

# ON INDIAN AND BURMESE EARTHWORMS OF THE GENUS *GLYPHIDRILUS*

By G. E. GATES

This note reports results of study of material of Indian species of *Glyphidrilus* received for identification during the last fifteen or twenty years. Most of the lots were small but one fairly long series (from Saharanpur) provided an opportunity for obtaining much needed information as to variation in certain taxonomically important characteristics about which nothing had been previously recorded. A little Burmese material (8 specimens) received after completion of the original draft of the manuscript is also considered.

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## Genus *Glyphidrilus* Horst 1889

*Definition.*—Body wall protuberant, at maturity, in a longitudinal lamellar ridge ("wing") in *bc* on each side, across several clitellar segments. Polythecal, spermathecae behind testis segments, the pores in three or more intersegmental furrows beginning with 12/13, 13/14 or 14/15. Setae, eight per segment, in four pairs. Clitellum, annular (?), extending over a number of segments including all with reproductive apertures (?), intersegmental furrows not obliterated. (No dorsal pores.) Prostomium zygalobous. Anus dorsal, body nearly circular in cross section anteriorly, becoming more elliptical posteriorly, quadrangular after preservation, with setae at the four corners and *dd* only slightly larger than *aa*.

Gizzard oesophageal, in region of vii-viii (not strictly confined to one segment?). Typhlosole present, rather low and thickly lamelliform (?). (No calciferous glands). Vascular system with a subneural trunk, single dorsal trunk, and one or more pairs of latero-oesophageal hearts. Excretory system holonephric, nephridia lacking in first twelve (or so) segments. Holandric. Seminal vesicles four pairs, in ix-xii (?). Spermathecae adiverticulate, ducts at least confined to parietes.

*Remarks.*—Organs present only in one of the species scarcely merit mention in a generic definition and so reference to "prostates" has

been omitted. Mention of male pores is also omitted as locations of those apertures have been recorded only for three species and also because of uncertainty as to the significance of the variation apparently indicated by some of those records.<sup>1</sup>

The definition above is tentative as we still are ignorant of important characteristics in a large proportion of the species. It is offered as one more contribution to a less artificial taxonomy of earthworms than that of the past which has been based on the so-called "phylogenetic" diagnoses.

A first attempt (below) at a key to any considerable section of the genus has succeeded only in pairing species that probably are morphologically and/or geographically distant. This may however be due only in part to the lack of information about internal organization.

Key to Oriental species of *Glyphidrilus*

|                                                                |   |   |   |                     |
|----------------------------------------------------------------|---|---|---|---------------------|
| 1. a. Gizzard in vii or mainly so                              | . | . | . | 2                   |
| b. Gizzard in viii or mainly so                                | . | . | . | 3                   |
| 2. a. Intestinal origin in xv                                  | . | . | . | <i>tuberosus</i>    |
| b. Intestinal origin behind xv                                 | . | . | . | <i>ceylonensis</i>  |
| 3. a. Intestinal origin in xv                                  | . | . | . | 4                   |
| b. Intestinal origin behind xv                                 | . | . | . | 6                   |
| 4. a. Wings begin in region of xvii-xix                        | . | . | . | <i>papillatus</i> * |
| b. Wings begin behind xx                                       | . | . | . | 5                   |
| 5. a. No genital markings in <i>aa</i>                         | . | . | . | <i>birmanicus</i>   |
| b. Unpaired, median markings in <i>aa</i>                      | . | . | . | <i>annandalei</i>   |
| 6. a. Intestinal origin in xvi, dorsal blood vessel ends in ix | . | . | . | <i>gangeticus</i>   |
| b. Intestinal origin in xviii, dorsal blood vessel ends in ?   | . | . | . | <i>malayanus</i> †  |

*Glyphidrilus annandalei* Michaelsen 1910

1925. *Criodrilus* sp. (? *lacuum*), Stephenson, *Proc. Zool. Soc. Lond.*, pp. 903-905.

Bangalore, Mysore State, 5 clitellate specimens. Prof. C. R. N. Rao.

Bhadravati, Shimoga district, Mysore State, December, 1 clitellate specimen.  
H. S. Rao. (Indian Mus.)

Mettupalayam, "from deep places along edge of Bhavani River", 16-9-25,  
1 clitellate specimen. Dr. S. L. Hora. (Indian Mus.)

Bangalore, "dhobie ghat", May 12, 1 fragment. Miss Dorothy Pearson.

*External characteristics.*—Nephropores, on the *b* lines, are recognizable only from xiv or xv even though nephridia are present from ix posteriorly (small in xi-xiv). Female pores are on xiv, on *b* lines, nearer the setal equator than 13/14 (7 specimens). The wings are 1¼-1½ mm high. Genital markings are located as follows: unpaired medians, on xii-xxii (2), xiii-xv (2), xiii-xx (1), xiii-xxi (1), xiii-xxii (1); paired laterals, xiii-xxiv (7), xxxii-xxxiii (5), xxxiii-xxxv (1), xxxiv but on right side only (1). Rims of markings are conspicuously raised peripherally

(<sup>1</sup>) Male pores have been said to be on 21/22, 27/28, 29/30, in *annandalei*, on 21/22 in *quadrangulus*, on 27/28 in *weberi*.

\**G. spelaeotes* Stephenson 1924 drops out here. It is not, at present, distinguishable from *papillatus*.

†*G. malayanus* Michaelsen 1903 is even more inadequately characterized than *spelaeotes* but may have (Gates, 1938, *Bull. Raffles Mus.*, Singapore, 14, p. 221) an intestinal origin in xviii.

(1 from Shimoga and 1 from Bangalore) so as to form deep cups within which the central tubercle is equally protuberant. The central tubercle of four markings, on xiv-xv, is doubled.

*Remarks.*—The three specimens from South Malabar of "*Criodrilus* sp.", in absence of wings, genital markings and spermathecae, must have been juvenile. The location of the gizzard muscularity and the ornamentation of the setae obviously are not as in the genus *Criodrilus*. Indeed, location of a gizzard in viii and vii not only rules out assignment to *Criodrilus* but invites consideration of reference to *Glyphidrilus*. *G. annandalei* is the only species of the genus that has been found in South India from whence the South Malabar specimens came. The zygalobous prostomium, ornamentation of the setae, location of gizzard, the segment of intestinal origin, the typhlosole, presence of hearts in vii-xi, and the presence of nephridia from xi posteriorly, all support an identification as *annandalei*.

### *Glyphidrilus gangeticus*, sp. nov.

1909. *Glyphidrilus* sp. ?, Michaelsen, *Mem. Indian Mus.* I, p. 244. (Kichha near Naini Tal, Kumaon district, base of western Himalayas. 2 juveniles.)
1920. *Glyphidrilus papillatus*, Stephenson, *Mem. Indian Mus.* VII, pp. 258-260 (Lucknow.)
1923. *Glyphidrilus papillatus* (part), Stephenson, *Fauna Brit. India. Oligochaeta*, p. 493. (Excluding all but Lucknow worms.)
1947. *Glyphidrilus* sp., Gates, *Proc. nat. Acad. Sci. India*, (B), XVII, pp. 121-122. (Ahraura in Allahabad sector of the Indo-Gangetic plain, U. P.)
1948. *Glyphidrilus papillatus*, Gates, *Growth*, XII, pp. 175-176. (Location of anus in younger and older tail regenerates.)
1951. *Glyphidrilus papillatus*, Gates, *Proc. nat. Acad. Sci. India*, (B), XXI, p. 17. (Saharanpur.)

*Glyphidrilus* sp., Gates, (in press). (Sohagi.)

Saharanpur, United Provinces, October, 19 juvenile, 6 acelitellate and 110 clitellate specimens. M. Mathur. (Along banks of a river, at a depth of about eighteen inches.)

*External characteristics.*—Length, 85-140 mm (preserved in a strongly contracted state). Diameter, 4-5½ mm. The prostomium is zygalobous. Nephropores have not been definitely identified, *i.e.*, actual openings have not been seen, but they probably are located on the *b* lines. Spermathecal pores have not been recognizable (because of strong contraction) but are in 12/13-16/17. Female pores are on xiv, on *b* lines, about midway between 13/14 and the setal equator. Male pores were not found. Variation in segmental location of the wings is shown in the table below. Genital markings are postsetal and are differentiated into well marked rim and central portion. Variation in segmental locations of the markings is also shown in Table I.

*Internal anatomy.*—The gizzard is mainly in viii (30 specimens). The intestinal origin is in xvi (30). The typhlosole begins in xvii or xviii and is fairly well developed relative to the size of the gut, rather thick, not blade-like (lamelliform).

The dorsal blood vessel (single) ends exactly with the commissures of ix (28), with a left commissure of viii (1), or with a pair of commissures to the ventral trunk in viii (1). The ventral trunk bifurcates over the

subpharyngeal ganglia or a little more posteriorly, the branches passing up around the gut and uniting under the brain so as to form a circumpharyngeal ring. From this ring small vessels may pass back, in some specimens apparently, to join branches of the supra-oesophageal trunk. This trunk is large, disappearing from view in xiii-xiv, bifurcating anteriorly, each branch passing anterolaterally to join the anterior lateroparietal trunk in ii. The supra-oesophageal gives off in each of segments vi and vii a pair of asymmetrical vessels which pass to the anterior lateroparietal trunks. Because of the close crowding in a small space these asymmetrical branches and the supra-oesophageal trunk could easily be mistaken for segmental commissures and a continuation of the dorsal vessel. A pair of smaller vessels from the supra-oesophageal is occasionally recognizable in segment v. A pair of small vessels from the supra-oesophageal pass downward just behind septum 7/8 on the gizzard. These vessels either unite midventrally to form a short, median suboesophageal vessel or pass into two suboesophageals, or unite and then join one of the suboesophageals. Suboesophageal vessels, on the ventral face of the gut from which they can be dissected off, may be paired, unpaired and median, or large on one side and small on the other, or lacking on one side but present on the other, or the condition may vary from one segment to another. This suboesophageal complex may be connected by a pair of large vessels in each of viii to xiii and on the anterior faces of the septa with the anterior lateroparietal trunks, or the lateroparietal trunks may turn mesially on one or both sides of any of those segments to join the suboesophageal. In the latter case the segmental branches from the suboesophageal complex pass straight laterally in the more posterior segments behind the junction. The anterior lateroparietals, in a few specimens, bend mesially in xii, xiii or xiv and on the anterior face of the septum unite with the posterior lateroparietal, the united vessel then joining the suboesophageal complex. The subneural trunk is large, with a pair of branches passing laterally just behind each septum. Any one, or any pair, of those branches, in the region of xxiii-xxviii may be much enlarged. An enlarged branch in xxvii or xxviii after passing straight laterally for some distance, turns almost at a right angle and then continues forward as the posterior lateroparietal trunk. This vessel may be joined in any of segments xviii-xxiii by another large branch from the subneural or, if the subneural has disappeared in the meanwhile, the two lateroparietals may be connected by a large commissure on the ventral parietes. The posterior lateroparietal vessels either join the anterior lateroparietals or open into or become the suboesophageal vessels in xii (1), xiii (5), or xiv (8) or xii on one side and xiii on the other, or xiii on one side and xiv on the other. The relationships of these vessels appear to differ constantly from one worm to another. The subneural disappears without exception before reaching xvii and is never recognizable anteriorly as in species of *Perionyx*, *Drawida*, etc.

The last pair of hearts, in xi (30 specimens), is latero-oesophageal, the bifurcations to the dorsal trunk always small, and white, the bifurcations to the supra-oesophageal always large and filled with blood. Hearts of ix and x always appear to be lateral, opening directly into the

dorsal trunk. If any bifurcation to the supra-oesophageal is present in segments ix and x it must be morphologically and physiologically different from that in xi. Segmental commissures of viii, when present, are lateral.

Seminal vesicles of xii are always elongated anteroposteriorly and push 12/13 back, into contact with 13/14. Small pseudovesicles are present in xiii and in one specimen are filled with dark brown granular debris such as is aggregated into the brown discs or bodies. Similar pseudovesicles are usually present in xiv where they presumably function as ovisacs. A pair of pseudovesicles is present in each of segments xiii, xiv, xv, and xvi, in one specimen, the size decreasing posteriorly.

*Abnormality.*—The left heart and both vesicles of ix are lacking in the worm in which the dorsal trunk ended with two commissures in viii (the specimen with post-alar unpaired median genital markings).

TABLE I

Variation in location and segmental length of the wings in one colony of *G. gangeticus*

| Location.                               |    |    |    |    |    |    | Number of<br>segments<br>involved. | Number<br>of<br>specimens. |
|-----------------------------------------|----|----|----|----|----|----|------------------------------------|----------------------------|
| 16/17-25/26                             | .. | .. | .. | .. | .. | .. | 9                                  | 1                          |
| $\frac{1}{2}$ xvii— $\frac{1}{2}$ xxv   | .. | .. | .. | .. | .. | .. | 8                                  | 1                          |
| *17/18— $\frac{1}{2}$ xxv               | .. | .. | .. | .. | .. | .  | 7 $\frac{1}{2}$                    | 51                         |
| *17/18-25/26                            | .. | .. | .. | .. | .. | .. | 8                                  | 9                          |
| 17/18— $\frac{1}{2}$ xxvi               | .. | .. | .. | .. | .. | .. | 8 $\frac{1}{2}$                    | 2                          |
| 17/18—26/27                             | .. | .. | .. | .. | .. | .. | 9                                  | 1                          |
| $\frac{1}{2}$ xvii— $\frac{1}{2}$ xxv   | .. | .. | .. | .. | .. | .. | 7                                  | 32                         |
| $\frac{1}{2}$ xviii—25/26               | .. | .. | .. | .. | .. | .. | 7 $\frac{1}{2}$                    | 1                          |
| $\frac{1}{2}$ xviii— $\frac{1}{2}$ xxvi | .. | .. | .. | .. | .. | .. | 8                                  | 5                          |
| $\frac{1}{2}$ xviii—26/27               | .. | .. | .. | .. | .. | .. | 8 $\frac{1}{2}$                    | 2                          |
| 18/19— $\frac{1}{2}$ xxv                | .. | .. | .. | .. | .. | .. | 6 $\frac{1}{2}$                    | 5                          |
| 18/19—25/26                             | .. | .. | .. | .. | .. | .. | 7                                  | 1                          |
| Not determinable because of condition   | .. | .. | .. | .. | .. | .. |                                    | 5                          |
| Total                                   |    |    |    |    |    |    |                                    | 116                        |

The " $\frac{1}{2}$ " indicates that the wings extend onto the postsetal portion of the segment in case of the first figure of a pair, or onto the presetal portion in the case of a second figure. It does not indicate exact extent across a postsetal or presetal half, one quarter and three quarter (usually plus) extent being omitted to save space.

Asymmetry in extent of wings of an individual is slight but present in some specimens, though amounting only to one segment or less. In such cases, again to save space, only the greater extent is indicated, but by recording the more anterior beginning and the more posterior ending.

\*The presetal portion of the wing, on the first segment, often is only about half the ight of the remainder of the wing.

TABLE II

Variation in number and segmental location of genital markings in one colony of *G. gangeticus*

| Segment. |    |    |    |    |    |    | Median, unpaired markings. | Paired markings, in <i>bc</i> . |
|----------|----|----|----|----|----|----|----------------------------|---------------------------------|
| x        | .. | .. | .. | .. | .. | .. | 2                          | ..                              |
| xi       |    | .. | .. | .. | .. | .. | 12                         | ..                              |
| xii      |    | .. | .. | .. | .. | .. | 53                         | 35                              |
| xiii     | .. | .. | .. | .. | .. | .. | 44                         | 70                              |
| xiv      | .. | .. | .. | .. | .. | .. | 17                         | 71                              |
| xv       | .. | .. | .. | .. | .. | .. | 2                          | 92                              |
| xvi      | .. | .. | .. | .. | .. | .. | 6                          | 107                             |
| xvii     | .. | .. | .. | .. | .. | .. | 52                         | 107                             |
| xviii    | .. | .. | .. | .. | .. | .. | 67                         | 1                               |
| xix      | .. | .. | .. | .. | .. | .. | 2                          | ..                              |
| xxiv     | .. | .. | .. | .. | .. | .. | ..                         | 9                               |
| xxv      | .. | .. | .. | .. | .. | .. | ..                         | 94                              |
| xxvi     | .. | .. | .. | .. | .. | .. | ..                         | 83                              |
| xxvii    | .. | .. | .. | .. | .. | .. | ..                         | 8                               |
| xxviii   | .. | .. | .. | .. | .. | .. | 1                          |                                 |
| xxix     | .. | .. | .. | .. | .. | .. | 1                          | 1                               |
| xxx      | .  | .. | .. | .. | .. | .. | 1                          | ..                              |
| xxxi     | .. | .. | .. | .. | .. | .. | 1                          | ..                              |
| xxxii    | .. | .. | .. | .. | .. | .. | 1                          | ..                              |

Arabic numerals show the number of times a genital marking is found on a particular segment in 116 specimens, asymmetrical conditions disregarded, *i. e.*, occasional absence of one of a pair.

The markings on xxiv always are asymmetrical and present only when one wing ends at 23/24 or on the anterior portion of xxiv.

All the post-alar median markings (of xxviii to xxxii) are on one worm.

*Remarks.*—Spermatozoal iridescence was evident in the spermatheca ampullae of each of the dissected specimens.

Variation in number of segments crossed by the wings, in the Saharanpur specimens, is slight,  $2\frac{1}{2}$ ;  $6\frac{1}{2}$  segments (5 specimens), 7 (33),  $7\frac{1}{2}$  (52), 8 (15),  $8\frac{1}{2}$  (4), 9 (2). The wings, as Table I shows, begin on one of three segments, xvii, xviii or xix, and end on one of two segments, xxv or xxvi. Although much more variation was shown in the number of genital markings (Table II), none of the worms had paired markings in *aa* (as was also the case in the Lucknow specimens examined by Stephenson, 1920).

Variation in segments crossed by the wings in "a considerable number, (Stephenson, 1920, p. 259) of Lucknow worms was of about the same order, 6-8½, as in worms from Saharanpur. But the wings apparently always began on xviii though ending on any of several segments, xxiii, xxiv, xxv, or ½ xxvi. Unfortunately we do not know how many adult specimens were available to Stephenson nor the size of the sample on which wing locations were precisely determined.

Internal organization of the Saharanpur material was uniform and showed no variation that might be expected to be of taxonomic importance. Although the segment in which the dorsal blood vessel ends was not mentioned by Stephenson there is no good reason, at present, for suspecting that Lucknow worms differ in that respect alone from those obtained at Saharanpur.

Identification of five young worms from Ahraura (Gates, 1947) and others from Sohagi (Gates, in press) was not attempted. These juveniles, as well as the two from Kichha (Michaelsen, 1909) are assumed to be of *gangeticus* in absence of any reason for suspecting presence of another species of the genus in the western portion of the Gangetic plain.

*G. gangeticus* is very clearly distinguished from *G. papillatus* (Rosa) 1890, with which it has been confused, by the termination of the dorsal blood vessel with the hearts of ix, as well as by the intestinal origin in xvi.

*Definition.*—Wings begin on one of segments xvii-xix and end on one of xxiii-xxvi. Genital markings primarily postsetal: unpaired and median on (*x*), xi-xiv, (xv-xvi), xvii-xviii, (xix, xxviii-xxxii); paired, lateral to *aa*, xii-xviii, (xix, xxiii), xxiv-xxvii, (xxviii-xxx). Spermathecal pores on 12/13-16/17 Female pores on *b* lines midway between setal arc of xiv and 13/14. (Male pores?) Clitellum on xiii or xiv to xxxiv or so (anterior and posterior limits rather indefinite). Segments, 202 (±?). Length, 85-140 mm. Diameter, 3-5½ mm.

Gizzard mainly in viii. Intestinal origin in xvi. Dorsal blood vessel ends with hearts of ix. Last hearts in xi, only this pair latero-oesophageal.

*Distribution.*—Western portion of the Gangetic plain from Saharanpur to Lucknow, Ahraura and Sohagi. Replaced in the eastern portion of the plain by *G. tuberosus*?

### ***Glyphidrilus tuberosus* Stephenson 1916**

1914. *Criodrilus lacuum*, Stephenson, *Rec. Indian Mus.* X, p. 256.

Bayrani, near Kallikote, Ganjam district, Madras Presidency, 7. iv. 1924, 8 clitellate specimens. Dr. S. L. Hora. (*Indian Mus.*)

*External characteristics.*—Length, 70-118 mm. Nephropores are on the *b* lines and are recognizable only from xv posteriorly. Spermathecal pores are minute, on 13/14-14/15, 4-6 on each furrow, on the *a* and *b* lines and in *bc*. Females pores are minute, very slightly lateral to *b* lines and nearer to the setal equator than to 13/14. The wings are low and on xx-xxiv. Grooves from the wings may pass forward to

xiv and back to xxvi, xxvii or xxviii. The genital markings are postsetal, small, circular to elliptical tubercles, slightly depressed peripherally, located on x-xiii, xvi-xix and xxiv-xxx, in *aa* (1, 2, or 3 markings), *ab* and *bc*. Each of these markings appears to be the equivalent of the central tubercle of an *annandalei* marking and without any indication of the wide marginal rim of *annandalei*.

*Internal anatomy*.—Gizzard small, apparently in vii (3 specimens). Intestinal origin in xv (3). Last hearts in xi (3).

*Remarks*.—The low height of the wings, the absence thereon of the tuberosities for which the species was named, and the lack of marginal rims on genital markings presumably cannot, be attributed to incomplete development as presence of spermatozoa in the spermathecal ampullae shows that these worms are mature enough to have completed copulation.

*G. tuberosus* has been known hitherto only from the original description. The present specimens are from a somewhat more southerly portion of the peninsula.

The specimens of "*Criodrilus lacuum*" from the shore at Satpara in Puri district of Orissa, in absence of wings, genital markings and spermathecae, must have been juvenile. The little information that was recorded with regard to these specimens is insufficient even for a generic identification but if the worms are actually of a species of *Glyphidrilus*, as now appears to be probable, they are more likely to be referable to *tuberosus* than to species from more distant regions.

(An attempt to determine the segment in which the dorsal blood vessel ends in this species was made by Dr. S. L. Hora. He states (*in lit.*) that the specimens are "too old and on opening they break in bits" and in the type "I could not possibly trace the vessels".)

### **Glyphidrilus papillatus** (Rosa) 1890

Burma, 1 juvenile, 1 acitellate and 2 clitellate specimens with label that had become illegible. (GEG/JS per N. Tebble.)

*External characteristics*.—Length of juvenile, *ca.* 57 mm. Diameter (adults) in clitellar region, *ca.* 5 mm, but less than 3 mm elsewhere. Anus wholly dorsal, with posterior lobe. The red clitellar coloration extends across xiv-xl at least.

Wings extend across xviii-xxvi and just onto xxvii (3). Unpaired, median genital markings are present in *aa* on xi-xvii and xxix-xxx, xii-xiv and xvii-xviii, xi-xiv and xviii. Paired genital markings, each in median part of *bc* are present on xiv-xvii (1) or xv-xvii (2). Markings are primarily postsetal.

*Internal anatomy*.—Gizzard in viii but apparently reaching well into vii (4). Intestinal origin in xv (4). Typhlosole begins about in xviii and is thickly lamelliform.

The dorsal blood vessel ends with the hearts of vii (4). Last hearts are in xi (4). Hearts of vii-ix are lateral, those of x-xi latero-oesophageal with the larger of the dorsal bifurcations passing to the supra-oesophageal trunk.



Spermathecae are mostly within the parietes, in xiv-xvii with pores on 13/14-16/17 (no spermatozoal iridescence).

*Remarks.*—A posterior portion of each specimen, except the juvenile, is lacking.

The red coloration, which may have been developed since preservation, gradually fades to disappearance both anteriorly and posteriorly so that recognition of definite clitellar boundaries is not possible from external inspection.

*G. papillatus* was erected for a single "mal conservato" specimen and Rosa made no mention of several characteristics on which information is now necessary. Records of the author's re-examination of the type were destroyed during the war. Attempts to arrange for determination of certain characteristics of digestive and vascular systems have been unsuccessful. The specimen may, after more than sixty years, have little or no value as a type.

The worms characterized above can be distinguished from the type only as follows: wings cover 9+ instead of 7 segments and end on an anterior portion of xxvii instead of at 24/25, presence of paired genital markings on xxiv-xxv. These differences certainly cannot be regarded, at present, as justification for erection of a new species. Since *papillatus* must now be defined as having an intestinal origin in xv, and a termination of the dorsal blood vessel in vii, the Indian forms from the western part of the Gangetic plain had to be placed in a different species (p. 55). This in turn makes it doubtful that identification of Hainan worms as *papillatus*<sup>1</sup> is correct. No information as to any taxonomically important characteristics of the Hainan material was supplied.

#### *Glyphidrilus birmanicus*, sp. nov.

Burma, 1 large juvenile, 1 clitellate specimen and anterior portions of 2 clitellate worms with label that had become illegible. (GEG/JS per N. Tebble).

*External characteristics.*—Length, 95-103 (+) mm. Diameter 6 mm. in clitellar region, as much as 5 mm. elsewhere. Prostomium zygalobous. Anus dorsal or dorsoterminal. Nephropores on *b* lines. Clitellar coloration, a deep red, extends across xii or xiii to xliii or xlvi but disappears gradually both anteriorly and posteriorly.

Wings are rather low, on xxi-xxix, in *bc*, just lateral to the genital markings (3). Genital markings are present only in a median portion of *bc*, and as usual are postsetal, on xii to xxi, xxii or xxiii, and xxx to xxxi, xxxiii or xxxiv.

*Internal anatomy.*—Gizzard in viii but apparently extending also through part of vii. Intestinal origin in xv (3). Typhlosole begins about in xviii and is rather thickly lamelliform.

The dorsal blood vessel ends exactly with the hearts of vii (4). The last hearts are in xi (4). Hearts of vii-ix are lateral, of x-xi, latero-oesophageal. A large vessel from the supra-oesophageal runs downwards on each side in vii.

<sup>1</sup>Chen, Y., *Cont. Biol. Lab. Sci. Soc. China*, (Zool.), xii, p. 426 (1938).

Nephridia, in these contracted specimens, fill the space between gut and body wall nearly to the mid-dorsal region. Nephridia lacking in first 11 or 12 segments.

Holandric, male funnels iridescent. Seminal vesicles in ix-xii. Pseudovesicles present in xiii and xiv, in the latter segment larger than in xiii. Spermathecae mostly concealed in the parietes but easily discovered by removal of superficial tissues. Number, 2 to 8 on each side in segments xiv-xviii, with pores on 13/14-17/18.

*Remarks.*—The juvenile is longer than the clitellate worm but even so had lost a posterior portion. Rudiments of wings and genital markings are unrecognizable in spite of the size.

Reproductive apertures, as in *G. papillatus*, were not identified definitely (specimens preserved in strongly contracted state).

Some internal organs had been removed from one of the anterior fragments. Exact site of insertion of septum 7/8 on the gut has not been determined, in these specimens as well as in those of *papillatus* and *gangeticus*. The septum, perhaps as a result of strong contraction, preservation or subsequent maceration, seems not to be attached to the gut. Two gizzards might have been said to be present in one worm (in vii and viii) if a more definite, non-muscular node had been recognizable.

*G. birmanicus* is distinguished from *papillatus* by the larger size, absence of genital markings in *aa*, location of wings on segments xxi-xxix.

#### Glyphidrilus sp.

Rangoon, Burma, 1 juvenile with label that is partly illegible. (GEG/JS per N. Tebble.)

Toungoo, Burma, 2 juveniles. (GEG/JS per N. Tebble.)

*Remarks.*—Internal organization is the same as in *G. papillatus* and *birmanicus*. The size of these juveniles is such as to indicate greater probability of being *birmanicus* than *papillatus*. Gizzard muscularity of the Rangoon worm is confined to viii.

#### Glyphidrilus sp.

1931. *Glyphidrilus papillatus* (part, Gates, *Rec. Indian Mus.* XXXIII, pp. 431-433.

*Remarks.*—A discontinuity in wing location is shown by data for Rangoon worms previously identified as *papillatus* (Gates, 1931, p. 431). The wings in 47 of a series of 71 worms crossed five to ten segments, beginning on xvii, xviii, or xix and ending on xxiii (once), xxiv, xxv, xxvi, xxvii (six times). Although this variation is greater than was found in *gangeticus* the identification, in each of these cases, presumably could have been correct. However, wings began on xxi in 19 and on xxiii in 5 specimens of the series and in each of them ended either on xxv or xxvi. These worms, with wings of four to six segments, may prove to be taxonomically separable from *papillatus*.

#### DISCUSSION

*Species of Glyphidrilus* have been erected in the past, on one to several specimens and characterized mainly or wholly by reference to external characteristics though some, such as locations of male and female pores,

were undetermined and ever since have remained unknown. By far the most important of the external structures have been the wings though some taxonomic value also has been attributed to genital markings. Intraspecific variation in number of segments and in the particular metameres crossed by the wings has now been demonstrated by a fairly long series from a single colony of one species (*gangeticus*). Genital markings, in the same series, varied in intrasegmental location and in number from eight to forty. Markings always were unpaired in the *aa* region of the body, but the value even of that characteristic is uncertain because of the presence on single individuals, of two or possibly three species, of paired and unpaired markings in *aa*. At present, use of genital markings in the taxonomy of *Glyphidrilus* appears to be limited to four pairs of + and — characteristics: presence or absence of markings, presence or absence in *aa*, presence or absence lateral to the *a* line, presence or absence of pairing in *aa*. The wings showed less variation in number of segments involved than the markings. When the range of variation can be anticipated these structures doubtless will continue, because of their immediate visibility, to have considerable taxonomic value.

Little or no variation was found in the same series with respect to five characteristics of internal organization which now appear to be of very considerable phylogenetic as well as taxonomic significance. These internal characteristics have shown that *gangeticus* is not even closely related to *papillatus* with which it had been confused because of similarity in the wings and the genital markings. One of the two remaining cases of discontinuous specific distributions, *papillatus* in Burma and Hainan, apparently rests on identification by external characteristics and information as to internal organization is lacking. In the other case *weberi* of Sumatra, Java, Flores and Celebes, even such facts as were recorded sixty years ago suggest failure to distinguish two or three distinct species. The genus *Glyphidrilus*, in spite then of past opinions to the contrary because of the semi-aquatic habitat of these worms, now promises to be of considerable zoogeographical interest.

The internal organization of the Burmese worms now appears to be more like that of *annandalei* from the southern tip of India than of the species in adjacent regions on either side of Burma. Anomalous distributions and morphological relationships of this same sort are being recognized in various other genera of earthworms. In these cases a sort of reversed phylogeny is attempted.

Specializations and conditions that can be regarded as derived are cancelled out from each species to obtain a primitive generic type. A "proto-glyphidrilus" so obtained is characterized in part only as follows: Digestive system with a single oesophageal gizzard in *vi* and an intestinal origin in *xv*. Circulatory system with a single, uninterrupted dorsal trunk, a pair of commissures connecting that trunk to the ventral vessel in each segment, the commissures of some segments anteriorly from *xi* enlarged and heart-like but lateral. Excretory system with a pair of holonephridia in each segment from *ii* posteriorly.

From the ancestral proto-glyphidrilus, *ceylonensis* is derived by translocation of the gizzard into vii and development of vessels connecting hearts of ix-xi to the supra-oesophageal trunk. Across the straits in southern India, *annandalei* is derived by translocation of the gizzard into viii, abortion of the dorsal blood vessel in i-vi and most of vii along with the commissures of i-vi, and the development of connectives between hearts of x-xi and the supra-oesophageal. Absence of such connectives in ix makes direct derivation from *ceylonensis*, which would otherwise be possible, inadvisable. Far to the north, *gangeticus* has its gizzard in viii, has inhibited development of intestinal characteristics by the gut in xv with resultant addition of one segment to the oesophagus and transfer of intestinal origin to xvi, but has developed connectives to the supra-oesophageal only for the hearts of xi. The latter characteristic contraindicates a direct derivation from *annandalei* that would otherwise be possible. In Burma, the derivation for both species involves the same changes as in *annandalei*. To the east, the gizzard has been transferred into viii in all Malaysian species. The oesophagus has been extended through xvii in one species from Malay Peninsula but only through xv in a Sumatran form. The one evolutionary change in the circulatory system that circumstances permit mentioning is the addition, in *malayanus* (Malay Peninsula), of a pair of hearts in xii that apparently have not yet been added elsewhere. To the far west, in Tanganyika, the derivation involves translocation of gizzard to vii, extension of oesophagus through xvii and addition of two pairs of hearts, in xii-xiii (dorsal trunk?).

The anterior nephridia probably have been aborted in all species and from the first 10 to 14 segments. Intraspecific variation, along with frequent reduction in size of the first few pairs, suggest that this evolutionary process is still going on. Spermathecae, likewise omitted from the preceding portion of this discussion, may also give evidence for present as well as past developments. The supposed rudiments of these organs in the testis segments of an African species provide a link to a stage with pregonadal locations. From that remote ancestor proto-glyphidrilus is derived by multiplication of the spermathecae, translocation of theca-producing capacity through the testis region into more posterior segments and development of the generically unique wings. The polythecal condition, like meronephry in other genera, may have arisen through early embryonic fragmentation of originally paired segmental anlage.

Since establishment of those conditions there has been no uniformity in the evolution of the group. Though subsequent changes are few they appeared in various portions of the proto-glyphidrilus range, from Borneo to Africa, in independent order and at different times. One of these standard changes, foreshortening of the dorsal blood vessel, has taken place in other families of earthworms. Abortion of the trunk back to the commissures of vii, as in *annandalei*, has been found in *Eudrilus* (Eudrilidae) and *Eutyphoeus* (Megascolecidae). In the latter genus this change certainly has been brought about, in some cases, at one step. As such a drastic change can be attributed, in *Eutyphoeus*, to a mutation for histolysis of appropriate sections in the circulatory

system during embryonic development, it seems unnecessary to assume a different origin in other genera.

Greater foreshortening, as in *gangeticus*, may have been due to repeated mutations as also seems required for the one, two, three step changes in connection with the latero-oesophageal hearts, the addition of hearts in xii and then in xiii, the extension of the oesophagus through xv, then xvi and finally xvii, as well as by the still continuing abortion of anterior nephridia. Although backward translocation of the gizzard in phylogeny is obvious, frequent records suggesting transgression of internal intersegmental boundaries makes this one alone of the evolutionary changes difficult to explain by single-step abrupt mutations.

In one portion of the *Glyphidrilus* range, Burma, two or more species are known to be present. One, *birmanicus*, is distinguished by absence of genital markings in *aa* and differences in location of the wings. A mutation for inhibition of genital markings in *aa*, already suggested by rare individuals of *papillatus*, provides for one of the changes. No evidence for abrupt mutational transfer of wings has been found and phylogenetic requirements can be met in this case by assuming varying reductions in size of wings that originally were much longer. This derivation again is indirect and from a common ancestor rather than from an existing form. If an anticipated third species is characterized by pairing of genital markings in *aa*, it may represent continuation of a local ancestral condition prior to establishment of a mutation for mid-ventral union of anlage of paired markings.

#### SUMMARY

Internal organization, which now has been studied in three species enabled examination of the phylogeny of *Glyphidrilus* for the first time. Of the several major and standard evolutionary changes throughout the genus, one can be attributed to a mutation of drastic effect. Others are attributed to repetitions of one-step-at-a-time mutations. These mutations have become established in different sequences at various parts of the generic range which extends from Borneo to Tanganyika. Origin of closely related species in a single area is also attributed to establishment of mutations but this time affecting external characteristics.