TAXONOMY AND DISTRIBUTION OF THE METAPHERETIMA ELONGATA SPECIES-COMPLEX OF INDO-AUSTRALASIAN EARTHWORMS (MEGASCOLECIDAE : OLIGOCHAETA)



BY EDWARD GLYNN EASTON

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SYNOPSIS

Following studies on the setal and spermathecal systems of the *Metapheretima elongata* species-complex five species, *elongata*, *everetti*, *kinabaluensis*, *phacellotheca* and *stelleri* are recognized. The taxonomy and indigenous distributions of each are described.

INTRODUCTION

DURING their numerical revision of the oriental earthworm genus *Pheretima* auct. Sims & Easton (1972:252) proposed that the Indo-Australasian earthworm *Meta-pheretima elongata* (Perrier, 1872) and its allies should be recognized as a single species-complex. They assigned eighteen nominal species and subspecies to the complex and tabulated the variation in expression of several characters. The lack of obvious correlations, however, prevented the delineation of discrete groups of taxa from among the relatively short series of material which they examined.

Subsequently more detailed investigations have continued into the taxonomy of the acaecate members of the *Pheretima* group of genera (*Archipheretima*, *Ephemitra*, *Metapheretima* and *Planapheretima*) and in particular into the members of the *Metapheretima elongata* species-complex which have received special scrutiny. During this latter study the material was located on which many of the taxa and records of the *elongata* species-complex were based. Additionally material of the species *Metapheretima phacellotheca* (not previously included in the *elongata* group of species) was also examined from which it was concluded that this species too is closely allied to the complex. Recent additions to the collections of the British Museum (Natural History) also included many examples of the species-complex. Examination of all this material has provided the data presented in this report from which it is possible to recognize five species and to establish the indigenous distributions of each.

METHODS

During revision of the genus *Metapheretima* it became evident that discrete taxonomic assemblages could be recognized in the *elongata* species-complex on the expression of three characters :

- 1. The volume of a single segment. This value is derived from measurements of the diameter and length of the segment. In specimens that have been dissected the circumference is measured instead of the diameter. For convenience during the study, the segment selected for measurement was *vii* since the volume determination could be assessed when making the setal count (see below) so that a direct correlation could be established between segmental volume and setal number.
- 2. Number of setae. During preliminary studies it was observed that the setal number of vii, in addition to being easier to determine, was also less variable than that of xx, the other segment sometimes selected for study.
- 3. Number of spermathecae. The spermathecae of members of the *elongata* species-complex, although occasionally absent, are usually arranged in paired, ventrolateral batteries of up to 28 spermathecae, opening into intersegmental furrows 5/6 and/or 6/7. The number of pores in each spermathecal battery was recorded.

The three characters employed here as taxonomic criteria differ somewhat from those utilized by Sims & Easton (1972:256). These authors used the length of an individual as an expression of size since this value was readily available in published descriptions. During the present study it became evident that segmental volume provided a more accurate indication of size owing to the vicissitudes of relaxation and fixing techniques causing wide fluctuations in overall length in similarly proportioned individuals. Initially segment number was also employed in this study but the large proportion of the specimens available for examination proscribed by damage or regeneration caused the data to lack significance. Some authors (Beddard & Fedarb, 1895; Michaelsen, 1899, 1922) considered the number of segments bearing genital markings to be of taxonomic importance for distinguishing the species of the *elongata* species-complex. However, when this character was assessed and correlated with the other results the degree of overlap of the groups made it impractical to utilize it as a taxonomic criterion although several groups of individuals could be recognized which were related to those established using the criteria discussed above.

The majority of the taxa included within the *elongata* species-complex by Sims & Easton (1972) are known only from one or two series and whenever possible all the members of those series were examined in this study. Only in the cases of the

common forms *biserialis* and *elongata*, often recorded from outside the *Pheretima* domain, were the number of specimens examined restricted by sampling. These two forms are usually considered synonymous and Sims & Easton (1972:256) suggested that they originated probably in the area bounded by Sumatra, Philippines, Celebes and Java. They concluded that all other records were the result of introduction. Gates (1972:182) however was of the opinion that these forms had originated in a smaller area: Borneo, Celebes and Philippines. All the records that could be traced from these areas were included in the study as well as a selection from several new series collected recently in Bali, Lombok, Sumbawa and Komodo. For many years *phacellotheca* has been known only from the type-series which is now unsuitable for study. It was found however that two specimens from Buru identified by Michaelsen (1934a) as *stelleri bonensis* so closely resembled the original description of *phacellotheca* as to require re-identifying with the result that they were included in the study as representatives of this species.

RESULTS

Correlation between each pair of characters was studied separately.

I. Setal number : segmental volume. The relationship between setal numbers and the volume of segment vii was tested (Fig. 1) and found to provide a means of

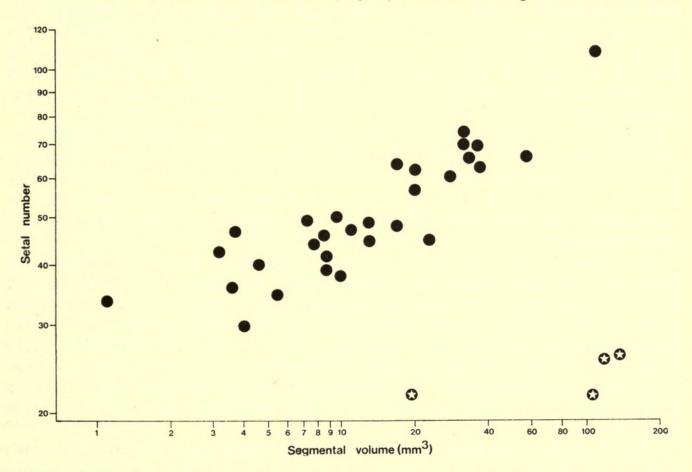


FIG. I. Relationship between the setal number and segmental volume of segment vii (scales logarithmic). Origins of material: Mt Kinabalu (above 2100 m); ● other localities.

recognizing two distinct groups of individuals. The smaller cluster (depicted by circular symbols with star-shaped centres) includes only examples from the upper slopes of Mt Kinabalu, Sabah (*series A*: Sims & Easton, 1972:253), while the larger cluster (depicted by solid circular symbols) contains examples from all other parts of the *elongata* species-complex range. Examples from the larger cluster have considerably higher setal numbers for a given segmental volume than those of the smaller cluster. Examination of the other individuals from the samples identified as *series A* revealed that the majority of them belong to the smaller cluster.

In both groups there is a positive correlation between setal number and segmental volume. The size of an individual, and therefore the segmental volume, increases during an individual's life and it may be deduced from Fig. I that the number of setae also increases. This conclusion has a wide significance in view of the diagnostic value usually attributed to setal number. It is implicit from the literature that the setal number of a segment is assumed to remain fairly constant (allowing for loss, etc.) throughout the life of an individual; indeed, many of the 'species' in the *Pheretima*-complex have been distinguished by smaller differences in the setal numbers than are recorded here.

2. Anterior spermathecal batteries : posterior spermathecal batteries. In the specimens studied each spermathecal battery of an individual rarely contained an identical number of pores although the discrepancies occurring between the right and left batteries within a furrow were small and apparently haphazard. The relationship between the mean number of spermathecae in a battery in furrow 5/6 and in 6/7 was tested (Fig. 2). A positive correlation was established between the sizes of the anterior and posterior batteries for most of the specimens with the posterior pair containing, on average, 20% more spermathecal pores than the anterior pair.

Two specimens, both from Buru (depicted by star-shaped symbols), depart significantly from the general trend. Both these specimens lack spermathecal batteries in furrow 6/7 (confirmed by internal examination) although there are large anterior batteries. Some of the other specimens also lacked posterior spermathecal batteries, but in all these individuals the anterior spermathecal batteries were very small or absent.

Some signs of clustering may be detected in the larger group of specimens, i.e. those with the usual spermathecal arrangement. Specimens from Sumbawa and Komodo (solid square symbols) and Lombok (open square symbols) have small spermathecal batteries, individuals from Borneo (solid circular symbols) and Celebes (open triangular symbols) have batteries of intermediate size while those from Balabac Island (open circular symbols) and Sangihe (solid triangular symbols) have large spermathecal batteries. The individuals from Mt Kinabalu (noted in Fig. I because of their low setal numbers) were indistinguishable from other specimens from Borneo.

3. Setal number : size of spermathecal batteries. Because of the strong positive correlation noted between the relative sizes of the anterior and posterior spermathecal batteries in the main cluster in Fig. 2 the regression line of the main cluster has been utilized as an axis in Fig. 3. Since this line passes close to the origin of

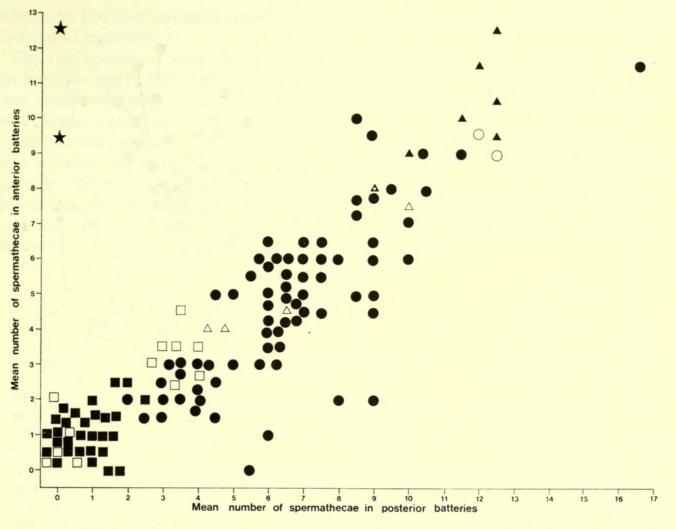


FIG. 2. Relationship between the mean number of spermathecae in the anterior (5/6) and posterior (6/7) batteries. Origins of material: ■ Sumbawa and Komodo; □ Lombok;
Borneo; ○ Balabac Island; ▲ Sangihe; ▲ Kepulaud Taulaud; △ Celebes;
Buru.

Fig. 2 the positions of specimens along this axis are determined by the distance each occurs from the origin. (The positions of specimens along this axis may be calculated directly from the formula $x = \sqrt{(a^2 + b^2)}$, where a and b are the mean sizes of the anterior and posterior spermathecal batteries.) To facilitate the recognition of clusters, members of each sample are linked.

Most of the specimens plotted in Fig. 3 form two discrete clusters. The remaining individuals are scattered in an area, peripheral to the larger of these clusters, which is characterized by large spermathecal batteries and low setal numbers. The first cluster, characterized by high setal numbers and small spermathecal batteries, contains all of the specimens from Java, Bali, Sumbawa and Komodo (depicted by solid square symbols). The series from which these specimens were selected were remarkable in the high proportion of athecate individuals present : approximately half the clitellate portion of each series lacked spermathecae and therefore had to be excluded from this figure. Setal numbers of athecate individuals agreed closely with the thecate individuals plotted. The second cluster, containing individuals

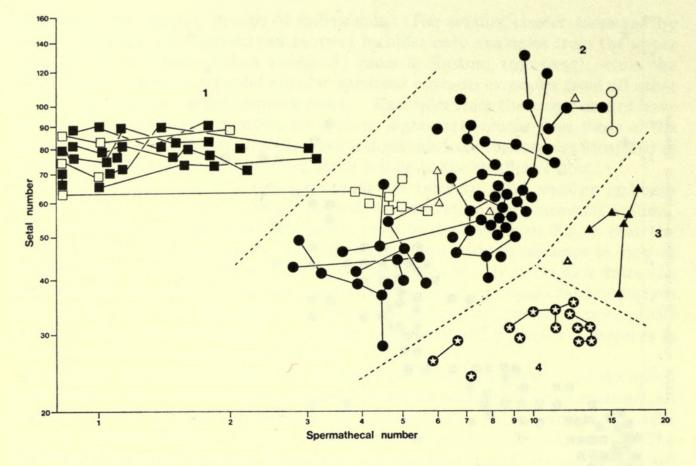


FIG. 3. Relationship between the setal number of segment *vii* and the spermathecal number, $\sqrt{(a^2 + b^2)}$ (scales logarithmic). Members of each series are linked. Origins of material: Sumbawa, Komodo, Bali and Java; \Box Lombok; \bullet Borneo (individuals with a high setae : volume ratio); \bigcirc Borneo (individuals with a low setae : volume ratio); \bigcirc Balabac Island; \blacktriangle Sangihe; \bigstar Kepulaud Taulaud; \triangle Celebes.

with a greater range of setal numbers and larger spermathecal batteries, includes all of the specimens from Balabac Island (open circular symbols), Celebes (open triangular symbols) and Borneo (solid circular symbols) with the exception of the individuals from Mt Kinabalu (circular symbols with star-shaped centres) which were noted (FI) for their low setal numbers.

Specimens from Lombok (open square symbols) occur in both clusters. Individuals from low altitudes (c. 50 m) however belong to cluster I while, with one exception, those from high altitudes (c. 400 m) belong to cluster 2.

The specimens situated peripherally to cluster 2 are those from Sangihe (solid triangular symbols), Kepulaud Taulaud (partially filled triangular symbols) and Mt Kinabalu (circular symbols with star-shaped centres). Since these may be distinguished by the difference in their setal development it is considered that two further clusters should be recognized among material from this area; one containing the specimens from Sangihe and Kepulaud Taullaud(cluster 3) and the other the Mt Kinabalu specimens (cluster4). Although the individuals of cluster 4 resemble those of cluster 3 in their relationships between setal and spermathecal development, it should be recalled (Fig. 1) that the setal development, compared with the segmental volume, is reduced in members of cluster 4, while the relationship of the segmental

volume to the spermathecal development in individuals in this cluster is closer to that found in cluster 2.

The two specimens from Buru (depicted by star-shaped symbols in Fig. 2) have not been plotted in Fig. 3 since they did not occur in the main cluster in Fig. 2. They most closely resemble specimens from Sangihe and Kepulaud Taulaud (cluster 3) on setal numbers and the size of the anterior spermathecal batteries.

The marker attributes of the five groups of individuals recognized above have been tabulated in Table I. Morphologically groups I, 2 and 3 form a series in which the only differences noted are increases in the sizes of spermathecal batteries in individuals of a similar size. Group 4 resembles group 2 but has lower setal numbers. Group 5 differs from group 3 only in lacking spermathecal batteries in furrow 6/7.

TABLE I

M	arker	attributes	of	the	morp	ho	logical	group	S
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	Group	Setae : segmental volume (Fig. 1)	Positions of spermathecal pores (Fig. 2)	Size of spermathecal batteries (Fig. 3)
Ι.	(elongata)	high	5/6 and 6/7	small (cluster 1)
2.	(everetti)	high	5/6 and 6/7	intermediate (cluster 2)
3.	(stelleri)	high	5/6 and 6/7	large (cluster 3)
4.	(kinabaluensis)	low	5/6 and 6/7	intermediate* (cluster 4)
5.	(phacellotheca)	high	5/6 only	large

* See text.

NOMENCLATURAL CONSIDERATIONS

The type-series of nine of the eighteen nominal species and subspecies assigned to the *elongata* species-complex were examined during the preparation of this report, thus permitting these names to be readily allocated to the appropriate morphological group. The types of *elongata* Perrier, 1872 and *biserialis* Perrier, 1875 were not examined, but Michaelsen (1910c) had previously synonymized the taxa and there is no evidence to dispute this decision. On the basis of Michaelsen's published description, as well as those of more recent workers (Stephenson, 1923; Gates, 1972) the types as well as the majority of records of both *elongata* and *biserialis* can be assigned to group I as also may one other taxon, *acystis* Beddard, 1895.

Although the type-series of seven other taxa could not be located during the preparation of this report, it is possible to estimate approximate co-ordinates in Figs 1, 2 and 3 for each of the taxa from the original descriptions. None of the original descriptions recorded segmental volume but approximate values have been calculated based on the mean segmental lengths (total length/segment number) and the maximum diameters. The estimated co-ordinates and the group to which each taxon is assigned are shown in Table 2 where data regarding *stelleri everetti*: Michaelsen, 1899 are also recorded.

In Table 2 it is uncertain to which group *kinabaluensis* Beddard & Fedarb, 1895 should be assigned. The original description lacks any data regarding setal numbers

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TABLE 2

	Segmental volume (mm ³)	Setal number on vii	Positions of spermathecal batteries	Size of spermathecal batteries	Group
Taxon					
baritoensis	11.5	49	5/6/7	4.7	2
beranensis beranensis	I·I	47	5/6/7	8.1	2
kinabaluensis	47.7	-	5/6/7	10.1	2, 3 or 4
phacellotheca	14.2	46	5/6	_*	5
stelleri annectens	28.8	40	5/6/7	26	3
stelleri bonensis stelleri everetti	95.4	131	5/6/7	31	2
(sensu Michaelsen, 1899)	126.2	85	5/6/7	28	3
stelleri koroensis	176.6	60	5/6/7	8	2

Estimated co-ordinates based on published data

* Size of spermathecal batteries not recorded.

so it could belong to any of groups 2, 3 or 4. It seems unlikely to belong to group 3 because the type locality of *kinabaluensis* is Tamburungare, Mt Kinabalu, Sabah, at an altitude of 2350 m (7700 ft) and only groups 2 and 4 are known from Borneo. It is however proposed to assign *kinabaluensis* to group 4 since it is evident from Sims & Easton (1972) that group 4 (*series A*) is the commonest form at altitudes of more than 2100 m.

Information on three records from the Borneo-Celebes area, *stelleri*: Michaelsen, 1896:202; *stelleri*(*typica*): Ude, 1932:155 and *elongata*: Ude, 1932:155, lacks sufficient detail to establish even approximate co-ordinates for this material. Never-theless, as the two records of *stelleri* are from Borneo at altitudes at which group 2 is believed to be the only representative of the complex present, both are assigned to that group, while the record of *elongata*, from south Celebes, is allocated to group I. Although all other records from Celebes have been assigned to groups 2, 3 or 5, they are from the north and west which are ecologically distinct from the south which resembles Lombok and Sumbawa where group I is indigenous (see Distribution).

Each morphological group may be recognized as forming a distinct taxonomic unit. The status of each and its relationships with the others still require considerable study but since there is no evidence of hybridization, although several samples studied contain representatives of more than one group, it is proposed to consider each as a distinct species while retaining them within the *elongata* speciescomplex. The senior synonym allocated to each group is given in Table 1.

TAXONOMY

Metapheretima elongata species-complex

Metapheretima elongata species-complex : Sims & Easton, 1972 : 252. Metapheretima phacellotheca : Sims & Easton, 1972 : 233. DIAGNOSIS. *Metapheretima* with male pores within copulatory pouches lacking stalked glands. Spermathecae in paired, ventrolateral batteries opening in intersegmental furrows 5/6 and/or 6/7. Genital markings simple, large, paired, presetal, on *xix* and successive segments in line with or slightly ventral to the male pores.

DESCRIPTION. External characters. Length 40-360 mm, diameter 1.5-10 mm. 100-220 segments. Clitellum xiv-xvi. First dorsal pore 12/13. Setae regularly distributed around each segment, 20-130 on vii, 36-86 on xx; setal distance aa = 1-2ab; occasionally setae a and b enlarged. Male pores paired on short penes within shallow copulatory pouches on xviii, c. 0.25 body circumference apart. Female pore single; midventral xiv. Sperma-thecal pores small, numerous, arranged in paired, ventrolateral batteries each com-prising up to 28 pores, intersegmental in 5/6 and/or 6/7. Genital markings (Fig. 5a): paired, simple, large, oval presetal papillae on xix and successive segments in line with or slightly ventral to the male pores; occasionally present on vi, vii and xvii. Internal characters. Septa 4/5-7/8 thickened. 8/0 membranous o/10 absent

Internal characters. Septa 4/5-7/8 thickened, 8/9 membranous, 9/10 absent, 10/11-13/14 thickened. Intestine begins in xv. Lateral hearts in x, xi, xii, usually xiii.

Holandric; testes sacs large, paired, extending to the dorsal line in x and xi; seminal vesicles paired in xi and xii, the anterior pair enclosed in the posterior testes sacs. Coelomic sacs in xiii, xiv. Spermathecae (Fig. 5b) numerous, in paired batteries of up to 28 in vi and/or vii. Copulatory pouches shallow, confined to the body wall of xviii.

DISTRIBUTION. Indigenous records: Kepulaud Taulaud; Sangihe; Celebes; Buru; Balabac Island, Palawan; Borneo; ? Madura; east Java; Bali; Lom-bok; Sumbawa; Komodo; ? Gt Bastard Island, Flores. Four of the five species included in this species-complex are known only from the indigenous range. The fifth, *elongata*, has been introduced into many parts of the

world.

world. REMARKS. This species-complex is readily recognized by the positions of the spermathecal pores and the form of the male pores. Three other species of *Meta-pheretima* with similar features may be distinguished either by the absence of genital markings in the case of *M. annamanensis*, a bithecal species known only from the Lang Biang Peaks, Vietnam, or by the form of the genital markings in the cases of *aringeana* from Kelantan, Malaya, and grata from New Guinea. In aringeana the postclitellar genital markings are paired and occur only on xvii and xix as circular pads with many small pores while in grata they are small and numerous, being present only in the region of the spermathecal pores. This latter species also has stalked glands discharging into the copulatory pouches which are large and invade the coelom. Clitellate individuals from the indigenous range of the species-complex are rarely athecate but the majority of specimens examined from introduced popu-lations lack spermathecae. In these populations athecate individuals may be identified by the arrangement of the genital markings and the form of the copulatory pouch. Outside of the *Pheretima* domain, identification is easier since only one

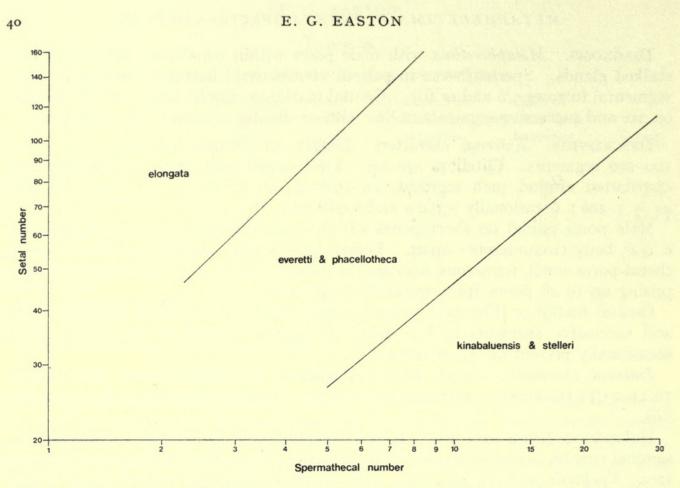


FIG. 4. Metapheretima elongata species-complex. Relationship between the setal number of segment vii and the spermathecal number, $\sqrt{(a^2+b^2)}$, for the member species.

other species of *Metapheretima* is commonly encountered. This species, *M. tapro*banae, has paired spermathecal pores in furrow 7/8 and genital markings on vi-ixand xviii-xxii. Additionally it is considerably smaller than the members of the elongata species-complex, rarely exceeding 140 mm in length.

The species of the *elongata* species-complex may be distinguished from one another by comparison of the setal number on *vii* and the size of the spermathecal batteries (Fig. 4). (The size of the spermathecal batteries is calculated by substituting the mean size of anterior and posterior spermathecal batteries of an individual for *a* and *b* in the formula $x = \sqrt{(a^2 + b^2)}$.)

Two pairs of species, everetti-phacellotheca and stelleri-kinabaluensis, need additional characters to be assessed for differentiation. In the first pair, M. everetti has spermathecae in furrows 5/6 and 6/7 while phacellotheca has spermathecae in furrow 5/6 only. In the second, M. stelleri has very numerous setae on vii (up to 130) while kinabaluensis has few setae (less than 40).

Metapheretima elongata (Perrier, 1872)

Perichaeta elongata Perrier, 1872:124; Beddard, 1895:431.

Megascolex elongata : Vaillant, 1889 : 81.

Amynthas elongatus : Beddard, 1900 : 650.

Pheretima elongata: Michaelsen, 1900: 265; Cognetti, 1905a: 33; Michaelsen, 1910a: 252; (= biserialis) Michaelsen, 1910c: 84; Michaelsen, 1913: 262; Michaelsen, 1920: 68; Stephenson, 1920: 222; Michaelsen, 1922: 32; Stephenson, 1922: 433; Stephenson, 1923: 298; Stephenson, 1924: 339; Gates, 1926a: 208; Gates, 1926b: 444; Gates, 1926c: 183; Gates, 1926d: 153; Stephenson, 1926: 256; Stephenson, 1929: 237; Gates, 1930: 309; Gates, 1931: 378; Stephenson, 1931: 58; Gates, 1932: 391; Gates, 1933: 525; Cernosvitov, 1934: 49; Cernosvitov, 1935: 11; Gates, 1936: 413; Gates, 1937a: 318; Gates, 1937b: 352; Gates, 1937c: 201; Gates, 1939: 87; Daweini, 1940: 110; Gates, 1954: 86; Gates, 1959: 9; Gates, 1960a: 57; Gates, 1960b: 256; Gates, 1961a: 62; Gates, 1961b: 308; Gates, 1972: 182; [non Ohfuchi, 1956: 148 (= Amynthas morrisi)].

Pheretima (Pheretima) elongata : ? Ude, 1932 : 155 ; Michaelsen, 1934a : 108.

Perichaeta biserialis Perrier, 1875: 1044; Beddard, 1890: 63; Beddard, 1895: 430; Michaelsen, 1897: 226; (= acystis) Horst, 1899: 202; Beddard & Fedarb, 1899: 803.

Megascolex (Perriera) biserialis : Vaillant, 1889 : 76.

Amynthas biserialis : Michaelsen, 1899 : 21 ; Beddard, 1900 : 638.

Pheretima biserialis: Michaelsen, 1900:256; Michaelsen, 1902:9; Michaelsen, 1904:285; Cognetti, 1905a:30; Cognetti, 1905b:2; Ude, 1905:471; Michaelsen, 1907:44; Michaelsen, 1908a:187; Michaelsen, 1908b:14; Ohfuchi, 1940:13; Ohfuchi, 1956:151.

Perichaeta acystis [nom. nov. pro biserialis : Beddard, 1890 (non Perrier, 1872)] Beddard, 1895 : 423.

Perichaeta monocystis (lapsus pro acystis) Horst, 1899: 202.

Metapheretima elongata species-complex : Sims & Easton, 1972 : 256, footnote 1.

Metapheretima elongata : Jamieson (in press).

TYPE LOCALITY. Peru.

DIAGNOSIS. *M. elongata* species complex with numerous setae (usually about 80 on *vii* but up to 130 on large individuals) and small spermathecal batteries (rarely more than 3 spermathecae in a battery) in furrows 5/6/7, or 5/6 or 6/7 only or absent. Spermathecal batteries usually present in about 50% of the clitellate portion of indigenous populations to about only 15% of the clitellate portion of introduced populations.

DISTRIBUTION. Indigenous records (Fig. 6). ? Madura; east Java; Bali; Lombok; Sumbawa; Komodo; ? Gt Bastard Island, Flores; ? south-east Celebes. The establishment of the indigenous range of this species is discussed below (see Distribution). The specimens identified from Bali, Lombok, Sumbawa and Komodo represent new indigenous records for the species.

Introduced records. This species has been introduced into many parts of the world; for a summary of these records see Gates (1972). During the preparation of this paper specimens from Queensland, Australia; Tahiti; Antigua, West Indies; and Oman were identified. These represent new introduced records for the species.

Metapheretima everetti (Beddard & Fedarb, 1895)

Perichaeta everetti Beddard & Fedarb, 1895:69; Beddard, 1895:428 (non Amynthas stelleri everetti : Michaelsen, 1899:43).

Perichaeta stelleri : Michaelsen, 1896 : 202 ; (non Michaelsen, 1891 : 39) ; Horst, 1899 : 205. Amynthas stelleri (typica) : Michaelsen, 1899 : 83.

Perichaeta papillata Beddard & Fedarb, 1895: 71; Beddard, 1895: 428.

Perichaeta sarawacensis Beddard & Fedarb, 1895: 71; Beddard, 1895: 429.

Perichaeta barami Michaelsen, 1896 : 203.

Amynthas stelleri barami : Michaelsen, 1899 : 41.

Pheretima stelleri (typica) : Michaelsen, 1922 : 25.

? Pheretima (Pheretima) stelleri (typica): Ude, 1932: 146.

Amynthas stelleri seriatus : Michaelsen, 1899 : 44.

Amynthas stelleri klabatensis Michaelsen, 1899: 46.

Amynthas stelleri bonensis Michaelsen, 1899: 45.

Pheretima stelleri bonensis : Michaelsen, 1900 : 307.

[non Pheretima (Pheretima) stelleri bonensis : Michaelsen, 1934a : 108 (= M. phacellotheca)]

Pheretima stelleri koroensis Michaelsen, 1910b : 109.

Pheretima stelleri mahakkami Michaelsen, 1922:25.

Pheretima (Pheretima) beranensis Michaelsen, 1928: 23.

Pheretima (Pheretima) baritoensis Michaelsen, 1932:9.

? Pheretima (Pheretima) elongata : Ude, 1932 : 155 ; (non Perichaeta elongata Perrier, 1872).

Pheretima (Polypheretima) beranensis tinjarana Michaelsen, 1934b: 25.

Metapheretima elongata species-complex [series B (part)] : Sims & Easton, 1972 : 253.

TYPE LOCALITY. Balabac Island, Palawan. Beddard & Fedarb reported that the type locality of *Perichaeta everetti* is Mt Kinabalu, Sabah. The type series of this species in the collections of the British Museum (Natural History) is labelled as originating from Balabac Island, Palawan. Although Beddard & Fedarb wrote in their introduction that the collection they were reporting was collected from both Borneo and Palawan, no reference to Palawan is made in the general text. It is

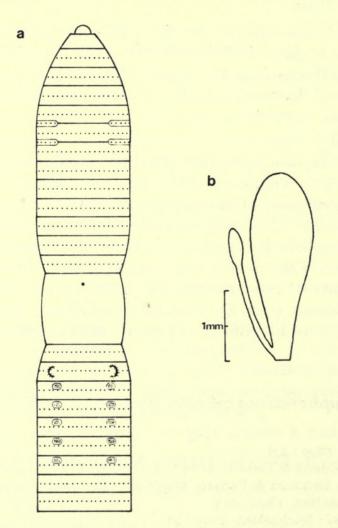


FIG. 5. Metapheretima everetti. (a) Diagram of the papillae pattern on the ventral surface of the anterior region of the body. (b) Spermatheca.

proposed to follow Recommendation 72E of the International Code of Zoological Nomenclature and redesignate Balabac Island, Palawan as the type locality for *Perichaeta everetti* Beddard & Fedarb, 1895.

DIAGNOSIS. *M. elongata* species-complex with numerous setae (up to 130 on *vii* in large individuals) and intermediate-sized spermathecal batteries (usually 6-12 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals.

DISTRIBUTION. Indigenous records (Fig. 6): north and west Celebes; Balabac Island, Palawan; Borneo (up to altitudes of 2400 m); Lombok (c. 350-450 m only).

This species is unknown outside its indigenous range.

REMARKS. On Lombok this species has been recorded only from localities at altitudes between 350 and 450 m. (Samples from lower altitudes contained the species *elongata* which is rare at the higher altitudes. No samples of earthworms are known from above 450 m on Lombok.) Although altitude would appear to be the primary factor governing the distribution of both *everetti* and *elongata*, it should be noted that, on Lombok, the samples of *everetti* were from natural woodland while those of *elongata* were from cultivated land. All the records of *everetti*, *stelleri* and *phacellotheca* from Celebes are from the northern and western region, an area of forest, while the single record of *elongata* (as yet unconfirmed as an indigenous population) is from the southeast which is an area of savannah. On Mt Kinabalu, Borneo, the species *everetti* occurs at altitudes up to 2400 m, being sympatric from 2100 m with the high altitude species *kinabaluensis*.

Although on Lombok and Mt Kinabalu *everetti* is sympatric with other members of the *elongata* species-complex, there is no indication of hybridization among them.

Metapheretima kinabaluensis (Beddard & Fedarb, 1895)

Perichaeta kinabaluensis Beddard & Fedarb, 1895: 71; Beddard, 1895: 429. Metapheretima elongata species-complex [series A & series B (part)]: Sims & Easton, 1972: 253.

TYPE LOCALITY. Tamburgare, Mt Kinabalu, Sabah, 2350 m (7700 ft).

DIAGNOSIS. *M. elongata* species-complex with few setae (less than 40 on *vii* in large individuals) and intermediate-sized spermathecal batteries (usually 6-12 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals.

DISTRIBUTION. Indigenous records (Fig. 6) : Mt Kinabalu, Sabah (2100–2750 m). This species has not been recorded outside its indigenous range.

REMARKS. This species is known only from high altitudes on Mt Kinabalu where the fauna and flora are of a distinct montane type. It is probable that future investigations of the high-altitude earthworm fauna in the Borneo-Celebes area will reveal other population of this species. Although samples collected at 2100 and 2400 m on Mt Kinabalu contained both *everetti* and *kinabaluensis* there is no indication of hybridization between these two forms.

Metapheretima phacellotheca (Michaelsen, 1899)

Amynthas phakellotheca (sic) Michaelsen, 1899:47.

Amynthas phacellotheca : Beddard, 1900 : 640.

Pheretima phacellotheca : Michaelsen, 1900 : 293 ; Gates, 1961 : 304.

Pheretima (Polypheretima) phacellotheca : Michaelsen, 1934b : 15.

Metapheretima phacellotheca : Sims & Easton, 1972 : 233.

Pheretima (Pheretima) stelleri bonensis : Michaelsen, 1934a : 108 ; (non Amynthas stelleri bonensis Michaelsen, 1899 : 45).

TYPE LOCALITY. Mt Masarang, above Tomohon, northeast Celebes.

DIAGNOSIS. *M. elongata* species-complex with numerous setae (up to 80 on vii in large individuals) and large spermathecal batteries (9–12 spermathecae in each battery in large individuals) in furrow 5/6. Spermathecal batteries present in aclitellate as well as clitellate specimens.

DISTRIBUTION. Indigenous records (Fig. 6) : northeast Celebes, Buru.

This species has not been recorded outside its indigenous range.

REMARKS. This species is the only member of the *elongata* species-complex known from Buru which is the most easterly indigenous record of the complex. Morphologically it most closely resembles *stelleri* from which it may be distinguished only by the restriction of spermathecal batteries to furrow 5/6. Its relationships with *everetti* and *stelleri*, which also occur in north Celebes, are unknown.

Metapheretima stelleri (Michaelsen, 1891)

Perichaeta stelleri Michaelsen, 1891: 39; (non Michaelsen, 1896: 202; Horst, 1899: 205). [non Amynthas stelleri (typica): Michaelsen, 1899: 83.]

[non Pheretima stelleri (typica) : Michaelsen, 1922 : 25.]

Pheretima (Pheretima) stelleri (typica) : Michaelsen, 1934a : 108 (non Ude, 1932 : 146).

Amynthas stelleri annectens : Michaelsen, 1899 : 42.

Amynthas stelleri everetti : Michaelsen, 1899 : 43 ; (non Perichaeta everetti Beddard & Fedarb, 1895 : 69).

TYPE LOCALITY. Sangihe.

DIAGNOSIS. *M. elongata* species-complex with very numerous setae (up to 130 on *vii* in large individuals) and large spermathecal batteries (up to 28 spermathecae in each battery of large individuals) in furrows 5/6/7. Spermathecal batteries present in aclitellate as well as clitellate individuals.

DISTRIBUTION. Indigenous records (Fig. 6): Kepulaud Taulaud; Sangihe; north Celebes.

This species has not been recorded outside its indigenous range.

REMARKS. In Celebes *stelleri* has been recorded from Bone Valley (c. 400 m) and the Matinang range (c. 1500 m). In both of these areas *everetti* has also been recorded but the relationship between the two species and the factors governing their distribution are unknown. No information is available regarding the relationship between *stelleri* and *phacellotheca*.

DISTRIBUTION

All the records attributed to *everetti*, *stelleri*, *kinabaluensis* and *phacellotheca* (groups 2, 3, 4 and 5) are from Borneo, Celebes or nearby islands and it is considered that these records indicate the indigenous ranges of the species. The species *elongata* (group I) has been recorded from islands as far apart as Luzon, New Guinea and Sumatra in the Indo-Australasian Archipelago (as well as many other localities throughout the world) but it is thought that this distribution is not entirely natural and that it has been augmented through accidental introduction by man. In the area adjacent to the range of the other members of the complex *elongata* has been recorded from Sumatra, Java, Madura, Bali, Lombok, Sumbawa, Komodo, Gt Bastard Island, Celebes, Kepulaud Taulaud and the Philippines and it is suspected that at least some of these records are from indigenous populations. Among these localities Lombok and Celebes are of particular interest since the most closely related member of the complex, *everetti*, has also been recorded from these islands.

Although the majority of species of the *Pheretima* group possess normal hermaphrodite reproductive systems and are assumed to reproduce only sexually, several species are known to occur as morphs lacking portions of the reproductive system. Gates (1972) recognized four principal morphs: H morph, the normal hermaphrodite form; A morph, lacking spermathecae; R morph, lacking male terminalia; and Z morph, lacking testes. (In addition to these basic forms he also recognized AR and ARZ morphs.) He considered that, with the exception of the H morph, all these forms reproduced by parthenogenesis. He recorded 70 species of the *Pheretima* group from Burma of which 42 were known only from Burma and the adjacent area while 19 were peregrine; only 6% of the indigenous species but 47% of the peregrine forms are known to possess non-hermaphrodite morphs. This correlation between non-hermaphrodite morphs and peregrine distributions led Gates (1956) to suggest that the peregrine species *Metaphire anomala* (Michaelsen, 1907) had originated from eastern Burma where the H morph was more common.

TABLE 3

Population characteristics of M. elongata from selected islands

Island	Number of clitellate specimens examined	Proportion of H morphs (%)
Jamaica	84	18
Sumatra	47	15
west & central Java	13	15
east Java	22	50
Madura	3	(2)*
Bali	27	44
Lombok	19	26
Sumbawa	59	
Komodo	4 5	51
Kepulaud Taulaud	I	(o)*
Philippines	9	(1)*

* For small samples (less than 10 individuals) the number of thecate individuals (rather than the percentage) has been recorded and placed in parentheses.

Metapheretima elongata similarly occurs as H and A morphs so if the hypothesis is valid then the H morph will be more common in its indigenous range than elsewhere. Samples of island populations were examined and the incidence of H morphs was calculated from among the clitellate portion of each series. The results of this study are shown in Table 3. (Java was treated as two regions since it may be considered to be composed of two ecologically distinct areas, tropical rain forest in central and west Java and savannah in east Java.) To obtain a comparative value for a population which was known to be introduced, the incidence of H morphs was assessed in a population from Jamaica. The low incidence of H morphs in the introduced Jamaican population (18%) agrees very well with that of the populations from central and west Java and Sumatra (both 15%) but contrasts strongly with populations from east Java, Bali, Sumbawa and Komodo (44-51%). The value calculated for Lombok (26%) is intermediate between the two classes and somewhat anomalous in view of the geographical position of the island. Possibly the small size of the sample may be the causative factor. Assuming the basic assumption to be valid, these calculations indicate that elongata is indigenous in east Java, Bali, Lombok, Sumbawa and Komodo, while the form which is morphologically the most similar, everetti, occurs at high altitudes (c. 400 m) in Lombok. These values are consistent in the degree of magnitude with those recorded by Gates (1956) when he recorded 20% H morphs of anomala in eastern Burma but only 0-7% in other parts of Burma.

Samples from Kepulaud Taulaud, Philippines and Madura were too small to derive any reliable conclusions from them but it seems unlikely that elongata is indigenous in either Kepulaud Taulaud or the Philippines, although it may possibly occur naturally in Madura. There have been single inconclusive records of elongata from south-east Celebes and Gt Bastard Island but in the former case the specimens cannot be located and in the latter the single extant specimen proved to be indeterminate and the occurrence of indigenous populations of elongata in both of these islands has yet to be confirmed. The known indigenous distributions of the members of the elongata species-complex are shown in Fig. 6. The earthworm fauna of south-east Asia has been extensively studied (Gates, 1972) and data from this work and other recent collections in the British Museum (Natural History) have allowed the establishment of the western limit of the indigenous range of the complex. Unfortunately the earthworm faunae of the Philippines, Celebes, Moluccas and Lesser Sunda Islands still require considerable study and it is not practical to establish the northern and eastern limits of the distribution of the complex. However, recent extensive collecting in New Guinea (Easton, in preparation) indicates that the complex is absent from this island except for introduced populations of elongata.

The form *kinabaluensis* is known only from Mt Kinabalu, Sabah, at altitudes of over 2100 m. It is probable that future collections will reveal that it also occurs on some of the other high mountains in Borneo and possibly even Celebes. Likewise the occurrence of *everetti* in Lombok at altitudes of 400 m may indicate that it occurs at high altitudes throughout the Lesser Sunda Islands.

Metapheretima stelleri has been recorded from Sangihe, Kepulaud Taulaud and north Celebes. Michaelsen (1934b) was of the opinion that this species had been

METAPHERETIMA ELONGATA SPECIES-COMPLEX

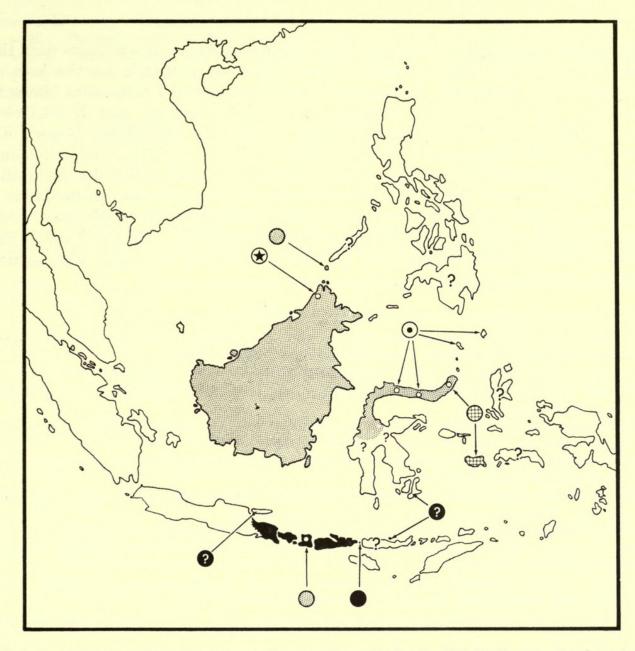


FIG. 6. Metapheretima elongata species-complex. Endemic distributions: ● elongata;
● everetti; ● kinabaluensis; ● phacellotheca; ● stelleri; ? limits of range uncertain;
o isolated or minor localities.

introduced into both Sangihe and Kepulaud Taulaud, but this view is inconsistent with the species' restricted distribution in Celebes. (At the time of Michaelsen's paper the species was thought to be widespread in both Borneo and Celebes.) The wide distribution of the species-complex, crossing both the Flores Sea and the Makassar Strait, suggests that the complex is of considerable antiquity and M. stelleri may have reached both Sangihe and Kepulaud Taulaud at a time when land bridges existed between these islands and Celebes.

In Celebes the ranges of each of the three forms occurring there as well as the natural occurrence of *elongata* have still to be established.

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APPENDIX

MATERIAL EXAMINED AND OTHER RECORDS FROM THE INDO-AUSTRALASIAN ARCHIPELAGO Museums :

- Amsterdam Zoologisch Museum, Universiteit van Amsterdam
- Institut für Spezielle Zoologie und Zoologisches Museum, Berlin Berlin
- BM(NH)British Museum (Natural History), London
- Bogor Museum Zoologicum Bogoriense, Bogor
- Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg Hamburg
- Leiden Rijksmuseum van Natuurlijke Historie, Leiden
- Museum National d'Histoire Naturelle, Paris Paris

The suffixes C and A refer to the numbers of clitellate and aclitellate individuals in each series respectively.

Metapheretima elongata (Perrier, 1872)

I. MATERIAL COLLECTED BY DR G. A. LINCOLN DURING THE BRITISH UNIVERSITY DRAGON EXPEDITION, May-September 1973. BM(NH) 1975.7.59-302.

Sumatra: Simabur, IC; Sungalamas, 4C 5A; Kalianda, 6C.

Java: village 16 km north of Balaradja, 1C; plantation 11 km west of Tomo, 11C 5A; Krijan, 3C; cultivated area 6 km east of Bangil, 10C 2A; Pasir Putih, 7C 4A; Baluran, 1C; Sukamade, 2C.

Bali: Udjung, 15C 1A; foothills 8 km north of Klungkung, 12C 12A.

Lombok : Surawadi, IC ; Songian, 26C IIA

Sumbawa: Alas, 15C; Kanar, 14C; Lape, 7C; Lampang, 9C; Napa, 9C 1A; cultivated area 5 km east of Dompu, 10C 11A; forest 8 km west of Bolo, 7C 1A.

Komodo; Komodo village, 4C.

2. OTHER MATERIAL EXAMINED.

Philippines: Bataan, Luzon, 4C, Paris AE 634, 638, 643 (elongata: Jamieson, in press); Mindoro, 6C, Paris AE 639-642, 644* (elongata: Jamieson, in press); Manila, Luzon, 2C 1A, BM(NH) 1904.10.5.1-2 (biserialis: Beddard, 1890; syntypes of acystis).

Kepulaud Taulaud : Salibaboe Liroeng, Salibaboe Island, 1C 1A, Amsterdam V.ol 254 (elongata : Michaelsen, 1934a).

Sumatra: Bindjey Estate, 3C 1A, Hamburg v.352 (biserialis: Michaelsen, 1899); north-east Sumatra, 2C 1A, Hamburg v.5060; Poeloe-Weh, 33C 11A, Leiden 1879, 1882, 1887, 1888 (elongata: Michaelsen, 1922); Nias Island, 1A, Leiden.

Madura : 3C 1A, Leiden 1880, 1883 (elongata : Michaelsen, 1922).

Java: Cimaja, Pelabuhanratu, 15C 1A, Bogor Ann. 090 & BM(NH) 1975.5.1-4.

Flores: Groot Bastaard Island, I macerated specimen, Leiden 1886 (elongata: Michaelsen, 1922). Jamaica: 84C, 99A; BM(NH).

3. OTHER RECORDS FROM THE INDO-AUSTRALASIAN ARCHIPELAGO.

Kei Islands : Elat, Gross Kei (elongata : Michaelsen, 1910).

Java : Malang (elongata : Michaelsen, 1922).

Celebes : Boeton (elongata : Ude, 1932).

New Guinea : Kila Kila, Madang district (elongata : Sims & Easton, 1972).

Metapheretima everetti (Beddard & Fedarb, 1895)

I. MATERIAL COLLECTED BY DR G. A. LINCOLN DURING THE BRITISH UNIVERSITY DRAGON EXPEDITION, August 1973. BM(NH) 1975.57-58, 303-313.

Lombok : Bentak, IIC 2A.

2. OTHER MATERIAL EXAMINED.

Celebes : Minahassa, IC, Hamburg v.3836 (barami : Michaelsen, 1896) ; —,† 2C IA, Hamburg v.5197, 5198 (types of stelleri seriatus) ; Klabat, IC, Hamburg v.5196 (holotype of stelleri klabatensis).

* A specimen from this series was examined by Sims & Easton (1972 : 254) and referred to as a syntype of *Perichaeta biserialis* Perrier, 1875. Further information has now been obtained and it is now certain that the specimen is not typical since it was not collected until 1876.

[†] The material on which the subspecies *stelleri seriatus* was described came from the Uangkahulu valley; north side of Matinang range; south side of Matinang range and Buol. There is no indication from which of these localities the two series in the Hamburg Museum were collected.

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Palawan: Balabac Island, 2C, BM(NH) 1904.10.5.38-40 (syntypes of everetti).

Borneo: Mt Kinabalu, Sabah, 6C 3A, BM(NH) 1971.19.12-20 [series A (part), series B (part): Sims & Easton, 1972]; Baram river, Sarawak, 1C, Hamburg v.3835 (holotype of barami); Labuan, 1C, BM(NH) 1904.10.5.150 (holotype of sarawacensis); Sarawak, 8C 6A, BM(NH) 1904.10.5.1336-1340; Long Lejok, Sarawak, 6C 13A, BM(NH) 1933.10.6.36-42 & Hamburg v.11956 (stelleri everetti: Michaelsen, 1934); Tinjar river, Long Lejok, Sarawak, 8C 10A, BM(NH) 1933.10.6.12-20 & Hamburg v.11951 (syntypes of beranensis tinjarana); Merabah, Sarawak, 14C 12A, BM(NH) 1904.10.5.1265-70 (syntypes of papillata); Putussibau, Kalimanton, 10C 13A, Leiden 1091 (stelleri: Horst, 1899); Nangaraun, Kalimanton, 5C 9A, Leiden 1903 (stelleri: Horst, 1899); 'the Liang Koeboeng' (the exact location of this locality could not be established), 1C, Leiden 1904 (stelleri; Horst, 1899); Bendjermasin, Kalimanton, 1C, Hamburg v.4024 [stelleri (typica): Michaelsen, 1899]; Bo river, Kalimanton, 3C, Leiden 1900 & Hamburg v.9307 [stelleri (typica): Michaelsen, 1922]; above Mahakkam rivers, Kalimanton, 1C, Leiden 1897 (holotype of stelleri mahakhami); Birang river, Beran district, Kalimanton, fragments of one or more specimens, Hamburg v.10576 [type(s) of beranensis].

Lombok: Swela, IC, Berlin 7214 [this specimen is here separated from the type series of Metapheretima badia (Ude, 1932)].

3. OTHER RECORDS.

Celebes: Koro valley [type(s) of stelleri koroensis]; Bone valley (types of stelleri bonensis).

Borneo: Baram river, Sarawak (stelleri: Michaelsen, 1896); Dorf Poh Trap, Brunei [stelleri (typica): Ude, 1932]; Boentok, on the Barito river, Kalimanton [type(s) of baritoensis].

Metapheretima kinabaluensis (Beddard & Fedarb, 1895)

I. MATERIAL EXAMINED.

Borneo : Mt Kinabalu, Sabah, 12C 2A, BM(NH) 1971.19.1-11, 21-23 [series A (part), series B (part) : Sims & Easton, 1972].

2. OTHER RECORDS.

Borneo: Tamburungare, Mt Kinabalu, Sabah [type(s) of kinabaluensis].

Metapheretima phacellotheca (Michaelsen, 1899)

MATERIAL EXAMINED.

Celebes : Mt Masarang, above Tomohon, several spermathecae and fragments of body wall, Hamburg v.5195 [type(s) of *phacellotheca*].

Buru : between Mnges'wain and Leksula, IC, Amsterdam V.ol 302 (stelleri bonensis : Michaelsen, 1934) ; Leksula, IC, Amsterdam.

Metapheretima stelleri (Michaelsen, 1891)

I. MATERIAL EXAMINED.

Sangihe : —, 7C 1A, Hamburg v.338, BM(NH) 1904.10.5.162 & Leiden 1903 (syntypes of stelleri).

Kepulaud Taulaud : Lobo, Karakelang, IC, Amsterdam V.ol 303.

2. OTHER RECORDS.

Celebes : Matinang range (stelleri everetti : Michaelsen, 1899) ; Bone valley [type(s) of stelleri annectens].

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