 98 and 127 mm (from anterior end) in worms 200 and 250 mm long respectively.

Testis sac annular (almost always). Male funnels of x and their deferent ducts almost always present. The funnels may be as large and of same shape and appearance as those of xi, little more than small rounded knobs, or variously intermediate between those two extremes, the several conditions shown by worms from each of the localities. Deferent ducts are almost always smaller, occasionally much smaller, than those of the posterior funnels. Ducts of a side usually come into contact in xii and run side by side to xvii where they unite, but they may separate from each other at irregular intervals between xii and xvii, be twisted around each other, or (very rarely) be widely separated until xvii.

Spermathecal duct short, with thick wall, lumen irregularly slit-like in cross section due to presence of vertical ridges. One on the posterior wall often enlarged and with a slight vertical groove. A similar ridge occasionally present on anterior wall. Ampulla usually rather longitudinally sausage-shaped, often asymmetrical with relation to duct. Diverticula lateral and median (498 spermathecae), right spermatheca lacks median diverticulum (1 Syriam), both diverticula lacking (1 Syriam, Abn. No. 2). An additional one or two small diverticula present on posterior faces of ducts (1 Hlegu). Diverticula may be ovoidal, ellipsoidal, digitiform and in latter case bent, twisted or with very slight marginal indentations as if indicating a very slight zigzag looping. Sperm in each diverticulum usually in one continuous mass. A pyriform sperm mass with head embedded in granular contents of ampulla very frequently resting on aperture into duct, a narrowed ectal continuation translucent to transparent and occasionally protuberant to exterior through spermathecal pore.

Longitudinal musculature uninterrupted over genital markings though body wall may be bulged more or less conspicuously into coelomic cavities according to the depression of the markings.

Penial setae (60 Rangoon) 1·0-1·88 mm long, 33-55μ thick at base, 30-40 at neck, 37-50 at blade, 11-20 at tip.* Shaft usually straight, occasionally with a slight ectal curve. Tip widened and flattened, tapering to a point, or a short spine (once) or to a knob (4) or with rounded ectal margin. Ornamentation of thorn-like teeth in short transverse rows. Number, 6-10 ; 6 (2 batteries), 7 (5), 8 (9), 9 (12), 10 (2). Functional setae yellow. Reserve setae pink with widened, oar-like blade

* Measurements at tip made at a level 10μ down from ectal margin.

usually tapering to a point. The blade-like widening of the tip is lacking on 20 setae from five Rangoon earthworms that have no genital markings, the setae 35-40μ thick at midshaft. Ornamentation of these setae is restricted to a region between levels 0·3 and 0·4 mm down the shaft. Ornamentation continued further ectally on setae of worms with genital markings, occasionally even to very ectal margin.

Penial setae may lack a blade-like widening of tip in inornate worms from other localities, but outside of Rangoon absence of blade may also characterize setae from worms that do have genital markings. Measurements of smaller penisetal samples are included in the table below.

| Length in mm | Thickness in μ at | | | | Number measured | Number per battery | Genital markings on segment | Locality |
|---|---|---|---|---|---|---|---|---|
| | base | neck | blade | tip | | | | |
| 1·8—2·0 | 53—60 | 31—32 | 38—39 | 15—17 | 2 | 7 | xix | Kyauktan |
| 1·6—1·9 | 31—40 | 34—38 | 41—46 | 12—13 | 4 | 6—7 | xxii | Syriam |
| 1·82—1·87 | 36—38 | 39—41 | | 11—15 | 4 | 7—8 | xx | Hmawbi |
| 1·7—1·82 | 33—38 | 36—38 | | 10—11 | 4 | 8 | xix | Hmawbi |
| 1·6—1·81 | 42—50 | 38—48 | | 11—14 | 6 | 8—13* | xx | Taukkyan |
| 1·5—1·79 | 47—70 | 47—50 | | 12—15 | 6 | 8—9 | xx | Hlegu |
| 1·78—1·96 | 40—47 | 38—45 | | 11—15 | 6 | 6—8 | 0 | Wanetchaung |

*Juveniles.*—Genital markings and male porophores are still lacking on the three Pantenaw worms. Supra-intestinal glands in ciii-cviii.

*Abnormality.*—(No. 1) An extra, median suboesophageal testis sac in xii, containing a male funnel on left side from which a deferent duct runs posteriorly to unite with other two deferent ducts of same side in xvii.

(No. 2) Right spermatheca represented only by two spheroidal vesicles sessile on parietes (Syriam).

*Remarks.*—The funnel-shaped protuberances bearing the male pores are so fragile as to be easily eroded and occasionally little evidence of their former presence is recognizable (erosion subsequent to preservation?).

Aclitellate specimens with a brownish or greyish discoloration of clitellar segments appear to be postsexual. Testis sacs are empty, testes large and fan-shaped, male funnels and spermathecae without iridescence, spermathecal ampullae filled with granular material. Genital markings are unrecognizable though their sites are discolored in the same way as clitellar segments.

Lateral typhlosoles (as in other species) are often unrecognizeble even when intestinal contents have been carefully washed out and then become recognizable only after a firmly adherent, coagulated slime has been scraped off. In cases when coagulum was especially refractory the typhlosoles may also have been scraped off.

A slight sheen indicative of presence of muscle fibres is recognizable on the nerve cord under careful scrutiny. The cord breaks readily, usually close to level at which tension was exerted.

*Includes several very small reserve setae, scarcely more than the apices.

The worms characterized above are topotypical and, in addition, include those similar to topotypes in absence of clitellar genital markings, in size of postclitellar markings as well as of male porophores, and in eccentric location of fissures in posterior halves of male porophores. Localities from which these worms were obtained are all in the Irrawaddy Delta region

The size of the male porophores, together with an ability to depress them in a concave manner, is thought to indicate a sucker-like function at time of copulation. Genital markings, of similar size and capacity, lacking coelomic glands, may have the same function.

2

Duyinzeik (Thaton), September, 0-1-2. K. John.
Kyaikto (Thaton), August, 0-3-22. September, 0-6-48. K. John.
Kinmunsakhan (Thaton), September, 0-1-3. K. John.
Mupun (Amherst), October, 0-0-2. K. John.
Kawkareik (Amherst), 0-0-1.

*External characteristics.*—Length, to 160 mm. Diameter, to 7 mm. First dorsal pore on 11/12 (46, 14 of which have a more or less pore-like marking on 10/11 that is almost certainly imperforate in 12), 12/13 (3).

Spermathecal pores in median portion of *BC*, or with centers occasionally just lateral to *B*. Female pores both present (60). Male porophores small, circular, reaching from or about *A* into *BC*, nearly all of the porophore raised in a rounded, mound-like fashion, fissure central and about at *B*.

Genital markings slightly larger than male porophores, circular or nearly so, or transversely extended, from slightly lateral to mV into *BC*, or to or beyond *mBC*.

*Location of genital markings*

| Locality | Number of specimens with genital markings on | | | | |
|---|---|---|---|---|---|
| | xvi | xix | xx | xxi | xxii |
| Kyaikto . . | 69 | 65 | 4 | | .. |
| Kinmunsakhan . | 4 | 4 | .. | .. | .. |
| Duyinzeik . . | 3 | .. | .. | 2 | 1 |
| Mupun . | 2 | | .. | 2 | .. |
| Moulmein . . . | 35 | .. | .. | 35 | .. |
| Chaungson | 10 | .. | .. | 10 | .. |
| Kya In . . . | 18 | | .. | 18 | .. |
| Ye . | 5 | .. | .. | 5 | .. |

Kyaikto : Rxv, xvi and xix (3); Lxv, xvi and xix (1) ; xvi, Rxx, Rxxi (1) ; xvi, xix, Lxx (1) ; xvi, Rxx Lxxi (1) ; Lxvi, xx (1) ; xix (1) ; Rxx, Rxxi (1).

*Internal anatomy.*—Lateral typhlosoles always present (88). Lateral intestinal caeca usually present, in xxviii (29), dorsally directed (7), ventrally directed (8), laterally directed (5). Ventral caeca : in xxxiv-lvi (2 Kyaikto), xxxiv-lviii (1 Kyaikto), xxxiv-lxi (1 Kinmunsakhan), xxxv-lii (1 Kyaikto), xxxv-lxii (1 Mupun), xxxv-lxv (1 Duyinzeik).

*Location of supra-intestinal glands*

| Segments | Number of specimens from | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| 84—87 | 3 | .. | .. | .. | .. | .. | .. | .. | .. |
| 85—88 | 3 | .. | .. | .. | .. | .. | | .. | .. |
| 85—89 | 7 | .. | .. | .. | .. | .. | .. | | |
| 86—89 | 5 | .. | .. | .. | .. | | | | |
| 86—90 | 3 | .. | .. | .. | | .. | .. | .. | |
| 87—90 | 4 | .. | .. | .. | .. | .. | .. | .. | |
| 87—91 | 3 | .. | .. | .. | .. | . | .. | | .. |
| 88—92 | .. | .. | 1 | .. | .. | .. | .. | | .. |
| 89—93 | .. | 1 | .. | .. | .. | .. | .. | .. | |
| 90—93 | .. | .. | | 1 | .. | .. | .. | .. | |
| 90—94 | .. | | 1 | .. | | | .. | .. | |
| 91—95 | .. | | | 2 | .. | | .. | | .. |
| 92—96 | .. | .. | .. | 1 | .. | 1 | | .. | |
| 93—97 | .. | | | .. | 1 | .. | | | .. |
| 94—98 | .. | .. | .. | .. | 1 | 1 | | | .. |
| 95—98 | .. | .. | .. | | 1 | | | | . |
| 95—99 | .. | .. | .. | | .. | | 1 | 1 | 3 |
| 95—100 | .. | .. | .. | | .. | | | | 1 |
| 96—100 | .. | .. | .. | .. | .. | | 1 | 2 | 5+1 |
| 97—101 | .. | .. | | .. | .. | | 2 | .. | 12+3 |
| 97—102 | .. | .. | .. | .. | .. | .. | 2 | .. | 2 |
| 98—101 | .. | .. | .. | .. | .. | .. | | 1 | .. |
| 98—102 | .. | .. | .. | .. | .. | .. | 3 | .. | 13+3 |
| 99—102 | .. | .. | .. | .. | .. | .. | 1 | .. | .. |
| 99—103 | .. | .. | .. | .. | .. | .. | 3 | .. | 4+1 |
| 99—104 | .. | .. | .. | .. | .. | .. | 2 | | 1+1 |
| 100—104 | .. | .. | .. | .. | .. | | 4 | .. | .. |
| 102—106 | .. | .. | .. | .. | .. | | .. | .. | 1 |

1 Kyaikto. 2 Kawkareik. 3 Mupun. 4 Kinmunsakhan.
5 Duyinzeik. 6 Kyaiktiyo. 7 Taungzun. 8 Naunggala.
9 Thaton.

Numbers to right of + indicate specimens with genital markings on xvi.

Dorsal blood vessel ends, with, or as a triangular tag just in front of, commissures of vi (usually), rarely continued as a slender (and functionless ?) filament to posterior face of 5/6.

Testis sac u- or U-shaped, rarely annular (2 Mupun and several Kyaikto).

Spermathecal diverticula median and lateral (174 spermathecae), median diverticulum lacking on left (1 Kyaikto) or right (1 Kinmunsakhan) spermatheca.

Penial setae (16 Kinmunsakhan) 1·35—1·99 mm long, 45—65μ thick at base, 32—42 at neck, 36—53 at blade, 20—35 at tip, 6—7 per battery (8 batteries); (16 Kyaikto) 1·73—1·96 mm long, 42—60μ thick at base, 33—43 at neck, 33—50 at blade, 20—30 at tip, 7—8 (8 batteries); (6 Duyinzeik) 1·72—1·98 mm long, 40—60μ thick at base, 37—45 at neck, 42—58 at blade, 22—30 at tip, 7—8 per battery (3 batteries).

*Remarks.*—These worms are distinguished from those of the delta region by the presence of clitellar genital markings, smaller size of male porophores, central location on porophores of the penisetal fissure, smaller size of the genital markings which are however larger than the porophores, and more anterior location of the supra-intestinal glands. They are distinguished from the worms of section 3 by the anterior location of the supra-intestinal glands and usually by the presence of intraclitellar markings. Location of the glands in the other Thaton district worms (below) is more nearly as in the delta region.

3

Kyaiktiyo (Thaton), September, 0-0-2. K. John.

Taungzun (Thaton), September, 0-2-24. K. John.

Naunggala (Thaton), September, 0-0-4. K. John.

Thaton, September, 0-76-33. K. John.

*External characteristics.*—First dorsal pore on 10/11 (4), 11/12 (53, on several of which a pore-like but obviously imperforate marking is present on 10/11).

Spermathecal pores in median or lateral halves of *BC*, or with centers at m*BC*. Female pores both present (31).

Male porophores small, circular, about as wide as *AB* but centered at *B*, flat or raised in a more or less mound-like fashion, definitely demarcated by a completely circumferential furrow, with central fissure (Thaton). Circular, distinctly demarcated, about twice width of *AB*, flat, fissure central (Naunggala). Fissure on a mound-like protuberance, possibly in the posterior portion of an indistinctly demarcated porophore of variable size (Taungzun, Kyaiktiyo).

Genital markings circular or nearly so, occasionally transversely or more rarely longitudinally extended, reaching from near mV or nearer *A* to m*BC* or further laterally. Slightly larger than male porophores (Taungzun) or smaller (Kyaiktiyo). A longitudinally elliptical or crescentic (and then concave laterally) marking just median to each male porophore (Thaton, others ?).

*Location of genital markings*

| Locality | Number of specimens with markings on | | | |
|---|---|---|---|---|
| | xvi and xx | xix and xx | xx | xxi |
| Taungzun | | 1 | 25 | .. |
| Naunggala | .. | .. | 4 | |
| Thaton | 11 | .. | 98 | .. |
| Kyaiktiyo | | | .. | 2 |

*Internal anatomy.*—Lateral typhlosoles always present (141). Lateral intestinal caeca in xxviii (30), or xxxix (5), ventrally directed (9), dorsally directed (11), posteriorly directed (10), scarcely constricted off from gut (4). Ventral caeca in xxxv-lxiv (1), xxxv-lxv (1), xxxv-lxviii (1), xxxvi-lxiv (2), all from Thaton.

Dorsal blood vessel usually ends with hearts of vi.

Testis sac u- or U-shaped and in latter case often reaching to or nearly to dorsal vessel, rarely annular (1 Naunggala, 8 Thaton). Annular sacs present in some aclitellate individuals, aclitellate ventral sacs present in some clitellate worms. Anterior male funnels and their ducts lacking in one Kyaiktiyo worm.

Spermathecal diverticula median and lateral (282 spermathecae).

Penial setae (12 Naunggala), 1·6—1·93 mm long, 37—65μ thick at base, 35—48 at neck, 42—62 at blade, 20—30 at tip, 8—12 per battery (6 batteries); (2 Taungzun) 1·75—2·05 mm long, 45—50μ thick at base, 41—43 at neck, 50 at blade, 22—30 at tip, 7 (1 battery); (4 Kayiktiyo) 1·51—1·91 mm long, 38—42μ thick at base, 40—45 at neck, 44—58 at blade, 20—25 at tip, 8—9 (2 batteries).

4

Kamaungthwe River, east (Tavoy), August, 0-1-3. W. D. Sutton.

Tavoy district (Site No. 9), August, 0-0-3. W. D. Sutton.

*External characteristics.*—Spermathecal pores centered at m*BC* or mesially. Male porophores large and like those of topotypical worms. Genital markings lacking as on all previous specimens from Tavoy and Mergui districts.

*Internal anatomy.*—Supra-intestinal glands in lxxxviii-xci (2), lxxxviii-xcii (4), lxxxix-xcii (1), xc-xciii (1). Dorsal blood vessel ends with commissures of vi (8). Testis sac annular (8). Anterior male funnels and deferent ducts lacking (1 Kamaungthwe), funnels well developed but ducts lacking (2 Kamaungthwe), funnels and ducts present (5).

Penial setae (14) 1·63—1·92 mm long, 40—60μ thick at base, 30—38 at neck, 32—40 at blade, 20—30 at tip, 6—8 per battery (7 batteries).

5

Shwegyin (Toungoo), October, 0-0-15. Saw Marshall Shwin.
Kyaukkyi (Toungoo), October, 0-0-3. Saw Marshall Shwin.

*External characteristics.*—Length, to 310 mm. Diameter, to 10 mm. First dorsal pore on 11/12 (15, of which 4 have a pore-like but imperforate marking on 10/11).

Spermathecal pores in lateral portion of *BC*, occasionally reaching beyond C, or centered about at m*BC*. Female pores both present (17). Male porophores mound-like protuberances or flat discs with one portion (posterior, median or central) bearing the fissure protruded in a mound-like manner.

Genital markings of about the same size as male porophores or larger, median margins about at *A* or just lateral to mV, on xvi and xx (18).

*Internal anatomy.*—Lateral typhlosoles always present (19). Intestinal caeca in xxvii (1), xxviii (12), or in xxviii but opening into gut through 28/29 (3), posteriorly directed (1), anteriorly directed (1), dorsally directed (6), ventrally directed (1), Ventral caeca in xxxv-lxix (1 Shwegyin). Supra-intestinal glands as shown in table below.

Dorsal blood vessel ends with commissures of vi (17), continued into v where it bifurcates, the branches passing ventrally just in front of 5/6 (1 Shwegyin).

Testis sac ventral (8 Shwegyin, 1 Kyaukkyi), U-shaped and reaching to or nearly to dorsal vessel, or annular (2 Shwegyin). Anterior male funnels and their ducts present or lacking (1 Shwegyin).

Spermathecal diverticula median and lateral (36 spermathecae).

6

Toungoo, October, 0-0-40. K. John.
Toungoo district, September, 0-0-8. G. E. Blackwell.

*External characteristics.*—Spermathecal pores centered at or just lateral to *B* or near m*BC* (8 district).

Male porophores small, about as wide as *AB* but centered at *B*, clearly demarcated, mound-like, fissures central (40 Toungoo and 2 district), porophores large, disc-shaped, fissures on local mound-like protuberances from median portions (6 district).

Genital markings extending from or just median to *A* to m*BC* or nearly to *C*, usually longitudinally extended, occasionally transversely; on xix (40 Toungoo), xx (2 district, with small porophores), xxi (1), Rxix and Rxx (1), Rxx (1), Lxx and Rxxi (1), Lxix and Lxx (1), xix and Rxx (1). A transverse greyish translucent area with distinctly demarcated and slightly raised rim and each of its four sides slightly concave is present in *AA* on xvii (most Toungoo). A more or less clearly demarcated, rather crescentic area (concave mesially) may be marked off just lateral to each male porophore (14 Toungoo).

*Internal anatomy.*—Lateral typhlosoles always present (48). Ventral caeca in xxxiv-lxvii (1 district). Supra-intestinal glands as in table.

*Location of supra-intestinal glands*

| Segments | Number of specimens from | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| 92— 96 | 1 | .. | | 1a | |
| 93— 96 | . | 1 | | | .. |
| 93— 97 | | 1 | | 1a | .. |
| 94— 98 | | 1 | .. | | .. |
| 94— 99 | 2 | | | | .. |
| 95-- 99 | | | 4 | | .. |
| 96—100 | .. | .. | 1 | 1 | .. |
| 96—101 | | .. | 1 | 1 | |
| 97—101 | | .. | 3 | 2 | .. |
| 97—102 | .. | . | .. | 1 | .. |
| 98—102 | | .. | 2 | .. | .. |
| 99—103 | 1 | .. | 1 | | .. |
| 99—104 | 2 | | | | 3 |
| 99—104, 106 | | | 1 | | .. |
| 100—104 | 2 | | .. | .. | 2 |
| 100—105 | 3 | | 1 | .. | 2 |
| 101—104 | 1 | | .. | .. | .. |
| 101—105 | 2 | | .. | .. | 2 |
| 101—106 | | | .. | | 4 |
| 102—106 | | .. | | .. | 1 |
| 102—107 | 1 | . | .. | | 5 |
| 103—108 | .. | .. | .. | .. | 1 |

1 Shwegyin. 2 Kyaukkyi. 3 Toungoo.

4 Toungoo district. 5 Pyinmana.

(a) Specimen with small male porophores. Others with larger porophores.

The dorsal blood vessel usually ends with the hearts of vi but may be continued very shortly as a tag or to 5/6 as a slender (functionless ?) filament (4 Toungoo, 2 district with small porophores) or even to 4/5 and with thread-like commissures in v (6 district with larger porophores).

Testis sac ventral, U-shaped or annular.

Spermathecal diverticula median and lateral (96 spermathecae).

Penial setae (8, from one of the localities) 1·76—1·91 mm long, 45—65μ thick at base, 40—50 at neck, 55—75 at blade, 20—30 at tip, 6—7 (4 batteries); (12 from the other locality) 1·86—2·09 mm long, 43—65μ thick at base, 40—47 at neck, 40—47 at blade, 22—30 at tip, 6—8 (6 batteries).

7

Pyinmana (Yamethin), August, 0-2-19. K. John.

*External characteristics.*—Length, 180—250 mm. Diameter, 6—8 mm. First dorsal pore on 11/12 (19, of which one has a pore-like but imperforate marking at 10/11).

Spermathecal pores large, reaching nearly to *B* and *C*, centers usually slightly nearer *C*. Female pores both present (18).

Male porophores distinctly demarcated, reaching from region of *A* nearly to *C*, nearly circular, the fissure at center of ventral face of a fairly large, mound-like protuberance from a median portion. The prostatic pore is minute and located on a small spheroidal protuberance from the anterior margin of the fissure, the male pore on a larger protuberance from the posterior margin.

Genital markings of about the same size as the porophores, nearly circular, transversely or longitudinally extended, always slightly nearer posterior than anterior intersegmental furrow: on xx (9), and Lxxi (1), xxi (1), Lxx and Rxxii (1), Rxxi (1), xix (2), Lxiv, xix and xx (1), Lxiii, xx and xxi (1), Lxx and Rxxi (1), Rxii, xiii, xxi and xxii (1), none (1).

*Internal anatomy.*—Lateral typhlosoles always present (20). Lateral intestinal caeca lacking (1), in xxviii (10), xxix (10, but opening anteriorly through 28/29 into gut of xxviii in 3), retracted into gut (1). Ventral caeca in xxxiv-lxx (1). Supra-intestinal glands as in table above (p. 139).

Dorsal blood vessel usually continued anterior to commissures of vi, often filled with blood to 5/6, in v slender to filamentous (functionless ?), colorless, no commissures in v (5), or thicker and red to 4/5 with red commissures just anterior to 5/6 (6, in two of which commissures have been traced to ventral trunk), or ending with commissures of v (2).

Testis sac annular (20).

Spermathecal diverticula median and lateral (39 spermathecae), lateral diverticulum of left spermatheca lacking (1).

Penial setae (28), 1·85—2·32 mm long, 55—75μ thick at base, 48—60 at neck, 49—75 at blade, 20—40 at tip. Shaft straight except for a slight ectal curve, tip pink, flattened on one side, widened, tapering to a blunt point (7 of 40 setae), spoon-shaped (2), wrinkled, bent, cracked or broken off and missing (31). Number, 6—9 (14 batteries). Reserve setae red, tapering to a blunt point ectally, the smaller straight, the longer ones bent at tip. Two batteries had three functional (yellow) setae. Ornamentation of thorn-like teeth, scattered or ental to neck in irregular circles.

*Remarks.*—Occasional continuation of the dorsal blood vessel anterior to its usual level of termination, in this and several other species, and association therewith of the various segmental commissures that are ordinarily absent, indicates that the vascular system is laid down during

embryonic development as in most earthworms. Later on, the appropriate portions, according to the species, together with the associated segmental commissures to the ventral trunk, are histolyzed.

*E. peguanus* apparently can be derived directly from *E. constrictus* by a mutation ("foreshortening") for abortion of an anterior portion of the dorsal trunk during ontogenetic development. Occasional presence in adults of a posterior section of the usually aborted portion, together with the appropriate segmental commissures, presumably results from incomplete or delayed penetrance of the mutation. Presence of the useless male funnels of x, and usually also of their ducts, suggests rapid establishment of the foreshortening mutation soon after the metandric mutation that gave rise to *constrictus*. Support for this belief is also provided by the distributions of the two species. The annular tumescence around the fissure of the male porophore, which seems to be developing now in both *hastatus* and *constrictus* has never been found in *peguanus*.

The *peguanus* genotype expresses itself, throughout the recent alluvium of the deltas region, in a phenotype characterized by large genital markings, equally large male porophores and the postclitellar and intrasegmental situation of the markings. Markings and porophores are of such similarity that the fissures almost appear to have been accidentally included. Both markings and porophores may have a sucker-like function at copulation. Equally characteristic seems to be the funnel-shaped, male pore bearing protuberance from the anterior wall of the fissure.

Segmental location of the genital markings is however variable and they may be on xix (f. *promotus*), xx (f. *intermedius*), xxi (f. *typicus*), or xxii (f. *postremus*). Occasionally both markings may be lacking (f. *simplex*).

Worms from Tavoy and Mergui districts always have lacked genital markings which seems to indicate that f. *simplex* is a true breeding type. Almost equal uniformity has characterized the material (f. *postremus*) secured at Syriam over a period of years. A similar uniformity is shown by the collections (f. *intermedius*) at Hlegu, Taukkyan, and to a less extent at Wanetchaung. If *simplex*, *intermedius* and *postremus* are true breeding types then the same may also be true of *typicus*. Rare cases of asymmetry (each marking on a different segment), perhaps also still rare cases of markings on two different segments, may result from hybridization of two of the true breeding forms. At one time it was thought that f. *promotus* might be a hybrid between *simplex* and *typicus* but the materials and records are no longer available. However, it can be stated that during all the years of collecting in Rangoon and immediate vicinity only three forms, *simplex*, *typicus* and *promotus*, were secured.

Worms from isolated colonies at Mandalay, Nyaungyo (Arakan Yomas) and Chaukma (Chindwin Valley), were all of f. *simplex* but the Myitkyina colony comprised *simplex*, *typicus* and *promotus*. Persistence of isolated remnants at the periphery of a once greater range scarcely seems possible in these cases. Of the alternatives, independent origin *in situ* from *constrictus*, or transportation from the deltas region, the latter now seems more probable. Monsoon flood waters, which may have been an agency of distribution in some of the deltas region, cannot

be invoked in the cases of these colonies. Of the agents that are known, or have been postulated, to be responsible for transport of earthworms, man seems to be the most likely. Although *peguanus* has not been found in Rangoon in earth around roots of potted plants, it is frequently present in flowerbeds around houses and in gardens from whence soil containing cocoons or small juveniles could easily have been taken on many occasions. Admittedly however, Mergui and Tavoy distributions, except for Tavoy town itself, seem much less obviously attributable to agency of man than the above-mentioned isolated colonies.

With the deltas forms thus geographically limited it will be convenient to treat them all collectively as a subspecies, *peguanus* n. subsp. The other forms also can be treated as a geographical subspecies which takes the name *similis* (n. subsp.) of one originally thought to be of species status.

In subspecies *similis* male porophores are small, usually smaller than the genital markings and with no sucker-like appearance. Instead they are raised (after preservation) *in toto* so that the fissure is on the rounded apex of a rather mound-like tough protuberance which presumably functions as a sort of intromittent organ in copulation. At greatest protuberance the organs appear to be the equivalent, in larger size, of the firm cone-like penis of *compositus* and closely related species.

Genital markings, in a region from the southern border of Amherst district north to Shwegyin and Kyaukkyi (Toungoo) usually are two pairs, one of which is intraclitellar and on xvi. The second pair, in Amherst district worms from the sea to the Siamese border as well as in various localities of Thaton district, is on xxi (f. *similis*) but in some Thaton localities and in the southern part of Toungoo district is on xx (f. *praecox*). Intraclitellar markings are omitted in some of the Thaton district localities and from Toungoo town north to the end of the range at Pyinmana. The remaining pair may be on xx (Thaton) or xix (Toungoo, f. *tumidus*) or in the north may occasionally be omitted. A peripheral region of the body wall around the mound-like protuberance has a tendency, in the older alluvium from Toungoo north, to assume an appearance of the *peguanus* male porophore. The testis sac, in the Shwegyin region and certain Thaton localities appears to be undergoing a further reduction to a suboesophageal chamber.

*E. peguanus* is quite common in the southern half of the Pegu Yomas which is part of the *constrictus* range but consideration of the very interesting material from that area has now become impossible.

**Eutyphoeus plenus**, sp. nov.

Pyinmana (Yamethin) and vicinity, August, 73-26-239. K. John.

*External characteristics.*—Length, 210-335 (clitellate specimens only). Diameter, 7—10 mm. First dorsal pore on 10/11 (2), 11/12 (203, of which 88 have a pore-like but imperforate marking on 10/11, 12/13 (5, of which 1 has pore-like markings on 10/11—11/12 and 2 have a marking 11/12).

Spermathecal pores in *BC*, occasionally with centers close to or rarely actually at *C*. Female pores both present (147).

Male porophores rather small, slightly wider than *AB*, circular or transversely elliptical, flat or protuberant in a mound-like fashion, not reaching intersegmental furrows, with central fissure. A crescentic area concave towards male porophore, partly or largely greyish translucent, with a more or less definite, opaque, white rim often recognizable just median to each male porophore. A similar area but concave mesially may be visible just lateral to each male porophore.

Genital markings reach from or close to *A* to or nearly to *C* and are usually longitudinally elliptical, touching or dislocating intersegmental furrows.

*Location and number of genital markings*

| Segments | Number of specimens |
|---|---|
| 15, 16 | 1 |
| 15, 16, R19 | 1 |
| 15, 16, 19 | 1 |
| 15, 16, 19, L20 | 1 |
| 15, 16, L19, 20 | 1 |
| 15, 16, L19, R20 | 8 |
| 15, 16, R19, L20 | 5 |
| 15, 16, R19, 20 | 4 |
| 15, 16, 19, 20 | 2 |
| 15, 16, 20 | 219 |
| R15, 16, 20 | 1 |
| 15, 16, 20, R21 | 2 |
| 15, 16, 20, L21 | 3 |
| 15, 16, 20, 21 | 2 |
| 15, 16, R18, 20 | 1 |
| 15, 16, R20, L21 | 1 |
| 15, 16, 21 | 1 |
| 15, 16, L19, 20, R21 | 1 |
| 15, 16, R19, 20, R21 | 1 |
| 15, 16, L18, 19, R20 | 1 |
| 16, L20 | 1 |
| 16, 20 | 3 |
| 16, R20, L21 | 1 |
| R14, 15, 16, 20 | 1 |
| L14, 15, 16, 20 | 1 |

R a marking present on right side only.

L a marking present on left side only.

*Internal anatomy.*—Typhlosole begins in region of xxviii (?). Lateral typhlosoles always present, often small. Lateral intestinal caeca in xxvii (5), xxviii (25), xxix (8), about equally in xxviii and xxix (8), in different segments on opposite sides (a number); dorsally directed (28), ventrally directed (40), anteriorly directed (25), posteriorly directed (51), completely retracted into gut lumen (10), lacking (1). Ventral caeca and supra-intestinal glands located as shown in table below.

*Location of ventral intestinal caeca and supra-intestinal glands*

| Segments | Number of specimens | Segments | Number of specimens |
|---|---|---|---|
| 34—73 | 1 | 106—110 | 4 |
| 35—72 | 2 | 106—111 | 8 |
| 35—73 | 1 | 107—111 | 5 |
| 35—75 | 2 | 107—112 | 16 |
| 35—76 | 2 | 108—112 | 1 |
| 35—77 | 1 | 108—113 | 16 |
| 35—78 | 2 | 108—114 | 1 |
| 35—79 | 1 | 109—113 | 4 |
| | | 109—114 | 7 |
| | | 110—114 | 2 |
| | | 110—115 | 5 |
| | 12 | | 69 |

Circulatory system as in *gigas* except that the extra-oesophageals are connected by a transverse vessel just behind 5/6. The dorsal vessel ends with or just in front of the hearts of vii (286) or is represented anteriorly by a functionless translucent strand (1) or a white and apparently solid cord (3) passing forward to 5/6, or by a slender white strand ending at 4/5.

Testis sac annular (all aclitellate and clitellate worms). Anterior male funnels and ducts lacking (1), the funnels of x rudimentary (14 in 5 of which both ducts are lacking, right duct lacking in 5, left duct in 4). Three deferent ducts on left side (1), from xv to bulbus ejaculatorius, the third duct passing laterally in xiv nearly to *D* and then into xiii where it disappears.

Spermathecal diverticula median and lateral (580 spermathecae), the sperm within often looped or twisted in a somewhat spiral manner.

Nerve cord with a markedly pink sheen due to presence of a strong muscular sheath. This sheath is 130—190μ thick in region of 5/6 and gradually becomes thinner posteriorly but even in xx may still be 100μ thick.

Penial setae (20) 2·09—2·99 mm long, 36—75μ thick at base, 40—70 at neck, 60—115 at blade, 25—45 at tip. Shaft straight except for an ectal curve, yellow except at the ends which are red, with dark segments, tip widened and flattened. Ornamentation of fine thorn-like spines so closely crowded as to have an appearance of fur or in distinct and irregularly interrupted circles and in this case disappearing at a greater distance from the ectal margin. Number, 8—15 (30 batteries), usually 11-15, Reserve setae entirely red, with oar like blade, bent terminally and usually wrinkled in region of bend (softened ?).

*Juveniles.*—Identified by the thick muscular sheath on nerve cord anteriorly. Genital markings and male porophores still lacking on specimens that had reached a size of 150—230×5—7 mm Spermathecal pores represented only by greyish translucent, slight puckerings of the epidermis. Fissures are present in *AB* but usually slightly nearer to *B*. Minute male pore behind the fissure and about half way between equator of xvii and 17/18. Penial setae may protrude slightly from the fissure through a cuticular aperture but in some of the worms the cuticle apparently has no aperture and is continuous across the fissure though tips of penial setae are recognizable therein.

Supra-intestinal glands in civ-cxiii (10). Dorsal blood vessel ends with hearts of vii (9) or on 5/6 (1) and then continued from hearts of vii as a slender transparent thread without blood and presumably functionless.

*Abnormality.*—(No. 1) A wedge-shaped half segment with four setae intercalated behind vii on right side only. Right male porophore on xvi, left on xvii (disregarding the half segment in the present enumeration). Genital markings on Rxiv, xv, Lxvi, Rxix, Lxx.

An extra half septum on right side inserted on gut just in front of gizzard and on parietes just in front of spermatheca. Three commissures from dorsal trunk on the right side anterior to 8/9. The dorsal trunk is continued anteriorly to level of half septum and then passes ventrally as a left commissure of vi (none on right side). Right male funnel of xi large, left rudimentary. A rudimentary seminal vesicle in xi on right side, the right vesicle in xii. Right heart of xiii lacking. Intestinal origin in xiv on right and in xv on left side. Right ovary and female funnel in xii, left in xiii.

*Remarks.*—The region of the body wall peripheral to the small male porophore that would be part of a sucker-like area if in subsp. *peguanus* seems here to be developing, as in some populations of subsp. *similis* and of *constrictus*, into two genital markings with some other function.

The anterior migration, during late juvenile growth, of male pores from their earlier postequatorial site to one nearer the prostatic pores appears to recapitulate part of one of the evolutionary changes of the classical megascolecid phylogeny. The union of male deferent and

prostatic ducts to open by a single pore that was assumed by the proponents of that scheme is not achieved in this case. Nor has it been found in any other species of *Eutyphoeus*.

Absence of pigment, superficial fissures, an annular testis sac, the long series of midventral intestinal caeca, location of the supra-intestinal glands, bidiverticulate spermathecae and a blade-like thickening of the penisetal shaft all indicate close relationships to *E. hastatus*, *constrictus* and *peguanus*. To the last two, closer relationship is indicated by the metandry. *E. plenus* is distinguished from *constrictus* by the ontogenetic abortion of an anterior portion of the dorsal blood vessel and associated segmental commissures, from *peguanus* by abortion of another section of the dorsal trunk along with the commissures of vi. Additionally *plenus* is distinguished from subsp. *peguanus* by the small male porophores and the intra-clitellar genital markings, from subsp. *similis* by a second pair of intraclitellar markings and location of the postclitellar markings on xix. The thickness of the muscular sheath around the anterior end of the nerve cord appears to be unique in the genus but no information is available as to this sheath in other species.

Lateral intestinal caeca, absent only in one of 290 specimens, are more frequently developed than in the related species but here also show variation in site and method of growth.

A "foreshortening" mutation such as has been invoked (pp. 141 and 112) to explain phylogenetic origin of *peguanus* and *bullatus* also can be postulated in the ancestry of *plenus*. Distributions are such that *plenus* can be derived from *constrictus* or *peguanus*. The first alternative involves abortion, in a single step, of more of the circulatory system than in the cases previously considered. This may not be impossible. Incidence of complete penetrance in *plenus* is high, unhistolyzed portions of the dorsal trunk having persisted only in 4 of 293 specimens (*ca.* 1·4 per cent). The second alternative, involving a second foreshortening mutation or some sort of an intensification or extension factor, requires retention of male funnels of x, even though their ducts are disappearing in *plenus*, during the time required for establishment of three consecutive species stages. *E. plenus* is known only from the vicinity of Pyinmana where it presumably arose too recently to have achieved a greater distribution.

### **Eutyphoeus ferinus**, sp. nov.

Myitkyina, September, 0-9-5. K. John.

*External characteristics.*—Length, of largest clitellate specimen, 230mm. (all clitellate worms posterior amputees), of longest complete aclitellate specimens, 270 mm. Diameter, 7 mm. Unpigmented. Setae begin on ii, on xx $AB$=or slightly $<BC<AA$, $DD>\frac{1}{2}$C. Tips of *a* and *b* setae of xiii ornamented by short transverse rows of fine teeth. First dorsal pore on 11/12 but with a non-functional porelike marking on 10/11 (4), without marking on 10/11 (10). Clitellum dark blueish, annular, from 12/13 or just behind equator of xii to 17/18, functional dorsal pores on 12/13 and 17/18 only, intersegmental furrows lacking, setae present.

Spermathecal pores small transverse slits in *CD* or with centers on or just median to *C*. Female pore on left side (most clitellate specimens), a rudimentary (?) right pore present on one clitellate and a punctated depression at site of pore on aclitellate specimens. Male porophores small, firm, with slightly convex surface, circular to shortly elliptical (transversely placed) in *BC*, usually well lateral to *B*. A very small slit, through which tips of penial setae may protrude, is the only aperture that has been recognizable. A crescentic whitened area with concave side laterally may be present median to each porophore or replaced by two smaller, shortly elliptical and slightly diagonal areas.

Genital markings paired, transversely elliptical to circular areas of epidermal thickening, postsetal on xiv-xvi and on 18/19-20/21 as follows : on xvi (1 clitellate), on xiv, xv, xvi (1 clitellate, 6 aclitellate), on xvi and 19/20-20/21 (1 clitellate, 1 aclitellate), on xvi and 18/19,19-/20 (1 clitellate), on xvi and on 19/20 (1 clitellate). Markings of xiv almost meet at mV, the interval between increasing posteriorly. Postclitellar markings extend from *A* or just lateral to mV to m*BC*, or nearly to *C*, *a* and *b* included in anterior marking.

*Internal anatomy.* Typhlosole begins in xxvii. Lateral typhlosoles unusually well developed and folded like the main typhlosole, in xxvii-xxx. Lateral intestinal caeca apparently lacking. Ventral caeca in xxxvii-xxxix (2), xxxvii-xxxviii (1). Supra-intestinal glands in xciv-xcvii (3), c-ciii (1).

Circulatory system as in *gigas* except that extra-oesophageals are connected by a transverse vessel just behind 5/6. Dorsal trunk, ending with commissures of vi, abruptly just in front of the commissures of vi, or continued as a fine white thread to posterior face of 5/6.

Metandric, testis sac ventral. Seminal vesicles push 12/13-13/14 into contact with 14/15. Funnels of x very small club-shaped rudiments (recognized only in aclitellate specimens). Prostatic ducts 15-17 mm. long. Bulbus ejaculatorius fairly large and coelomic.

Spermathecal duct short, stout, lumen irregularly crescentic in cross section due to presence of a high vertical ridge (with vertical groove) on posterior wall and several smaller ridges laterally and anteriorly. Ampulla flattened, anteriorly directed. Diverticulum a bi- or tri-lobed horizontal ridge on posterior face of duct near ampulla. Two apertures (at least?) are present on inner wall of duct from the diverticulum, one just lateral and one just median to the large vertical ridge.

Penial setae (functional) 1·6-2 mm long. Shaft nearly straight except for an ectal curvature, tapering slowly to a rounded tip without terminal spine. Ornamentation of numerous short transverse rows of fine spines. Number, 7 (1 battery of five pink to red reserve and two light yellow functional setae).

No glandular material recognizable over sites of genital markings.

*Remarks.*—In aclitellate specimens seminal vesicles are well developed testis sac filled with coagulum, spermathecae fairly well developed but anteriorly directed ampullae are short and flattened, genital markings indistinctly delimited or (2) primordia unrecognizable.

Morphologically *E. ferinus* appears to be related to *constrictus*, *peguanus* and *plenus* and is distinguished from each of them only by the single functional female pore and the single spermathecal diverticulum perhaps also though with less certainty by the intersegmental location of the postclitellar genital markings.

The morphology of the circulatory system in particular indicates closer relationship to *peguanus* than to *constrictus* or *plenus* but the distributions imply a much closer relationship to *constrictus*. This apparent anomaly seems capable of resolution by a phylogeny in the same manner as for *peguanus*, *plenus*, *bullatus*, and other species. Here again a foreshortening mutation is required but in order to derive *ferinus* from *constrictus* two additional mutations must be assumed. The first of these ("oviductless") is for abortion during ontogenetic development of the right oviduct. The right oviducal or female funnel is retained and seems to be of normal size but the duct is rudimentary or lacking distally. Once again, incomplete or delayed penetrance of a mutation is indicated, here by presence of a rudimentary right female pore on several individuals. The second additional mutation (stalkless 1) is for abortion of the stalks of the spermathecal diverticula so that the seminal chambers are developed in a single horizontal row on the posterior face of the spermathecal duct. An ancestral bidiverticulate conditon is still indicated, in *ferinus*, by the two openings into duct lumen, or the two groups of openings, one on each side of the large vertical ridge on the posterior wall of the duct. This stage may well have been preceded by one in which the two diverticula, instead of growing straight out from the duct in a median and lateral direction, were turned posteriorly and more or less closely approximated. Such a stage is shown today by the spermathecae of *E. macer*.

*E. ferinus* seems not to have initiated development of the lateral intestinal caeca that are now becoming established in *peguanus* and *constrictus*. Reduction of the testis sac to a suboesophageal chamber, which has been found only rarely in *peguanus*, appears to have become customary in *ferinus*.

### The *levis* group

#### **Eutyphoeus levis** (Rosa) 1890

Kyaiktiyo Hill (Thaton), September, 0-0-1 K. John.

Kyaiktiyo (Thaton), September, 0-0-5. K. John.

Thaton, September, 0-5-4. K. John.

*External characteristics.*—Length, to 62 mm. Diameter, to 3 mm. Unpigmented. The *d* setae definitely dorsal (10) in a posterior portion of the body, about at mL or very slightly dorsal (2 posterior amputees). First dorsal pore on 11/12 (12), 12/13 (2), 13/14 (1). Clitellum lacking at mV (10) and between male porophores where body wall is so thin that nerve cord is visible externally.

Spermathecal pores with centers on or close to *B* (15). Female pores both present (10). Male porophores slightly protuberant, transversely and shortly elliptical, rather sharply demarcated areas, with

centers at or slightly median to *B* and reaching mesially to or nearly to *A*. At the center of each porophore a very shallow, transversely slit-like depression contains two pits from which penial setae may protrude, discrete apertures apparently of two penisetal follicles. The marginal region around the slit is slightly tumescent, distinctly demarcated peripherally by a slight, completely circumferential and circular groove. On the tumescence, which looks like a rudimentary penial annulus there is occasionally visible a minute pore, smaller than the penisetal pits, and presumably the aperture of male deferent ducts.

Definite genital markings lacking but in *AB* and on a presetal portion of xvii there may be visible (7) a slightly raised circular area but which has no grey translucent central portion.

*Internal anatomy.*—Typhlosole begins in xxi (4) or xxii (4). Lateral typhlosoles, in first two typhlosolar segments, low, continuous, simple lamellae. Ventral caeca in xxviii-xix (3), xxix (1), xxix-xxx (1). Supra-intestinal glands in lvii-lix (5), lviii-lx (3).

Dorsal blood vessel though unrecognizable in front of vii must be uninterrupted as hearts of vi are always present and blood-filled segmental commissures are recognizable in v (4) or even in iv (1).

Male funnels present in x (8), anterior ducts passing posteriorly for some distance before coming into contact with posterior deferent ducts. Testis sac annular (8), hearts of xi apparently imbedded in the testicular coagulum but dorsal blood vessel probably not included. Prostates confined to xvii-xviii (8), prostatic ducts *ca.* two mm long. Bulbus small, white, soft, confined to parietes or only slightly protuberant into coelomic cavity.

Spermathecal duct with thick wall, lumen small and slit-like in cross section. Diverticulum (single) always lateral (16), digitiform to pyriform and with a single seminal chamber (14), or bifid and with two shortly ellipsoidal seminal chambers (2 spermathecae from the same worm).

Penial setae (20) are (according to Miss Chapman's measurements) 1·0-1·13 mm long, 10-15μ thick at tip, 24-30 at midshaft, 29-49 at base. Shaft slightly curved as in blade of a scythe. Tip tapering and bluntly rounded or, occasionally, slightly widened and spoon-shaped, deformed only in 5 of 50 setae. Ornamentation of long spines in practically unbroken circles between 0·01 and 0·2 mm levels down the shaft. Number, 2 (24 batteries), 3 (2), 1 (2, from one worm).

*Remarks.*—*E. levis* was erected for a single specimen that was considered, even in 1890, to be in too poor condition for study of internal anatomy. The type is broken just behind the prostatic region and intestinal characteristics are not determinable. Spermathecae are however clearly unidiverticulate and the diverticulum is lateral. No positive contraindications against identity with *E. falcifer* Gates 1933 were found. Type localities of the two forms probably are very near each other. The only solution to the problem posed by *levis*, in absence of adequate collections from the region of the type locality, is to supress *falcifer* and define the former as the latter.

**Eutyphoeus pusillulus** Gates 1931

Body wall of the type opaque at mV.

Typhlosole begins in xxii. Lateral typhlosoles low, continuous, simple lamellae in xxii-xxiii. Supra-intestinal glands in lvi-lviii.

*Remarks.*—Sexual maturity is indicated by spermatozoal iridescence on the male funnels but there is no iridescence in the spermathecae to show that copulation had taken place.

*E. pusillulus* is close to *E. levis* from which it can be distinguished at present by the proandry and, of course associated therewith, absence of posterior male funnels, deferent ducts and seminal vesicles.

No evidence of production of sperm in x by *levis* has been found, nor other support for a suggestion previously made that the type of *pusillulus* might be an aberrant individual of *falcifer* (= *levis*).

Ye, the type locality of this species, is at the southern border of Amherst district which must also be considered the southern boundary of the *Eutyphoeus* range. The jungles and uncultivated areas of the southern part of Amherst district to the Siamese border scarcely have been entered by collectors.

**Eutyphoeus pius**, sp. nov.

Kyaiktiyo (Thaton), September, 0-0-2. K. John.

*External characteristics.*—Length, 40 (incomplete posteriorly) to 42 mm. Diameter, 2½-3 mm. Unpigmented. Setae begin on ii (2), *a* and *b* more closely paired than *c* and *d*, *d* setae posteriorly at or only very slightly dorsal to mL. First dorsal pore on 11/12(2). Clitellum annular (?), the body wall though with clitellar coloration so thin near mV that nerve cord is visible externally, definitely lacking near mV on xiii and xvii, extending dorsally from equator of xiii to 17/18 ; dorsal pores and intersegmental furrows lacking, setae present.

Spermathecal pores transverse slits, in lateral half of *BC* but reaching very slightly beyond *C* (1), or with centers about at *C* (1). Both female pores present (2). Penes annular, each in a slight, rather regularly concave depression, the latter in an indistinctly delimited area of slight tumescence (and possible parietal thickening), the annulus just lateral to *B*, the male porophore probably reaching from *A* to or beyond m*BC*.

Genital markings paired, in *AB* but reaching slightly lateral to *B*, apparently postsetal on xiii, xiv and xv (2) as anterior margins quite definitely are nearer segmental equators than the posterior margins (but sites of intersegmental furrows crossed ?).

*Internal anatomy.*—Septa, digestive, circulatory and excretory systems as usual in the genus (2). Lateral intestinal caeca in xxv but opening to gut in xxvi (2). Typhlosole begins in xxvi. Lateral typhlosoles low, simple lamellae in xxvi. Ventral caeca in xxxi-xxxiv (2). Supra-intestinal glands in lxv-lxvi or lxv-lxvii. Dorsal blood vessel continued certainly to 4/5 with commissures in v (1, doubtful in the other).

Testis sac U-shaped (2), reaching up only slightly at sides of gut, ventral portions of hearts of xi apparently imbedded in coagulum. Anterior

wall of sac in region of mV bulged forward half way through segment x. Semimal vesicles extend back to 13/14. No male funnels in x. Bulbus ejaculatorius soft, bound loosely to parietes. Prostates in xvii-xx, ducts 2-3 mm long, slender, white.

Spermathecal duct short, lumen slit-like in cross section, without posterior vertical ridge. Diverticula median and lateral (4 spermathecae), simple, rather elongate and looped in a shortly zigzag fashion.

Genital marking glands (soft) sessile on parietes.

Penial setae 1·45-1·5 mm long (measured along straight line from tip to base), 29-30μ thick at neck (just ental to bowl or widened part of tip), 40μ at midshaft, 51-70 at base. Shaft curved in a rather spiral fashion but when flattened by cover glass has a bow or crescent shape. Tip spoon-shaped (1), thickened but without concavity (1). Ornamentation of slightly irregular, closely crowded circles of very fine spines, frequently and irregularly broken entally. Number, 2 (2 batteries).

*Remarks.*—Clitellar thickening of the epidermis is slight in the smaller worm though intersegmental furrows are unrecognizable, dorsal pores not only present but actually open. As spermatozoal iridescence in the spermathecal diverticula proves that copulation had taken place, condition of the clitellum may be due to postsexual regression.

The penial annulus appears to be a permanent structure seated on a discoidal region of parietal thickening that is slightly depressed, on the types, in a regularly concave manner so as to bring the annulus below general level of body surface. Better protection still for the soft annulus would be provided by apposing anterior and posterior (or median and lateral) margins of the porophore, if that is possible. A vestibulum, eversible as in *macer*, certainly is lacking but a somewhat similar sort of intromittent organ might be attainable, during copulation, by raising the male porophores in a mound-like fashion, as in *constrictus*, with penes at distal extremities.

*E. pius* is morphologically similar to *E. lippus* Gates 1934 from Ramechap district of Nepal in various ways. Differences have to do with : First dorsal pore, on 11/12 instead of 10/11 or anteriorly. Spermathecal pores, centered lateral to m*BC* rather than mesially. Genital markings, several pairs on clitellar segments rather than one pair on x. Lateral intestinal caeca, in xxv rather than xxiv. Ventral caeca, in 3 consecutive segments of xxxi-xxxiv rather than in 4-7 of xxx-xxxvii. Supra-intestinal glands, in 2-3 segments of lxv-lxvii rather than 3-5 of lxvi-lxx.

*E. pius* is distinguished from *E. macer*, present in the same Burmese district, as follows. By absence of eversible vestibula, presence of three pairs of intra-clitellar genital markings instead of one and with a more anterior location (on xiii-xv instead of xvi), lateral intestinal caeca in xxv instead of xxiv, typhlosolar origin and lateral typhlosoles in xxvi instead of xxv, ventral caeca in 3 segments of xxxi-xxxiv rather than 4-6 of xxviii-xxxiv, supra-intestinal glands in 2-3 segments of lxv-lxvii instead of 3 in lxiii-lxvi. Except the vestibula, these differences are of about the same order as those distinguishing *lippus* and *pius*. In these circumstances geographical relationship must be given greater weight

than the structural similarities. The latter then, insofar as *lippus* and *pius* are concerned, are indicative only of similar stages in independent lines of evolutionary development.

**Eutyphoeus macer** Gates 1933

Thaton, September, 0-0-21. K. John.
Bilin (Thaton), September, 0-0-1. K. John.
Kyaikto (Thaton), August, 0-0-1. K. John.

*External characteristics.*—The *d* setae are not noticeably dorsal on any of these specimens. First dorsal pores on 11/12 (15), 12/13 (2).

Spermathecal pores usually in lateral half of *BC*, just reaching to *C*, rarely (1) reaching into *CD* and then with centers at or close to *C*. Female pores both present (23). Vestibular apertures small, centers about at *B*. Vestibula small, practically filled by annular penes. Posterior half of annulus slightly thickened and continued ventrally into two pointed flaps usually bent anteriorly. Penes may be withdrawn into vestibula so that only tip of a single flap is visible (7), or both flaps of each penis may be slightly protuberant to exterior (2), or vestibula may be completely everted (14). Penis and everted vestibulum have a columnar appearance and rather like that of a tubular penis but a more or less definite circular furrow marks off the ventral and penial portion of the column from a dorsal part representing everted vestibulum.

Genital markings postsetal, on xvi (19), in *AB*, usually continued slightly beyond both *A* and *B*. Right marking (2) or both (2 specimens) lacking.

*Internal anatomy.*—Lateral intestinal caeca in xxiv (13) but opening into gut in xxv. Typhlosole begins in xxv (10) but may be slightly protuberant into xxiv. Lateral typhlosoles simple, low lamellae in xxv. Ventral caeca in xxviii-xxxii (2), xxviii-xxxiii (1), xxix-xxxii (4), xxix-xxxiii (2), xxix-xxxiv (2). Supra-intestinal glands in lxiii-lxv (3), lxiv-lxvi (9).

Dorsal vessel empty in front of commissures of vi and unrecognizable in front of 4/5 probably because of absence of blood. Segmental commissures of v usually recognizable though small and white. Transverse connectives between extra-oesophageal trunks are present just behind 5/6 and just in front of 8/9.

Testis sacs U-shaped, limbs not quite reaching to dorsal trunk (10), limbs possibly united above dorsal trunk to form an annular sac (1).

Spermathecal duct short, rather soft, lumen slit-like ectally, crescentic entally due to presence on posterior wall of a high vertical ridge. Diverticula always median and lateral (20 spermathecae), usually more or less digitiform but may be bilobed (4) or trilobed (6). Ampulla usually bent anteriorly as in types.

Penial setae (22 Thaton) are 2·03-2·53 mm long, 11-16$\mu$ thick at tip widening to 16-22, 13-18 at neck, 19-27 at base. Shaft with slight spiral curve ectally. Tip flattened, only slightly widened, usually bent and wrinkled, occasionally narrowing to a sharp point or a short spine.

Ornamentation of irregular rows of spine-like teeth, between levels of 0·05 and 0·3 mm down the shaft. Number, 2 (25 batteries), 3 (1).

Genital marking glands small, soft, sessile on parietes.

*Remarks.*—The penial annulus, in absence of immature worms for growth stages, is assumed to develop around a fissure of the usual sort and in this species to be a permanent structure. The pointed projections from the thickened posterior portion of the annulus presumably are inserted into spermathecal pores of a copulatory partner and in absence of any contraindication likewise appear to be permanent. On more complete retraction of the penes than has characterized any of the material hitherto available, some protrusion is expected of the vestibular roof into the coelomic cavity.

No variation as to male terminalia, presence or absence, shape or site of lateral intestinal caeca, number of supra-intestinal gland segments, or as to segment of origin and intrasegmental situation of genital markings, has been found, though four specimens suggest a trend in some populations towards elimination of the markings. A variation of but one segment in axial location of the supra-intestinal glands, with regard to size of the sample, also is unusual. Even as to number and axial location of ventral caeca, variation is slight.

Posterior direction and approximation, in this species, of spermathecal diverticula originally more anterior and directed laterally or mesially, appears now to be in a line of development that ends in a unidiverticulate condition characteristic of *ferinus*.

Male funnels of x and their ducts, as in *pius* and the remaining species of this group, apparently have disappeared.

**Eutyphoeus sejunctus** Gates 1930

Pelachi (Toungoo), on road to Thandaung, September, 0-0-4. G. I. Marshall.

Shwenyaungbin (Toungoo), on road to Thandaung, September, 0-0-1. H. I. Marshall.

Dawpakho, Thandaung Reserve, (Toungoo), September, 0-0-5. H. I. Marshall.

*External characteristics.*—First dorsal pore on 11/12 (10). The *d* setae are dorsal (10) posteriorly. Clitellum thinner or lacking (?) at mV(10).

Spermathecal pores with centers on or close to *B* (10). Female pores both present (10). Vestibular apertures always open, nearly circular, in *AB*, occasionally reaching just beyond *B*. Vestibula small, practically filled by small, firm, smooth-surfaced, conical penes, less than ½ mm long.

Genital markings postsetal, on xi, in *AB* (10). Indistinctly demarcated, translucent areas with centers at or near *A* occasionally recognizable on sites of 16/17 and 17/18, a transverse strip between those patches with unusually thin epidermis.

*Internal anatomy.*—Typhlosole begins in xxvii (or just reaches into xxvi). Lateral typhlosoles low simple lamellae, in xxvii (5). Ventral caeca in xxxii-xxxviii (1), xxxii-xl (1), xxxii-xli (1), xxxii-xlii (1), xxxii-xliv (1). Supra-intestinal glands in lxiii-lxv (1), lxiv-lxv (1), lxiv-lxvi (2) lxvi-lxviii (1).

Testis sac slightly U-shaped, lower portions of hearts of xi apparently imbedded in testicular coagulum. Bulbus ejaculatorius firm, with slight pink sheen, bound to parietes, Vestibular roof conspicuously protuberant into coelomic cavity as a columnar, bluntly conical or rather ovoidal, solid body with muscular sheen, into which prostatic duct, penisetal follicle and bulbus pass ectally.

Spermathecal duct *ca.* one mm long (including parietal portion), lumen small, slit-like in cross section. Diverticula median and lateral (20 spermathecae), usually with a single seminal chamber, or, occasionally, with one or two additional and much smaller chambers. Ampulla bound down around ental portion of duct.

Genital marking glands conspicuously protuberant into coelomic cavity. The gland though soft is sufficiently coherent, in this material to be pulled out from parietes taking away the marking on its ventral face.

Penial setae (according to Miss Chapman's measurements) are 2·46—2·48 mm. long, 38-40μ thick at tip, 45 at midshaft, 48-50 at base. Ornamentation, extending 150μ down the shaft, of small spine-like teeth, in regular unbroken circles ectally, in scattered rows of two or three entally. Number, 9 (1 battery of a Thandaung worm). Functional setae yellow, reserve setae red.

*Remarks.*—Fissures, in absence of immature specimens, are assumed to develop as usual in the genus though here always small and with a definite smooth margin that has been lacking in previous species of the present group. The margin of the fissure, as in subsequent species of the *levis* group, instead of becoming soft and tumescent, is firm and glistening. The penis formed as the vestibular invagination developed is tough and somewhat resembles the hard, mound-like protuberance from the male porophore of *peguanus*. The thickened vestibular roof in the coelomic cavity suggests a muscular bulb to evert the vestibulum as a temporary intromittent organ with the conical penis at its distal extremity. The testis sac which has been annular in previous species of this group has now been reduced to a suboesophageal chamber occasionally with a u—or even a U-shape. The secondary nature of these distentions, in comparison with an earlier U-shaped stage in the reduction, is shown by exclusion therefrom of the hearts of xi.

No variation, even as to presence or absence of genital markings and lateral intestinal caeca, has been found in any of the localities. Variation in number and axial location of ventral caeca is greater than in some of the previous species but, as also in case of supra-intestinal glands, is less than that prevailing in *hastatus*, *constrictus* and *peguanus*.

Development of a battery of reserve setae and the dorsal dislocation of the *d* setae are innovations in this group.

### **Eutyphoeus strigosus** Gates 1933

*External characteristics.*—Penes firm, shortly conical. The pore at apex of the penis is small, with firm smooth margin and is slit-like to circular.

*Internal anatomy.*—Typhlosole begins posteriorly in xxvii but is higher from xxviii. Lateral typhlosoles low, simple lamellae in xxvii. Ventral caeca in xxxiv-xlvii (1). Supra-intestinal glands in lxix-lxxi (2), lxx-lxxii (2).

Circulatory system as in *gigas*, except for anterior continuation of dorsal trunk. Extra-oesophageals almost come into contact behind 5/6 so that the commissure between is very short.

Testis sac u - or U-shaped, limbs not adherent to gut, hearts of xi entering sac only beneath gut.

Spermathecal duct *ca.* one mm long, lumen slit-like in cross section. Diverticula median and lateral, simple, bent at right angles, or slightly looped as in *pius*, or bi- or tri-lobed.

Genital marking gland sessile on parietes, soft, but not easily scraped away from body wall.

*Remarks.*—The oval papilla with follicle apertures, inside the penis, shows that the smooth-margined pore at apex of the organ is a fissure and, despite appearances, of the same nature as throughout most of the genus. Discrete male and prostatic pores may then be expected. Only slight protrusion of the penis has been shown but eversion of the vestibula is anticipated in view of the presence of vestibular bulbs.

The worms from three localities showed no variation as to : site and method of development of lateral intestinal caeca, secondary typhlosoles origin of main typhlosole, axial and intrasegmental location of the genital marking. Incidence of absence of markings was 11·5 per cent as compared with 8 per cent in *macer*. Variation as to ventral caeca and supra-intestinal glands appears to be greater than in previous species except *sejunctus*. With those two species the most posterior location of lateral intestinal caeca has been attained, the axial location being anteriorly in species both to the north and to the south. Typhlosolar origin and lateral typhlosoles, as in general throughout the genus, are closely associated with the lateral caeca.

The genital marking showed no evidence of the union of paired anlage that seems to be required phylogenetically.

As in *sejunctus* the dorsally directed limbs of a U-shaped testis sac appear to be secondary distentions.

### **Eutyphoeus compositus** Gates 1933

*External characteristics.*—Spermathecal pores may be just lateral to C. Vestibular apertures small, circular to elliptical, at or close to *B*, each in a flat, slightly protuberant, distinctly demarcated, circular field extending from *A* into *BC*. Vestibula small, well-like, almost completely filled by rather conical penes which are less than $\frac{1}{2}$ mm long. A small greyish translucent, transversely elliptical area, with boundaries recognizable only in brilliant illumination, is present just anterior and just posterior to each vestibular aperture.

*Internal anatomy.*—Typhlosole begins abruptly in xxiv (9) or xxv (1) but is not as high as in xxv or xxvi. A small secondary typhlosole which may be also folded slightly is present laterally on each side in xxiv-xxv and reaching into xxvi. A slight protuberance that looks like a rudimentary caecum is present on each side of the gut, in nine of the ten dissected specimens, in the first typhlosolar segment. Each protuberance is slightly constricted off from the gut, dorsally (8) or ventrally (1). The dorsal constriction is continued ventrally, in one case, on the anterior side of the protuberance.

Location of supra-intestinal glands

| Segments | Specimens |
|---|---|
| 58—60 | 1 |
| 58—61 | 5 |
| 59—62 | 2 |
| 59—63 | 1 |
| 60—63 | 1 |

Circulatory system as in *gigas* except that dorsal trunk is continued anteriorly and extra-oesophageals are connected by a transverse commissure just behind 5/6.

Testis sac ventral (1), u-shaped (3), U-shaped (6), reaching nearly (1) or actually to dorsal trunk (1). Hearts of xi pass into testis sac ventrally.

Spermathecal duct *ca.* ½ mm long, slightly bulbous, slenderer than in *annulatus*, a vertical ridge not certainly recognizable on posterior wall of lumen. Diverticula median and lateral (20 spermathecae), digitiform, usually bent anteriorly or anteriorly and then ventrally.

Glands of the small genital markings on male porophores are usually (6 specimens) recognizable in coelomic cavity after removal of concealing nephridia, but the glands of three specimens appear to be entirely within the parietes.

Penial setae (36, mostly from Kyauk-kyone worms) are 1·2—1·65 mm. long, 10—18μ thick at tip, 24—33 at midshaft, 28—43 at base. Shaft bowed. Tip softened, wrinkled or cracked. Ornamentation of very fine spines in closely crowded circles. Number, 5-7 (18 batteries). Functional setae yellow, reserve setae red.

*Remarks.*—Vestibula may be eversible in this form in spite of apparent absence of thickening of roofs sufficient to be recognizable in the coelomic cavity.

Ventral intestinal caeca were 3-6 (usually 4) in xxviii-xxxiv (25 specimens). Reduction of the testis sac to a ventral chamber either has been completed or is under way, brown pigment has been acquired, but the lateral intestinal caeca appear to be in an early stage of evolutionary development though site seems to have been fixed. Incidence of absence of genital markings, and the variation as to axial and intrasegmental location, in 142 worms from two localities, was zero. In view of such uniformity, as also characterizes related species to the south, this taxon is treated for the present as a species in spite of similarities to *annulatus* and the geographical contiguity.

*E. compositus* is distinguished from *sejunctus* by the lateral position of the spermathecal pores, lateral position of the *d* setae posteriorly, presence of genital markings on x and xvii, rudimentary condition and more anterior location of lateral intestinal caeca, more anterior location of supra-intestinal glands and absence of vestibular bulbs. From *annulatus*, *compositus* is distinguished by the smaller vestibula, presence of genital markings on the circular areas bearing the vestibular pores, restriction of genital markings to x-xi and xvii, presence of rudimentary lateral intestinal caeca in xxiv, and a slightly more anterior location of supra-intestinal glands.

### **Eutyphoeus annulatus** Gates 1931

Kin-U (Shwebo), September, 0-0-4. Saw San Thwe.

Kyaukmyaung (Shwebo), September, 0-1-3. Saw San Thwe.

*External characteristics.*—Length, to 55 mm. Diameter, to 3 mm. Pigmentation sparse behind clitellum, dense anteriorly. First dorsal pore on ?11/12(4), 11/12 (4). Clitellum reddish, protuberant, lacking at mV except on a portion of xiv and from 16/17 posteriorly where the musculature is no longer visible externally through the epidermis.

Spermathecal pores nearer to *C* than *B* or close to *C* (Kin-U), slightly nearer *B* (Kyaukmyaung), at m*BC*, just median to, at or just lateral to *C* (Sagaing, Kaungmudaw). Female pores both present (7). Vestibular apertures, in *AB* but usually reaching into *BC*, rather slit-shaped, transverse or slightly diagonal. Body wall somewhat thickened around the apertures, slightly less so mesially. Penes small; less than ½ mm. long, rather conical, invisible until vestibula are cut open.

Genital markings postsetal: On vii, in *BC* (1-Sagaing, 3-Kaungmudaw) ; on x, in BC (7) ; on xviii (6) ; on xix and xx (1, Kyaukmyaung). Postclitellar markings extend from *A* or slightly lateral to *A* into *BC*. Opaque rims of preclitellar markings, when recognizable, may cross intersegmental furrows but the greyish translucent central area appears to be strictly segmental.

*Internal anatomy.*—Typhlosole begins abruptly in xxiv (3) or xxv (5). A smaller secondary typhlosole, also slightly folded (16), is present laterally on each side in first two typhlosolar segments. Lateral intestinal caeca lacking (16). Ventral intestinal caeca in xxix-xxxi (2 Kyaukmyaung), xxix-xxxii (1 Kaungmudaw), xxix-xxxiii (1 Kaungmudaw).

*Location of supra-intestinal glands*

| Segments | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| 62—66 | 1 | | .. | .. |
| 63—66 | | 1 | | 1 |
| 63—67 | 1 | .. | .. | .. |
| 64—68 | .. | .. | 2 | 1 |
| 65—68 | | .. | 1 | 1 |
| 65—69 | .. | .. | .. | 1 |

1 Kyaukmyaung. 2 Kin-U. 3 Sagaing.
4 Kaungmudaw.

Testis sac ventral (Kin-U and Kyaukmyaung), u-shaped(4-Sagaing 1-Kaungmudaw) or U-shaped (3 Kaungmudaw) and then reaching to or almost to dorsal blood vessel. Hearts of xi not included in dorsal limbs. Bulbus ejaculatorius white or with pink muscular sheen, protuberant into coelomic cavity but sometimes covered over by transparent tissue. Vestibular roof slightly protuberant into coelomic cavity.

Spermathecal duct (coelomic portion) nearly or actually one mm long, bulbous, narrowed at parietes. Lumen slightly eccentric due to presence on posterior wall of a high vertical ridge on which there is usually a slight vertical furrow. Ectally this furrow widens and deepens so that ridge appears to bifurcate. Diverticula median and lateral (32 spermathecae), usually directed anteriorly and then ventrally.

Glandular material (soft) protrudes slightly into coelomic cavity just over each genital marking including those on vii.

Penial setae (22 from Kyaukmyaung and Kin-U worms) are 1·95-2·98 mm long, 12-25μ thick at tip, 27-39 at midshaft, 30-50 at base. Shaft bowed, *i.e.*, curved in a semicircle. Tip pink, usually cracked or softened, otherwise tapering to a point. Ornamentation of closely crowded, unbroken circles of spines, extending 0·5 mm down the shaft. Number, 6-8 (22 batteries). Functional setae yellow except for tip, reserve setae red.

*Remarks.*—Circumferential constrictions on the penial setae, as well as the dark and light segments, now have been found occasionally in other species and have been lacking in some of the recent specimens of *annulatus*.

Complete protrusion of the penes has been recognized, perhaps all that is permitted by the small vestibular bulbs (proximal portion of the temporary intromittent organ of *macer* lacking here ?).

Ventral intestinal caeca have varied in number (29 specimens) from 3-7 (usually 4-6) in xxviii-xxxv and supra-intestinal glands have been in 4-5 of eight segments, lxii-lxix. Lateral intestinal caeca have not begun to develop though the typhlosolar correlation indicates they may be anticipated in xxiv or xxv. Brown pigment has been acquired and

is more dense in a postclitellar region of the body than in *compositus.* The testis sac has been reduced to a suboesophageal sac but secondary dorsal distentions may be present. Male funnels of x almost have disappeared, a pair without ducts having been found only in one of 25 worms. The genital markings, though always restricted as to pairing and postsetal location, have been on any of segments vii-xxi except viii, xiii and xvii. Incidence of absence of the markings, in the type series of 22 specimens, was 4·5 per cent and certainly has been low in subsequent lots though definite percentages cannot be mentioned.

## THE PHYLOGENY OF THE *levis* GROUP

The dorsal blood vessel has been retained in its primitive uninterrupted condition in each species of this group. Both female pores have been retained and also without variation. The first dorsal pore is on 11/12 and with equal uniformity the clitellum is thin or lacking just at mV. Genital markings have been restricted throughout the group to a postsetal location and always are associated with coelomic glands of unknown function but possibly for production of an adhesive substance at time of copulation.

The history of the supra-intestinal glands and of the ventral intestinal caeca apparently can be read from the available data in either of two directions but for the present it is assumed, in each case, to involve reduction in number.

Interspecific variation as to the lateral intestinal caeca, male genital terminalia, axial location of the genital markings, supra-intestinal glands and ventral caeca, is such as to indicate segregation in a common ancestral form of local populations into a number of small-range species, as now seems to be under way in the Pegu Yomas populations of *hastatus* and *constrictus* that are not mutating to other species. The small size of these *levis* group species and the infrequency with which they have been found, in comparison with somatic size and frequency of individuals of species just to the west, may indicate that morphological stabilization has been attained at cost of adaptability. The numbers and size of *peguanus* individuals in Thaton and Amherst districts rules out the explanation once advanced that "the mighty genus *Pheretima* has crushed all competitors" (Stephenson, 1923, Fauna British India, p. 30), in its westward advance.

The range in which segregation took place extends from Ye, at the southern border of Amherst district as well as of the *Eutyphoeus* domain, to Mandalay and then, west of the Irrawaddy river, north through Sagaing district and well into Shwebo. Extensions of this range may perhaps be anticipated as the fauna of the east bank of the Irrawaddy above Mandalay is largely unknown and not much more has been learned about that of the opposite side above Shwebo.

From the common ancestral form, which would have to be close to the proto-eutyphoeus, *pusillulus* has been segregated at the southern frontier, by establishment of the unidiverticulate mutation along with reduction in number of ventral caeca and supra-intestinal glands (as in

the other seven species), elimination of genital markings as well as posterior testes and male ducts though not before evolution of an annular testis sac had taken place. In the rest of the range holandry was also completely eliminated but by establishment of the metandric mutation.

To the north *levis* has been derived by establishment of the unidiverticulate mutation, elimination of genital markings and by dorsal dislocation of the *d* setae posteriorly. If retained male funnels of x indicate recent origin, *levis* is the youngest species of the group. *E. pius* has been derived by a restriction of genital markings to xiii-xv, development of intestinal caeca in xxv and of a sucker-like male porophore with a penial annulus. *E. macer* has been derived by restriction of markings to xvi, development of intestinal caeca in xxiv and of eversible vestibula into which the penial annulus, now with posterior protuberances, has been withdrawn. *E. strigosus* is derived by restriction of genital markings to xii and their union at mV, development of intestinal caeca in xxvii and of vestibula so invaginated as to leave the fissure at apex of a tough conical penis without annulus. *E. sejunctus* has been derived by restriction of genital markings to xi, reduction of the annular testis sac to a suboesophageal chamber, development of intestinal caeca in xxvi, of batteries of reserve penial setae along with *strigosus* terminalia, and by dorsal dislocation of the *d* setae posteriorly. *E. compositus* has been derived by restriction of genital markings to x-xi and development of *sejunctus* terminalia but only now is in process of developing lateral caeca in xxiv. *E. annulatus* has been derived by development of *sejunctus* terminalia and like *compositus* has acquired brown pigment. Though the species still shows the presumed primitive variation in location of genital markings some populations have an obvious tendency for restriction to xv.

A mutation seems to be required to explain appearance of individuals without genital markings in the " marked " species of this group, as well as in *peguanus*, *constrictus* and *marmoreus*. Such a mutation has become established in the northern part of the *constrictus* range and in *peguanus* has given f. *simplex* which breeds true in isolation. This mutation, " inornate ", for inhibition of development of genital markings, characterizes the holotype of *pusillulus* and is assumed in the phylogeny of *levis*.

Though anterior testes have been eliminated in genera of more than one family, proandry is rare and no evidence of the usual sort can be adduced as to its origin. Since the posterior testes can be aborted mutationally a similar cause for abortion of the anterior gonads is assumed in the phylogeny of *pusillulus*.

Approximation of diverticula on the posterior side of the spermathecal duct in *macer* provides just the stage on which stalkless subscript 1 can operate most easily to bring about the unidiverticulate condition reached in *E. ferinus*. Slight dorsal dislocation posteriorly of *d* setae to or just above mL (*pius*, *macer*, *strigosus*) similarly seems preliminary to the more marked dislocation of *levis* and *sejunctus*. If there is involved in this case a single mutation, it has become established in the southern half

of the range though its effect has been partially masked, or its penetrance delayed, in three of the five species.

## THE *foveatus* GROUP

### Eutyphoeus foveatus (Rosa) 1890

1

Mupun (Amherst), October, 0-0-3. K. John.
Moulmein (Amherst), October, 0-0-58. K. John.
Kyaikto town (Thaton), August, 0-0-6. October, 0-0-30. K. John.
Boyagyi (Thaton), October, 0-0-2. K. John.
Syriam (Hanthawaddy), August, 0-0-9. K. John.
Kyauktan (Hanthawaddy), September, 0-0-1. K. John.
Twante (Hanthawaddy), September, 0-0-72. K. John.
Taikkyi (Insein), September, 0-2-26. K. John.
Wanetchaung (Insein), September, 0-0-31. K. John.
Taukkyan (Insein), September, 0-0-22. K. John.
Hmawbi (Insein), September, 0-0-16. K. John.
Hlegu (Insein), September, 0-0-20. K. John.
Dam site, M5-6 (Insein), September, 0-0-17. K. John.
Hlawga (Insein), September, 0-0-9. K. John.
Maubin, October, 0-0-17. Maung Ohn Maung.
Danubyu (Maubin), October, 0-0-4. Maung Ohn Maung.
Pantanaw (Maubin), October, 0-0-3. Maung Ohn Maung.
Pegu, August, 0-1-5. K. John.
Pegu, jungles to the east, August, 0-0-4. K. John.
Thanatpin (Pegu), August, 0-2-3. K. John.
Ingabu (Henzada), October, 0-0-2. Maung Ohn Maung.
Zalun (Henzada), October, 0-0-1. Maung Ohn Maung.
Henzada, October, 0-0-2. Maung Ohn Maung.
Pyu (Toungoo), hills to the west, September, 0-0-32. H. I. Marshall.
Toungoo, October, 0-0-1. K. John.
Paukkaung (Prome), September, 0-0-28. K. John.
Prome, September, 0-0-25. K. John.
Allanmyo (Thayetmyo), September, 0-0-5. K. John.
Thayetmyo, September, 0-0-5. K. John.
Naba (Katha), September, 0-0-25. Saw San Thwe.

*External characteristics.*—A size of 380×9 mm is reached by some of the Paukkaung worms. First dorsal pore on 10/11 (1), 11/12 (38), 12/13 (1).

Spermathecal pores small slits, usually centered at *B*, rarely slightly median or very rarely slightly lateral to *B*. Female pore on left side (59), on right side also (3), represented by a punctate but possibly functionless marking on right side (4). Vestibular aperture, always open usually nearly circular, rarely hexagonal, square, longitudinally elliptical or rectangular, usually restricted to *AA*, occasionally reaching slightly beyond *B*. Vestibulum deep, body wall around vestibular aperture thickened in an annular fashion, roof thin, never showing indications of eversion. Penes slenderly tubular, one mm or more long or, lateralmost portion of vestibular roof, directed ventrally or ventromesially, invisible from rexterio

Genital marking reaches *A*, into *AB*, to or rarely very slightly beyond *B*, almost to equator of xvi and to site of 14/15 or onto posterior portion of xiv, usually indented at equator of xv, *a* within or outside. The following variations were found in present material : Portion of marking in front of equator of xv much reduced (3 Paukkaung, 1 Prome, 5 Pyu), or lacking (1 Paukkaung), or separated from the equisized posterior part by an unmodified transverse band of epidermis containing ventral setae of xv (1 Paukkaung, 1 Thayetmyo, 1 Syriam, 1 Twante, in the latter case anterior marking about twice size of posterior). No genital marking, epidermis wrinkled and whitish ventrally on xv-xvi (1 Pyu). An additional small marking in *AA* on 13/14 (1 Thayetmyo).

*Internal anatomy.*—Typhlosole begins in xxvii (3) or xxviii (25). Longitudinal rows of small patches, as in *excavatus*, always present in first one or two typhlosolar segments ; one patch on each side (1), two (5), three (20), four (25), five (1). The anteriormost usually is slightly median to caecal aperture. Protuberances that look like unconstricted lateral caeca may be recognizable (34) but in some other worms were not certainly distinguishable from sacculations present in neighbouring segments, in nine specimens even sacculations lacking. Small incompletely constricted caeca present in xxviii or xxix. Two pairs of caeca in two successive segments xxvii-xxviii (1), xxviii-xxix (3), or smaller but both pairs in the same segment and one dorsal to the other (1).

Circulatory system as in *gigas* except that the extra-oesophageals are connected by a transverse vessel just behind 5/6. The dorsal trunk (1 Pyu) is continued well onto gizzard where it bifurcates, the branches disappearing ventrally at sides of the gizzard, or continued further and nearly to 5/6 where it passes ventrally on left side as a heart-like commissure (1 Pyu).

Testis sac suboesophageal (64). Bulbus ejaculatorius firm, with muscular sheen, conspicuously protuberant into coelomic cavity (64), sometimes more than two mm long.

*Location of supra-intestinal glands and ventral caeca*

| Segments | Number of specimens from | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| 85-91 | | .. | .. | .. | | .. | .. | 1 | .. | | |
| 86-90 | | .. | .. | | .. | | | 1 | | | .. |
| 86-91 | .. | .. | 1 | 1 | | | | 1 | .. | | . |
| 87-91 | | .. | 2 | .. | | .. | | .. | .. | .. | .. |
| 87-92 | | | 2 | 1 | .. | .. | | 1 | | 1 | .. |
| 87-93 | | .. | | 1 | .. | 1 | .. | .. | | .. | .. |
| 88-92 | 1 | | 5 | 2 | .. | .. | | .. | .. | 1 | 1 |
| 88-93 | .. | | 2 | 1 | .. | .. | | . | | 2 | 1 |
| 88-94 | 1 | | .. | 1 | 1 | .. | | .. | | .. | .. |

*Location of supra-intestinal glands and ventral caeca*—contd.

| Segments | Number of specimens from | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| 89-93 | 2 | .. | 6 | 2 | .. | .. | .. | .. | .. | 1 | 5 |
| 89-94 | 1 | 4 | 4 | 1 | 1 | .. | 1 | .. | 2 | 8 | .. |
| 89-95 | 1 | 2 | 1 | .. | .. | 1 | 1 | .. | .. | 1 | .. |
| 90-94 | 2 | 2 | 4 | .. | 1 | .. | .. | .. | .. | 2 | 2 |
| 90-95 | .. | 2 | 5 | 2 | 1 | 2 | 1 | 1* | .. | 2 | |
| 90-96 | .. | 1 | .. | | .. | .. | 4 | .. | 1 | .. | .. |
| 91-95 | 2 | | 1 | 2 | | | .. | .. | .. | .. | .. |
| 91-96 | 1 | 1 | .. | 1 | | 1 | 1 | .. | 1 | 1 | .. |
| 91-97 | 1 | 3 | .. | | | | 2 | .. | 1 | .. | .. |
| 92-96 | | | | 1 | | .. | .. | .. | .. | .. | .. |
| 92-97 | | 2 | .. | 2 | 1 | | 2 | .. | .. | .. | .. |
| 92-98 | 1 | 1 | .. | | .. | .. | .. | .. | .. | .. | .. |
| 93-98 | .. | 1 | | 1 | | .. | .. | .. | .. | .. | . |
| 93-99 | | | .. | 1 | .. | .. | .. | .. | .. | .. | .. |
| 94-100 | | 1 | | .. | | | .. | .. | .. | .. | .. |
| 95-99 | .. | | | .. | .. | | 1 | .. | | .. | .. |
| 95-100 | | 2 | | | .. | .. | .. | .. | .. | .. | .. |
| 95-101 | | 2 | | | | | .. | | | .. | .. |
| 33-53 | .. | .. | | 1 | | | | .. | .. | .. | .. |
| 34-53 | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | .. |
| 34-56 | .. | .. | .. | 3 | | .. | .. | .. | .. | .. | .. |
| 34-57 | .. | | .. | 1 | .. | | .. | | .. | .. | .. |
| 34-58 | .. | .. | .. | | | .. | .. | 1 | .. | .. | .. |
| 34-59 | .. | .. | .. | 1 | .. | 1 | .. | .. | .. | .. | . |
| 35-54 | .. | | .. | 1 | | | .. | .. | .. | .. | .. |
| 35-55 | | | | 1 | | | .. | .. | .. | .. | .. |
| 35-56 | | | .. | 2 | .. | .. | | .. | .. | . | .. |
| 35-57 | .. | | | 4 | | | .. | 1 | .. | .. | .. |
| 35-58 | .. | | .. | 1 | .. | | .. | .. | | .. | .. |
| 35-59 | .. | | | 2 | | .. | .. | | .. | | .. |

*Abnormal or mutant.

*Location of supra-intestinal glands and ventral caeca*—contd.

| Segments | Number of specimens from | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| 35-60 | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | .. |
| 36-54 | .. | .. | .. | .. | .. | .. | .. | 2 | .. | .. | .. |
| 36-57 | .. | .. | .. | 1 | .. | .. | .. | .. | .. | .. | .. |

1 Rangoon and vicinity. 2 Naba. 3 Pyu.
4 Paukkaung. 5 Kyaikto. 6 Allanmyo.
7 Prome. 8 Thayetmyo. 9 Laboo.
10 Thanbula. 11 Moulmein.

Spermathecal duct 2-3 mm long, with brilliant muscular sheen markedly bulbus, ampulla bound down around entalmost portion, wall thick. Lumen small except in region of diverticular junctions where it may be slitlike or widened horizontally and then on floor of widened portion two, three or four lobes with high and regularly rounded surfaces. Diverticula median and lateral on each spermatheca except as noted below. Seminal chambers in a diverticulum usually five or less.

Median diverticulum of right spermatheca lacking (1 Pyu, 1 Thanatpin, 1 Allanmyo). Median diverticulum of left spermatheca lacking (1 Henzada, 1 Taukkyan). Median diverticulum of each spermatheca lacking, duct abnormally short and without sheen (3 Taikkyi, 1 Dam site). An extra small diverticulum of about same height as the other two but on anterior face of duct (1 spermatheca, each of 2 Naba worms).

Body wall occasionally rather conspicuously protuberant into coelomic cavity over genital marking as a result of depression of the marking, the longitudinal musculature uninterrupted over site of marking.

Penial setae (60 from 6 localities), 3·0-4·6 mm long, 30-51$\mu$ thick at base, 22-46 at midshaft, 11-30 at tip. Shaft with spiral curves ectally, assuming under pressure of cover glass a question-mark shape. Tip flattened but not widened, tapering to a point, thin and almost transparent. Ornamentation of spine-like teeth in irregular transverse grooves ectally, more or less regular and possibly unbroken circles entally. Number, 8-16 (30 batteries). Reserve setae may be pink. Functional setae of 130 additional specimens from the various localities have the spiral curvature ectally, unless otherwise indicated.

Penial setae of four Taikkyi and Damsite worms with unidiverticulate spermathecae, 11-16 per battery, 3·05-3·44 mm long, 41-52$\mu$ thick at base, 31-39 at neck, 44-47 at blade, 13-18 at tip. Shaft practically straight except for slight curve at ectal end. Tip flattened, widened, occasionally with a longitudinal ridge at middle of blade. Tips of smaller reserve setae only slightly widened and very similar to those from worms with bidiverticulate spermathecae.

*Abnormality.*—(No. 1) An extra half vestibulum on left side of xviii, containing a penis and penial setae. A prostate and duct of about same size as those in xvii, and a penisetal follicle present in xviii on left side. Left male deferent duct passes into parietes normally in xvii, no bulbus ejaculatorius in xviii (Moulmein).

(No. 2) Right spermathecal pore on 8/9. Genital marking extending to equator of xvi on left side, to equator of xvii on right side. A half vestibulum present on left side of xvii, another on right side of xviii. Clitellum on xiii-xviii on left side, xiv-xix on right side. Septum 11/12 thickly muscular but present only on right side. Intestinal origin in xvi and last heart in xiv on right side. No testis sac, a rudimentary male funnel in xi on right side, a large male funnel in xii on right side but none on left side, rudimentary seminal vesicles in xii (left side) and xiii (right side). No ovary on right side (Taikkyi).

*Remarks.*—Types are softened. One is aclitellate, avestibulate penes represented only by very small rudiments, and without a genital marking. Vestibulum and penes are recognizable on another but the genital marking is incompletely developed or abnormal. Penes are visible on a third but the vestibulum is scarcely recognizable presumably as a result of relaxation associated with maceration.

The penes almost completely protrude in anesthetics but eversion of the vestibulum has never been observed.

The genital marking has been lacking only once, in the entire range, and an extra genital marking has been present only twice, once each on 13/14 and 18/19, the three worms from or near the northern boundary. The anterior portion of the marking, between equators of xiv and xv, has been lacking on three specimens from two localities, one of which is at the northern periphery, the posterior half absent on but one worm also from near the northern limit. The marking has been separated into two parts by an unmodified strip of epidermis at equator of xv in one worm from each of seven localities. This variation may result from premature cessation of growth in separate anlage thereby resulting in reversion to an ancestral state characterized by two discrete intersegmental markings such as still prevails in *excavatus*.

The dorsal blood vessel usually ends with or as a short stump just in front of the hearts of vii. Continuation, in 3 of 104 specimens examined in this connection, onto gizzard (2) and then bifurcating or turning ventrally on one side or passing on nearly to 5/6 (1) before turning ventrally, represents partial reversion to an ancestral condition in which the trunk was uninterrupted and with paired commissures to ventral vessel in each segment. The reversion is attributable to inhibition, during development, of the reorganization process that eliminates the segmental commissures and produces the foreshortening.

Variation in number of segments provided with supra-intestinal glands appears to be about the same throughout the range, glands having been found only in 5, 6, 7 segments. Number of segments

in which glands have been found, in a local population, is 8-14, and in the species, 17.

| Number of segments in which glands have been found | Number of specimens in sample | Segments involved | Locality |
|---|---|---|---|
| 8 | 10 | 88—95 | Moulmein |
| 9 | 5 | 89—97 | Laboo |
| 10 | 33 | 86—95 | Pyu |
| 10 | 5 | 88—97 | Kyaikto |
| 10 | 5 | 87—96 | Allanmyo |
| 10 | 14 | 87—96 | Thanbula |
| 11 | 5 | 85—95 | Thayetmyo |
| 11 | 13 | 89—99 | Prome |
| 13 | 24 | 89—101 | Naba |
| 14 | 13 | 85—98 | Rangoon |
| 14 | 20 | 86—99 | Paukkaung |

Glands in five segments, 49 worms.
Glands in six segments, 66 worms.
Glands in seven segments, 31 worms.

Variation as to presence or absence of lateral intestinal caeca, degree of constriction from gut wall, shape and direction as well as number, throughout the range, indicate the species has been found in an early stage of evolution of a new organ. In marked contrast is the constancy of the seemingly insignificant red patches at sites of lateral typhlosoles. Variation in number of spermathecal diverticula is considered below.

The abnormal specimen (No. 1) shows that development of the vestibulum also is induced by the prostate but only unilaterally. Further, development of the penis likewise is prostate induced and that development may be perfectly normal in absence of a male deferent duct.

Mandalay and Naba populations now appear to be local colonies established after accidental transport from the proper range well to the south. Small individuals of this species occasionally have been found in earth around roots of the potted plants that have been carried around Burma for many years. Locations of supra-intestinal glands in the Naba worms are almost exactly the same as in those from Prome. Several attempts to find the species again at Mandalay, to secure data on location of supra-intestinal glands, were all unsuccessful. The colony at Mandalay probably was not large and may have become extinct. The distribution in Amherst and Thaton districts now appears to be marked by significant discontinuities and at least in part by isolation from the main range. The Moulmein-Mupun colony, which is well established

is thought to be a result of accidental transportation by man. Although the same agent can have responsibility for the introductions into Thato district, transport by flood waters from across the Sittang, either directly or indirectly, may require consideration.

With these deletions the *foveatus* range is limited to the southern hills of the Arakan Yomas, the recent alluvium of the Irrawaddy-Sittang rivers and adjacent higher land. The species has not been found as yet in Myaungmya and Pyapon districts where the alluvium presumably is of latest deposition.

2

Laboo (Prome), September, 0-0-6. K. John.
Thanbula (Thayetmyo), September, 0-0-14. K. John.
Thayetmyo, September, 0-0-1. K. John.

*External characteristics.*—Spermathecal pores small, almost without exception in *AB*, often nearer *A* than *B*, occasionally just lateral to *A*. (Genital marking normal.)

*Internal anatomy.*—Typhlosole begins in xxvii (2), xxviii (14), xxix (4). Red patches always present in first one or two typhlosolar segments, two in a row (4), three (12), four (4). Lateral intestinal caeca rudimentary, in xxviii (3 Laboo) or lacking. Ventral intestinal caeca in ; xxxiv-lviii (1), xxxiv-lx (1), xxxv-liv (2), xxxvi-li (1), xxxvi-liii (1).

Spermathecal duct slightly more than one mm long, lumen small with several fairly high vertical ridges on the wall. Median diverticulum lacking (42 spermathecae). Lateral diverticulum usually a horizontal ridge of five to nine seminal chambers, rarely a vertical ridge (2). Seminal chambers occasionally few, five to two or even one and then more protuberant and ovoidal to spheroidal.

Penial setae have no blade-like widening of tips and are spirally curved ectally.

*Abnormality.*—(No. 1) A very small vestibular invagination containing a rudiment of a penis present on right side of xv. A prostatic duct about one mm long passes into wall of vestibular invagination but entally duct ends abruptly without a gland. A follicle containing three penial setae associated with the prostatic duct. Penial setae 1·34-1·6 mm long, 45-46μ thick at base, 39-40 at midshaft, 25-26 at tip. (Right male deferent duct passes into parietes of xvii normally.)

*Remarks.*—These worms have normal *foveatus* genital markings and penial setae. Spermathecae also are as usual except for absence of the median diverticulum. No other species is present in or near the region with which the worms could be confused so no question arises as to their identification or their mutant nature. Each individual of the sample of the populations at Laboo and Thanbula is a mutant (unidiverticulate). At Thayetmyo, where the species is not common, only one individual, 16·6 per cent., of the small sample secured, is a mutant. Thanbula and Thayetmyo are at or near the northern border of the *foveatus* range. Laboo though well inside is near the foothills of the southern Arakan Yomas.

Three specimens of the Taikkyi and one of the Damsite samples, 10·7 per cent. and 5·8 per cent., with normal genital markings, show the unidiverticulate mutation which presumably has appeared *in situ*. The spermathecal duct in these worms is abnormally short. Penial setae are like those of *spinulosus* and have a neck of the same width though the blade is not quite as thick and does not narrow to a spin. Younger reserve setae are more like those of *foveatus* than similar stages in *spinulosus*. Identification of these worms would have to be *spinulosus*, though genital markings are quite normal, if the localities were unknown.

### **Eutyphoeus spinulosus** Gates 1926

Padaukchaung (Bassein), nearby jungle, October, 0-4-46. K. John.
Bassein, October, 0-4-28. K. John.

*External characteristics.*—Spermathecal pores centered at or just median to *B*. Female pore on left side (48), a pore also present on right side but like area around it smaller than that of left side (10 Bassein, 3 Padaukchaung).

Genital marking with a deep V-shaped incision at equator of xv on each side, *a* and *b* of xv in the incision rather than in the marking (60), the portion in front of equator of xv definitely smaller (53). Genital marking nearly reaching equators of xv and xvi only (4 Padaukchaung, 2 Bassein). Two distinct markings, the smaller on 14/15 (6 Padaukchaung, 1 Bassein).

*Internal anatomy.*—Typhlosole begins in xxviii (3), or just in front of 28/29 (2). Small patches at sites of lateral typhlosoles in longitudinal rows of three (2) or four (3), in first one or two typhlosolar segments. No lateral intestinal caeca. Ventral caeca in xxxv-lxii (1), xxxv-lxiii (1), xxxv-lxv (1), xxxvi-lxiv (1), xxxvi-lxvi (1).

*Location of supra-intestinal glands*

| Segments | Number of specimens |
|---|---|
| 87—91 | 2 |
| 88—92 | 6 |
| 89—93 | 7 |
| 90—93 | 1 |
| 90—94 | 1 |
| 90—95 | ? |
| 91—96 | 1* |

*The only pair of glands in xcvi of this worm is smaller than those of preceding segment

Circulatory system as in *foveatus*.

Testis sac suboesophageal (82). Bulbus ejaculatorius protuberant into coelomic cavity though covered with transparent tissue (Bassein), in parietes, or covered over by opaque tissue (Padaukchaung).

Spermathecal duct usually about one mm long, abruptly narrowed in parietes, with marked sheen. Lumen irregularly slit-like in cross section, with several fairly high vertical ridges on wall. Diverticulum a low ridge rather diagonally placed with anterior end ventrally, always lateral (164 spermathecae). Definite seminal chambers not marked off externally but five to nine spheroidal masses of spermatozoa may be visible through outer tissues. Only one opening into duct lumen was found from diverticulum (8 spermathecae).

Penial setae (10 each from Bassein and Padaukchaung), 3·5-4·37 mm long, 32-45μ thick at base, 31-40 at neck, 45-59 at blade. Shaft practically straight except for a slight curve ectally. Tip flattened, widened (also in functional setae of 71 other specimens), tapering to a sharp point or a spine. Ornamentation of small thorn-like teeth in regular circles about 5 micra apart. Number, 6-8 (10 batteries). Reserve setae red, thick basally, tip often slightly concave like a spoon bowl.

*Abnormality.*—(No. 1) No male genital terminalia on right side, right deferent duct dwindling to disappearance before reaching xvii (Bassein). (No. 2) Spermatheca lacking on left side (Bassein).

*Remarks.*—This species is distinguished from *foveatus* by absence of the median spermathecal diverticulum, absence of spiral coiling of an ectal portion of the penial setae and by the shape of the thickened ectal portion of the penisetal shaft. The anterior portion of the *foveatus* genital marking here seems to be gradually disappearing. Incidence of inornate individuals certainly is much higher than in *foveatus* though statement of percentages now has become impossible.

*E. spinulosus* has been found only in the recent alluvium of Bassein district. It must have arrived there recently, perhaps from the southern hills of the Arakan Yomas the fauna of which is entirely unknown south of the Taungup pass.

### **Eutyphoeus planatus** Gates 1929

Allanmyo (Thayetmyo), August, 0-0-45. K. John.
Thayetmyo, August, 0-0-15. K. John.
Magwe and vicinity, August, 1-0-44. K. John.
Minbu and vicinity, August, 3-0-120. K. John.

*External characteristics.*—Length, 100-240 mm. Diameter, 5-9 mm. Pigmentation dense anterior to, in and just behind clitellum, sparse posteriorly. First dorsal pore on 10/11 (4), 11/12 (86).

Spermathecal pores centered at or close to *B*, more often slightly lateral, or pores in median half of *BC* (Allanmyo). Female pore on left side (79), a smaller pore present on right side (5) or represented by an imperforate punctation (10).

Vestibular aperture (Allanmyo-Thayetmyo), in *BB*, usually transverse, often slightly wider anteriorly as in types (fig. 20*a*, Gates 1929,

p. 36), occasionally rectangular, nearly square (2), longitudinally rectangular (2), wide open except when longitudinally rectangular. Tow pairs of slightly raised, longitudinal areas with somewhat of an appearance of genital markings present on vestibular roof mesially, close to mV (epidermis between opaque) or slightly more lateral (epidermis between so thin that fibres of longitudinal musculature beneath are visible).

Vestibular aperture Y-shaped (Minbu-Magwe), limbs of about the same length, one median and posterior, the others directed anterolaterally. The Y-shape due to presence of a ridge on anterior wall of vestibulum that may almost touch posterior wall in which case vestibular aperture is almost V-shaped (2 Minbu). Vestibular aperture closed, by apposition of margins of limbs of Y, or open. The wider the opening the less prominent the anterior ridge which is however always distinct even in relaxation so complete that vestibular lumen is almost obliterated (1 macerated Minbu worm). Two pairs of slightly raised areas present on vestibular roof mesially but the two anterior areas are here on lateral sides of the anteromedian ridge.

Penes small, soft, annular, or quite unrecognizable (specimens from each of the four localities) in which case two penial setae usually protuberant from the transverse fissure.

Genital marking (single, 208) transverse, in *BB*, rarely extending slightly into *BC*, on postsetal portion of xiii, occasionally (?) reaching slightly across site of 13/14. Asymmetrical, from mV to *A* on left side (1 Allanmyo). An additional marking on xiv (14 Allanmyo, 1 Thayetmyo), usually in AA (13), reaching into *AB* (1) or to *B* (1), possibly crossing site of 14/15 in some cases, but always smaller than the anterior marking. A rather indefinite rudiment of an extra marking on xiv (4 Minbu).

*Internal anatomy.*—Typhlosole begins in xxvii (1), xxviii (13), xxix (1, Thayetmyo), xxvii (3), xxviii (19, Allanmyo), xxviii (1), xxix (15, Minbu), xxviii (1), xxix (16), xxx (1, Magwe). Lateral typhlosoles represented by small, dark red, transversely elliptical patches in longitudinal rows of one (4), two (14), three (21), four (27), five (1). Lateral intestinal caeca lacking, a slight lateral bulge occasionally recognizable in xxviii, xxix or even xxx (1). Ventral caeca rather large, often bent backwards or coiled when length is greater than that of its segment. The largest caecum (each of several worms) may have one, two or three small, shortly ellipsoidal, whitish swellings posteriorly on the widened proximal portion. Ventral caeca and supra-intestinal glands as in table (p. 171).

Circulatory system as in *gigas* except that extra-oesophageals are connected by a transverse vessel just behind 5/6 and the supra-oesophageal occasionally is continued forward to hearts of xi. Dorsal trunk continued onto gizzard as a colorless (functionless ?) filament (1), ending with commissures of vii, or just in front of them as a bluntly rounded or a conical protuberance (225). Right heart of xiii lacking (1 Minbu).

Testis sac apparently suboesophageal (Thayetmyo-Allanmyo), a small cord apparently of testicular coagulum continued up to or nearly to dorsal blood vessel on anterior face of each heart of xi (1 Thayetmyo), dorsal halves of hearts of xi recognizable without opening the sac. Testis sac annular (Minbu-Magwe), passing over dorsal trunk, usually conspicuously distended dorsally as well as laterally by coagulum. When there is little or no coagulum dorsally and laterally, lumen of sac can still be traced to or nearly to dorsal vessel though the upper portion of the sac appears to be strongly contracted. Hearts of xi are invisible in distended sacs but attached to posterior wall and within a delicate tube.

*Location of supra-intestinal glands and of ventral caeca*

| Segments | Number of specimens from | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| 85—90 | | 6 | | .. |
| 86—90 | | 1 | | .. |
| 86—91 | 1 | 8 | .. | .. |
| 87—91 | | 2 | .. | .. |
| 87—92 | 3 | 4 | .. | .. |
| 87—93 | 1 | 1 | | |
| 88—92 | 3 | 1 | .. | .. |
| 88—93 | 5 | 2 | | .. |
| 88—94 | 1 | .. | | |
| 90—95 | .. | 1 | 1*a* | .. |
| 91—96 | .. | | 1*a* | .. |
| 91—97 | .. | | 2*a* | .. |
| 92—97 | .. | .. | 1 | .. |
| 92—98 | .. | .. | 2*a* | |
| 93—97 | .. | .. | .. | 1 |
| 93—98 | .. | .. | 3*a* | 2*b* |
| 93—99 | .. | .. | 1*a* | 1 |
| 94—98 | .. | .. | .. | 2 |
| 94—99 | .. | .. | 2 | 2 |
| 94—100 | .. | .. | 2 | 3 |
| 95—100 | .. | .. | .. | 6 |
| 95—101 | .. | .. | 2 | .. |
| 95—102 | | .. | 1 | .. |

*Location of supra-intestinal glands and ventral caeca*—contd.

| Segments | Number of specimens from | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| 96—101 | .. | .. | 2 | 2 |
| 96—102 | .. | .. | 3 | .. |
| 96—103 | | .. | 1 | .. |
| 97—101 | .. | .. | | 1 |
| 97—103 | .. | .. | 4*c* | .. |
| 97—105 | .. | .. | 1 | .. |
| 98—102 | .. | .. | .. | 1 |
| 98—103 | .. | .. | 1 | .. |
| 99—104 | .. | .. | 1 | .. |
| 33—36 | .. | 2 | .. | .. |
| 33—37 | 1 | 2 | | .. |
| 33—38 | 1 | .. | .. | .. |
| 33—39 | 1+1 | .. | .. | .. |
| 34—37 | 1+2 | 11 | .. | .. |
| 34—38 | 6+7 | 5 | 3*a* | .. |
| 34—39 | 3+7 | .. | .. | 2 |
| 34—40 | .. | .. | 1 | 1 |
| 35—38 | .. | .. | 3 | 3 |
| 35—39 | 1 | .. | 5 | 3 |
| 35—40 | .. | | 2 | 1 |
| 36—38 | | | 1 | .. |
| 36—39 | . | .. | 3 | 2 |
| 36—40 | | | 5 | 3 |
| 36—41 | .. | | 1 | 2 |
| 37—40 | .. | .. | 1 | 1 |
| 37—41 | .. | .. | | 1 |

1 Thayetmyo. 2 Allanmyo. 3 Minbu. 4 Magwe.

*a* All unusually small worms, 100-130 × 5-6 mm.

*b* Including one juvenile. *c* Including one small worm.

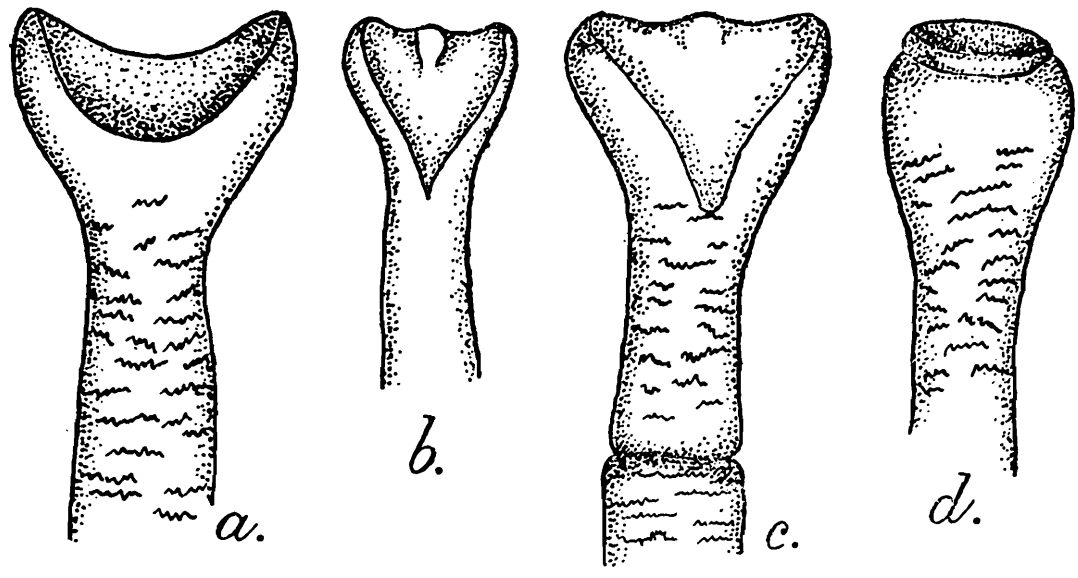
+ Previous records (Gates, 1933, p. 593).

Vestibular roof somewhat protuberant into coelomic cavity, somewhat thinner, especially in Thayetmyo-Allenmyo worms, mesially. Bulbus ejaculatorius small, rather soft, white, in posterior wall of vestibulum.

Spermathecal duct (Minbu-Magwe) bulbous, flask-shaped, constricted at or within parietes, with narrow but definite neck entally, two or slightly more mm long, with marked pink sheen. Lumen irregularly slit-like in cross section due to presence of vertical ridges on anterior and posterior walls. Number of ridges variable but twelve in several spermathecae, all of about the same height and quite regularly placed. Duct (Allanmye-Thayetmyo) less than two mm long, white, no sheen recognizable, constricted in parietes but without a definite neck region entally. Lumen crescentic in cross section due to presence of a fairly high and thick ridge with a slight vertical groove on posterior wall. Diverticula small, often with but one shortly ellipsoidal seminal chamber or with ental end marked off into two to seven (rarely) lobes, median and lateral (449 spermathecae). Lateral diverticulum lacking on right spermatheca (1 Minbu, 1 Thayetmyo), on left spermatheca (1 Minbu, 1 Thayetmyo). An extra diverticulum on posterior face of one spermatheca (1 Magwe), on anterior face of each spermatheca (1 Thayetmyo).

Body wall bulged slightly into coelomic cavity over genital marking but not thickened (Allanmyo-Thayetmyo). Coelomic surface of protuberance firm, longitudinal musculature uninterrupted. A slight layer of soft (glandular ?) material on coelomic face of protuberance in Minbu-Magwe worms. This layer is easily scraped off to display small, circular greyish translucent spots (ends of glandular cords ?) between longitudinal muscle fibres.

Penial setae (40 Allanmyo-Thayetmyo) 1·9-2·7 mm long, 30-45μ thick at base, 20-60 at neck, 30-57 at blade. Shaft nearly straight except for a slight ectal curve, occasionally with one or more circumferential constrictions. Tip widened, flattened, rather spade-shaped, truncate




TEXT-FIG. 1.—*E. planatus*. Tips of penial setae, x *ca.* 560.

*a*. From clitellate worm (Magwe); *b*. From juvenile (Magwe); *c*. From clitellate worm (Minbu); *d*. Tip abnormal. From clitellate worm (Minbu).

[Camera lucida sketches by Miss Chapman. (Other sketches of penial setae, vestibula, and genital markings were destroyed during world war ii)].

or ectal margin with central protuberance rarely tapering to a point. Ornamentation of small triangular teeth in transverse rows ectally, in circles entally, 3-4 circles in 10 micra. Number, 4-8 (20 batteries). Width of blade, 32-42μ in Allanmyo, 35-57 in Thayetmyo worms.

Penial setae (68 Magwe-Minbu) 1·0-2·3 mm long, 25-50μ thick at base, 12-30 at neck, 28-60 at blade. Shaft curved in half parabola. Tip widened, scoop-shaped, ectal margin concave, ending in annulus (4, fig. 1). Ornamentation of thorn-like teeth in rows or circles as before. Number, 5-11 (34 batteries). Functional setae yellow, reserve setae pink and usually with central protuberance of ectal margin (Magwe) quite obvious. Four functional setae, from juveniles with batteries of 10-11, are 1·34-1·8 mm long, 30-47μ thick at base, 15-21 at neck, 34-45 at blade.

*Juveniles.*—Anlage of vestibular invaginations are represented in these Magwe-Minbu worms, 65-100×4 mm, by a greyish translucence of body wall in diagonal, anterolaterally directed areas within each of which is a transverse fissure through which penial setae project. A median region on presetal half of xvii, of triangular shape with apex posteriorly, is more or less markedly tumescent. Grey areas are slightly depressed (1) or, in largest juvenile, depressed, enlarged and united at mV posteriorly on xvii. Margins of fissures very slightly tumescent on one of the juveniles. The rudiment of the genital marking is postsetal on xiii. Spermathecal pores exactly centered at *B*. Testis sac annular, with delicate coagulum extending dorsally through sac and above dorsal trunk. Spermathecal duct bulbous and even at this stage with a definite though short neck. Ampulla shorter than duct, rudiments of diverticula recognizable.

*Parasites.*—Gregarines are present in numbers, in coelomic cavities of postprostatic segments of three of the juveniles.

*Remarks.*—The genital marking according to evidence provided by juveniles belongs to xiii though it may cross site of 13/14 in its growth. The marking has been absent only twice. Additional markings have been present on xii (or 12/13 ?) thrice, on xiv (or 14/15 ?) in a score of cases. The latter location is the same as that of the anterior marking of *excavatus*.

Populations from opposite sides of the Irrawaddy River have similar characteristics but those at northern and southern limits of the unusually small range differ with respect to shape of vestibular aperture and lumen, shape of testis sac, shape and length as well as muscularity of spermathecal duct and the ridging of its inner wall, curvature and shape of tip of functional penial setae, color of reserve setae, segment in which typhlosole begins, segmental location of supra-intestinal glands, and possibly in development of glandular material associated with genital marking.

Penial annuli, on the contrary have been recognized in individuals from each of the localities though absent in others from the same populations. The variation here, as in other species, may be due merely to

degree of outrolling of lining of fissure at time of preservation rather than in development of a permanent structure.

**Eutyphoeus excavatus** Gates 1929

Meiktila, September, 0-0-33. K. John.
Taungtha (Myingyan), September, 0-0-1. K. John.
Myingyan, September, 0-0-21. K. John.
Kyaukse, hills to the west, September, 0-5-50. K. John.
Kyaukse, two miles to the west, September, 4-1-49. K. John.
Dwehla (Kyaukse), September, 0-4-29. K. John.
Myotha (Sagaing), September, 0-0-10. K. John.
Tada-U (Sagaing), September, 0-0-2. K. John.

*External characteristics.*—Smallest clitellate specimen 110 mm long and 4 mm thick. First dorsal pore on 10/11 (2), 11/12 (58), 12/13 (3).

Spermathecal pores small, with centers on or median to *B*, rarely in median half of *AB*. Female pore on left side only (149), paired (11, but both functional?). An imperforate punctation at approximate site of right pore on nine specimens.

Vestibular aperture transversely slit-like, extending into lateral half of *BC*, margin especially strengthened from *A* laterally. Vestibular lumen transversely dumbbell-shaped in horizontal section (full contraction), often much shallower in region of *AA* than laterally and then lips usually in contact with each other in region of *AB* on each side. Vestibulum may be relaxed so that there is no trace of an aperture recognizable in *AA*, the worms then apparently bivestibulate. A slightly raised, circular to shortly elliptical area is present, about in *AB*, on each side of the anterior and posterior vestibular walls, and on these areas occasionally are distinguishable an opaque whitish rim and greyish translucent central portion. Penes are represented only by small, low, whitish annuli on the vestibular roof at or slightly lateral to *B*. The annulus may be anteroposteriorly flattened (many Myingyan specimens) and even slightly extended so as to appear tubular but is still less than one half mm long. The annulus is unusually small in some of the Meiktila specimens and in worms from other localities appears to be entirely lacking though the rim of the aperture into the fissure is slightly softer than the rest of the vestibular roof. Median to the annulus and centered at *A* there is often a slightly raised circular patch.

Genital markings (median) reach laterally to *A*, into *AB*, to or just lateral to *B* and may nearly meet or actually be in contact at equator of xv. Markings are sharply demarcated by a slight, (usually) completely circumferential groove. Just internal to this groove the marking is slightly raised and whitish but this margin is not clearly marked off from the greyish translucent portion which is usually depressed in a regularly concave fashion. The usual two markings are present (199) except as follows: Anterior marking lacking (1 Kyaukse, 1 Dwehla). Posterior marking lacking, a marking on 13/14 (1 Myingyan). An extra marking on 13/14 (2 Myingyan, 1 Meiktila). An anterior half portion of a marking present on the posterior part of xvi (1 Dwehla) in addition to the usual markings.

*Internal anatomy.*—Typhlosole begins in xxvi (1), xxvii (7), xxvii (10), xxix (1). A very slight but definite white ridge, continuous or variously interrupted, often present forward into xv. A short intermediate zone less than one segment in length usually present but pressed against front end of typhlosole and unrecognizable unless gut wall is stretched. Lateral typhlosoles represented only by longitudinal rows of patches, two in a row (3), three (10), four (9), five (3). Patches shortly oval to elliptical or spindle-shaped thickenings of wall gorged with blood, usually unrecognizable externally. Location of ventral caeca and supra-intestinal glands as shown in table. Two ventral caeca, both median and with apertures close together have been found in a single segment (of four specimens).

Circulatory system as in *gigas* except that the extra-oesophageals are connected by a transverse vessel just behind 5/6 and the dorsal trunk ends with hearts of vii (209).

Testis sac annular (209). Hearts of xi at first appear to be within the sac and adherent to its posterior wall but each heart is within a tube of delicate tissue which can be dissected off as also in case of hearts of xii. The dorsal trunk also at first appears to be included in the sac but delicate longitudinal mesenteries pass down from the vessel to dorsal surface of gut shutting off a small space that contains no testicular coagulum.

*Location of ventral caeca and of supra-intestinal glands*

| Segments | Number of specimens from | | |
|---|---|---|---|
| | 1 | 2 | 3 |
| 33-38 | 1 | — | — |
| 33-42 | 1 | — | — |
| 33-43 | 1 | — | — |
| 34-38 | 2 | — | — |
| 34-39 | 1 | — | 1 |
| 34-40 | — | 1 | — |
| 35-39 | 2 | — | — |
| 35 40 | 2 | — | — |
| 35-41 | 2 | 2 | — |
| 36-38 | 3 | — | — |
| 36-39 | 2 | — | — |
| 36-40 | 1 | 2* | 2 |
| 36-41 | 1 | 1 | — |
| 36-42 | 1 | — | — |
| 37-38 | 1 | — | — |
| 37-42 | 1 | — | — |

* Including the only record of caeca for a Taungtha worm.

*Location of ventral caeca and of supra-intestinal glands*—contd.

| Segments | Number of specimens from 1 | 2 | 3 |
|---|---|---|---|
| 92-97 | 1 | — | — |
| 92-98 | 2 | — | — |
| 93-97 | 2 | — | — |
| 93-98 | 7 | — | — |
| 93-99 | 3 | — | — |
| 94-98 | 2 | — | — |
| 94-99 | 2 | — | — |
| 94-100 | 1 | — | — |
| 95-99 | 1 | — | — |
| 95-100 | 3 | — | — |
| 95-101 | 2 | — | — |
| 96-100 | 1 | 2 | — |
| 96-101 | 2 | 3 | — |
| 96-102 | — | 1 | — |
| 97-101 | 1 | 1 | — |
| 97-102 | — | 3 | 2 |
| 97-103 | — | 3 | 3 |
| 98-102 | — | 3 | 1 |
| 98-103 | — | — | 5 |
| 98-104 | — | — | 1 |
| 99-103 | — | — | 1 |
| 99-104 | — | 1 | 1 |
| 99-105 | — | — | 1 |
| 100-105 | 1 | — | |
| 101-105 | — | — | 1 |

1. Kyaukse and Dwehla. 2. Myingyan and Taungtha. 3. Meiktila.

Bulbus ejaculatorius markedly protuberant into coelomic cavity bound down to parietes, or within body wall, rather soft or firm, without muscular sheen. Vestibular roof thin in *AA*, thickened laterally and there slightly protuberant into coelomic cavity.

Body wall often conspicuously protuberant into coelomic cavity over each genital marking due to depression of a central portion of marking. Longitudinal musculature though thin, continued across the protuberances.

Spermathecal duct short, abruptly narrowed deep in parietes, lumen slit-like in cross section. The diverticulum, always single (418 spermathecae), lateral, rarely with an appearance of being more anterior than lateral (3 Myingyan specimens), usually manicate, with 6-8 finger-like lobes. Only one aperture in duct lumen ( 8 spermathecae) has been found.

Penial setae (36 Myingyan and Meiktila) 2·95-4·95 mm long, 40-75μ thick at base, 20-38 at neck, 27-63 at tip ; 3·2-4·05 (40 Dwehla), 40-75μ thick at base, 30-50 at neck, 30-50 tip. Shaft straight except for curvature from neck ectally. Tip widened, flattened tapering to a point or, occasionally, slightly concave like a bowl of a spoon. Ornamentation of spine-like teeth irregularly scattered ectally, in broken circles entally. Number, 8-16 (20 batteries, Dwehla), 5-17 (18 batteries, Myingyan and Meiktila). Reserve setae, paler than yellow functional setae, bowed slightly (quarter of a circle), with widened spoon-shaped tip.

*Remarks.*—The patches at sites of lateral typhlosoles are not always present in the same number on both sides of a worm. Counts were recorded for a single side only as the difference between the two sides usually was but one.

A female pore has been present on the right side in 11 of 149 specimens examined in this connection. Range of spermathecal pore location is even smaller than in *bifovis*.

At least one genital marking has been present in every worm, that of 14/15 lacking on two, that of 15/16 on one. An extra marking has been present on 13/14 of five specimens.

Each of 468 (+) spermathecae examined in this connection was unidiverticulate, the diverticulum lateral except in three worms where it had the appearance of being more anterior.

Number of segments with supra-intestinal glands in an individual was 5-7. Number of segments in local populations 9 (16 and 17 specimen samples from Meiktila and Myingyan respectively), 14 (31 specimen sample from Kyaukse-Dwehla). Number for the species, only 14.

Greater variation was found in number of ventral intestinal caeca 211. The number of segments involved in this species is the same as the maximum for a single individual.

All degrees between extremes of variation as to condition of margin of fissure containing penisetal follicle pores have been found in a single population, annulus lacking, doubtfully indicated, small, anteroposteriorly flattened and in a slightly longer tubular form.

### **Eutyphoeus cochlearis** Gates 1951

*Internal anatomy.*—Typhlosole begins abruptly in posterior portion of xxvii (2), or xxviii (1), but reaches maximum height only in xxvii or xxix. Lateral typhlosoles represented only by longitudinal rows of

3-6 small, oval reddish patches in first typhlosolar segment. Ventral intestinal caeca in xxxiv-xxxix (1), xxxvi-xxxix (2). Supra-intestinal glands in xciii-xcviii (1), xciv-xcviii (1), xcv-xcix (1). Circulatory system, in these types, as in *gigas* except that extra-oesophageal trunks are connected by a transverse vessel just behind 5/6.

Testis sac annular and above dorsal trunk (1), or U-shaped, limbs reaching up to dorsal vessel (2). Vestibular roof thin midventrally. Penial setae (reserve) in two longitudinal ranks with the largest setae anteriorly and the smallest posteriorly, one rank in median, other in lateral wall of an entally closed cylinder, the two ranks almost meeting posteriorly. The two functional setae in softer tissue at anterior face of cylinder.

Spermathecal duct (coelomic portion) about 2 mm long, not bulbous. with fairly thick muscular wall, lumen rather crescentic in cross section due to presence on posterior wall of a fairly high ridge with a vertical groove at least ventrally.

Penial setae (6 Pakokku), 3-4·4 mm long, 40-50μ thick at base 30-40 at midshaft, 20-25 at neck, 35-39 at tip. Shaft curved into an S-shape. Tip slightly flattened, truncate, more or less spoon-shaped. Ornamentation of circles of spines that become smaller ectally. Number, 11-13 (3 batteries). Reserve setae shorter but thicker, tips more markedly spoon-shaped, bowl of spoon of smaller reserve setae occasionally ending in a slight protuberance.

### **Eutyphoeus bifovis** Gates 1929

Taungdwingyi (Magwe), August, 1-1-14, K. John.
Taungdwingyi, hills to the east, August, 0-0-30, K. John.
Magwe, and vicinity, August, 0-0-34. K. John.
Nyaungbinywa (Magwe), August, 0-0-43. K. John.
Myingyan, September, 1-1-2. K. John.
Tada-U (Sagaing), September, 0-0-7. K. John.
Kin-U (Shwebo), September, 0-0-1. Saw San Thwe.

*External characteristics.*—Length, 140-220 mm. Diameter, 4·9 mm. First dorsal pore on 10/11 (2), 11/12 (42).

Spermathecal pores with centers at or near *C* (some Mandalay), pores lateral to *C* (Tada-U), in lateral part of *CD* (Myingyan), center at or close to *D* (some Mandalay), one pore only at m*BC* (2 Nyaung binywa). Female pore on left side (79, two of which have an imperforate punctation at site of right pore), right pore present but usually smaller and the whitened area around it smaller than that on left side. Vestibular apertures in *AB*, longitudinally elliptical to slit-like, always open. Midventral region between apertures slightly tumescent and cross-hatched as on relaxed specimens of *excavatus*. A ventral region including both vestibular apertures may be slightly depressed in which case a slight longitudinal elevation is present just lateral to each of the apertures. The median wall of each vestibulum is thin, with two rather conspicuous, circular to shortly elliptical protuberances, as anterior and posterior corners. Penes (?) small, white, annular, anteriar portion of each annulus slightly thickened and with a transversely ellipsoidal appearance.

Genital markings transverse, reaching laterally to or slightly beyond *B*, on 15/16 and 18/19 (121) except as follows. Anterior marking lacking but site white, slightly tumescent, cross-hatched with numerous furrows (3 Taungdwingyi). No genital markings (1 Taungdwingyi). An asymmetrical marking on 19/20, from near mV to *A* on left (2) or right (1) side (Taungdwingyi and Nyaungbinywa). A marking on 14/15 (3 Taungdwingyi and Nyaungbinywa), as large as that on 15/16 (1) or smaller (2) and then in one case from mV to *A* on left side. Marking on 18/19 small, from near mV to *A* on left side (1 Nyaungbinywa).

*Internal anatomy.*—Typhlosole begins in xxvii (1), xxviii (48) or xxix (6). Lateral to the typhlosole there is always present on each side, in the first one or two typhlosolar segments or occasionally in the segment next in front as well, a longitudinal row of protuberant, dark red, transversely placed patches, one to six in a row ; one (1), two (3), four (23), five (8), six (1). Ventral caeca and supra-intestinal glands located as shown in table.

Circulatory system as in *gigas* except as follows : Extra-oesophageals connected by a transverse vessel just behind 5/6. Supra-oesophageal usually a definite median vessel terminating with oesophageal bifurcations of hearts of xi and xiii. An extra connective between extra-oesophageals, in one specimen, is fairly large and just anterior to 5/6. Dorsal vessel terminates with hearts of vii (130).

*Location of ventral caeca and of supra-intestinal glands*

| Segments | Number of specimens from | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 33-38 | 1 | — | .. | — | — | — | — |
| 34 38 | — | 4 | | — | — | — | 1 |
| 34-39 | 4 | — | | 2 | 1 | — | — |
| 34-40 | 1 | 1 | .. | — | — | 1 | — |
| 34-41 | — | — | .. | 3 | — | — | — |
| 34-42 | — | — | | 1 | — | 1 | — |
| 35-38 | 1 | — | | — | — | — | — |
| 35-39 | 3 | 4 | | — | 6 | 2 | — |
| 35-40 | 2 | 3 | .. | 9 | 2 | — | — |
| 35-41 | 1 | — | | — | — | — | — |
| 35-42 | — | — | .. | 3 | — | — | — |
| 35-43 | — | — | .. | 1 | — | — | — |
| 35-44 | — | — | | — | 1 | — | — |
| 36-40 | — | 1 | .. | — | — | — | — |
| 36-41 | 1 | — | .. | 1 | — | — | — |
| 37-41 | | — | .. | — | 2 | — | — |

*Location of ventral caeca and of supra-intestinal glands*—contd.

| Segments | Number of specimens from | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 86-91 | — | — | — | — | — | — | 1 |
| 86-92 | — | — | 1 | — | — | — | — |
| 87-92 | — | — | 2 | — | — | — | — |
| 87-93 | 1 | 1 | 1 | — | — | — | — |
| 87-94 | — | — | 1 | — | — | — | — |
| 88-92 | — | — | 1 | — | — | — | — |
| 88-93 | — | — | 1 | — | — | — | — |
| 88-94 | 3 | 2 | — | — | — | — | — |
| 89-94 | 1 | 1 | — | 4 | — | — | — |
| 89-95 | 5 | — | — | — | — | — | — |
| 90-95 | 2 | 5 | — | — | — | — | — |
| 90-96 | 3 | 1 | — | 2 | — | — | — |
| 91-96 | 1 | 4 | — | 1 | 1 | — | — |
| 91-97 | — | — | — | 11 | 8 | 1 | — |
| 92-97 | — | — | — | 5 | — | — | — |
| 92-98 | — | — | — | 9 | 5 | — | — |
| 92-100 | — | — | — | — | — | 1 | — |
| 93-98 | — | — | — | — | — | 1 | — |
| 93-99 | — | — | — | 3 | 1 | — | — |
| 94-100 | — | — | — | 1 | — | 1 | — |

1. Taungdwingyi. 2. Hills east of Taungdwingyi.
3. Mandalay. 4. Magwe and vicinity.
5. Nyaungbinywa. 6. Myingyan. 7. Kin-U.

Testis sac annular (135), passing over dorsal blood vessel. Hearts of xi within the sac but each in a tube of delicate tissue as are also hearts of xii. Bulbus ejaculatorius small, white, covered over or within posterior wall of vestibular bulb.

Spermathecal duct usually less than two mm long, constricted in parietes, not narrowed entally, with no externally recognizable muscular sheen. Lumen transversely slit-like in cross section ectally, rather crescentic entally due to presence on posterior wall of a rather wide and fairly high ridge on which there is a vertical groove. The ridge is especially obvious at opening into ampulla. Three high ridges are present on posterior wall of duct in Tada-U and Kin-U material. Diverticula are shortly ellipsoidal to digitiform, median and lateral (268 spermathecae) except as noted below. A length of more than two mm was attained by five diverticula of Tada-U and Kin-U worms.

Body wall bulged into coelomic cavity over genital markings but not thickened, longitudinal musculature apparently continued across the protuberances but thin, especially over posterior genital marking.

Penial setae (16 Mandalay) 1·85-2·55 mm long, 23-34μ thick at base 14-22 at midshaft, 18-32 at tip. Number, 10-12 (8 batteries). In Taundwingyi material (32) 2. 53-2.98 mm long, 32-45μ thick at base, 22-36 at tip. Number, 7-10 (16 batteries). In worms from Magwe, Nyaungbinwa and Myingyan (68) 2·5-3·06 mm long, 32-51μ thick at base, 20-32 at tip. Number, 7 (2 batteries), 8 (13), 9 (13), 10 (4), 12 (2). Shaft straight with slight curvature of terminal ectal portion (Mandalay) or sigmoid and occasionally (7 setae) with spiral twisting more (Taungdwingyi) or less (Magwe) marked. Tip widened, thinner at edges, tapering to a point, occasionally more or less hollowed as in bowl of a spoon and (except at Taungdwingyi) pink. Ornamentation of small thorn-like to triangular teeth in more or less regular circles. A segment of the shaft, 0·5 to 0·7 mm from tip is dark (Mandalay). Reserve setae (Mandalay) are deep red. The tip of the shorter ones usually is distinctly spoon-shaped but the bowl becomes increasingly less distinct as size increases. Reserve setae may be bowed but show no spiral twisting.

*Abnormality.*—(No. 1) Left spermatheca with no median diverticulum, duct only about half the usual thickness (Magwe). (No. 2) Left spermatheca with an extra diverticulum of one seminal chamber on posterior face of duct about halfway between lateral and median diverticula (Taungdwingyi). (No. 3) Right spermatheca lacking (Taungdwingyi).

*Parasites.*—Nematodes are present in numbers in the coelomic cavity of xii of each Taungdwingyi specimen. One only was found (same place) in each of two Magwe specimens, two in a Nyaungbinywa worm. Nematodes were numerous in the testis sac of several Tada-U specimens.

*Remarks.*—Little variation has been found in this species with respect to various taxonomically important characteristics. A female pore was present on right side of seven of the 110 specimens examined in this connection, but in each case the pore, as well the whitened field around it, was smaller than that of the right side. The range in location of spermathecal pores, even including two somewhat aberrant worms, is just a half that of *constrictus*.

Genital markings have been lacking in only one of all worms collected, an anterior marking in two other specimens. An extra marking has been present, on 14/15 (six times), on 17/18 (once), on 19/20 (seven times). Two diverticula have been present in 348 (+?) spermathecae, the median diverticulum of a left spermatheca lacking in one worm an entire right spermatheca lacking in another specimen.

Number of segments with supra-intestinal glands, in an individual, was 5-9, but eight and nine segments were obtained only once each. Number of segments in a local population was 9-11, as indicated by

samples of 4 specimens (Myingyan) to 32 (Magwe). The number for the species only 15, lxxxvi-c. Number of intestinal caeca was 4-10 and number of segments involved only twelve, xxxiii-xliv.

## THE PHYLOGENY OF THE *foveatus* GROUP

The inornate mutation, except in *spinulosus*, has been recognized in this group of species only three times, in one individual of *foveatus* and in two of *planatus*. Variation in number of genital markings is slight in each species. Lateral intestinal caeca are lacking except in *foveatus* where rudimentary pockets are just beginning to appear in some of the populations. Supra-intestinal glands usually are in 5-7 metameres and the axial locations, throughout the entire group, involves only 21 segments.

In addition to this high degree of species stabilization, the group as a whole, is uniform with respect to the following characteristics: Location of first dorsal pore, on 11/12. Presence of brown pigment. Invagination of both fissures into a single vestibulum. Restriction of the genital markings, always unpaired and median, to *BB*, and absence of coelomic glands. Right female pore lacking. Lateral typhlosoles replaced by a row of flat red patches. Abortion of the dorsal blood vessel and associated commissures anterior to the hearts of vii. Absence of anterior testes as well as the male funnels of x and their ducts. Presence of a battery of reserve penial setae.

Another species, *bifovis*, is similarly characterized (1 inornate individual) except that two discrete vestibula are invaginated and for present convenience is appended to the *foveatus* group.

The common ancestral form that apparently should be assumed for such a group of species arose by establishment of three of the standard mutations postulated above, metandric, foreshortening and oviductless. Absence of records of male funnels in x agrees with the scarcity of cases in which vestiges of the dorsal trunk are retained to indicate long establishment for the first two. Incidence of persistence of an apparently functional right female pore, 4·8 per cent. in *foveatus*, 5·9 per cent. in *planatus*, 7·3 per cent. in *excavatus*, 6·3 per cent. in *bifovis*, 21·3 per cent. in *spinulosus*, indicates more recent establishment of the third. Possibly the three were established in the order already mentioned. Absence of any unpigmented individuals, in each of the species, is thought to indicate ancient acquisition of a chemical process possibly for elimination of certain metabolic wastes. Similarly absence of any variation as to pairing of genital markings or a situation in *BB* indicates that the restrictions on those structures were acquired early in the evolution of the group. This also may have involved the union at mV of originally paired and postsetal anlage suggested above for *strigosus* though a location on the intersegmental levels apparently crossed in present ontogenetic development is assumed for greater convenience in the subsequent part of the discussion. The vestibulum, in this line of evolution appears to be as ancient as anything just mentioned. Invagination of this pocket, like the development of a battery of reserve penial setae, is induced by the prostate anlage These growth centers

presumably have been responsible for development of the fissures throughout the *Eutyphoeus* phylogeny. A mutation for considerable subsequent extension and prolongation of that induction effect in individual ontogeny might conceivably give rise to the vestibulum at one evolutionary step. Presence of penisetal batteries in *hastatus*, *constrictus* and other uninvaginate species proves that a separate mutation is necessary if these ranks of reserves are also to be achieved in a single step.

From the advanced proto-foveatus thus characterized, *foveatus* is derived by restriction of number of markings to two, on 14/15 and 15/16, their subsequent enlargement and union to form a single area often showing at the equator of xv more or less obvious evidence of a double origin. Additionally, a temporary annular tumescence around each fissure became extended into a permanent tubular penis, and the testis sac was reduced to a ventral chamber. The range of *foveatus*, as now delimited (p. 167), includes a southern sector of the Arakan Yomas and the recent alluvium of the deltas region. If an origin of *foveatus* almost in historical times is to be avoided, its site must be placed in the yomas, presumably on the eastern slopes or in the eastern ranges. Migration thence eastwards may have been speeded by flood-water transportation.

*E. spinulosus* apparently can be derived directly from *foveatus* by establishment of the mutation unidiverticulate along with a modification of penial setae and acquisition of a tendency to reduce the size of the anterior portion of the genital marking or even to eliminate the whole area. In this change the standard mutation inornate presumably is involved and if so the restricted anterior abortion may then be attributable to incomplete penetrance. Also apparently indicated is a trend toward reduction in number of supra-intestinal glands and ventral caeca. The species is known today only from the recent alluvium of Bassein district which is of later deposition even than that where *foveatus* is found. Accordingly, an origin of the species in the eastern slopes or hills of the Arakan Yomas and at the southern frontier of the *foveatus* range is predicted. This geographical origin again involves eastward migration and/or transportation to explain present distribution.

To the north of the *foveatus* range *planatus* has been derived from the proto-foveatus by reduction of the ancestral genital markings to one on 13/14 and by reduction in number of intestinal caeca to four to seven. Reduction of the testis sac to a suboesophageal chamber is under way. Even within the vertically short range of about a hundred miles half a dozen easily recognizable differences apparently could be used to distinguish two subspecies, one northern and one southern. Indeed, all but one of the dissected specimens can be referred by supra-intestinal glands alone to one or the other of two such taxa though only twenty segments are involved in the entire range. Relatively recent transport of both types across the Irrawaddy is indicated by the restricted distribution on the east bank. An origin in the eastern ranges of the Arakan Yomas and eastward migration again is anticipated.

Well above the *planatus* area as now known *cochlearis* was derived by elemination of a genital marking on 14/15 to leave one on 15/16

A tendency to more posterior location of supra-intestinal glands is indicated. The species is, of course, distinguished from previously discussed members of the group, as they are from each other, by characteristics of vestibula and penial setae less amenable at present to phylogenetic exploitation. The range extends from Pakokku north along the west bank of the Chindwin river. Some unconfirmed records indicate a possibility of fairly recent transport across the river.

*E. excavatus* has been derived by establishment of the unidiverticulate mutation and has retained the genital marking on 14/15 lost by *cochlearis*. Otherwise there seems to be little to differentiate the species for vestibula are identical and penial setae more difficult to distinguish than previously. The range is on the wrong side of the Chindwin-Irrawaddy axis and the distribution apparently is such as to require crossing at an earlier period than for the previous species, possibly before the Irrawaddy had broken through to the Chindwin, in order to permit migration north into Sagaing district. The unknown fauna of the region between Minbu and Pakokku on the west bank of the Irrawaddy may be expected to throw some light on this question of appearance of the unidiverticulate mutation with reference to the crossing.

*E. bifovis* has a genital marking on 15/16 as in each of the *foveatus* group except *planatus* but is distinguished from all of that group by presence of a postclitellar marking on 18/19, and by a marked lateral migration of spermathecal pores. The vestibulate induction may not have been sufficiently strong or continued long enough to invaginate a median portion of xvii thus leaving two discrete vestibula. A penial annulus may have become permanent around each fissure. The 200 mile vertical range in central Burma, without indication of segregation of variants, parallels the ranges of three *foveatus* group species to the west. Origin directly from *excavatus* is contraindicated by the bidiverticulate spermathecae, and there are distributional difficulties involved in local derivation together with *excavatus* from a common ancestor. These difficulties are temporarily avoided by placing origin in the north where the fauna is largely unknown and from whence migration to south may have taken place before junction of the Irrawaddy with the Chindwin.

### THE *gigas* GROUP

#### **Eutyphoeus gigas** Stephenson 1917

Sandoway, September, 0-0-1. I. M. Ismailjee.
Taungup (Sandoway), September, 0-13-0. I. M. Ismailjee.
Myebon (Kyaukpyu), September, 0-2-0. I. M. Ismailjee.
Myohaung (Akyab), September, 0-1-10. I. M. Ismailjee.
Kyauktaw (Akyab), September, 68-0-2. I. M. Ismailjee.
Buthidaung-Maungdaw (Akyab), September, 0-24-5. I. M. Ismailjee.
Akyab, September, 9-0-0. I. M. Ismailjee.
Paletwa (Arakan Hills), September, 0-0-40. I. M. Ismailjee.

*External characteristics.*—Pigmentation may be continued ventrally into *BC* or even to *B* or *A* (Paletwa). First dorsal pore usually on 11/12.

Spermathecal pores usually in median portion of *BC*, occasionally centered at *B*. Female pore, whenever recognizable, on left side.

Two penisetal follicle pores on a distinct tubercle. Two setae occasionally protrude through one of the apertures. A fairly large and firm annulus, with appearance of being a permanent organ, always seated on body wall at periphery of penisetal pore tubercle. Ventral margin of the annulus softer and slightly but variously lobed and capable of some ventral extension. Annulus centrally or laterally located on male porophores. These may be large, longitudinally elliptical, tough discs of slight parietal thickening (1 Paletwa and Sandoway worms), smaller and then circular to transversely elliptical. The surface is smooth (Sandoway) or cross-furrowed and with an appearance of slight tumescence (preservation artefact ?). Porophores may be transversely depressed in front of the annulus so as to approximate, more or less closely, the anterior and posterior margins, or the entire porophore may be depressed in a regularly concave manner so as to bring annuli below general level of body surface, or a portion of the porophore just in front of or behind or to one side of the annulus may be deeply depressed. The entire peripheral portion of the porophore is occasionally depressed deeply in which case (5) the annulus is seated on a central protuberance and with a superficial appearance of a large tubular penis in a well-like vestibulum, with roof slightly protuberant into coelomic cavity.

| | | Localities | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Unpaired and median | Presetal on viii | 1 | .. | .. | .. | .. | .. | 10 |
| | Postsetal on viii | .. | .. | .. | .. | .. | | 1 |
| | Postsetal on ix | 1 | .. | .. | .. | .. | .. | .. |
| | On 11/12 | .. | 1 | .. | .. | .. | .. | .. |
| | On 12/13 | .. | 1 | .. | .. | .. | .. | .. |
| | Postsetal on xiii (or on 13/14) | .. | .. | .. | 1 | 1(*a*) | .. | 1 |
| | Postsetal on xiv (or on 14/15) | .. | .. | .. | 1 | 2(*a*) | 3 | 18 |
| | Postsetal on xv (or on 15/16) | .. | .. | .. | 1 | 2(*a*) | 1 | 24 |
| | 18/19 | .. | .. | .. | .. | .. | .. | 3(*d*) |
| | 19/20 | 1 | .. | .. | .. | .. | .. | .. |
| | 20/21 | 1 | .. | .. | .. | .. | .. | .. |
| Paired, in *AA* | Postsetal on xv | .. | .. | .. | .. | .. | 5 | .. |
| | ,, ,, xvi | .. | .. | .. | .. | | 2 | 1 |
| | ,, ,, xviii | .. | .. | .. | .. | .. | 5 | 7(*c*) |
| | ,, ,, xix | .. | .. | .. | .. | .. | .. | 2 |
| Paired, in *AB* | Postsetal on viii | .. | .. | .. | .. | .. | 5 | .. |
| | ,, ,, ix | .. | .. | .. | .. | .. | 1 | .. |
| | ,, ,, xvi (*b*) | .. | .. | .. | .. | .. | .. | 36 |
| | On 18/19 | .. | .. | .. | 2 | .. | .. | 13 |
| | ,, 19/20 | .. | .. | .. | 7 | 3 | 1 | 25 |
| | ,, 20/21 | .. | .. | 2 | 7 | 2 | 1 | 7 |
| | ,, 21/22 | .. | .. | 2 | .. | .. | .. | .. |
| Paired, in *BC* | Postsetal on vii, just in front spermathecal | .. | 1 | 2 | 6 | 1 | 2 | 3 |
| | Presetal on vii, just behind spermathecal pore. | .. | 2 | .. | .. | .. | .. | |
| | Postsetal on viii | .. | 6 | .. | .. | .. | .. | .. |
| | ,, ix | .. | 2 | .. | .. | .. | .. | .. |
| | Postsetal on xv (or on 15/16) | 1 | .. | .. | .. | .. | 2 | .. |
| | Postsetal on xvi (or on 16/17) | .. | .. | .. | 1 | .. | 1 | .. |

(*a*) Juveniles. Markings rudimentary, posterior margins at intersegmental furrows, anterior margins some distance behind equators.

(*b*) These markings may replace the greyish, transverse crescentic areas often present in front of the male porophores, or may be united with the crescents or even within the crescents.

(*c*) Markings on two of these worms are united mesially although the double origin is clearly indicated.

(*d*) Median marking is united with markings of *ab* in two of these worms.

Postclitellar markings of *ab* may extend deeply into *aa*, occasionally almost to the midventral line as well as into *bc* although usually not so far.

Genital markings transverse and shortly elliptical to spindle-shaped.

Localities, 1-7. Key sheet or localities was destroyed along with other records.

*Internal anatomy.*—The mid-dorsal, longitudinal muscle band is pigmented.

Typhlosole begins in caecal segment but with a slight protuberance into xxvii. Lateral typhlosoles represented by a dark red elliptical area which is present only in about half the specimens and which may be continued around anterior margin of caecal aperture. Lateral intestinal caeca distinctly marked off, long, rather digitiform, usually ventrally directed, rarely turned upwards, in xxviii (25). Ventral intestinal caeca in xxxii-lx (1), xxxii-lxi (1), xxxiii-lviii (1), xxxiii-lix(1). Supra-intestinal glands in four to six segments as shown in the table.

*Location of supra-intestinal glands in* E. gigas

| Segments | Number of specimens from | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 82—85 | | | 1 | | | | . | |
| 82—86 | | | | | . | | 1 | |
| 82—87 | | | | | | | | 2 |
| 83—86 | | | . | | .. | | 1 | .. |
| 83—87 | | | 1 | | | | 3 | 2 |
| 83—88 | | | .. | | | | .. | 1 |
| 84—87 | | | 1 | | | | .. | .. |
| 84—88 | | | | | | | 5 | 4 |
| 84—89 | | | | | | | .. | 4 |
| 84—90 | | .. | | | | | | 1 |
| 85—89 | | | | | | | | 7 |
| 85—90 | | | | | . | . | | 5 |
| 86—89 | .. | | | . | 1 | 3 | | .. |
| 86—90 | | | | 2 | 5 | 1 | | 3 |
| 86—91 | | | .. | 2 | 1 | .. | .. | 2 |
| 87—90 | | . | | . | . | 3 | | . |
| 87—91 | | 1 | | 2 | 2 | 2 | .. | 5 |
| 87—91 | | 1 | | 2 | 1 | | | 2 |
| 88—92 | .. | 3 | | .. | 2 | | | .. |
| 88—93* | 1 | 2 | .. | 1 | . | | .. | |
| 89—93 | 3 | 2 | | . | 1 | | | |
| 89—94 | 3 | 1 | | 2 | | | | |
| 90—94 | 1 | 2 | | | | | | |
| 90—95 | 1 | 1 | | | | | .. | |

1. Sandoway 2. Taungup. 3. Myebon.
4. Myohaung. 5. Kyauktaw. 6. Akyab.
7. Buthidaung-Maungdaw. 8. Paletwa.

Dorsal blood vessel ends with commissures of vii (104), with a pair of (functionless ?) commissures just in front of gizzard (1 Myohaung), or turning ventrally in front of gizzard on left side as a (functionless ?) commissure of vi (1 Paletwa). Supra-oesophageal trunk usually represented by an X-shaped figure on gut in xii-xiii, posterior limbs of the "x" joining hearts of xiii, anterior limbs disappearing into gut wall. Junction of the four limbs occasionally elongated so as produce a short median vessel, the figure then more like that of parentheses in contact by their convex sides. A median vessel formed by junction of anterior bifurcations of hearts of xiii is long enough, in just one worm, to be joined by oesophageal bifurcations of hearts of xi. Extra-oesophageals

* As in type from Rangamati in Chittagong Hill Tracts of Bengal.

turn upwards just in front of 4/5 and anteriorly in v unite, separating again slightly behind 5/6, then dropping nearly to ventral parietes. The trunks again turn upwards just in front of 8/9 and are there connected by a short transverse vessel just before passing through 8/9. In x the trunks pass on to ventrolateral or lateral aspect of gut and anteriorly in xi into gut wall. A small branch may pass ventrally at anterior end of calciferous gland but this is often unrecognizable so that the whole trunk appears to be continued posteriorly on dorsal margin of median wall of calciferous gland, turning ventrally at hind end of gland. The ventral trunk bifurcates in region of subpharyngeal ganglia, branching as it passes dorsally along the circumpharyngeal nervous commissures. No subneural trunk (106). Lateroparietal trunks, which have been recognizable in *BC* as far back as lx, pass in xiii onto ventral face of gut and disappear from sight on posterior face of calciferous gland. A median vessel on the floor of the post-typhlosolar portion of the gut bifurcates anteriorly, the branches passing dorsally and then anteriorly at lateral margins of supra-intestinal glands. Hearts of xi-xiii latero-oesophageal, bifurcations of hearts of xiii continued as posterior limbs of the X-shaped figure mentioned above, oesophageal bifurcations of hearts of xii opening into anterior limbs of the figure. Oesophageal bifurcations of hearts of xi pass into a transverse vessel which may be recognizable on each side of gut almost to mL. Commissures of x-vii lateral, no oesophageal bifurcations having been recognizable in any specimen in x.

Nephridia of iii are aggregated into a rope-like cord which is zigzag looped on the parietes.

Testis sac ventral (106).

Spermathecal duct 1-2 mm long, lumen irregularly slit-like in cross-section, two high, narrow vertical ridges, each with a groove, on the posterior wall between diverticular apertures. Diverticula elongate, median and lateral (212 spermathecae). An elongate stalk is often recognizable with a cluster of the seminal chambers at ental end, or additional chambers may be located on what appears to be the stalk, or the whole diverticulum may be filled with sperm in a zigzag looped cord. The lateral diverticulum of the right spermatheca of a Taungup worm is bifid nearly to the duct.

Genital marking glands sessile on parietes, a few nearly transparent (longitudinal muscle ?) fibres sometimes recognizable across the gland.

Penial setae (12) 6·45-8·25 mm long, 70-90μ thick at base, 52-61 at midshaft, 24-38 at tip. Shaft usually straight but may be bowed or slightly sigmoid and then with two curves in opposite directions. Tip red, slightly flattened but not widened, tapering to a short spine. Ornamentation of small spine-like teeth in scattered rows beginning 0·2 mm from ectal margin. Number, 6-12 (6 batteries). The terminal spine is characteristic of functional setae of more than a hundred worms but is rarely perfect. Reserve setae red, bowed.

*Abnormality.*—(No. 1) Ventral setae of xvii on right side sigmoid of about the same size and with same ornamentation as those of xvi,

and xviii. Male genital terminalia lacking on right side, right vas deferens continued into xxvii (Kyauktaw).

*Parasites.*—Nematodes are present in coelomic cavities of several Paletwa worms and in smaller numbers in worms from other localities. Elongate but unbranched gregarines of about the same size as *A. singularis* are present in coelomic cavities of Paletwa worms as well as in some from other localities.

*Juveniles.*—Male porophores and genital markings are unrecognizable on Akyab juveniles. A small, transverse fissure is present in *AB* at equator of xvii, within which tips of two penial setae are usually visible, slightly behind and about at m*AB* the minute, transversely slit-like to crescentic male pore is recognizable.

*Remarks.*—The penial annulus in this species seems to be permanent. It must develop around the fissure present in young juveniles (later juvenile stages unavailable). The male porophore on which the annulus is seated in adults is more variable than in most species. Large porophores of especial toughness may serve as suckers to grip the region around a spermathecal pore of a copulatory partner while temporary extensions (?) of the annulus are inserted into the pore. A small porophore may be protrusible, with annulus at tip as an intromittent organ inserted more deeply into lumen of spermathecal duct. Live specimens that would have shown how the annulus is protected from friction during locomotion have not been seen.

A Lucknow record of this species (Bahl, 1927) rests on misidentification of *E. nicholsoni* (p. 203). *E. gigas* is known only from a southern portion of the western mountain wall between India and Burma.

### **Eutyphoeus quinquepertitus** Gates 1930

*Internal anatomy.*—Typhlosole begins in xxviii (2). Lateral typhlosoles simple, low lamellae in xxviii. Lateral caeca in xxviii (2). Ventral caeca in xxxii -lv (1), xxxiii-lii (1). Supra-intestinal glands in lxxix-lxxxiii (1), lxxx-lxxxiv (1).

Spermathecal duct about two mm long, lumen irregularly slit-like in cross section due to presence of vertical ridges on anterior and posterior walls. Diverticula stalked.

Body wall not especially protuberant into coelomic cavity over large genital marking, glandular (?) tissue associated with the marking apparently in the parietes and covered by a thin, tough layer of longitudinal muscle.

*Remarks.*—Brown pigmentation of the types has become unrecognizable (formalin preservation). Worms are not white, however, but grey ventrally as well as dorsally.

The ' tubular penis .. with two marginal lips ' of one type, and the ' annular penis ' of another, may represent different but early stages (apical) of eversion of the vestibulum and in such a manner that prostatic and male pores are within the lumen of the protrusion into vestibular cavity.

**Eutyphoeus rarus** Gates 1925

Kungyangon (Hanthawaddy), September, 0-0-3. K. John.
Twante (Hanthawaddy), September, 0-0-11. K. John.
Wanetchaung (Insein), September, 0-0-3. K. John.
Taukkyan (Insein), September, 0-0-1. K. John.
Bassein, October, 0-0-23. K. John.
Prome, August, 0-0-5. K. John.
Labu (Prome), August, 0-0-7. K. John.

*External characteristics.*—First dorsal pore on 11/12 (12). Clitellum reddish or brownish, protuberant or not.

Spermathecal pores centered about at *B* (Prome, Labu), laterally but usually at or just median to m*BC* (others). Female pore on left side (50).

Posterior protuberance from penis may be enlarged and gorged with blood, the pointed flaps bent up against the gorged portion.

A genital marking present just in front of each spermathecal pore (1 Labu). Unpaired median markings increasing in size posteriorly, on xii-xvi or xiii-xvi (2 Labu).

*Internal anatomy.*—Typhlosole begins in xxviii (53) but projects slightly into posterior portion of xxvii. Lateral typhlosoles low, in xxviii (46), occasionally (7) unrecognizable, possibly as a result of maceration of intestinal wall. Lateral intestinal caeca ventrally directed, in xxviii (53).

*Location of genital markings in* E. rarus

| | | Twante | Kungyangon | Wanetchaung | Bassein |
|---|---|---|---|---|---|
| Unpaired, median. | On 18/19 | 7 | .. | 3 | .. |
| Unpaired or paired. but united in *AA*. | Postsetal on xiii | 1 | .. | .. | 2 |
| | „ „ xiv | 6 | .. | 1 | 21 |
| | „ „ xv | 6 | 1 | 2 | 24 |
| | „ „ xvi | .. | .. | .. | 24 |
| Paired but united. | Postsetal on xviii | .. | .. | .. | 6 |
| Paired, in *AB*. | Postsetal on xvi | 11 | 2 | 3 | .. |
| Paired in *A*-m*BC*. | on 21/22 | 2 | 3 | .. | .. |
| | on 22/23 | .. | 1 | .. | .. |

*Location of supra-intestinal glands and ventral caecain* E. rarus.

| Segments | Number of specimens from | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| 73—76 | .. | .. | 1 | .. | .. | .. | .. | .. | .. |
| 73—77 | .. | .. | 1 | .. | 1 | .. | .. | .. | |
| 74—77 | .. | .. | .. | .. | .. | .. | 1 | | .. |
| 74—78 | .. | 2 | 2 | .. | .. | .. | 9 | | |
| 74—79 | .. | 2 | 1 | .. | .. | .. | .. | . | .. |

| Segments | Number of specimens from | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| 75—78 | .. | .. | 1 | 2 | .. | .. | 1 | .. | .. |
| 75—79 | .. | 1 | 1 | 1 | .. | .. | 8 | 1 | 2 |
| 75—80 | 1 | 1 | 1 | .. | .. | .. | .. | .. | .. |
| 76—79 | .. | 3 | .. | .. | .. | .. | .. | .. | .. |
| 76—80 | .. | .. | 1 | 1 | .. | .. | 4 | 3 | .. |
| 76—81 | 3 | .. | 2 | .. | .. | .. | .. | .. | .. |
| 77—81 | .. | .. | 4 | .. | .. | .. | .. | 5 | .. |
| 77—82 | 2 | .. | .. | .. | .. | .. | .. | .. | .. |
| 78—81 | .. | 1 | 1 | .. | .. | .. | .. | .. | .. |
| 78—82 | .. | .. | 1 | 2 | 1 | .. | .. | .. | 1 |
| 78—83 | 1 | .. | .. | .. | .. | .. | .. | .. | .. |
| 79—82 | .. | .. | 1 | .. | .. | .. | .. | .. | .. |
| 79—83 | .. | .. | 1 | .. | .. | .. | .. | 2 | .. |
| 79—84 | .. | .. | 1 | .. | .. | .. | .. | .. | .. |
| 80—83 | .. | .. | 1 | .. | .. | .. | .. | .. | .. |
| 80—84 | .. | .. | .. | 2 | 1 | .. | .. | .. | .. |
| 80—85 | .. | .. | .. | .. | 1 | 2 | .. | .. | .. |
| 80—86 | .. | .. | .. | .. | .. | 1 | .. | .. | .. |
| 81—86 | .. | .. | .. | .. | .. | 1 | .. | .. | .. |
| 32—43 | 1 | .. | .. | .. | .. | .. | .. | .. | .. |
| 32—44 | 1 | .. | .. | .. | .. | .. | .. | .. | .. |
| 32—45 | 2 | .. | .. | .. | .. | .. | .. | .. | .. |
| 32—51 | .. | .. | .. | .. | .. | 1 | .. | .. | .. |
| 33—43 | 1 | .. | .. | .. | .. | .. | .. | .. | .. |
| 33 46 | .. | 1 | .. | .. | .. | 1 | .. | .. | .. |
| 33—48 | 1 | .. | .. | .. | .. | 1 | .. | .. | .. |
| 33—51 | .. | .. | .. | .. | .. | 1 | .. | .. | .. |

1. Labu.
2. Rangoon.
3. Rangoon and Sandoway, var. *deminutus* Gates 1930.
4. Sandoway, var. *duplex* Gates 1930.
5. Sandoway, var. *simplex* Gates 1930.
6. Prome.
7. Bassein.
8. Twante.
9. Kungyangon.

Circulatory system as in *gigas*. The extra-oesophageals may be united shortly in a posterior portion of v (1), within 5/6 (1), posteriorly in v and in 5/6 (1), or from just behind 4/5 to just behind 5/6 (47), not united but connected by a transverse vessel just behind (2) or just in front (1) of 5/6. Dorsal blood vessel continued anteriorly along right side of gizzard to which it is adherent, passing ventrally just in front of gizzard to ventral trunk (1). Left heart of xiii lacking (1 Kungyangon).

Testis sacsuboesophageal (52). Bulbus ejaculatorius small, whitish, in parietes (Prome and Labu).

Spermathecal duct about one mm long, muscular. Lumen rather crescentic in cross section due to presence on posterior wall between diverticular apertures of two or three fairly high vertical ridges. Diverticula median and lateral (106 spermathecae).

Penial setae (102 from various localities) 2·99-4·7 mm long, 30-80μ thick at base, 22-47 at midshaft, 18-51 at tip. Shaft straight except for a slight curve at ectal end. Tip pink, tapering to a sharp spine which may be about 10μ long but is undamaged in only 4 of the 146 functional setae examined in this connection. The tip in some Bassein, Prome and Labu worms somewhat widened, the blade 5-10μ thicker than entally. Ornamentation of very small thorn-like teeth in circles 8-20μ apart, irregularly broken into rows of 2-8 teeth. Number, 5-11 (50 batteries). Reserve setae with straight or bowed shaft, red (except Prome and Twante), tip tapering to a terminal spine which is bifid in 5 setae.

*Remarks.*—Protrusion of the penes has been secured in anesthetics but eversion of the vestibula has never been observed though not, perhaps, impossible.

Incidence of inornate individuals in one Sandoway collection, 20·8 per cent, suggests that the taxon resulting from that mutation, f. *simplex*, may be true-breeding in isolation.

### Phylogeny of the *gigas* group

Species of this group are all characterized as follows: Presence of brown pigment. Location of first dorsal pore on 11/12. Right female pore lacking. Lateral intestinal caeca present. Ventral caeca numerous. Abortion of the dorsal blood vessel and associated segmental commissures anterior to hearts of vii. Absence of anterior testes as well as the funnels of x and their ducts. Reduction of the testis sac to a suboesophageal chamber.

Unpigmented individuals never have been found though deposition seems always to be sparse, especially posteriorly, in two species. Intestinal caeca always are well developed and in xxviii, an occasional individual varying only as to direction of the pocket. The typhlosole, of more variable origin in the *foveatus* group, here always begins in xxviii, the caecal segment. Incidence of presence of male funnels (one or two) in x was 2·5 per cent in 40 specimens of *gigas*, 2·3 per cent in 86 of *rarus*, and in each of these cases deferent ducts were not developed. Incidence of persistence of vestiges of the dorsal trunk anterior to the hearts of vii was 1·8 per cent in 106 specimens of *gigas*. A right

female pore has not been found in any of these species, condition may have prevented its recognition in some specimens of *gigas*, even though the right funnel always seems to be normally developed. Associated with this high degree of stabilization is the usual variation in number and location of ventral caeca and supra-intestinal glands.

Although the morphology agrees with the distributions to support a common origin for the *gigas* and *foveatus* groups, presumably in the Arakan Yomas, the phylogenetic separation took place before the proto-foveatus had modified its lateral typhlosoles or acquired its restrictions on the genital markings, but after establishment of the mutations brown (for pigment), metandric, foreshortening, oviductless and battery. Lateral intestinal caeca were acquired and stabilized as to form and location (in xxviii) presumably before segregation of the extant species.

From the common ancestor of the group *gigas* has been derived by elimination of the lateral typhlosoles, development of (or retention?) of coelomic glands in association with the genital markings, development of a permanent penial annulus around each fissure. The primitive multiplicity and indefiniteness of axial and intrasegmental location of the genital markings has been retained. The *gigas* range extends from the Arakan Yomas into Chittagong at least to Rangamati. The species is thought to have migrated west into Bengal from the southern yomas.

*E. rarus* has been derived by development of a small penial annulus with protrusible posterior flaps, as in *macer*, and the withdrawal of each annulus into a small, well-like vestibulum possibly eversible as in some of the *levis* group. Lateral typhlosoles were retained as well as the primitiveness of genital markings (with coelomic glands) but the inornate mutation may be spreading in some Sandoway population. The *rarus* range extends from the Sandoway coast across the yomas and into the recent alluvium of the deltas region. Arrival in the latter part of the range, where it is still rare, must have been recent and a result of eastward migration and/or transportation. Westward migration from its source in the yomas has been stopped by the sea.

*E. quinquepertitus* has been derived by acquisition of large and presumably completely eversible vestibula with a muscular bulb in the roof but with loss, of the penial setae. Lateral typhlosoles were retained but the genital markings have been stabilized in a five-sited arrangement. A vestibulate mutation must be associated here with another mutation for early abortion of the setal follicles adjacent to the prostates for no traces of them have been recognized. Nor have fissures been recognized though beginning eversion of the vestibular apex seemingly produces an appearance of a fissure surrounded by an annulus. The species must be assumed for the present to have originated *in situ*.

## INDIAN SPECIES

### **Eutyphoeus incommodus** (Beddard) 1901

*External characteristics.*—Length, 40-120 mm. Diameter, 2½-6 mm. size, at Madhosingh, 25-80×3-6 mm., the majority at or close to the lower limit; at Robertsganj, 40-75 × 2½-4 mm., except one worm which is 140 × 6 mm. Segments, to 156. Pigmentation unrecognizable behind

*Lacation of genital markings in* E. incommodus

| Locality | Markings on segment | | | | | | | | | | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No marking | 11—15 | 12—15 | 12—16 | 12—16, 18 | 13 | 13—14 | 13—15 | 13—16 | 13—16, 18 | 13—16, 18—19 | 13—16, 19 | 14 | 14—15 | 14—16 | 14—16,18 | 15—16 | |
| Ghakla | .. | 1 | .. | .. | .. | .. | 1 | 28 | 27 | 1 | .. | 1 | .. | 1 | 1 | .. | .. | | 56 |
| Ahraura | .. | .. | .. | .. | .. | .. | 1 | 21 | 8 | .. | .. | .. | .. | 1 | 1 | .. | .. | | 30 |
| Benares | | .. | 1 | 1 | .. | .. | .. | 1 | 43 | 2 | .. | .. | .. | 1 | 1 | .. | 1 | | 52 |
| Chunar | .. | .. | .. | 1 | .. | .. | 1 | 4 | 1 | .. | .. | .. | .. | .. | .. | .. | .. | | 7 |
| Madho Singh | 1 | .. | .. | .. | .. | .. | 12 | 243 | 20 | .. | .. | .. | .. | .. | 1 | .. | .. | | 276 |
| Zafarabad | .. | .. | .. | .. | .. | .. | .. | 25 | 54 | .. | .. | .. | .. | .. | 1 | .. | 1 | | 80 |
| Jaunpur | .. | .. | .. | .. | .. | .. | .. | 6 | 64 | 2 | .. | .. | .. | .. | 2 | .. | 1 | | 75 |
| Janghai | .. | .. | .. | 3 | .. | .. | .. | 6 | 140 | 2 | .. | .. | .. | 2 | 3 | .. | .. | | 156 |
| Jhusi | .. | .. | .. | 1 | | .. | .. | 18 | 101 | 2 | .. | .. | .. | .. | .. | .. | .. | | 122 |
| Allahabad-- | | | | | | | | | | | | | | | | | | | |
| (1) | 6 | 1 | 29 | 1 | .. | .. | .. | 26 | R | 2 | 2 | | .. | 3 | 4 | .. | 1 | | 75+ |
| (2) | .. | .. | 1 | .. | .. | .. | .. | 13 | 40 | .. | .. | | . | .. | .. | .. | .. | | 54 |
| (3) | 2 | .. | .. | .. | .. | 3 | 1 | 82 | 11 | .. | | .. | .. | 1 | .. | .. | .. | | 100 |

| | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ghoorpur | .. | .. | 2 | 2 | 1 | .. | .. | 85 | 94 | 8 | .. | .. | .. | | | .. | .. | 140 |
| Partabgarh | .. | .. | .. | 4 | .. | .. | .. | .. | 169 | 1 | .. | .. | .. | .. | | .. | .. | 174 |
| Sultanpur | .. | .. | .. | 1 | .. | .. | .. | 3 | 94 | 2 | 1 | 1 | .. | .. | 2 | .. | .. | 104 |
| Fyzabad | .. | .. | .. | 4 | 1 | .. | .. | .. | 87 | .. | .. | .. | .. | .. | .. | .. | .. | 92 |
| Fatepur | .. | .. | .. | 1 | .. | .. | .. | 11 | 81 | .. | .. | .. | .. | .. | .. | .. | .. | 93 |
| Rae Bareilly | .. | .. | .. | 8 | .. | .. | 12 | 8 | 207 | 3 | 1 | .. | .. | .. | .. | .. | 1 | 229 |
| Lucknow | 2 | .. | .. | .. | .. | .. | .. | 2 | 89 | .. | .. | .. | 2 | .. | 1 | .. | .. | 96 |
| Bara Banki | .. | .. | 3 | .. | .. | .. | 1 | 113 | 6 | .. | .. | .. | .. | 2 | .. | | .. | 125 |
| Fatehpur (4) | .. | .. | .. | .. | .. | .. | .. | 30 | 22 | .. | .. | .. | .. | .. | .. | .. | .. | 52 |
| Rewa | .. | .. | .. | .. | .. | .. | 1 | 10 | .. | .. | .. | .. | .. | .. | .. | .. | .. | 11 |
| Robertsganj | .. | .. | .. | .. | .. | .. | 2 | 198 | 24 | .. | .. | .. | 1 | .. | .. | .. | .. | 225 |
| Larhaoti | .. | .. | .. | .. | .. | .. | .. | 4 | 192 | .. | .. | .. | .. | 1 | 2 | .. | .. | 199 |
| Totals | 11 | 1 | 36 | 27 | 2 | 4 | 20 | 889 | 1,574 | 19 | 4 | 1 | 3 | 11 | 17 | 1 | 3 | 2,623+ |

(1) Near Jumna River
(2) Bund Road, Allengang.
(3) McPherson lake.
(4) Bara Banki District.
Remainder of specimens were not counted.
All Markings are lacking on left side (1 Janghai, 1 Rae Bareilly) or on right side (1 Zafarabad), of three specimens.
Occasional absence of one marking of a pair is not recorded.

the clitellum, usually very slight in the preclitellar dorsum but in three specimens (Allahabad, October) pigmentation is obvious anteriorly and in one of them about as dense as in *nicholsoni*. First dorsal pore on 10/11(1), 11/12 (61, but with a pore-like though apparently imperforate marking on 10/11 in several cases), 12/13 (9). The clitellum may be thinner or even totally lacking ventrally. In the latter case ventral boundaries are rather indefinite or very conspicuous and then sometimes sinuous.

Spermathecal pores always in median port of *BC*. Female pores both present. Genital markings postsetal, in region of *AB*, on some of xi-xvi as shown in the table below.

*Internal anatomy.*—Typhlosole begins in the region of xxii-xxiv. Ventral caeca and supra-intestinal glands as in table. Dorsal blood vessel uninterrupted (71), paired commissures or hearts always present in v-xiii, except that in one worm the left commissure of vii is represented only by a short dorsal stump with a rounded end. Commissures of iv were not found. Lateroparietal trunks are clearly visible, in juvenile specimens, back to the region of the supra-intestinal glands but in adults usually have been recognized only from *ca.* xix-xx anteriorly, as well as from the gland region posteriorly.

*Location of ventral caeca and supra-intestinal glands*

| Segments | Number of specimens from | | | | Segments | Number of specimens from | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | | 1 | 2 | 3 | 4 | 5 | 6 |
| 27—31 | .. | 1 | .. | .. | 62—64 | .. | .. | .. | 1 | .. | .. |
| 27—33 | 6 | .. | .. | .. | 62—65 | .. | .. | .. | 3 | .. | .. |
| 27—34 | .. | .. | 1 | .. | 63—66 | .. | .. | .. | 5 | .. | .. |
| 28—31 | .. | 4 | .. | .. | 63—67 | .. | 4 | .. | .. | .. | 1 |
| 28—32 | .. | 1 | .. | .. | 63—68 | .. | 1 | .. | .. | .. | .. |
| 28—33 | 7 | .. | .. | .. | 64—67 | .. | .. | .. | 1 | .. | .. |
| 28—34 | 22 | .. | .. | .. | 64—69 | .. | 1 | .. | .. | .. | .. |
| 28—35 | 3 | .. | .. | .. | 65—68 | .. | .. | .. | .. | .. | 1 |
| 29—31 | .. | 1 | .. | .. | 66—70 | 4 | .. | .. | .. | .. | 1 |
| 29—32 | .. | 1 | .. | .. | 66—71 | .. | .. | .. | .. | .. | 1 |
| 29—33 | 1 | .. | .. | .. | 67—70 | 1 | .. | .. | .. | .. | 1 |
| 29—35 | .. | .. | .. | 1 | 67—71 | 3 | .. | .. | .. | .. | .. |
| 30—32 | .. | 1 | .. | .. | 67—72 | 1 | .. | .. | .. | 1 | 1 |
| | | | | | 68—71 | 3 | .. | .. | .. | 1 | 3 |
| | | | | | 68—72 | 15 | .. | 1 | .. | .. | 4 |
| | | | | | 68 73 | 4 | .. | .. | .. | .. | .. |
| | | | | | 69—72 | 1 | .. | .. | .. | 3* | 2 |
| | | | | | 69—73 | 7 | .. | .. | .. | .. | 5 |
| | | | | | 69—74 | 2 | .. | .. | .. | .. | .. |
| | | | | | 70—73 | 4 | .. | .. | .. | 5 | .. |
| | | | | | 70—74 | 7 | .. | .. | .. | .. | 5 |
| | | | | | 71—74 | 1 | .. | .. | .. | 1 | .. |
| | | | | | 71—75 | .. | .. | .. | .. | .. | 1 |
| | | | | | 72—75 | .. | .. | .. | .. | .. | 2 |

1 Allahabad and Naini. 2. Rewa. 3. Nowgong.
4. Bara Banki. 5. Lakhaoti. 6. Previous records.

* In addition, one specimen with a single pair of rudimentary glands in lxviii.

Glands are in lxiii-lxvii (1 Saharanpur), lxx-lxxiii (1 Patna).

All of the Bara Banki specimens listed above are small and have genital markings on xiii-xv only.

Seminal vesicles of ix always well developed. Posterior vesicles usually reach back to 13/14, occasionally pushing 13/14 in to contact with 14/15, but may extend into xiv (11), xv (7), or even xvi (3).

*Life history.*—One postsexual aclitellate worm (March, Patna) has been found. Clitellar segments are marked by a slight brownish discoloration quite distinct from normal brown pigmentation and genital markings are quite unrecognizable. Spermathecal ampullae and seminal vesicles are shrunken and brownish. Prostates are also of the same brown color. Each penisetal battery has only one or two setae.

*Abnormality.*—(No. 1) An extra spermatheca on the right side with pore on 6/7 (No. 2) A half segment intercalated between xvi-xvii on the left side bears the male porophore. Left genital marking of xiv lacking, right marking of xvi doubled anteroposteriorly. (No. 3) An extra male porophore on the left side of xviii is associated with a prostate and a battery of penial setae (but no bulbus). (No. 4) Spermathecal pore on 6/7, female pore on xiii, male porophore on xvi, on the left side. Genital markings on left sides of xiv-xv, right sides of xiv-xvi. Septum 7/8 present on left side only. Intestinal origin in xiv, last heart in xii on left side. Testes and male funnels of left side in ix, x, xi, seminal vesicles in viii, and xii. Left ovary in xii. Left male terminalia in xvi. The gizzard is symmetrical. (No. 5) Genital markings on xiii-xv. Male porophores on xvi and xvii. Prostates and penial setae also present in xvi but male deferent ducts continued into xvii as usual. (No. 6) Left male porophore and terminalia lacking. Left male ducts become filamentous and translucent in xvi. (No. 7 and 8) Female pore on xiii, male pore on xvi on right side. Seminal vesicle in viii, testes and male funnels in ix and x, rudimentary seminal vesicle in xi, ovary in xii, heart of xiii lacking, male terminalia in xvi, on the right side.

*Remarks.*—The identification of some Lucknow specimens (Bahl, 1927, p. 485) was questioned in the revision of the Indian species (Gates, 1938, p. 118). The worms now have been examined. The identification was correct but the supposed penes are merely unusually protuberant margins of the fissures on the male porophores.

*E. incommodus* now appears to be the only holandric species that has acquired pigment.

The slight variation in location of supra-intestinal glands is especially noteworthy in view of the distribution. The range extends from Calcutta at least through the Gangetic plain. Extensions along river valleys into the Deccan, and across the Aravalli divide into the Indus valley may be due to migration or to transportation by man (as at Rawalpindi).

### **Eutyphoeus quadripapillatus** Michaelsen 1907

Chhitauni (Gorakhpur district, U. P.), October, 1-23-40. Cedric Shaw.

*External characteristics.*—Length, 88-100 mm. Diameter, 3-4 mm. Segments, 152-165. Unpigmented. First dorsal pore on 10/11 (4), 11/12 (48), 12/13 (4). Clitellum, of a faint yellowish or yellow brown, extends into xiii and xvii, occasionally (18) reaching 17/18, lacking in *BB* on xvii and thinner in *BB* on xiii-xvi.

Spermathecal pores in *AB*. Female pores both present (51, unrecognizable on the others). Male porophores may be perfectly flat discs or immediate margins of the fissures may be slightly protuberant, or the whole disc may be raised in a rather conical fashion.

Genital markings postsetal, in *AB*, or with centers at or lateral to *B* but reaching mesially to or nearly to *A*, on xiii-xiv (58), xiii-xv (1), xiii (3), lacking on 1 juvenile and 1 clitellate specimens.

*Internal anatomy.*—Ventral intestinal caeca and supra-intestinal glands as shown in the table. Dorsal blood vessel always (50 specimens) uninterrupted, with commissures and hearts in v-xiii, commissures occasionally (2) recognizable in iv (2). Lateroparietal trunks in one specimen are distended with blood and visible all the way back to the posterior end of the body.

*Location of ventral caeca and supra-intestinal glands*

| Segments | Number of specimens | Segments | Number of specimens |
|---|---|---|---|
| 27—30 | 1 | 63—66 | 2 |
| 27—31 | 7 | 64—67 | 19 |
| 27—32 | 23 | 65—67 | 1 |
| 27—33 | 4 | 65—68 | 22 |
| 27—35 | 1 | 66—68 | 2 |
| 28—31 | 2 | 66—69 | 3 |
| 28—32 | 7 | 67—70 | 1 |
| 28—33 | 4 | | |
| 29—32 | 1 | | |

Seminal vesicles of xii usually reach back at least into xxvi, once to lxxiii. Posterior end portions (2 specimens) are softened as if disintegrating. Although the vesicles in one worm reach only into xvi and show no indications of disintegration at their rounded posterior ends, there are, in a number of subsequent segments, septally constricted masses of tissue that seem quite different from the easily fragmented aggregations of coelomic corpuscles sometimes filling coelomic cavities between gut and parietes. Vesicles of one worm are under the gut behind xiv and unrecognizable until the intestine is rolled over to one side. Vesicles are confined to xii (no fragments recognized posteriorly) in one worm with spermatozoal iridescence in the spermathecae.

*Remarks.*—The ventral follicles of xvii are retained throughout life. Ability to produce normally shaped setal shafts is lost in some juvenile stage, the follicles of sexual animals containing numerous small spheroids and ovoids or larger bodies of more irregularly odd shapes (Gates, 1947). Appearance of follicle contents usually is such as to suggest discontinuous deposition of setal material. An undischarged sigmoid seta was once found in an adult (Gates, 1938, P. 108) and larger bodies may

sometimes look as if they had been irregularly eroded chemically. No evidence of fibrillation, as at ectal ends of penial shafts in macerated worms of other species, has been observed. Whether continued and disorderly secretion, or solution of undischarged shafts, is involved, the condition prevailing in this species seems to represent a stage in elimination of penisetal follicles, a process which has been completed in other species. As formation of penial instead of sigmoid setae is induced by growing prostate glands (p. 108), the disordered functioning of the follicles in *quadripapillatus* results from modification in the prostatic induction capacity. This may be brought about by the mutation "apenisetal" already suggested on another page. Penetrance at an earlier stage, and more effectively, would then permit abortion of the follicles before maturity is attained, as in *quinquepertitus*.

### **Eutyphoeus gammiei** (Beddard) 1888

Lokra (Balipara Frontier Tract, Assam), 8. xi. 1939, 0-1-0. Dr. S. L. Hora (Indian Museum.)

*External characteristics.*—First dorsal pore on 10/11. Spermathecal pores in median half of *BC*. The vestibulum is almost as deep in *AA* as laterally so that the worm can be characterized as definitely univestibulate. The genital marking, in *BB*, on 20/21, shows no indications of double origin.

*Internal anatomy.*—First recognizable ventral caecum in xl. Supra-intestinal glands in cxxxiv-cxl. Penial setae, including reserves, usually with chevron markings. An exceptional seta, with simple tip and ornamentation of closely crowded irregular circles of fine spines, has a single crack in the region where the splits of the chevron markings usually are located.

*Remarks.*—Although the genital marking is quite obvious and distinctly demarcated, no parietal modification is recognizable aside from the epidermal thickening. Any caeca anterior to xl might well have been unrecognizable because of maceration of gut wall forward nearly to xv (as in many preserved specimens of this as well as other genera).

Some thirty or so specimens, from a range larger than that of any Burmese species though less extensive than those of *incommodus* and *waltoni*, are all that have been available for study. They show that supra-intestinal glands are in 4-6 consecutive segments of xcviii-cxl. This variation in location is about twice that of some of the Burmese species and about four times that of *incommodus* and *waltoni*.

### **Eutyphoeus orientalis** (Beddard) 1883

Chhitauni (Gorakhpur district, U. P.), October, 0-1-1. Cedric Shaw.

*External characteristics.*—Pigmentation dense. Genital markings on ix (Chhitauni), xv (Chhitauni and 4 Dehra Dun), xvi (Chhitauni and 5 Dehra Dun), 18/19 (Chhitauni and 5 Dehra Dun), 19/20 (4 Dehra Dun), 20/21 (1 Dehra Dun).

*Internal anatomy.*—Supra-intestinal glands are in lxxxvi-xc (2 Dehra Dun), lxxxvii-xci (2 Dehra Dun), lxxxviii-xcii (1 Dehra Dun), xc-xcvi

Penisetal tips are usually softened but on one functional and one reserve seta are spoon-shaped. Ornamentation is readily recognizable under ordinary high power.

*Remarks.*—This species is distinguishable at present from *waltoni* only by the penes which are annular rather than elongate, presence of genital markings on xvi, and a more posterior location of the supra-intestinal glands—in lxxxvi-xcvi instead of lxxviii-lxxxvi. *E. orientalis* has been found hitherto only in a north-eastern part of the *waltoni* range and at Dehra Dun to which it may have been transported accidentally by man. Although the geographical range now appears to be so much smaller than that of *waltoni*, variation in location of supra-intestinal glands is of the same order in both species.

## **Eutyphoeus waltoni** Michaelsen 1907

*External characteristics.*—Length, to 180 mm. Diameter, to 8 mm. All worms larger than 140×8 mm. (strongly contracted at preservation) were obtained from compost heaps. Pigmentation dense. Genital markings are located as shown in the table.

*Location of genital markings*

| Segment | Number of specimens from | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| 8 | 1 | .. | .. | .. | .. | .. | 2 | .. | |
| 9* | 496 | 23 | 51 | 35 | 43 | 45 | 38 | 19 | |
| 10 | 6 | .. | 5 | 1 | 1 | 1 | 1 | 1 | |
| 13 | 1 | .. | .. | .. | .. | 2 | 2 | 1 | |
| 14 | 185 | 10 | 25 | 30 | 29 | 39 | 35 | 9 | |
| 15* | 496 | 25 | 50 | 36 | 46 | 48 | 37 | 15 | |
| 18/19* | 497 | 25 | 50 | 34 | 43 | 49 | 39 | 19 | |
| 19/20 | 99 | 3 | 19 | 4 | .. | 20 | 17 | 5 | |
| 20/21 | 14 | .. | 2 | .. | .. | 2 | 1 | 1 | |
| 21/22 | 3 | .. | .. | .. | .. | 1 | .. | .. | |
| | 500 | 25 | 51 | 36 | 46 | 49 | 40 | 19 | Number of specimens studied. |

1 Allahabad and Naini. 2 Gorakhpur and Chhitauni.
3 Chunar. 4 Rae Bareily.
5 Rewa. 6 Lucknow.
7 Fatehpur. 8 Benares.

Postclitellar genital markings are in sequence, if a marking is present on 21/22 markings are also present on 18/19-20/21.

*Two of these three pairs of markings are present in every worm of the Allahabad series.

Markings are entirely lacking on one worm of the Fatehpur series.

Markings occasionally are present on xi-xii and 14/15-15/16 : on ix-xiii, 14/15-15/16 18/19 (1 Udaipur), ix-xv (1 Sultanpur).

A perfectly developed genital marking, with distinctly demarcated rim and central portion, is present on xvi ,or 16/17 ,of one worm from Rae Bareily.

*Internal anatomy.*—Locations of supra-intestinal glands of a few specimens are shown in the table.

*Location of supra-intestinal glands*

| Segments | Number of specimens from | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | |
| 76—80 | 1 | .. | .. | | |
| 77—79 | | 1 | .. | | |
| 77—80 | 1 | .. | | | |
| 77—81 | 1 | .. | | .. | |
| 78—81 | 2 | 1 | .. | 1 | |
| 78—82 | 1 | .. | .. | .. | |
| 79—82 | 2 | 3 | 2 | 2 | |
| 79—83 | 4 | 1 | .. | .. | (Bahl and Lal, 1933.) |
| 80—83 | 1 | 2 | 1 | 3 | |
| 80—84 | .. | 1 | .. | 4 | (Also, Thapar, 1934.) |
| 81—84 | 2 | 3 | .. | 1 | |
| 81—85 | 1 | | .. | 3 | |
| 82—86 | .. | .. | .. | 1 | |

1 Allahabad. 2 Chittauni. 3 Fyzabad.
4 Previous records except for those of Bahl and Thapar.

*Abnormality.*—(No. 1) Left male terminalia lacking. Left male duct dwindles to a thread in xvii without entering the parietes. (No. 2) Spermathecal pores on 7/8, 8/9, L9/10. No genital markings on ix-x. Four spermathecae normal, the left posterior represented only by a muscular duct which tapers entally to a pointed end. (No. 3) Paired female pores. Genital markings on ix, 17/18, 18/19. Vestibula in xvi. A short but unusually stout penis (?) with distal aperture ends blindly, without a vestibulum, in parietes, on left side of 15/16. (No. 4) Left spermatheca lacking. (No. 5) A small penis present on xvi on left side, in a rudimentary vestibulum. Ventral setae of left side of xvi also penial. Left male duct continued normally into xvii.

### **Eutyphoeus nicholsoni** (Beddard) 1901

*Eutyphoeus gigas*, Bahl, 1927, Quart. J. Mic. Sci. 71, pl. 485.

*External characteristics.*—Size, to 270×10 mm all larger than 170×8 mm (preserved contracted as usual) obtained from compost heaps (manure and leaves) and when relaxed 300-450 mm long. Pigmentation dense. Female pores present on both sides, only five specimens.

Genital markings, except as noted below, are between equators of xv and xvi. Markings are transversely elliptical and obviously separated at mV in most Lucknow specimens and all from Fatehpur, Bara Banki, Benares, Moghul Serai, Chunar and Ahraura. In some worms from the latter localities markings may even be widely separated and restricted to *AC*. Markings are united at mV in all Sohagi specimens. In Chakia and Robertsganj series respectively, markings are obviously separate (58 and 42), almost in contact (5 and 6), united but with deep incisions of anterior and posterior margins at mV (2 and 4). Deviations from the normal pattern (of one or two markings on 15/16) were found occasionally. Right marking (4 specimens), left marking (1), both markings (1) lacking. An extra marking on left side (12), or right side (6), or right and left sides (6) of 14/15. An extra marking on left side (3), right side (4), or right and left sides (3) of 18/19. An extra marking on left side of 18/19 but left marking of 15/16 lacking (1). A marking on 18/19 is present in three of twenty Fyzabad worms.

*Internal anatomy.*—Supra-intestinal glands as in table. The dorsal blood vessel ends with or just in front of commissures of vii (76) or apparently, with a right (2) or left (1) or right and left (1) commissures of vi. These supposed commissures could not be traced in any of those four specimens to the ventral trunk. Pharyngeal nephridia, in relaxed specimens, quite obviously are aggregated into a zig-zag-looped cord on the parietes on each side.

*Location of supra-intestinal glands*

| Segments | Number of specimens from | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| 80—83 | 1 | | | | | |
| 80—84 | 6 | | | | | |
| 80—85 | 3 | 4 | | | | |
| 81—84 | 2 | | | | | |
| 81—85 | 19 | 7 | | | | |
| 81—86 | 3 | | | | | |
| 82—86 | 12 | 6 | | 1 | | 1 |
| 83—86 | 2 | | 2 | | | |
| 83—87 | 4 | 3 | 3 | | | 2 |
| 84—87 | | | 1 | | | 1 |
| 84—88 | | 2 | | | 1 | 4 |
| 84—89 | | | | | 1 | 1 |
| 85—88 | | | | | | 1 |
| 85—89 | | | 1 | | | 1 |

1 Allahabad. 2 Nowgong. 3 Lucknow.
4 Rewa. 5 Robertsgang. 6 Previous records, and includes Thapar's Lucknow record (83-87) and Beddard's Calcutta record (84-88).

Seminal chambers 5-11, rather digitiform but usually shortly looped, slightly zigzagged or distally branched, usually aggregated into a single fan-shaped cluster which has 2-5 separate openings into the spermathecal duct. One or two of the chambers occasionally are completely separated from the cluster.

*Abnormality.*—(No. 1) Genital markings, vestibula and penes lacking. Clitellum continued to 17/18 ventrally as well as dorsally Ventral setae and apertures of their follicles unrecognizable on xvii. Left male duct splits into two widely separated portions in xiv which unite in xvi and then in xvii dwindle to a filament that does not enter the parietes. Right male duct thickened in xv-xvii and in xviii, without entering the parietes, becomes attached to follicles of ventral setae. Rudimentary prostates (?) without ducts and penisetal follicles are present in xvii but do not enter the parietes! Spermatozoal iridescence in seminal chambers of the spermathecae shows that copulation had taken place. (No. 2) Genital marking, vestibulum, setae *a-d* of xvii-xix and male terminalia of left side lacking. Left male duct dwindles to a translucent cord in region of 15/16 and shortly disappears.

*Remarks.*—The identification of some Lucknow specimens (Bahl, 1927, p. 485) was questioned in the revision of the Indian species (Gates, 1938, p. 118). The worms in question now have been examined and quite obviously are referrable to *nicholsoni.*

The variation in location of supra-intestinal glands (Table) is slight and seems especially small in a range about as large as that of *incommodus* (after excluding extensions presumably due to accidental transportation). Midventral union of originally paired genital markings appears to be well under way and a uniformity of exial location comparable to that of *E. foveatus* has been achieved.

## PHYLOGENY OF INDIAN SPECIES

Holandric species are unknown from the almost unexplored region between the Burmese hills of the Arakan Yomas and the Gangetic Valley at longitude of Calcutta. It is necessary then, at present, to assume that the proto-eutyphoeus range extended across the Indo-Burmese mountain wall well towards or even into the Gangetic plain. There the proto-eutyphoeus became *incommodus* by acquisition of brown pigment, restriction of genital markings (paired) to intraclitellar and postsetal locations (on xiii-xvi) in region of *AB*, restriction of ventral caeca to xxvii-xxxv and of supra-intestinal glands to 4-6 of segments lxii-lxxv, and development of numerous diverticula on the spermathecae. The latter condition may well have been brought about by eliminating the stalks of a pair of polyloculate diverticula so that each seminal chamber now has its own opening directly into the spermathecal duct. This change could have been accomplished at a single step by a mutation which may be called "stalkless$_2$".

*E. quadripapillatus* apparently can be derived almost directly from *incommodus* by elimination of the genital markings in xv-xvi, inhibition of formation of penial setae, restriction of ventral caeca to xxvii-xxxii and of supra-intestinal glands to lxii-lxx. However, since segregation of the two species the spermathecal pores have migrated somewhat laterally in *incommodus* though retained in *quadripapillatus* in *AB*, the primitive position.

*E. annandalei* Michaelsen 1907, from the Kumaon region just west of Nepal, is known only from the very briefly characterized holotype,

The species seems to be distinguishable from *incommodus* by the primitive bidiverticulate spermathecae, absence of genital markings on xv-xvi, and location of the spermathecal pores. As the species cannot be derived directly from *incommodus* it must have evolved from the proto- eutyphoeus before establishment of stalkless$_2$. Along with acquisition of further restrictions on the genital markings, the spermathecal pores have been moved even further laterally than in *incommodus*.

A trans-Arakan equivalent of the metandric *levis* group in eastern Burma is present in the Himalayas through Nepal into Kumaon. The comparison is suggested by the absence of pigment, the uninterrupted dorsal blood vessel, the genital marking glands and especially by the lateral intestinal caeca. The latter are in xxiv, the segment in which they are now developing in *annulatus*, or possibly in *nainianus* Michaelsen 1907, in xxiii. Genital markings show some of the *levis* group restrictions, being in part postsetal in *AB*, on x in *lippus* Gates 1934, on xiv-xv in *nepalensis* Michaelsen 1907, on xvi in *nainianus*, though the intraclitellar locations are also shared by species of the *incommodus* group. Each of the Himalayan species, as in the *levis* group, can be derived from the proto-eutyphoeus by establishment of the metandric mutation. Additionally, stalkless$_2$ has been involved in the phylogeny of *nainianus* and *nepalensis*.

*E. pharpingianus* Michaelsen 1907 is of uncertain status but if it does belong in *nepalensis* group persistence of male funnels in x would seem to indicate, as in the case of *levis*, that the least specialized species insofar as lateral caeca are concerned is of most recent origin.

An Indian equivalent of the *constrictus* group in central Burma between the Chindwin-Irrawaddy and Irrawaddy-Sittang axes, must be sought among species known only from their types, sometimes unique or even juvenile. A *constrictus* stage with uninterrupted dorsal trunk is shown by *assamensis* Stephenson 1926, *festivus* Gates 1938 (*comillahnus* and *scutarius* Michaelsen 1907?), a *peguanus* stage of abortion possibly by *turaensis* Stephenson, 1920 (*comillahnus* and *scutarius*?), a *plenus* stage of foreshortening by *aborianus* Stephenson 1914 and *callosus* Gates 1938. The last two have lost the right female pore and have posteriorly united spermathecal diverticula (stalkless$_1$) as in the Burmese *ferinus*, but in *festivus* spermathecal diverticula may be as yet only posteriorly directed. Uncertainty as to important taxonomic characters of each species contra-indicates further discussion except to note that the range of these forms extends from Chittangong (*comillahnus* and *scutarius*) north through Cachar (*assamensis*) to the Khasi (*callosus*, *festivus*) and Garo Hills (*turaensis*) as well as to the Abor country (*aborianus*) of the far eastern Himalayas.

*E. gammiei* (Beddard), 1888, has four specializations of the *foveatus*—*gigas* groups; metandry, foreshortening, penisetal batteries, single female pore, and may prove to have the fifth, pigment. Invagination of the fissure-bearing regions and absence of lateral intestinal caeca suggest comparison with the *foveatus* group. Indeed, the vestibulum, in a considerable part at least of the range, is almost exactly the same as in *cochlearis* and *excavatus*. The genital marking system is less

restricted than in the *foveatus* group for little evidence of stabilization either as to number or axial location has been recognized and median union of paired markings is still under way. The protofoveatus ancestor, in its westward migration, did however acquire one specialization lacking in the *foveatus* group and rare in other Burmese groups, as spermathecal diverticula are either approximated posteriorly or actually united (stalk $less_1$). Other peculiarities are an increase in number of ventral caeca (xxv-c) and posterior shifting of the supra-intestinal glands, here in 5-6 of segments xcviii-cxxx. The *gammiei* range extends from Chittagong through Cachar into the Garo Hills and across the Brahmaputra plains into the Himalayas and there from Darjiling to the Abor country. The southern part of this range is at the *cochlearis* latitude. Much more material, in much better condition than in the past, is needed to show whether *gammiei* is a single species. *E. kempi* Stephenson 1914, from the Abor country, apparently is distinguished from *gammiei*, with which it had been united, by the elongate penes (*foveatus* type) and the stalkless, condition.

The rest of the Indian species, with nine specializations, metandry, maximal foreshortening, penisetal batteries, single female pore, pigment, coelomic glands associated with genital markings, a ventral testis sac, vestibula and definite penes, do lack lateral intestinal caeca. Penes, with the exception of *E. orientalis*, are elongate (as in *foveatus*) and at the terminal stage of evolutionary development of this organ. *E. waltoni*, like *orientalis*, has retained the primitive pairing of genital markings and still shows considerable variation in their number and axial location, though spermathecal pores have migrated well laterally. *E. nicholsoni* has reduced the markings to a single pair, on 15/16, but median union has not yet been completed throughout the species. One additional specialization in each species is shown by the spermathecae which are in one stage or another of the $stalkless_1$ development. Coincidence of the ranges with that of *incommodus*, which helped to convince Stephenson (1923, p. 428) that the Gangetic plain "could be looked on as the proper range of the genus" does at first seem to require origin of the *orientalis* group *in situ*. Indeed about all that is required to derive *waltoni* from *orientalis* is to elongate the annular penes of the latter. Nevertheless, in all the *Eutyphoeus* domain there is nowhere else such intraspecific uniformity throughout such large ranges (see for instance data on supra-intestinal glands locations). Nowhere else is there so great difference between holandric and metandric species. Further light on this, as well perhaps as other peculiar problems of the Gangetic valley, is anticipated from the area of unknown fauna east of Calcutta.

## DISCUSSION

### RELATIONSHIPS AND PHYLOGENY OF THE GENUS *Eutyphoeus*

The genus *Scolioscolides* Gates 1937, is remarkably like *Eutyphoeus* morphologically. Indeed, about all that is required to derive the former from the latter is transfer of capacity for developing prostates from xvii into xviii and in the proto-eutyphoeus stage. Such a transfer can be brought about, according to the evidence provided by aberrant individuals

in species of several genera by a single step. The prostates, from a more posterior location in *Scolioscolides*, exert their attractive influence on the male deferent ducts before the latter have passed through xviii and so effectively that they grow posteriorly straight toward and then into those organs. Further growth of the prostates then carries the level of junction considerably away from the body wall so that the male duct in the adult joins the ental end of the duct portion of the prostate.

*S. bergtheili* (Michaelsen) 1907, the single species found as yet, is known only from the type locality in the Darjiling district of the Himalayas. In this species the prostates not only have lost the capacity to induce production of penial setae but seem to have acquired the ability to inhibit setal production in the adjacent ventral follicles which presumably atrophy early in ontogenetic development leaving no evidence of their previous existence. Additionally in this species, the typhlosole has been reduced to a low ridge, ventral caeca have been restricted to xxiv-xxviii, the supra-intestinal glands to two consecutive segments (in region of lix-lxi), and originally paired genital markings (possibly now restricted to presetal locations on xi-xiii and xx-xxi) have been united at mV Lateral intestinal caeca have been developed, as in the *nepalensis* group of Himalayan *Eutyphoeus* species, but further anteriorly, in segment xxi. Intrageneric evolutionary developments excepting reduction of the typhlosole appear then to be of the same general nature as in *Eutyphoeus*, so far as can be estimated from our present knowledge of but one species. One of those developments may be attributable to the mutation apenisetal already postulated in the phylogeny of several *Eutyphoeus* species.

*Bahlia* Gates 1945, is more like *Eutyphoeus* morphologically than any other genus except *Scolioscolides* and has essentially the same male terminalia, at the same axial location, as in the proto-eutyphoeus, in addition to lateral typhlosoles. Derivation from the proto-eutyphoeus is however impossible. Since segregation of these two genera ventral intestinal caeca have been acquired, a pair of spermathecae opening on 8/9 has been eliminated, septa 5/6-7/8 have been aborted, and an extra diverticulum has been acquired on each spermatheca, in the *Eutyphoeus* line. Meanwhile spermathecae of viii were lost in the *Bahlia* line. Reduction in number of spermathecae may have taken place, in both lines, at about the same time (or subsequently?) a posterior pair of prostates was eliminated. With disappearance of the latter organs, the male ducts which previously had opened on xviii could be attracted towards the prostates of xvii. This attraction however becomes effective ontogenetically only after the ducts have nearly passed through xvii in their posterior growth so that they are now compelled to turn and grow down into the parietes behind the prostate gland.

The point on the evolutionary tree at which bifurcation of *Bahlia* and *Eutyphoeus* is to be placed, now seems to depend on structures barely mentioned in older taxonomic characterizations and usually ignored in phylogenetic theorizing. These calciferous glands are in x and xi in *Bahlia* but only in xi in *Eutyphoeus*. In preference to postulating addition of a pair of such highly developed structurs in *Bahlia*, and

rather than push segregation into a still more remote past before the organs had been closed off from the oesophageal lumen, it is assumed that the common ancestor was quadriglandular at least, and that one pair, in x, was eliminated in the *Eutyphoeus* branch. *Bahlia*, in this as well as other respects, is more like the common ancestral form than *Eutyphoeus* is.

*B. albida* Gates 1945, the single species, is known only from a very few individuals obtained in the Allahabad sector of the Gangetic plain and the immediately adjacent portion of the Deccan. The species must have lost the anterior testes long ago (possibly a generic characteristic?) as male funnels of x are lacking. Ventral setae of the spermathecal segment are enlarged and modified so that the shape of tip and ornamentation is much the same as in the copulatory setae developed in certain species of *Calebiella* Gates 1945, *Lennogaster* Gates, 1939, *Octochaetoides* Michaelsen 1922, and *Pellogaster* Gates, 1939. In spite of the common evolutionary potentiality demonstrated by those specialized setae, all of these genera, like *Hoplochaetella* Michaelsen 1900, and most other Indian octochaetines, must be placed in collateral lines.

*Ramiella* Stephenson 1922, can be associated more closely to the *Bahlia-Eutyphoeus* line but only through a form so primitive as to be able to give rise to all species of that genus. Such a proto-ramiella had a gizzard in v, an intestinal origin in xiv or even anteriorly, no calciferous glands or typhlosoles, the last pair of hearts in xii, paired male, female, prostatic and spermathecal pores (on 7/8-8/9) in region of *AB*, male pores on xviii, two pairs of prostates opening to the exterior on xvii and xix, and four pairs of seminal vesicles in ix-xii. Prostates had not acquired ability to induce modification of setal form and all ventral follicles of xvii-xix may have retained sigmoid setae throughout life. To give rise to the *Bahlia-Eutyphoeus* line three changes were necessary, transfer of the gizzard behind 5/6 into vi, elongation of the oesophagus to push intestinal origin back into xv, development of calciferous glands. The latter process can be visualized from conditions still prevailing today in certain species of *Pellogaster* and *Ramiella* as follows. A median fold grew out from the floor of the gut in the region of x-xii or xiii and after becoming more or less lamelliform was divided at its free margin into two parts as the intestinal typhlosole of certain species of *Octochaetoides* is today. Each secondary lamella, falling over laterally, in effect closed off ventrolateral portions of the oesophageal lumen from the ingesta. Thus protected against erosion by passing soil particles, transverse ridges containing the calciferous cells could become much thinner and their number much greater. Union of median margins of such thin lamellae with the enlarged adjacent half of the ventral typhlosole and of the latter to the gut wall at regions of septal insertions would then provide the required intramural, half-bean shaped calciferous glands opening into the central lumen through a dorsal slit. Only two pairs of glands are now needed in the common ancestor though three or even four in x-xii or xiii, may have been present (and retained in some as yet undiscovered types?). Rather than postulate independent acquisition of a long series of structures—intestinal typhlosole, lateral intestinal

typhlosoles, supra-intestinal glands at the posterior end of the median typhlosole, hearts in xiii—segregation of the two lines is placed after the development of those organs.

The proto-ramiella range may well have extended over most of India south of the Himalayas, possibly also well into Burma, but the various evolutionary changes just outlined presumably took place in the Gangetic valley or the adjacent Deccan. There at any rate the few subsequent modifications were made to give *Bahlia* while in some part of the region now occupied by the Indo-Burma mountain wall the longer series of changes resulted in the proto-eutyphoeus.

### Phylogency of the oriental Octochaetinae

The proto-ramiella also is primitive enough to provide an ancestral stage for the remainder of the Indian octochaetines with the single exception of *Howascolex*. Near universality of intestinal origin in xv or posteriorly in the group requires early extension of the oesophagus through xiv. Subsequently two major lines seem to be required by the gizzards. In the *Ramiella* branch of the one-gizzard line that organ has since been transferred into segment vi in all but one species, the oesophagus has been eztended additionally through xv in at least one species, and some have acquired an oesophageal or intestinal typhlosole or both. Minor evolutionary developments shown by extant species of *Ramiella* are : dislocation of spermathecal pores laterally or posteriorly, ontogenetic elimination of the ventral setae in the spermathecal segments, development of the rolled-tube type of penial setae.

The gizzard remained in v in another branch of the same line but the oesophagus was extended still further posteriorly. In the *Octochaetoides* descent, where all prostates (4) and spermathecae (4) were retained, oesophageal elongation put the intestinal origin back into xvii.

Subsequent development of calciferous glands was at two different levels. The two calciferous pockets are evaginated asymmetrically in one group and are constricted off so completely as to leave a short, slender stalk opening into gut at region of insertion of septum 15/16. In the excretory system the last remaining nephridial funnels have been lost, a development which now appears to be unique in the Octochaetinae. One species has become metandric and so recently that the male funnels are still present in x. Several species have acquired hearts in xiii. Two or three pairs of seminal vesicles have been eliminated, in ix-x, x-xi, or ix-xi. Species are found throughout much of peninsular India but little is known of their individual distribution or variation. Those with calciferous glands (of unknown structure) associated with 14/15 almost certainly should be generically separated and such information as is now available suggests a possibility that one other group of species may have to be split off.

In the far south of India, in forms that had also retained the gizzard in v, prostates long age were reduced to two, in xviii, where they acquired ability to attract posteriorly growing male deferent ducts into

an early ontogenetic junction. Seminal vesicles in ix-x were also eliminated, but all four spermathecae, as well as all testes, have been retained. *Travoscolides* Gates 1940 alone has retained the four-paired arrangement (lumbricin) of the setae and a short oesophagus (intestinal origin either in xv or xvi). Reniform calciferous glands, four pairs in xi-xiii, are so constricted off as to open through stalks from ventral poles into the oesophagus close to mV An early stage in the development of this type of gland, in which calciferous pockets are still only slight bulges from floor of gut, apparently is shown by species of *Pellogaster* in the two-gizzard line. A typhlosole has been developed, and hearts have been added in xiii. In the excretory system, the nephridial anlage from xiv posteriorly apparently have been split, in an embryonic stage, longitudinally and each of the 20-24 stomate derivatives, instead of boring through the parietes to an external nephropore, now grows on towards the intestine into which they all open through two postseptal canals *via* a single intratyphlosolar excretory duct. Nephridia of ii-iv have disappeared, those of v-xiii have become tufted with loss of funnels and acquired openings into the pharynx or oesophagus.

Number of setae has been increased in the rest of this group. In *Spenceriella* (Indian section only), the gizzard has been transferred to vi, the oesophagus has been extended into xvi but no typhlosole or calciferous glands have been developed. The setae are twelve per segment in two of the forms, the two extra on each side lateral to *D* and all in regular longitudinal ranks. In another form the number has been increased to 14 to 17 in the posterior segments where only *a* and *b* setae are in regular ranks. Regularity of ranks is said to be completely lacking in another species where the number is now 50 or so per segment. The other two genera have extended the oesophagus into xix, but, like *Spenceriella*, have not yet acquired hearts in xiii. In *Priodochaeta* Gates 1940, with 30-40 setae per segment, the typhlosole is still rudimentary but three pairs of out-pocketed calciferous glands, in xiv-xvi, have been acquired. Each gland is still constricted off only dorsally and ventrally so as to open widely at hilus by a vertical slit about as high as the oesophageal lumen. In *Priodoscolex* Gates 1940, which now has 75-80 setae per segment and a more definitely lamelliform typhlosole, large reniform calciferous glands are evaginated in xiv-xvii. These glands are constricted off so that the stalks of two glands of a side in a segment unite to open into the gut at mL by a single minute aperture (secondary division of a single gland?). In the circulatory system there is a subneural trunk, a vessel that is lacking in all other Indian Octochaetinae. Nephridial anlage in the last few segments apparently have been split longitudinally so as to provide 20-24 funnelled tubes each of which may still have its own epidermal nephropore. The gizzard, as in *Priodochaeta* has been considerably enlarged and is now three mm long but there has been no transgression of limits of segment v. Body length in these two genera is from 230 to 330 mm but is much shorter in other genera with male pores on xviii. The ranges appear to be limited in this line. *Spenceriella* is known only from the Palni Hills, *Priodochaeta* from the Nilgiris, *Priodoscolex* from Mysore, and *Travoscolides* from Cochin and Travancore.

In the rest of the one-gizzard line that organ has been transferred into vi, intestinal origin into xv or posteriorly and a typhlosole has been developed. In the evolution of *Calebiella* four pairs of reniform calciferous glands have been evaginated in x-xiii but are still incompletely constricted off so as to open directly through the hilus into the gut at or near mL. The typhlosole has been enlarged and become deeply bifid ventrally and at its hind end supraintestinal glands of a simple sort may have been developed. Seminal vesicles of x-xi have been eliminated in the only species. A pair of hearts has been added, in xiii.

In the evolution of *Hoplochaetella* the oesophagus has been extended into xvi and calciferous glands have been constricted off more completely so as to open through short slender stalks from the hilus into the gut ventrolaterally. Setae have been multiplied and are 50-80 per segment. Seminal vesicles of xi have been eliminated but those of x are still retained in some species. Hearts have been added, in xiii, in most species. Although the male deferent ducts still grow back into xviii, one on each side then turns forward to pass into the posterior face of the anterior prostatic duct while the other continues back and into the anterior face of the posterior prostatic duct. Even in the few species that have recently become biprostatic (with no reduction in number of spermathecae), the male ducts still pass into xviii though all then turn anteriorly to join the prostates of xvii. A muscular thickening of the male deferent duct (bulbus ejaculatorius) is developed, in some species, just prior to union with the prostatic ducts. The median nephridium on each side in an intestinal portion of the body, in at least one species, has been secondarily enlarged and its duct, instead of penetrating through the parietes, grows laterally to join with those of other segments in a longitudinal excretory canal eventually opening to the exterior in the anal region. Additionally, this nephridium in some posterior segments has become multistomate (Gates, 1940), a condition which may be attributed to longitudinal splitting of the preseptal portion of the original nephridial anlage. A continuation of this process into the postseptal portion of the embryonic organ presumably would result in a condition similar to that now prevailing in *Priodoscolex*. *Hoplochaetella* arose in the western portion of the Indian peninsula and *Calebiella* in the north, perhaps in the Gangetic valley.

The remainder of the Indian octochaetines (again excepting *Howascolex*) can be arranged in a single line initiated by addition of a gizzard in vi. Associated therewith have been the usual oesophageal extension, bringing intestinal origin into xv, and development (except in one small branch) of an intestinal typhlosole but no addition of hearts in xiii. *Pellogaster* has lost the seminal vesicles of ix-x and has a typhlosole that ends abruptly without special glandular tissues. Definite calciferous glands have not yet been developed. A bifid oesophageal typhlosole in x-xiii of one species provides an early stage from which the intramural type (*Bahlia-Eutyphoeus*) as well as one evaginated type (*Lennogaster-Eudichogaster*) of gland may have been developed. Extension laterally of the broad, dorso-ventrally flattened typhlosole of another species could cover slight ventrolateral depressions containing rudimentary lamellae,

with further evagination followed by constriction providing a series of four pairs of glands opening through oesophageal floor as in *Travoscolides*. The oesophagus may have been extended, in some forms, into xvi. Ventral setae of spermathecal segments are dehisced early in some species but become copulatory in others. The *Pellogaster* range apparently includes the north-eastern part of peninsular India and possibly some part of the Gangetic valley.

In another branch of the two-gizzard line, calciferous glands were evaginated in segments x-xii (one pair lost from xiii?) to open without stalks by dorsal poles into longitudinal grooves in the gut wall still shut off by median partitions. In the genus *Lennogaster*, lateral typhlosoles have appeared, and the posterior end of the median typhlosole has been enlarged, perhaps by differentiation of glandular tissue. Seminal vesicles of ix-x have been eliminated in some species, all four pairs in others. The anterior testes may have been lost in one species and posterior testes must have been aborted at two different times. Posterior prostates and spermathecae have been suppressed in one group of specise and male ducts are now attracted into parietes of xvii though opening independently there as in *Bahlia-Eutyphoeus*. *Lennogaster* apparently arose in the northern part of peninsular India but its range now appears to extend into Burma (2 species).

In another branch of the two-gizzard line, evaginated calciferous glands were reduced to two pairs, in xi-xii, and glandular tissue at the hind end of the typhlosole was segregated into discrete supra-intestinal glands but not in the same manner as in *Bahlia-Eutyphoeus*. Seminal vesicles of xi, or x-xi, have been eliminated. *Eudichogaster* presumably arose in the northwestern part of peninsular India to which it now seems to be confined.

In a *Barogaster* branch, calciferous glands also were reduced to two pairs, in xi-xii, but glands are so constricted off as to leave short stalks from dorsal poles opening directly into the oesophageal lumen, a longitudinal groove and median partition having disappeared (as also in *Rillogaster* Gates 1939). Glandular tissue has been differentiated at posterior end of typhlosole in a sort of grid-like thickening of the intestinal roof but without demarcation into discrete glands. One pair of prostates must have been eliminated and the other has been transferred into xviii where the male ducts are attracted into anterior faces of prostatic ducts at the parietal level. *Barogaster* apparently is restricted to the northern half of peninsular India.

A long isolated branch apparently never developed a typhlosole or associated glandular tissue but has shifted the gizzards back into vi-vii. Reniform calciferous glands are evaginated in xi-xiii and constricted off to leave a fairly long stalk passing from hilus to oesophagus just in front of the septa. Seminal vesicles of x-xi, posterior spermathecae and anterior prostates have been eliminated and male deferent ducts are now attracted into xix where they presumably join the prostatic ducts. The single species of *Rillogaster* is known only from one locality in western peninsular India.

Oviducts, it should also be mentioned, have been united ectally to open by a single median pore in four genera, *Hoplochaetella*, *Eudichogaster*, *Barogaster* and *Rillogaster*. The uniporal condition also has been found in one individual of *Pellogaster isabellae* Gates 1945.

*Howascolex*, the remaining Indian octochaetine, merits little more than passing mention. This genus has been a convenient depository of a geographical and morphological motley of little known species. The excretory system supposedly has been studied in one species but its name is known only from a museum label and the trivial portion of the nomen nudum, if correctly descriptive, means that the species cannot go in the egnus even in its present heterogeneity. Two evolutionary developments appear to be now under way in Indian species, multiplication of setae in the intestinal region and multiplication of nephridia in an anterior portion.

To trace the descent of the octochaetines still further back there now needed a form from which the proto-ramiella can be obtained with a minimum of modification and in accordance with limitations of known geographical distributions. A protoplutellus (Megascolecinae), obtained in the same way as other protoprimitive forms postulated above, is distinguished from the protoramiella by the desired holonephry but had already become biprostatic with pores on xviii. The required quadriprostatic stage may be obtainable in the Acanthodrilinae but that group is without indigenous representation in the oriental region. Slowly accumulating evidence however makes it increasingly possible that the remaining group of Stephenson's Megascolecidae, the Ocnerodrilinae, does have endemics in that region. A primitive form would necessarily have a short oesophagus, an intestinal origin in xii, only two pairs of hearts in x-xi, four pairs of seminal vesicles in ix-xii, but no calciferous glands, typhlosoles, supra-intestinal glands or caeca, nor a subneural trunk in the vascular system. It may have had a gizzard in v or none but was holonephric, *i.e.*, having a single pair of stomate nephridia with parietal nephrophores in each segment. Species similar in many of the most important respects to such a form are present in India and Burma and are unknown elsewhere. Of the changes necessary to derive the protoramiella from such an ocnerodriline, elongation of the oesophagus into xiv, and addition of a pair of hearts in xii, are of the same sort as had to be postulated in the various octochaetine lines. The other change requires only transverse fragmentation of the postseptal portion of the embryonic anlage of the holonephric tubules after which each fragment acquired its own parietal nephropore. The median fragment, retaining the original connection with the preseptal rudiment would develop into a stomate nephridium, the others, without such connection remaining astomate. This change now can be seen, in the backward look, to have been of major importance though at the time it would have seemed justification at most for generic separation. Such evidence as is available from *Howascolex* suggests that the fragmentation may have been confined at first to an anterior portion of the body and was later extended throughout the whole axis. Multiple organs presumable arising from

fragmentation of a single embryonic rudiment occasionally are noted in individual earthworms that presumably are to be regarded as mutants. Establishment of a mutation for transverse fragmentation of the postseptal portion of nephridial anlage appears then to be a possible explanation of the origin of the meronephric type of excretory system characteristic of most Indian octochaetines. Subsequent developments in the various lines have been limited to modifications that now appear to be minor, such as elimination of funnels of median nephridia, first anteriorly and then posteriorly, secondary enlargement of median tubules and development of longitudinal excretory ducts, development in a limited number of anterior segments of the habit of opening into a pharyngeal portion of the gut rather than through the parietes, suppression of nephridia in one or more anterior segments, increase or decrease in extent of fragmentation of nephridial anlage. Although of a somewhat similar nature, the longitudinal splitting of the preseptal rudiment, foreshadowed in *Hoplochaetella*, has ended in development of intestinal enteronephry, in the genus *Travoscolides*, but which has reached a greater degree of specialization in the Megascolecinae.

## SUMMARY

Gross anatomy of digestive, circulatory and excretory systems are remarkably uniform throughout all of the genus *Eutyphoeus*, in environments ranging from semidesert to rain forest and from tropical sea level to Himalayan heights. Intrageneric differences in these three systems are restricted to length of median intestinal typhlosole, number and axial location of ventral intestinal caeca as well as of two-paired sets of supra-intestinal glands, location of lateral intestinal typhlosoles and lateral caeca, number of nephridial ranks in posterior segments, number of such metameres in which median nephridia still retain funnels, extent of abortion of dorsal blood vessel and associated segmental commissures within the first seven segments. The relative uniformity in these organs is in striking contrast to the marked variability in the reproductive system. Here, differences in anatomy involve all structures except ovaries. Among the more important are the following : Two pairs of testes or one pair and then in x (proandry) or xi (metandry). Presence (with or without part or all of its deferent duct) or absence of male funnels after disappearance of corresponding gonads. Functional or functionless right oviduct. Testis sac lacking, annular, U-shaped or ventral and then without or with secondary dorsal extensions. Spermathecae uni-, bi-, or multidiverticulate. Spermathecal diverticula uniloculate or multiloculate. Male terminalia avestibulate, univestibulate or bivestibulate, with or without intromittent organs which may be porophores capable of temporary elevation with pores at apices, eversible invaginations, protrusible annular or tubular penes, without or with penial setae and in the latter case with or without batteries of size-graded reserves. Genital markings lacking or present and then paired or unpaired, segmental and pre- or post-setal or intersegmental, without or with coelomic glands which may or may not be capsulated.

Characteristics available for taxonomic use necessarily are mainly of the reproductive system with digestive and circulatory systems together

providing several others of more or less limited value. Lateral typhlosoles hitherto unrecognized, like the thickenings of the intestinal wall into which they are modified or by which they are replaced, apparently are always developed in species that have them. Presence and absence provide one pair of characteristics but these structures, so insignificant that any function is questionable, now appear to be more valuable for indication of intrageneric relationships. Lateral caeca, as well as typhlosoles, are always associated with the anterior end of the median typhlosole in a limited number of segments (xxii-xxviii) and supra-intestinal glands are always at the posterior end. Ventral caeca are always in typhlosolar segments and usually much nearer the anterior than the posterior end, neither of which is reached even in the longest series known. Funnels on median nephridia may prove to be confined to post-typhlosolar segments. In addition to the few characteristics provided by the typhlosolar portion of the gut there are only presence or absence of dark pigment and presence or absence of dorsal displacement of *d* setae, also of limited use. In the reproductive system, presence or absence of a vestibulum as well as number and certain conformations, presence or absence of penial setae, presence or absence of a battery of size-graded reserves, provide taxonomically useful characteristics, some of which may be recognizable only at maturity

Individual variation hampers use of all other characteristics regardless of system. Lateral intestinal caeca appear to be universally present, of characteristic conformation and definite axial location or always lacking in certain species but in others often are scarcely distinguishable from fortuitous bulges and at best are variable as to size, shape, direction, degree of constriction from gut, even location. Ventral intestinal caeca, like the supra-intestinal glands, apparently in all species, vary both as to number and axial location. Number of gland sets in this genus always is small, 2-9, but the region in which they are found may comprise ten or fewer segments in some species to forty or more in others. Genital markings generically confined to ventrum of some fourteen anterior segments, are present in most species but may be lacking in occasional individuals, small local populations or throughout a considerable portion of a species range. Critical ectal portions of penial setae, frequently damaged in use, distorted by strong mortal constriction or fibrillated during maceration, may be similar in closely related species but markedly different in an occasional individual, short series or local population. Penes may be absent in some individuals in a local population or represented by annular protuberances possibly only of a temporary nature. Although many more anatomical characteristics can be used for definition of species than was formerly recognized, they are inadequate individually as well as collectively in one situation or another. No "museum" criterion is available for determination of taxonomic status when material is limited to a single individual or a short series. Populations of rather similar anatomy, when geographically separated from each other by considerable distances, have been considered to be different species. Adjacent or overlapping populations that appear to be rather closely related to each other morphologically have been treated as species when they cannot be derived directly from each other but only from a common ancestral from no longer extant

(cf. *levis* group), except in case of *manipurensis* where the two subspecies now recognized may prove to be worthy of a higher status. Residues usually have been separated into species according to stages reached in evolutionary developments, as in the *constrictus* group; loss of anterior testes in *hastatus* —→ *constrictus*, in which loss of dorsal blood vessel and associated branches anterior to commissures of vi ———→ *peguanus*, in which loss of dorsal blood vessel anterior to commissures of vii ———→ *plenus*.

Within some of the species so delimited infra-specific taxa may be recognizable. One hundred percent of the material of *E. planatus* that has been available from an unusually small range could have been referred to two geographical subspecies by external as well as by various internal characteristics, and indeed, in almost the same percentage by locations of supra-intestinal glands alone. One hundred percent of the specimens of *peguanus* from the deltas region has been referable almost at a glance, by slight but easily recognizable external characteristics to subsp. *peguanus* and the same percentage of trans-Sittang worms has been referable to subsp. *similis*. Variation in internal organs such as supra-intestinal glands and intestinal caeca appears to be about the same in the two subspecific ranges. Within each of those ranges there can be further distinguished, again by external characteristics (axial location of genital markings), several formae each of which may prove to breed true (with reference to those characteristics) when isolated. *E. constrictus* apparently has no genital markings in the little known northern half of its unusually long range but the same "inornate" condition is found, though only in low frequencies, throughout the southern half. There, external characteristics (as well sometimes as certain aspects of internal organization) may be very similar to those of *hastatus* in the same locality. Solution of various taxonomic problems with reference to populations of the *hastatus-constrictus* complex, in the jungles of the Pegu Yomas, was postponed indefinitely by the late world war and determination of status of several India "species" still awaits acquisition of further material in better condition and longer series.

Discontinuities in geographical distribution of species of *Eutyphoeus* are few, rather small and restricted to the proper generic range with two exceptions. The latter, presence of Gangetic species in Pakistan and Bombay, obviously are attributable to transportation and presumably by man. Internal discontinuities, in absence of characteristic differences in variation, also are attributable to recent transportation by man, with estimates sometimes possible as to original sources. Ranges of three fairly stabilized Gangetic species probably have been extended recently by migration and/or transportation but only into adjacent areas along river valleys leading into the Deccan or across the Aravalli divide into the Indus Valley (Gates, in press). Outside of the generic range and contiguous areas worms of this genus apparently have been unable to avail themselves of the opportunities for new colonization that must have been increasingly provided by man during the last four centuries. The range of the genus now has been quite accurately determined as to southern, eastern and western boundaries. There remains to be learned just how far north the genus has been able to penetrate into the Himalayas,

as extension in those mountains east of Burma or west of Nepal is not anticipated. Species ranges, in Burma, appear to be of two distinct sorts. One, involving considerable north-south extent, characterizes three Burmese species, *hastatus*, *constrictus*, *bifovis*, and possibly one Indian species (*gammiei*). The other, is of a much shorter extent, with ranges of related species succeeding each other in a north-south direction (cf. *levis* and *foveatus* groups). Stabilization of genital markings and other external characteristics, as well as of supra-intestinal glands (typhlosolar termination) and intestinal caeca, in various combinations, possibly under way in local populations of *hastatus* and *constrictus* in the Pegu Yomas, may represent an earlier stage in the evolution of smaller range species.

The variation that has caused so much trouble to systematists in *Eutyphoeus* involves precisely those characteristics by which species must be distinguished and shows that evolution still is going on throughout the genus. Just as in the more remote past *hastatus* evolved into *constrictus*, so today small local populations of the former, in south-central Burma, appear to be passing (or to have passed very recently) into a *constrictus* stage. Passage from the *constrictus* to the *peguanus* stage, in at least one locality of the Pegu Yomas, must have been almost at once, if not directly from *hastatus*, as elsewhere, in the vicinity of Pyinamana, *constrictus* may have gone straight into a *plenus* stage. Several local populations of *foveatus* also appear to be evolving into a *spinulosus* stage. Rapid evolution at times is indicated by persistence of *hastatus* male funnels of x, now useless and usually lacking in metandric species, through the *constrictus-peguanus* and *constrictus-plenus* stages.

Direction of evolution sometimes is clearly indicated by certain organs : male funnels in segments from which the testes have disappeared, a right oviduct without external aperture, anterior portions of the dorsal blood vessel with associated segmental commissures that are of much less than normal size or even functionless, malfunctioning or even functionless penisetal follicles Some other trends can be deduced from comparative anatomy : Lateral dislocation of spermathecal pores. Increase in number of seminal chambers in spermathecal diverticula. Modification in activities of penisetal follicles to produce batteries of size-graded reserve setae apparently long before sexual maturity. Perfection of mechanisms for direct transfer of sperm into spermathecae of a copulatory partner, this having been anticipated, as it were, by the generically characteristic thick duct with lumen and aperture large enough to receive an intromittent organ. Trends with respect to structures such as genital markings, supra-intestinal glands, ventral intestinal caeca, penial setae, are much more difficult to recognize. Each of two opposites occasionally may be indicated. Some degree of stabilization as to number as well as location of markings, glands and caeca, however, has been achieved at various times and places.

Evolutionary changes have taken place repeatedly and independently in *Eutyphoeus* according to the evidence provided by distribution. Tubular penes have been developed, presumably by elongation of smaller but definite annular ones around fissures, in the Arakan Yomas of Burma,

in the Eastern Himalayas and the Gangetic valley. The dorsal blood vessel has been foreshortened in several sections of Burma, as well as in the plains of the Ganges, and the interspecific variation in incidence of persistent vestiges indicates that this change has taken place at different times. Metandry has been achieved in different parts of Burma, in the Himalayas and in the Gangetic area. Attainment of this meroandric reduction at different times is evidenced by presence or absence of seminal vesicles of ix, of anterior gonoducal funnels with or without their ducts and the various stages of regression in funnels as well as ducts. Intestinal caeca have been evaginated, though usually not in the same segments, in different parts of the eastern border of the generic range in Burma, in a northern as well as a southern section of the Indo-Burmese mountain wall and in the Himalayas. Median spermathecal diverticula have been lost twice in eastern Burma, once each in central Burma and in Manipur. Considerable similarity in gross anatomy need not then be evidence of close relationship, and contrariwise, closely related species may be distinguished from each other by structural differences about as great as are to be found in this genus.

Also involved in much of the present discussion are assumptions that issued from a study of aberrant or monstrous individuals and of juveniles in which development of various reproductive structures can be followed, as it were, merely by seriation of growth stages. (1) Development of gonoducal funnels is induced by the gonads, as presumably, development of seminal vesicles or ovisacs (when present) is induced by testes or ovaries. Persistence of male funnels of x in metandric species such as *peguanus* is explained as due to abortion of gonads only after funnel induction and in some cases only after the funnel ducts have acquired autogenous growth. Disappearance of the ducts and finally even of the funnels in older metandric species then must be attributed to increasingly earlier abortion of the testes. (2) Development of most of the male terminalia is induced by the prostates. If the prostates are lacking the terminalia do not develop and male deferent ducts, whether shorter or longer than usual, do not acquire external apertures. When prostates are shifted to another segment the rest of the terminalia also develop there. Included in the developments thus induced are; acquisition by male deferent ducts of superficial apertures, anterior migration of male pores from an original postequatorial position forward into fissures as the latter develop, protrusion of margin of each fissure as an annular penis, elongation of an annular to a tubular penis, invagination of the fissure areas into one or two chambers, or development around each fissure of some sort of a porophore, migration of apertures of setal follicles into closer proximity to prostatic and male duct pores, modification of activity of the adjacent follicles to produce penial setae, sometimes with size-graded reserves. Evolution, insofar as the terminalia are concerned, has involved increase in number of developments induced by the prostate, intensification or other modification of those inductions, all of which take place rather late in ontogenetic growth. When prostates are lacking all of those developments are of course omitted and follicle apertures of ventral setae remain in the usual locations. Follicles, as formerly in the long distant past, produce ordinary sigmoid rather than penial setae,

Loss of a late ontogenetic induction in this case then results in a return to an ancestral condition that was not anticipated previously (Gates, 1939, p. 183).

A hypothetical ancestral form has been obtained by subtraction of all species specializations in this genus. With that proto-eutyphoeus, species of *Eutyphoeus*, insofar as present knowledge of anatomy permits, have been filiated phylogenetically and arranged in groups according to phyletic relationships for the first time. The mountain wall between India and Burma now appears to have been the center of *Eutyphoeus* evolution, and perhaps a more appropriate one than the Gangetic plain (Stephenson, 1914, p. 323) for animals eventually to climb 15,000 feet into the Himalayas. From that wall an ancestral proto-eutyphoeus passed across Burma into a region comprising the western edge of the Shan Plateau as well as the southern hills down through Amherst district to the Ye River, where it became segregated into species of the meroandric *levis* group (proandric and metandric). In the opposite direction it penetrated into the Indian lowlands where, without loss of holandry it became differentiated into *incommodus*, *annandalei* and *quadripapillatus*. To the north and in the mountains, after giving rise to the genus *Scolioscolides*, it became segregated into species of the Himalayan equivalent of the *levis* group. Subsequently migration to the east from the mountain wall brought into Burma a form that became *hastatus* and which gave rise in the central yomas to species of the *constrictus* group. The oldest of these has hardly escaped from the Pegu Yomas, but another, *peguanus*, was able to cross the Sittang into the *levis* group territory but only down to the mouth of the Salween and more recently has spread throughout the deltas region. The same ancestor of *hastatus*, or a form with similar evolutionary capacity, passing westwards gave rise to a trans-Arakan equivalent of the *constrictus* group (*scutarius*, *comillahnus*, and others, all of uncertain status). Finally, from that same wall, a proto-foveatus, passing east into the Chindwin-Irrawaddy axis, was segregated into species of the *foveatus* group, due south in the Arakan Yomas into species of the *gigas* group, and to the west into the *gammiei* complex, possibly still further on, in the Indian lowlands, part or all of the *orientalis* group.

Hypothetical ancestral forms obtained for other oriental octochaetine genera in the same way as the protoeutyphoeus have been filiated first with the derived species (mostly without mention in the present contribution) and then with each other. This oriental phylogeny includes various genera erected since the last discussion of the subject by Stephenson (1930) and makes use of recently acquired information regarding calciferous glands (Gates, 1937-1940) and excretory systems (Bahl, 1919-1946). The evolution of the nephridial system in the oriental octochaetinae, as now outlined for the first time, is based, except for one assumption as to longitudinal splitting of nephridial anlage, on ideas advanced by Bahl which are however set in a more appropriate systematic framework because other organization also has been taken into consideration. Further studies like those of Bahl and his students are required, both for phylogenetic and taxonomic purposes, in meronephric genera and especially in the Megascolecinae. The best documented evolutionary

sequence in calciferous glands involves; appearance of a ventral oesophageal typhlosole, its heightening and bifurcation, appearance of transverse calciferous lamellae, union of median ends of those lamellae with the lateral faces of the typholosolar bifurcations to form the intramural sort of gland characterizing *Eutyphoeus*, *Scolioscolides* and *Bahlia*. Each lamella forming area, in another line, is evaginated laterally into a stalked sac and the typhlosole has been reduced to two small valves one over each stalk aperture still within a slight groove. Retraction of stalked extramural glands into an intramural situation, required at least twice in the classical phylogeny, still seems unlikely (Gates, 1938, p. 45). Other octochaetine methods of gland evolution are suggested by stalk-gut relationships; evagination from the ventral side close to mV, from the dorsal side, or from regions of septal insertion, sometimes with complications due to lobing of primary evaginations and acquisition by secondary lobes of their own stalks, etc. Such variety in development and gross anatomy, to say nothing of microscopic structure, together with differences in number and axial origin, require more consideration in phylogeny as well as taxonomy than the customary reference to absence or presence and then sometimes to number and segmental location. Even such casual characterization has been omitted in classical definitions of megascolecine genera.

Some of the evolutionary changes that have taken place in *Eutyphoeus* (such as acquisition of pigment, lateral migration of spermathecal pores, modifications in spermathecal diverticula, mercandric reductions, elimination of penial setae, etc.) also have been made within other octochaetine genera. Some changes, invagination of copulatory chambers, development of penes and intestinal caeca, fore-shortening of the dorsal blood vessel, absent elsewhere in the Octochaetinae, have taken place within genera of one or more other subfamilies or families. Only regression of the right oviduct, certainly a rather odd development in animals so fundamentally symmetrical as are earthworms, has not been found elsewhere and now seems to be unique.

Evolutionary changes such as migration of female pores mesially, ectal union of oviducts to open by a single pore at mV, dislocation of spermathecal pores mesially or away from the intersegmental furrows, and then anteriorly or posteriorly, loss of a pair of spermathecae or prostates, etc., not only have taken place independently within different octochaetine genera but also time and again within genera of other families. Variation in number and segmental location of gizzards, length of oesophagus, number as well as location of hearts and calciferous glands, number of setae, and as to presence or absence of typhlosoles, etc., is lacking, as in *Eutyphoeus*, in many genera of the Octochaetinae and other (sub) families. The single gizzard in *Perionyx* however may be in v, vi or vii, according to species. The number of gizzards as well as their location, in the Moniligastridae, may vary considerably from one individual to another in a local population of a species. Intestinal origin in *Perionyx* may be in any of segments xv to xx according to species but with frequent individual exceptions. Morphologically quite similar species of *Plutellus* may differ from each other mainly as to presence or absence of a typhlosole. Number of pairs of setae in *Spencriella*, as well as other

genera, varies from one species to another if not from one individual to another in the same species. The single morphological characteristic, union of male and prostatic ducts in xviii, that was supposed to distinguish the phylogenetic (sub) family Megascolecinae (Stephenson) or Megascolecidae (Michaelsen) now has been found in two other (sub) families. Individual variation in calciferous glands has not been found yet and most of the cases of interspecific differences are in phylogenetically defined genera (*Howascolex* and the Megascolecinae) obviously in need of revision. Meronephry is universal in the Octochaetinae, only generic in the Microchaetinae and Megascolecinae, but excretory systems have been studied too little to permit any conclusion with reference to intrageneric or individual variation. Lack of hierarchy in characteristics that must be used in earthworm taxonomy, frequent independent development of the same conditions in so many evolutionary lines, and paucity of unique major changes, has been responsible in part for the difficulties in classification of earthworms and its present unsatisfactory state.

In the Octochaetinae three genera clearly are more closely related to each other than usual in that family. One of them, *Scolioscolides*, can be derived directly from *Eutyphoeus*, certainly from a primitive form similar to the proto-eutyphoeus. This derivation requires little more than a single change, translocation of capacity for developing prostates from the *Eutyphoeus* segment to that next behind, which has taken place in intrageneric evolution (*Diplocardia*, *Pheretima*) and occasionally is found in mutant individuals of *Pheretima* sp. Other modifications involved in that derivation may arise from changes in induction resulting in part at least from the difference in axial location. The other genus, *Bahlia*, can be derived only from some extinct common ancestral form. Other oriental octochaetine genera, like *Bahlia*, usually can be filiated only indirectly. Direct filiations, with the ancestral genus surviving alongside daughter and grand-daughter genera, as in the classical earthworm phylogeny, must be very rare if at all possible.

The protoramiella which also can be ancestral to other Indian octochaetines except the little known and taxonomically confused *Howascolex*, differs significantly from the corresponding protoprimitive form in the nearest family (geographically as well as morphologically) only by one characteristic,—presence of two or more pairs of nephridia per segment instead of one. The initial evolutionary change then needed to derive the protoramiella and through that all other oriental octochaetines is merely transverse fragmentation, in an early embryonic stage, of the usual single pair of nephridial anlage. This fragmentation initially may have been a mere halving, to give, as in the microchaetine genus *Tritogenia*, four tubules per segment.

Hybridization between species has not been recognized in the genus *Eutyphoeus* and may well have had little or no importance in its evolution. This is in agreement with Pickford (1937, p. 46) who found "that species hybridization has played but a small part " in the evolution of the South African Acanthodrilinae. Vestigial anterior portions of the circulatory system could have been interpreted in certain Burmese localities as a result of a cross between *constrictus* (*dorsal vessel intact*) x *peguanus*

(vessel foreshortened). But the same vestigial conditions have been found in circumstances where that or any similar cross is impossible.

Some of the genetic changes that must have been the bases of evolution in this family bring about shifts in " developmental fields " and other gradual modifications. Some correspond to the classical " mutations " of the De Vriesian period. Such " mutations ", postulated to explain certain evolutionary changes in *Eutyphoeus* and other octochaetines, have been named, for convenience of discussion, at opportune places in the present contribution. The evidence for these hypothetical mutations is provided by aberrant or monstrous individuals of various genera as well as *Eutyphoeus* since identical evolutionary changes can be expected to originate in the same way in different lines. These mutations may produce their major recognizable effect at any stage of the life history; a meronephric mutation early in embryonic development, foreshortening perhaps somewhat later after the circulatory system has been well developed in the embryo, elimination of spermathecal diverticula late in ontogeny when worms have about attained adult size. Delayed penetrance of the metandric mutation, until after induction of spermiducal funnel development, is assumed, to explain persistence of these useless structures. Eventual disappearance of both ducts and funnels can then be attributed to earlier penetrance. Incomplete or delayed penetrance also has been invoked to explain persistence of the anterior section of the dorsal blood vessel in occasional individuals of species where foreshortening is usual. Genetic determiners for certain evolutionary changes may however be ineffective or become inoperative in later stages of embryonic development. Thus there are meronephric nephridia and two dorsal blood vessels in an anterior portion of the body in certain species of *Howascolex* and *Diplocardia* (Acanthodrilinae) respectively, the primitive condition (holonephridia and single dorsal vessel) retained posteriorly.

Mutation " athecal " has had no role in the evolution of *Eutyphoeus* or any other oriental octochaetine though involved in the ancestry of *Bimastos* (Lumbricidae) and *Criodrilus* (Criodrilinae), as well as of various other lumbricid and megascolecine species. Presumably the " prerequisites " for perpetuation and spread of the mutation, such as spermatophores that can adhere to the exterior of a copulatory partner (Criodrilinae) or uniparental and presumably parthenogenetic reproduction (sp. of the megascolecine *Pheretima*), have been lacking in the octochaetines. Mutation " aprostatic " may have had no evolutionary significance in the Octochaetinae because of inability of male deferent ducts, in absence of prostate glands, to acquire openings to the exterior.

*Scolioscolides* can be derived directly from *Eutyphoeus* or rather from the proto-eutyphoeus by a single change, shift of prostatic development from one segment to that next behind. Aberrant individuals in species of *Pheretima* indicate that such a change can be brought about at one step by mutation. A new genus of earthworms then apparently can arise by establishment of a mutation (along with associated changes of induction) and be characterized by a condition previously thought to distinguish an entire (sub) family (Megascolecinae or Megascolecidae).

Furthermore, the single change required to derive the basic octochaetine protoramiella from the protothatonia, transverse fragmentation of the single pair of nephridial anlage, presumably can result from mutation. Mutant individuals of that sort have not yet been recognized in holonephric species but aberrant individuals in which other embryonic anlage were fragmented have been found. A systematist already familiar with the protothatonia might well have disregarded a single individual of a protoramiella as an unimportant aberration, or for several individuals might have made a different species. Prior to writing this, the genus *Perionyx* was redefined so as to keep within it one species which differed from all others almost only in having had each of the embryonic nephridial anlage split longitudinally into five or six portions, each of which develops into an apparently normal nephridium. At most this unusual species will have to be transferred to a new genus. If however the species had happened to be one with considerable evolutionary potentiality it could in time have given rise to a group of genera possibly even requiring recognition as a subfamily or family. In the same way the Octochaetinae is today distinguished from the two most closely related subfamilies only by the meronephry.

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