

# Checklist of Pheretimoid Earthworms (Oligochaeta: Megascolecidae) of the World: I. Genera *Archipheretima* Michaelsen, 1928, *Begemius* Easton, 1982, *Dendropheretima* James, 2005, *Duplodicrodrilus* Blakemore, 2008, *Isarogoscolex* James, 2005, *Manus* Blakemore, 2010, *Planapheretima* Michaelsen, 1934, and *Pleionogaster* Michaelsen, 1892

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**ABSTRACT.** – This paper is the first of a series that aims to provide an updated checklist of all pheretimoid earthworm species recorded so far in the world after the latest pheretimoid checklist by Blakemore (2007). Eight out of 14 currently accepted pheretimoid genera are featured in this study, namely: *Archipheretima* Michaelsen, 1928, *Begemius* Easton, 1982, *Dendropheretima* James, 2005, *Duplodicrodrilus* Blakemore, 2008, *Isarogoscolex* James, 2005, *Manus* Blakemore, 2010, *Planapheretima* Michaelsen, 1934, and *Pleionogaster* Michaelsen, 1892. Altogether, a total of 67 nominal species and subspecies are included in this checklist, where the taxonomic treatments, diagnostic characters, the type locality and the status of type specimens of each taxon are provided.

**KEYWORDS:** megadrile, systematics, taxonomy

## INTRODUCTION

‘Pheretimoid’ earthworms, originally used by Sims and Easton (1972), denote a group of megascolecoid earthworm species most of which had been previously classified under the genus *Pheretima* Kinberg, 1867, but currently are reassigned to several other genera. The first pheretimoid species, *Perichaeta taitensis* (= *Amyntas taitensis*) was described by E. Grube (1866). Several authors then attempted to compile all pheretimoid species at that time, but the generic classification was indeterminate as the species were equivocally assigned to either *Megascolex* Templeton, 1844 or *Perichaeta* Schmarda, 1861 (Beddard, 1895; Vaillant, 1889). Later, W. Michaelsen (1899c) and F.E. Beddard (1900b) compiled the pheretimoid species under *Amyntas* Kinberg, 1867 (= *Amyntas* Kinberg, 1867), which was the first available pheretimoid genus described by J.G.H. Kinberg (1867). However, Michaelsen (1900) in his foundational monograph, perceiving that “*Amyntas*” sensu Kinberg, 1867 was the junior homonym of *Amyntas* Wollaston, 1865 (Insecta: Coleoptera), assigned all species possessing a more or less continuous ring of more than eight setae around each segment and one gizzard not in front of the septum 7/8 to *Pheretima*, the allegedly remaining available pheretimoid genus described by Kinberg (1867). Michaelsen (1900) also settled the taxonomic confusion among *Perichaeta*, *Pheretima*, and *Megascolex* (see more details in Sims and Easton (1972)), and the generic usage of *Pheretima* had ever

since been adopted by following preeminent earthworm taxonomists: H. Ude, L. Cognetti de Martiis, J. Stephenson, G.E. Gates, and Y. Chen.

At the time before Sims and Easton (1972), *Pheretima* constituted nearly 750 nominal species, making it the largest known genus of earthworms. In order to divide the genus *Pheretima* into smaller, more manageable taxa, Sims and Easton (1972) applied numerical analyses, where the resulting assemblages were then recognized as eight genera (one being divided into two subgenera). Within these genera, two were newly introduced (*Ephemitra* Sims & Easton, 1972 and *Pithemera* Sims & Easton, 1972), and three were elevated from the subgeneric rank (*Archipheretima* Michaelsen, 1928, *Metapheretima* Michaelsen, 1928, and *Planapheretima* Michaelsen, 1934). The genus *Pheretima* was retained, constituting the nominotypical subgenus and the subgenus *Parapheretima* Cognetti, 1912. For the remaining two genera, Sims and Easton (1972) opted *Amyntas* and *Rhodopis* Kinberg, 1867, being originally described together with *Pheretima* but often deemed synonyms of *Pheretima*, to represent two of the resulting assemblages. Therefore, *Amyntas* was resurrected, whereas *Rhodopis*, being the junior homonym of *Rhodopis* Reichenbach, 1854 (Aves: Trochilidae), was replaced by *Metaphire* Sims & Easton, 1972.

Regarding the selection of the generic name “*Amyntas*” as valid over its variant spelling “*Amyntas*”, Sims and Easton (1972) provided the history to some extent. In the original description of this monotypic genus, Kinberg (1867) established two

different original spellings: the first mention of “*Amyntas*” on p. 97 but with a variant spelling of “*Amyntas*” on p. 101. Later, some authors used these two variants inconsistently, as in Perrier (1872) and Vaillant (1889), whereas most other authors mentioned or adopted the spelling “*Amyntas*” only, as in Benham (1886), Beddard (1895, 1900b), and Michaelsen (1899b, c). However, the generic names “*Amyntas*” or “*Amyntas*” had not been used ever since the reclassification of all pheretimoid earthworms into *Pheretima* by Michaelsen (1900) until the resurrection of “*Amyntas*” by Sims and Easton (1972). Although Sims and Easton (1972) mentioned that Vaillant (1889) was the First Reviser to select the spelling “*Amyntas*” over “*Amyntas*”, this is incorrect since according to the Code, the First Reviser is the “first author to have cited them together and to have selected one spelling as correct” (ICZN 1999: Art. 24.2.3). Therefore, Sims and Easton (1972), complying with the Code, were the First Revisers to select “*Amyntas*” as the correct spelling.

Later in the revision of the acaecate pheretimoid earthworms, Easton (1979) synonymized *Ephemitra* with *Metapheretima*, resurrected *Polypheretima* Michaelsen, 1934, previously a synonym of *Metapheretima*, and included *Pleionogaster* Michaelsen, 1892 among the pheretimoids. Although Gates (1982) criticized the subdivision of pheretimoid and still classified all pheretimoid species under *Pheretima*, other authors largely adopted the classification scheme proposed by Sims and Easton (1972) and Easton (1979), as “a genus with more than 750 species has outlived its usefulness” (Reynolds and Reinecke, 1976). Since then, five more genera were newly described and included in the pheretimoid earthworms, namely: *Begemius* Easton, 1982, *Dendropheretima* James, 2005, *Isarogoscolex* James, 2005, *Duplodicrodrilus* Blakemore, 2008, and *Manus* Blakemore, 2010. Therefore, a total of 14 genera are currently recognized in the pheretimoid earthworms (Blakemore, 2020), where all generic names, along with the type species and diagnostic characters of each genus are given in Supplementary Table 1.

At present (as of 2023), a total of 1,552 available nominal species and subspecies of pheretimoid earthworms have been recorded, a number twice increased since Sims and Easton (1972), representing an expansion of earthworm taxonomic studies in mainland Southeast Asia, East Asia, and the Philippines (Fig. 1). This paper is thus the first of a series that aims to provide an updated checklist of all pheretimoid earthworm species recorded so far in the world after the latest pheretimoid checklist by Blakemore (2007), which contains approximately 930 valid species names. The part I here features the genera

*Archipheretima*, *Begemius*, *Dendropheretima*, *Duplodicrodrilus*, *Isarogoscolex*, *Manus*, *Planapheretima*, and *Pleionogaster*.

## MATERIALS AND METHODS

Taxonomic treatments, diagnostic characters, and the type locality of each species were assembled by examining and reviewing the literature published between 1866 and 2023. The generic placements mainly follow Sims and Easton (1972), Easton (1979), James (2005, 2006, 2009), and Blakemore (2007, 2019, 2020), and the genera and species in this checklist are listed alphabetically. Within each species or subspecies, the taxonomic treatment includes the original combination of the taxon name with original spelling, and references to the page(s) and plate and/or figures. The type locality is given as stated in that respective publication, and when possible, the modern name and/or regional name of those localities is provided in square brackets. In addition, when possible, the type materials with catalogue numbers are provided under the Remarks section. The status of type materials of some taxa is checked with the curator of each respective museum or checked via the collection database of each respective museum when available (as of August 2024) and given in Supplementary Table 2.

### Institutional abbreviations

**AMSS** = Australian Museum Department of Marine Invertebrates, Sydney

**HNUE** = Soil Organism Research Centre, Hanoi National University of Education, Hanoi

**KUNHM** = Kansas University Natural History Museum, Lawrence, Kansas

**MGDG** = Museo Civico di Storia Naturale “Giacomo Doria,” Genoa

**MNCN** = Museo Nacional de Ciencias Naturales, Madrid

**MZB** = Museum Zoologicum Bogoriense, Bogor

**MZUT** = Museo Regionale di Scienze Naturali, Turin

**NHM** = Natural History Museum, London

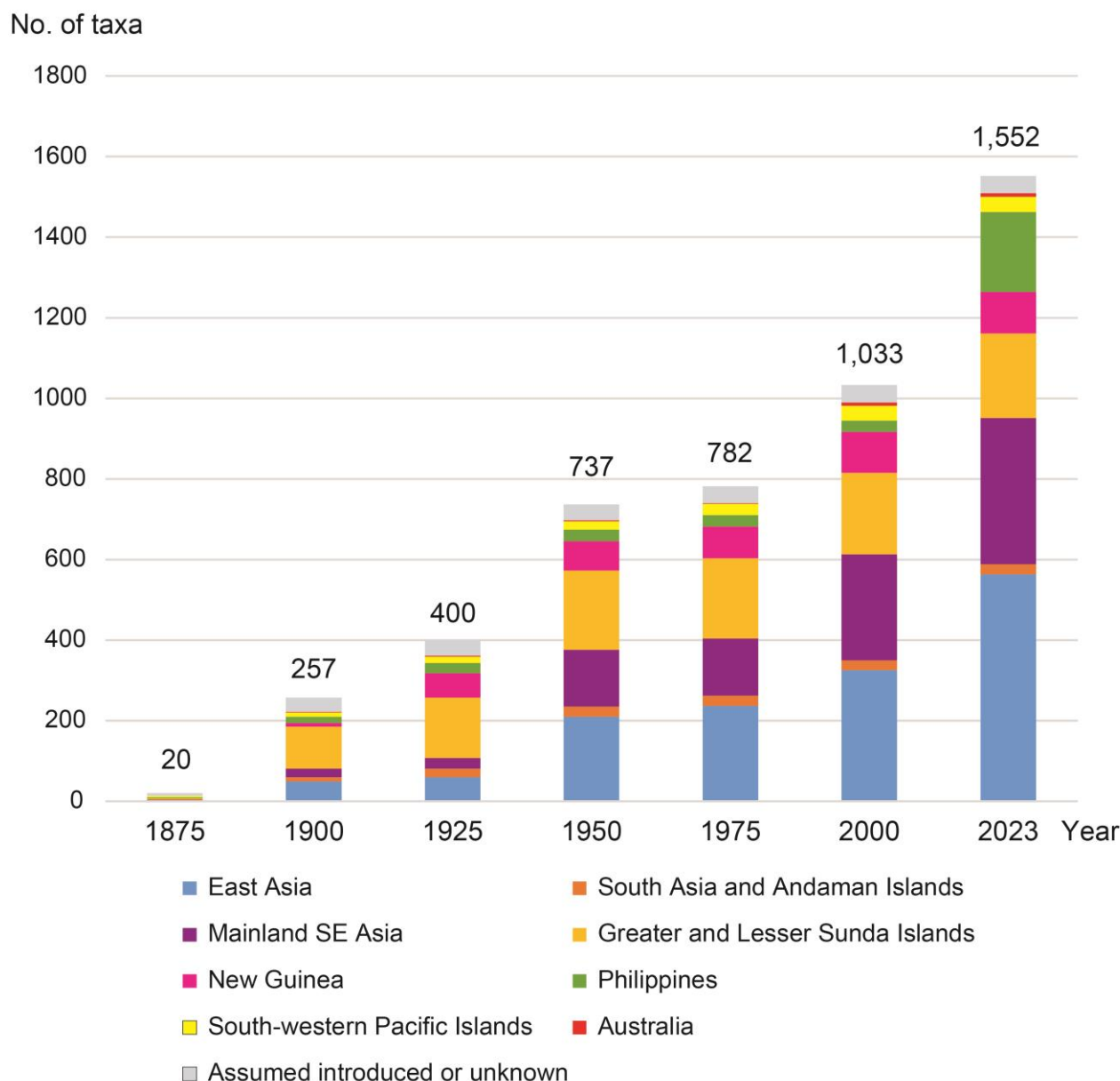
**NHMUK** = when citing specimen lots deposited in the NHM

**NMA** = National Museum of the Philippines Annelida collection, Manila

**NSMT** = National Museum of Nature and Science, Tokyo

**QMBA** = Queensland Museum, Brisbane

**RMNH** = Naturalis Biodiversity Center, Zoology Collections (Rijksmuseum van Natuurlijke Historie), Leiden



**FIGURE 1.** The number of available names of pheretimoid earthworm species per 25 years during 1875–2023. Each colour represents a different geographic region of the taxon's type locality.

**UPLBMNH** = University of the Philippines Los Baños  
Museum of Natural History, Laguna

**UPV** = University of the Philippines Visayas, Miagao  
Museum of Natural History, Laguna

**WNHM** = Naturhistorisches Museum Wien, Vienna

**ZMB** = Museum für Naturkunde – Leibniz-Institut für  
Evolution- und Biodiversitätsforschung, Berlin

**ZMH** = Museum der Natur Hamburg, Zoologie –  
Leibniz Instituts zur Analyse des Biodiversitätswandels,  
Hamburg

**ZMUM** = Zoological Museum, University of Moscow,  
Moscow

## RESULTS

### SYSTEMATICS

#### Family Megascolecidae Rosa, 1891

##### *Archipheretima* Michaelsen, 1928

*Pheretima* (*Archipheretima*) Michaelsen, 1928a: 7–8.  
Michaelsen 1934: 15.

*Archipheretima*—Sims and Easton 1972: 200–201,  
232. Easton 1979: 21–22. James 2009: 244.e3.

**Type species.**— *Megascolex iris* Michaelsen, 1892, by original designation.

**Other originally included species.**— *Pheretima* (*Archipheretima*) *picta* (Michaelsen, 1892) (= *Polypheretima picta*), *Pheretima* (*Archipheretima*) *beccarii* Cognetti, 1910 (= *Polypheretima beccarii*), *Pheretima* (*Archipheretima*) *zonata* Michaelsen, 1922 (= *Archipheretima zonata*), *Pheretima* (*Archipheretima*) *penrissenii* Michaelsen, 1928 (= *Archipheretima penrissenii*), *Pheretima* (*Archipheretima*) *moultoni* Michaelsen, 1913 (= *Planapheretima moultoni*), *Pheretima* (*Archipheretima*) *pallescens* Michaelsen, 1928 (= *Planapheretima pallescens*), *Pheretima* (*Archipheretima*) *maculata* Ude, 1925 (= *Planapheretima maculata*), *Pheretima* (*Archipheretima*) *scandens* Michaelsen, 1928 (= *Planapheretima maculata*), *Pheretima* (*Archipheretima*) *nieuwenhusi* [sic] Michaelsen, 1922 (= *Planapheretima nieuwenhuisi*)

**Diagnosis.**— Pheretimoid with male pores superficial; without copulatory pouches or other secondary male pore structure. Clitellum 12, 13–16, 17, ½18. Calciferous lamellae vertical in lateral esophageal pouches 11–13. Paired supraesophageal vessels with connectives to the calciferous lamellae. Dorso-lateral intestinal caeca three to six pairs in region of 29–35. Heart 13 attached post-septally. Spermathecal duct without nephridia. Holandric.

**Remarks.**— This taxon was formerly a subgenus of *Pheretima*, and later raised to the specific rank by Sims and Easton (1972). The generic diagnosis by Sims and Easton (1972) and Easton (1979) stated that the lamellae in the esophagus and the intestinal caeca were absent and did not mention the paired supraesophageal vessels. Later, James (2009) emended the diagnosis by including these characters.

### 1. *Archipheretima cofini* James, 2009

*Archipheretima cofini* James, 2009: 244.e12–244.e13, fig. 3c, d.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores face posteriorly on low rounded porophores on 18; male field sunken, surrounded by lateral ridges. Clitellum 13–16, 17 dorsal only. Genital markings paired ovals on 19/20, broad midventral 9/10, 20/21–½21; deep smooth-surfaced indentations flanking porophores 17/18, 18/19. Paired intestinal caeca pocket-shaped in 30–32, shallower in 33–36. Spermathecae octothecate; ampulla irregular ovate, broad duct shorter than ampulla, confined to body wall; diverticulum single shortly stalked or sessile transversely placed ovate receptacle with 2–3 internal

chambers; diverticulum attachment largely within body wall but receptacle not within.

**Type locality.**— Lower montane forest in climbing ferns, 17°07.34'N, 121°10.20'E, 1675 m asl, Barangay Lias of Barlig, Mt. Lamagan, Mountain Province, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004168) (James, 2009).

### 2. *Archipheretima gritzae* James, 2009

*Archipheretima gritzae* James, 2009: 244.e7–244.e9, fig. 1a, b.

**Diagnosis.**— Spermathecal pores paired on 6/7–8/9. Male pores transverse slits superficial on 18 on ovate low conical porophores. Clitellum ½13, 14–½17. Genital markings paired concavities with smooth, slightly darker surface posterior to male pores within 18, broad midventral oval on 19/20, midventral oval post-setal 9 to presetal edge of 10 or 10/11. Paired intestinal caeca simple in 29–32 or 30–33. Spermathecae sexthecate; ampulla ovate, broad duct shorter than ampulla; diverticulum single shortly stalked or sessile terminating in ovate receptacle with 2–4 internal chambers.

**Type locality.**— Low elevation forest north of Barangay Summit, Buradan, 13°46'N, 124°16'E, 275 m asl, Catanduanes Province, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004174), and three additional adult paratypes are housed in the KUNHM (Invertebrate Zoology No. 002355) (James, 2009).

### 3. *Archipheretima iris* (Michaelsen, 1892)

*Megascolex iris* Michaelsen, 1892: 244–245, fig. 24. Beddard 1895: 383.

*Amyntas* [sic] *iris*—Michaelsen 1899c: 15. Beddard 1900b: 647.

*Pheretima iris*—Michaelsen 1900: 276.

*Archipheretima iris*—Sims and Easton 1972: 200–201, 232, 243. Easton 1979: 26, figs 10d, 11d. Nakamura 1999: 16. Blakemore 2007: 51. James 2009: 244.e3–244.e4.

**Diagnosis.**— Spermathecal pores paired on 6/7–8/9. Male pores on 18, at peaks of conical porophores; porophores with smooth darkened surfaces. Clitellum 13–½17. Genital markings broad midventral oval on 17/18, but mainly on presetal half of 18, similar marking 18/19 mainly on postsetal 18, oval midventral

19/20, 20/21. Paired intestinal caeca simple in 31–32, 33. Spermathecae sixthecate; ampulla ovate, narrow duct shorter than ampulla; diverticulum single shortly stalked terminating in ovate receptacle with one internal chamber; diverticulum-duct junction within body wall.

**Type locality.**— Samar, Loquilocun, the Philippines.

**Remarks.**— The syntypes are housed in the ZMB (No. 565) and MZUT (MZUT O1122) (Easton 1979; James, 2009; Supplementary Table 2; R. Tota, pers. comm., 14 Aug 2024).

#### 4. *Archipheretima margaritacea* (Michaelsen, 1892)

*Megascolex margaritacea* Michaelsen, 1892: 245–246, fig. 25. Beddard 1895: 383–384.

*Amyntas* [sic] *margaritaceus*—Michaelsen 1899c: 16. Beddard 1900b: 647.

*Pheretima margaritacea*—Michaelsen 1900: 282.

*Archipheretima margaritacea*—Sims and Easton 1972: 232, 244. Easton 1979: 25–26, figs 10c, 11c. Nakamura 1999: 16. Blakemore 2007: 63. James 2009: 244.e4.

**Diagnosis.**— Spermathecal pores paired on 6/7–8/9. Male pores on 18, covered from the front by a small bulge. Clitellum 13, 14–16, 17. Genital marking one midventral at 10/11, composed of oval field with numerous small dark flecks; paired genital markings almost fused over 18/19. Genital markings at 9/10, 12/13, 19/20 in some specimens. Intestinal caeca not known. Spermathecae sixthecate; ampulla simply sac-shaped, without a clearly recognizable muscular duct; diverticulum sac-shaped, the length of which is approximately equal to half the length of the sac.

**Type locality.**— Samar, Loquilocun, the Philippines.

**Remarks.**— The syntype is housed in the ZMH (ZMH-ANN-V00361) (James, 2009; J. Moore, pers. comm., 8 Aug 2024).

#### 5. *Archipheretima mazarredi* (Rosa, 1894)

*Megascolex mazarredi* Rosa, 1894: 765–767, fig. 5.

*Amyntas* [sic] *mazarredi*—Michaelsen 1899c: 15. Beddard 1900b: 644.

*Pheretima mazarredoi* [sic]—Michaelsen 1900: 283. Gates 1970: 155–158.

*Archipheretima mazarredoi* [sic]—Sims and Easton 1972: 232, 244. Nakamura 1999: 16.

*Archipheretima mazarredi*—Easton 1979: 22–23, figs 10a, 11a. Blakemore 2007: 63. James 2009: 244.e4.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores superficial on 18, equatorial and rather widely separated; on male field at 17–20, transversal margins slightly marked, lateral margins swollen. Clitellum 13–16. Genital markings paired, as whitish transverse depressions about in line with the male porophores and so rather widely separated, at 17/18–18/19, or 18/19–20/21. Intestinal caeca absent. Spermathecae octothecate; ampulla ovate almost confined to the body wall, with a large and short duct; diverticulum small, heart-shaped to spheroidal, or very shortly ellipsoidal.

**Type locality.**— Marinduque Island, the Philippines.

**Remarks.**— Rosa (1894) stated that the type material is housed in the MNCN, but currently could not be located (S. T. Moreno, pers. comm., 19 Sep 2024).

#### 6. *Archipheretima middletoni* James, 2009

*Archipheretima middletoni* James, 2009: 244.e9–244.e11, figs 1c–e, 2.

**Diagnosis.**— Spermathecal pores paired on 6/7–8/9. Male pores transverse slits superficial on 18 on ovate to hemispheric porophores; male field strongly concave. Clitellum 12–17, ½18. Genital markings postsetal oblong flanking spermathecal pores in 6–8 encroaching on 6/7–8/9; genital markings intersegmental paired oval to lanceolate in line with male pores on 17/18–19/20, and some on 20/21, 21/22; those of 17/18–18/19 curved around porophores. Paired intestinal caeca simple in 29–32 or 30–33, 34 or 31–34. Spermathecae sixthecate; ampulla spherical, broad duct shorter than ampulla, duct fluted internally, confined to body wall; diverticulum simple, mostly or wholly within body wall.

**Type locality.**— Maria Aurora National Park, old growth remnant forest, 15°41'N 121°22'E, 725 m asl, Aurora Province, the Philippines.

**Remarks.**— The holotype and two adult paratypes are housed in the NMA (NMA 004171, NMA 004172), and five additional adult paratypes are housed in the KUNHM (Invertebrate Zoology No. 002349) (James, 2009).

#### 7. *Archipheretima ophiodes* (Michaelsen, 1929)

*Pheretima* (*Archipheretima*) *ophiodes* Michaelsen, 1929: 85–90, pl. 1, fig. a–c.

*Pheretima ophiodes*—Michaelsen 1930: 273–280, pl. 1, figs 1–3.

*Archipheretima ophiodes*—Sims and Easton 1972: 232, 244. Easton 1979: 27–28, fig. 12a. Nakamura 1999: 16. Blakemore 2007: 73. James 2009: 244.e7.

**Diagnosis.**— Spermathecal pores paired on 4/5–6/7. Male pores superficial on 18, on medial crest of transversely oval, strongly raised whitish porophores extending from 18 to 20. Lateral margin of porophores continues in a thick white wall. Intersegmental furrows between the male porophore and this wall at 17/18–19/20 with a dark, glandular appearance. Clitellum 12–17. Genital markings lacking. Intestinal caeca not known. Spermathecae sexthecate; ampulla pyriform to sac-like, not differentiated into main ampulla and duct; diverticula small, globular.

**Type locality.**— Mt. Azapan, Luzon, the Philippines.

**Remarks.**— The syntype is housed in the ZMH (ZMH-ANN-V10418) (James, 2009; J. Moore, pers. comm., 8 Aug 2024).

#### 8. *Archipheretima pandanophila* James, 2009

*Archipheretima pandanophila* James, 2009: 244.e13–244.e14, fig. 3e, f.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores face posteriorly on low hemispheric porophores on 18; male field sunken ½17–½20, surrounded by lateral ridges. Clitellum 13–17. Genital markings indistinct paired smooth-surfaced dark indentations flanking porophores at 17/18, 18/19. Paired pocket-shaped intestinal caeca in 30, 31–35. Spermathecae octothecate; ampulla cordate to ovate, broad duct shorter than ampulla, duct nearly confined to body wall; diverticulum single sessile transversely placed triangular receptacle with 3–4 internal chambers, attachment largely within body wall but receptacle not within.

**Type locality.**— Lower montane forest in pandan plants, 16°27.03'N, 121°13.06'E, 1274 m asl, Mt. Palali, Solano, Nueva Vizcaya Province, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004173), and one additional paratype is housed in the KUNHM (Invertebrate Zoology No. 002354) (James, 2009).

#### 9. *Archipheretima penrisseni* (Michaelsen, 1928)

*Pheretima* (*Archipheretima*) *penrisseni* Michaelsen, 1928a: 11–14, fig. 1. Nakamura 1999: 16. Blakemore 2007: 108.

*Archipheretima penrisseni*—Sims and Easton 1972: 232, 245.

*Archipheretima zonata* [in part]—Easton 1979: 23–25. ? *Archipheretima penrisseni*—James 2009: 244.e7.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores on 18, on fairly small, transversely oval, cushion-like, raised porophores quite close to the ventral median line; male field at 16–20; lateral margins curved. Clitellum ½13–17 at dorsal; 14–16 at ventral. Genital marking large, transversely oval, unpaired, incised by the intersegmental furrow, ventral median to these furrows at 17/18 and 18/19; genital markings paired, small, on 16/17 and 19/20, median to the ventral median line. Genital markings four pairs on 17/18 and 18/19 in some specimens. Intestinal caeca not known. Spermathecae octothecate; ampulla elongated, sac-shaped, somewhat narrowed in the apical half or irregularly shaped, and a sharply defined, duct very short and narrow completely hidden in body wall; diverticulum scarcely ¼ as long as the ampulla, with a thick, up to four chambers with different size, and a short, narrow stalk.

**Type locality.**— Berg Penrissen [Gunong Penrissen], ca. 1200 m., West Sarawak, Malaysia.

**Remarks.**— The syntypes are registered at the ZMH (ZMH-ANN-V10513), but currently stated as missing (J. Moore, pers. comm., 8 Aug 2024). Although Easton (1979) and Blakemore (2007) treated this species as a junior synonym of *A. zonata*, James (2009) posited that this species is distinct from *A. zonata* due to an unstriped body appearance, unpaired female pores, an absence of septa 8/9–9/10, testes and funnels within thin-walled sacs that may be joined ventrally and in segment 11 united with seminal vesicles, spermathecal duct entirely within body wall and spermathecal diverticula divided internally.

#### 10. *Archipheretima ricei* James, 2009

*Archipheretima ricei* James, 2009: 244.e11–244.e12, figs 1f, g, 3a, b.

**Diagnosis.**— Spermathecal pores paired on 6/7–8/9. Male pores face posteriorly on low rounded porophores on 18 with deep indentations anterior and posterior to porophores; male field sunken, surrounded by lateral ridges. Clitellum 13–15, incompletely developed. Genital markings paired ovals on these possible intersegmental furrows of 9/10–11/12, 19/20–21/22. Paired shallow intestinal caeca in 30, 31–33. Spermathecae sexthecate; ampulla ovate to knobby, broad duct shorter than ampulla; diverticulum single

shortly stalked or sessile terminating in ovate receptacle with 2–4 internal chambers; duct and diverticulum attachment largely within body wall.

**Type locality.**— Montane forest on Mt. Akbab, Kalahan Foundation land, 16°11.44'N, 120°52.21'E, 1675 m asl, Barangay Imugan of Santa Fe, Nueva Vizcaya Province, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA004169) (James, 2009).

### 11. *Archipheretima zonata* (Michaelsen, 1922)

*Pheretima zonata* Michaelsen, 1922: 42–44, fig. 13.

*Pheretima* (*Archipheretima*) *zonata*—Michaelsen 1928a: 11.

*Archipheretima zonata*—Sims and Easton 1972: 181, 232, 246. Nakamura 1999: 16. Nugroho 2010: 106 (appendix 1). Blakemore 2007: 108.

*Archipheretima zonata* [in part]—Easton 1979: 23–25, figs 10b, 11b.

? *Archipheretima zonata*—James 2009: 244.e6–244.e7.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores rather inconspicuous, marked by a pair of tiny, papillae-shaped, circular porophores standing close together on 18 and adjacent to the ventral median line. Clitellum 13–17. Genital markings lacking. Intestinal caeca not known. Spermathecae octothecate; ampulla ovate, narrow duct shorter than ampulla; diverticulum single shortly stalked terminating in ovate receptacle with 2–4 externally demarcated chambers.

**Type locality.**— Nanga Raoen, Borneo, Indonesia.

**Remarks.**— The holotype is housed in the RMNH (RMNH.VER.OL.1816) (James, 2009; Supplementary Table 2). James (2009) suspected that this species might not belong to *Archipheretima* due to the presence of striped pigmentation throughout, and esophageal hearts with the last hearts in 12.

### *Begemius* Easton, 1982

*Begemius* Easton, 1982: 713–716. Blakemore 2020: 461–462.

**Type species.**— *Begemius jamiesoni* Easton, 1982, by original designation.

**Other originally included species.**— *Begemius gavini* Easton, 1982, *Begemius jamiesoni hornensis* Easton, 1982, *Begemius lockerbiensis* Easton, 1982, *Begemius queenslandicus* (Fletcher, 1887), *Begemius raveni* Easton, 1982, *Begemius yorkensis* Easton, 1982,

*Begemius cyclops* (Cognetti de Martiis, 1911), *Begemius monoperus* (Cognetti de Martiis, 1911)

**Diagnosis.**— Pheretimid with male pores superficial; without copulatory pouches or other secondary male pore structure. Clitellum 14–16. Lateral crescentic genital markings usually associated above and/or below the male pores. Calciferous lamellae in paired dorsal esophageal pouches often present in 10, occasionally in 11–13. Dorso-lateral intestinal caeca one pair, starting from 25, 26. Spermathecal duct without nephridia. Metandric.

**Remarks.**— Xiao (2019) classified five Chinese pheretimid species (*dinghumontis* Zhang et al., 2006, *heshanensis* Zhang, Li & Qiu, 2006, *jiangmenensis* Zhang, Li & Qiu, 2006, *paraglandularis* Fang, 1929, and *yuhsi* Tsai, 1964) in *Begemius*. However, Xiao (2019) did not mention the important diagnostics of *Begemius*: (1) calciferous lamellae in paired dorsal esophageal pouches and (2) lateral crescentic genital markings associated with male pores, and these species have not been known to possess these characters. Therefore, the generic classification of these Chinese species in *Begemius* is dubious, and these species were not included in this checklist.

### 1. *Begemius cyclops* (Cognetti de Martiis, 1911)

*Pheretima cyclops* Cognetti de Martiis, 1911: 1. Cognetti de Martiis 1912: 554–556, pl. 22, figs 30, 31.

*Pheretima* (*Metapheretima*) *cyclops*—Ude 1932: 180–181.

*Amyntas cyclops*—Sims and Easton 1972: 234, 241.

*Begemius cyclops*—Easton 1982: 716. Nakamura 1999: 18.

*Begemius* ? *cyclops*—Blakemore 2006: 3. Blakemore 2007: 26.

**Diagnosis.**— Spermathecal pores single median on 5/6–6/7. Male pores small transverse slits on large porophores on 18, the base of which is as wide as the length of 18th segment. Female pores paired on 14, surrounded by 2 light-colored areas that merge in the middle. Clitellum 14–16. Genital markings paired circular, presetal, close to ventral midline on 7–9; paired as transversely oval papillae abutting the porophores and in line with male pores, postsetal on 17, presetal on 19, 20. Paired intestinal caeca simple, starting from 26, extending forward to 23. Seminal vesicles digitiform, one pair in 12, attached to the posterior surface of septum 11–12, extending to the sides of the esophagus from the ventral region. Spermathecae single median in 6–7; ampulla ovate, distinct from the robust duct by a slight constriction;

and with two simple, short subcylindrical diverticula, opening on the duct's anterior surface at half of its length.

**Type locality.**— Mt. Cyclops [Gunung Cycloop], West Irian [Papua], Indonesia.

**Remarks.**— The syntype is housed in the RMNH (ZMA.V.OL.251) (Reynolds and Cook, 1976; Supplementary Table 2). Ude (1932) reported that the intestinal caeca are very short and only limited to segment 26, whereas Easton (1982) stated that the intestinal caeca start on segment 25 and extend anteriorly to segment 24.

### 2. *Begemius gavini* Easton, 1982

*Begemius gavini* Easton, 1982: 717, figs 2a, 3a. Nakamura 1999: 19. Blakemore 2007: 41.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores superficial on 18, lacking perigenital ridge. Female pore single on 14. Clitellum 14–16. Genital markings large, paired, circular papillae; preclitellar slightly lateral to the line of the spermathecal pores, presetal on 7–9, postsetal on 5–9; postclitellar in line with the male pores, presetal on 17, 19–25; paired crescentic markings anterior and posterior to the male pores on 18. Paired intestinal caeca simple, starting from 25, extending forward to 23. Seminal vesicles extending to the dorsal line in 12; pseudoseminal vesicles absent from 13, vestigial or absent in 14. Spermathecae octothecate; ampulla round, duct very short; diverticulum simple, originating near the spermathecal base, with the same width throughout, as long as half of ampulla.

**Type locality.**— Horn Island, Torres Strait, Queensland, Australia.

**Remarks.**— The holotype and two paratypes are housed in the QMBA (No. GH197–198), and eight additional paratypes are housed in the NHM (NHMUK 1980.46.1–8) (Easton, 1982; Supplementary Table 2).

### 3. *Begemius jamiesoni hornensis* Easton, 1982

*Begemius jamiesoni hornensis* Easton, 1982: 720, figs 2c, 3b. Blakemore 2007: 51.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores on short, stout penes on 18, surrounded by incomplete perigenital ridge. Female pore single on 14. Clitellum 14–16. Genital markings paired circular to ovate papillae; preclitellar in line with or slightly lateral to the spermathecal pores, both presetal and postsetal on 6–9; postclitellar in line with or slightly

lateral to the male pores, presetal on 19–23; crescentic markings lacking. Paired intestinal caeca simple, starting from 25, extending forward to 24. Seminal vesicles large with slim dorsal processes, extending to the dorsal line; pseudoseminal vesicles absent. Spermathecae octothecate; ampulla ovate, duct nearly half as ampulla length; diverticulum simple, originating near the spermathecal base, widest at the middle, not extending beyond half of ampulla.

**Type locality.**— Horn Island, Torres Strait, Queensland, Australia.

**Remarks.**— The holotype and four paratypes are housed in the QMBA (No. GH 191–193), and 11 additional paratypes are housed in the NHM (NHMUK 1980.46.29–39) (Easton, 1982; Supplementary Table 2).

### 4. *Begemius jamiesoni jamiesoni* Easton, 1982

*Begemius jamiesoni* Easton, 1982: 717–719. Nakamura 1999: 19.

*Begemius jamiesoni jamiesoni* Easton, 1982: 719–720, fig. 2b. Blakemore 2007: 51.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores on short, stout penes on 18, completely encircled by perigenital ridge. Female pore single on 14. Clitellum 14–16. Genital markings paired circular to ovate papillae; preclitellar in line with or slightly lateral to the spermathecal pores, both presetal and postsetal on 6–9; postclitellar in line with or slightly lateral to the male pores, presetal on 20–23; crescentic markings lacking. Paired intestinal caeca simple, starting from 25, extending forward to 24. Seminal vesicles large with slim dorsal processes, extending to the dorsal line; pseudoseminal vesicles absent. Spermathecae octothecate; ampulla ovate, duct nearly half as ampulla length; diverticulum simple, originating near the spermathecal base, widest at the middle, not extending beyond half of ampulla.

**Type locality.**— Lockerbie East, Cape York, Queensland, Australia.

**Remarks.**— The holotype and five paratypes are housed in the QMBA (No. GH194–196), and 13 additional paratypes are housed in the NHM (NHMUK 1980.46.16–28) (Easton, 1982; Supplementary Table 2).

### 5. *Begemius lockerbiensis* Easton, 1982

*Begemius lockerbiensis* Easton, 1982: 720–721, figs 2d, 3c. Nakamura 1999: 19. Blakemore 2007: 59.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores superficial on 18, lacking perigenital ridge. Female pore single on 14. Clitellum 14–16. Genital markings large paired papillae; preclitellar median to the line of the spermathecal pores, presetal on 8–9; postclitellar with lateral margins in line with the male pores, presetal on 17 and 19; paired crescentic markings anterior and posterior to the male pores on 18. Paired intestinal caeca simple, starting from 25, extending forward to 23. Seminal vesicles extending to the dorsal line in 12; pseudoseminal vesicles absent from 13, vestigial in 14. Spermathecae octothecate; ampulla round, duct nearly half as ampulla length; diverticulum simple, originating at the spermathecal base, widest at the end, extending to nearly half of ampulla.

**Type locality.**— Lockerbie East, Cape York, Queensland, Australia.

**Remarks.**— The holotype and two paratypes are housed in the QMBA (No. GH186–187), and four additional paratypes are housed in the NHM (NHMUK 1980.46.40–43) (Easton, 1982; Supplementary Table 2).

#### 6. *Begemius monoperus* (Cognetti de Martiis, 1911)

*Pheretima monopera* Cognetti de Martiis, 1911: 5–6. Cognetti de Martiis 1912: 553–554, pl. 22, figs 25–29. Sims and Easton 1972: 225, 244.

*Begemius monoperus*—Easton 1982: 716.

*Begemius monopera*—Nakamura 1999: 18.

*Begemius ? monoperus*—Blakemore 2006: 3. Blakemore 2007: 66.

**Diagnosis.**— Spermathecal pore single median on 5/6 only. Male pores closely paired on short, stout penes on 18, each of which surrounded by a dark, somewhat depressed area, extending almost from the anterior edge of 18 to the posterior edge of 19, narrowing a little at 18/19. Female pore single on 14. Clitellum not recognizable. Genital markings paired papillae; postclitellar with lateral margins in line with the male pores, presetal on 17. Intestinal caeca not recognizable. Seminal vesicles possibly two pairs in 11 and 12; the second pair oblong, with a digitiform terminal appendage. Spermatheca single median in 5/6; ampulla subpyriform, duct distinct, nearly as long as ampulla length; and with two simple ental diverticula, each of which is half the length of the duct.

**Type locality.**— Joccha, on the shores of Lake Sentani, near Humholdt Bay [Papua], Indonesia.

**Remarks.**— The type material could not be located. Easton (1982) stated that the intestinal caeca start on 25 and extend anteriorly to 24. Blakemore (2007) stated that the prostatic ducts were provided with copulatory pouches as indicated in Cognetti de Martiis (1911), so this species is possibly not in *Begemius*. However, the exact translation in Cognetti de Martiis (1911, 1912) indicated that the prostate glands have no copulatory pouches.

#### 7. *Begemius queenslandicus* (Fletcher, 1887)

*Perichaeta queenslandica* Fletcher, 1887: 962–966, pl. 13, fig. 6. Beddard 1895: 407.

*Amyntas* [sic] *queenslandicus*—Beddard 1900b: 643.

*Pheretima queenslandica*—Michaelsen 1900: 297–298. Michaelsen 1917: 34–37, pl. 1, fig. 22. Nakamura 1999: 54.

*Amyntas queenslandicus*—Sims and Easton 1972: 237, 245.

*Begemius queenslandicus*—Easton 1982: 721–723, figs 2e, 3d. Nakamura 1999: 19. Blakemore 2007: 84. Blakemore 2020: 462–464.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores small transverse slits on conical to spherical penes on 18, lacking perigenital ridge. Female pores paired on 14. Clitellum 14–16. Genital markings large, paired, circular to oval papillae; preclitellar, in line with or slightly median to the spermathecal pores, presetal on 5–11; postclitellar, in line with the male pores, presetal on 17, 19–23; paired crescentic markings anterior and posterior to the male pores on 18. Paired intestinal caeca simple, starting from 25, extending forward to 21–22. Seminal vesicles extending to the dorsal line in 12; pseudoseminal vesicles absent from 13, vestigial in 14. Testes sac single in 11, horseshoe-shaped coalescing dorsally above oesophagus. Spermathecae octothecate; ampulla conical, duct nearly half as ampulla length, widest at the ampulla base; diverticulum simple, short, originating near the ampulla base and extending just shortly beyond the ampulla base. Glandular masses on coelomic body wall associated with genital markings in mature specimens longer than 150 mm.

**Type locality.**— Barron River District, North Queensland, Australia.

**Remarks.**— The syntypes are housed in the AMSS (No. W2399) (Easton, 1982; Supplementary Table 2).

**8. *Begemius raveni* Easton, 1982**

*Begemius raveni* Easton, 1982: 723–724, figs 2f, 3e.  
Nakamura 1999: 18. Blakemore 2007: 85.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. Male pores on small penes on 18, lacking perigenital ridge. Female pore single on 14. Clitellum not recognizable. Genital markings large, paired, circular to oval papillae; postclitellar, median to the line of the male pores at 17/18 and 19/20; paired crescentic markings posterior to the male pores on 18 closed to the intersegmental furrow, and in mature specimens somewhat invaginated as transversely oval region between furrow 17/18 and the setal line of 19. Paired intestinal caeca simple, starting from 25, extending forward to 24. Seminal vesicles extending to the lateral line in 12; pseudoseminal vesicles absent. Spermathecae quadrithecate, small; ampulla ovate, duct nearly half as ampulla length; diverticulum thick, coiled, originating at the spermathecal base and extending slightly beyond half of ampulla.

**Type locality.**— East, Cape York, Queensland, Australia.

**Remarks.**— The holotype and five paratypes are housed in the QMBA (No. GH199–200), and nine additional paratypes are housed in the NHM (NHMUK 1980.46.112–120) (Easton, 1982; Supplementary Table 2).

**9. *Begemius spectabilis* (Rosa, 1898)**

*Perichaeta neoguineensis* var. *spectabilis* Rosa, 1898: 60–61.

*Amyntas neoguineensis* var. *spectabilis* [sic]—Beddard 1900b: 642.

*Pheretima spectabilis*—Michaelsen 1900: 304–305.

*Pheretima* (*Metapheretima*) *spectabilis*—Ude 1932: 182–183.

*Amyntas spectabilis*—Sims and Easton 1972: 237, 246.

*Begemius* ? *spectabilis*—Blakemore 2006: 3–4. Blakemore 2007: 93.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. Male pores minute on transverse, slightly oval penes on 18, with flat, concentrically wrinkled, indecisive margins, not reaching the adjacent intersegments. Female pore single on 14. Clitellum 14–16. Genital markings large, paired, more or less oval papillae; postclitellar, in line with the male pores, on 19–25, 26. Paired intestinal caeca simple, starting from 26. Seminal vesicles single pair in 12; discoid, thick, non-lobed, with a small finger-like prolongation at the outer anterior margin. Spermathecae octothecate; ampulla

oval, duct short; diverticulum small, round, with racemose structure internally.

**Type locality.**— Hughibagu, New Guinea Britain [Papua New Guinea].

**Remarks.**— The syntypes are housed in the MGDG (MGDG 44005) and the MZUT (MZUT 159) (Reynolds and Cook, 1976; R. Tota, pers. comm., 5 Sep 2024). Ude (1932) reported a variation in some characters of this species, e.g., no setae in clitellar region, septa in all segments present, last hearts in 12, and intestinal caeca starting from 27, compared to setae found ventrally in clitellar region, septa 8/9 rudimentary and 9/10 missing, last hearts in 13, and intestinal caeca starting from 26 in Rosa (1898).

**10. *Begemius yorkensis* Easton, 1982**

*Begemius yorkensis* Easton, 1982: 724, figs 2g, 3f. Nakamura 1999: 19. Blakemore 2007: 107.

**Diagnosis.**— Spermathecal pores paired on 4/5, 5/6–8/9. Male pores superficial on 18, lacking perigenital ridge. Female pore single on 14. Clitellum 14–16. Genital markings large, paired circular papillae; preclitellar close to the median line, presetal on 5–9, in line with the spermathecal pores, postsetal on 6–9, usually only presetal or postsetal markings present; postclitellar, median to the line of the male pores, presetal on 17, 19–23; paired crescentic markings anterior and posterior to the male pores on 18. Paired intestinal caeca simple, starting from 25, extending forward to 22. Seminal vesicles extending to the dorsal line in 12; pseudoseminal vesicles absent from 13; vestigial 14. Spermathecae octothecate to decathecate; ampulla pyriform, ampulla-duct junction not clear; diverticulum simple, narrow, widest at the end, originating nearly at one fifth from the spermathecal base, and extending to nearly half of ampulla.

**Type locality.**— Lockerbie East, Cape York, Queensland, Australia.

**Remarks.**— The holotype and one paratype are housed in the QMBA (No. GH184–185), and four additional paratypes are housed in the NHM (NHMUK 1980.46.151–153) (Easton, 1982; Supplementary Table 2).

***Dendropheretima* James, 2005**

*Dendropheretima* James, 2005: 272–273.

**Type species.**— *Dendropheretima banahawensis* James, 2005, by original designation.

**Other originally included species.**— *Dendrophetima bicolensis* James, 2005

**Diagnosis.**— Pheretimid with male pores superficial; without copulatory pouches or other secondary male pore structure. Clitellum 13, 14–17. Calciferous lamellae on lateral expansions of the esophageal wall in the region of 11–13, 14. Dorso-lateral intestinal caeca one pair, starting from 25. Last hearts in 12. Spermathecal duct without nephridia. Holandric; testes free of sacs.

**1. *Dendrophetima banahawensis* James, 2005**

*Dendrophetima banahawensis* James, 2005: 273–275, fig. 1a, b. Blakemore 2007: 11.

**Diagnosis.**— Spermathecal pores paired on 6/7–8/9. Male pores superficial on 18, crescentic with concavity facing posteriorly, surrounded by roughly circular elevated papillae, pores in 3rd–4th setal line, 1.0–1.2 mm apart, 2–4 setae between male pores. Genital markings paired, intersegmental lenticular centers surrounded by white lips at 16/17, 17/18, 19/20, 20/21 in all specimens; at 21/22, single right 21/22, 22/23, 23/24 in some specimens. Oesophagus with vertical calciferous lamellae in ½11, 12–13, 14, lamellae within lateral pouches of oesophagus opening independently to oesophageal lumen. Paired intestinal caeca simple, dorso-lateral within 25. Spermathecae sexthecate; ampulla small rounded or scalloped-edge, large barrel shaped muscular duct longer than ampulla; diverticulum single stalked terminating in ovate to club-shaped reservoir.

**Type locality.**— Upper montane forest on Mt. Banahaw, Tayabas municipality, Batangas Province, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 003842), and five paratypes are housed in the KUNHM (Invertebrate Zoology No. 001893) (James, 2005).

**2. *Dendrophetima bicolensis* James, 2005**

*Dendrophetima bicolensis* James, 2005: 275–276, fig. 1c, d. Blakemore 2007: 14.

**Diagnosis.**— Spermathecal pores paired on 6/7–8/9. Male pores superficial on 18, crescentic with concavity facing posteriorly, on circular to ovate elevated porophores, pores in 7th–9th setal line, 1.8–2.3 mm apart, 9–12 setae between male pores. Genital markings paired, intersegmental lenticular centers surrounded by white lips at 16/17, 19/20, paired small

ovals 17 in line with male porophores; extra genital marking left or right side rarely present on 15/16 or 20/21. Oesophagus with vertical lamellae in ½11, 12–13, lamellae within segmental lateral pouches on oesophagus, pouches of a side connected to lateral channels parallel to oesophageal lumen, opening into oesophageal lumen in 13 or 14. Paired intestinal caeca simple, dorsolateral, starting from 25, extending forward to 24. Spermathecae sexthecate; ampulla spherical, stout muscular duct longer than ampulla; diverticulum single stalked terminating in club-shaped reservoir.

**Type locality.**— Upper montane forest arboreal habitats on Mt. Isarog, Camarines Sur Province, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 003844), and three paratypes are housed in the KUNHM (Invertebrate Zoology No. 001901) (James, 2005).

***Duplodicrodrilus* Blakemore, 2008**

*Duplodicrodrilus* Blakemore, 2008c: 24–25. Blakemore 2008b: 82–84. Blakemore 2020: 465–466.

**Type species.**— *Megascolex schmardae* Horst, 1883, by original designation.

**Other originally included species.**— *Duplodicrodrilus schmardae macrochaeta* (Michaelsen, 1899)

**Diagnosis.**— Pheretimid with male pores within copulatory pouches, eversible as large inflatable and doubled intromittant organs or pseudo-penes. Clitellum 14–16. Genital markings lacking. Calciferous glands and esophageal pouches absent. Dorso-lateral intestinal caeca one pair, simple or manicate, starting from 26, 27. Spermathecal duct without nephridia. Holandric.

**Remarks.**— Molecular phylogenetic analysis by Sato et al. (2023) revealed that *Duplodicrodrilus acinctus* and *D. schmardae* are not sister species. *D. acinctus* is retrieved to be more closely related to *Metaphire tosaensis* (Ohfuchi, 1938), whereas *D. schmardae* is sister to *Amyntas longisiphonus* (Qiu, 1988). Therefore, based on the current molecular phylogeny *Duplodicrodrilus* is not monophyletic.

**1. *Duplodicrodrilus acinctus* (Goto & Hatai, 1899)**

*Perichaeta acincta* Goto & Hatai, 1899: 16–17, fig. 6.

*Amyntas* [sic] *acinctus*—Beddard 1900b: 650.

*Pheretima acincta*—Michaelsen 1900: 252.

Yamaguchi 1962: 10–11, figs 2, 3. Ishizuka 1999: 56–57. Nakamura 1999: 37.

*Amyntas acinctus*—Sims and Easton 1972: 235, 240. Easton 1981: 48–49. Blakemore 2003: 242. Blakemore 2007: 3–4.

*Pheretima yezoensis* Kobayashi, 1938: 412–414, fig. 4a–c. Type locality: Hakodate, Japan. Nakamura 1999: 40.

*Metaphire yezoensis*—Easton 1981: 60. Blakemore 2003: 243.

*Metaphire acincta*—Ito et al. 2007: 49–53, figs 1, 2, table 1. Blakemore 2008a: 7. Blakemore 2008b: 18, 89–90. Blakemore 2012a: 19.

*Duplodicrodrilus acinctus*—Blakemore 2012b: 104–106, fig. 4. Blakemore 2019: 60.

**Diagnosis.**— Spermathecal pores paired on 5/6–7/8. Male pores as lateral slits on 18, within large wrinkled copulatory pouches extending into 17 and 19, with 7 or fewer setae between secondary male pores. Genital markings absent. Paired intestinal caeca simple, often with 4–8 incised ventral and dorsal margins, starting from 26–27, extending forward to 23–24. Spermathecae sexthecate; ampulla long, spatulate in shape and somewhat flattened, duct stout and shorter than the ampulla; diverticulum long, bent or twisted and tube-like, its distal portion showing frequently sausage-like swelling, being twice longer than the main portion of the spermatheca.

**Type locality.**— Tokyo, Japan.

**Remarks.**— The neotype of *D. acinctus* is housed in the NSMT (NSMT-An 429) (Blakemore, 2012b). The original description by Goto and Hatai (1899) stated that the intestinal caeca start on 26, but later descriptions reported the origin of intestinal caeca on 27 (Easton, 1981; Ito et al., 2007). See also the comprehensive taxonomic remarks in Ito et al. (2007) and Blakemore (2012b).

## 2. *Duplodicrodrilus schmardae macrochaeta* (Michaelsen, 1899)

*Perichaeta schmardae*—Michaelsen 1892: 235.

*Perichaeta schmardae macrochaeta* Michaelsen, 1899a: 227–228. Michaelsen 1900: 302.

*Pheretima schmardae*—Gates 1939: 482–485.

*Metaphire schmardae macrochaeta*—Sims and Easton 1972: 239, 243, 245. Blakemore 2003: 243.

*Duplodicrodrilus schmardae macrochaeta*—Blakemore 2007: 88. Blakemore 2008a: 7. Blakemore 2008b: 20, 88–89. Blakemore 2012a: 19. Blakemore 2019: 60. Blakemore 2020: 470.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. Male pores on the centre of huge eversible structures within copulatory pouches on 18. Genital markings

absent. Anterior segments with 50 or less setae, and those on segments 4–6 enlarged and ornamented. Paired intestinal caeca manicate with 3 or more branches, starting from 27, extending forward to 24. Spermathecae quadrithecate; ampulla large with short duct; diverticulum long bent.

**Type locality.**— Japan.

**Remarks.**— The syntypes are housed in the ZMH (ZMH-ANN-V00337) (J. Moore, pers. comm., 8 Aug 2024).

## 3. *Duplodicrodrilus schmardae schmardae* (Horst, 1883)

*Megascolex schmardae* Horst, 1883: 194–195. Vaillant 1889: 77–78.

? *Perichaeta sumatrana*—Beddard 1892: 155–156, pl. 9, fig. 4.

*Perichaeta schmardae*—Michaelsen 1899a: 224–229.

*Perichaeta trityphla* Beddard, 1896: 205–206. Type locality: Barbados.

*Amyntas* [sic] *schmardae*—Beddard 1900a: 426. Beddard 1900b: 619.

*Pheretima schmardae*—Michaelsen 1900: 302. Gates 1937: 368–371. Gates 1982: 65. Nakamura 1999: 61.

*Pheretima kikuchii* Hatai & Ohfuchi, 1936: 767–772, text-figs 1–10. Type locality: Mito and Onuki, Higashi-Ibaragi district, Ibaragi Prefecture; Hiragata, Taga district, Ibaragi Prefecture; Nakamura, Soma district, Fukushima Prefecture, Japan.

*Metaphire kikuchii*—Sims and Easton 1972: 239, 243.

*Metaphire schmardae schmardae*—Sims and Easton 1972: 239, 245. Blakemore 2003: 243.

*Metaphire trityphla*—Sims and Easton 1972: 239.

*Metaphire trityphia* [sic]—Sims and Easton 1972: 246.

*Metaphire schmardae*—Easton 1981: 58–59.

*Duplodicrodrilus schmardae schmardae*—Blakemore 2007: 88. Blakemore 2008a: 7. Blakemore 2008b: 20, 85–88. Blakemore 2012a: 19. Blakemore 2019: 60.

*Duplodicrodrilus schmardae*—Blakemore 2020: 466–470, fig. 217a–c.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. Male pores on the centre of huge eversible structures within copulatory pouches on 18. Genital markings absent. Anterior segments with more than 50 setae. Paired intestinal caeca manicate with 3 or more branches, starting from 27, extending forward to 24. Spermathecae quadrithecate; ampulla large with short duct; diverticulum long, bent.

**Type locality.**— Japan.

**Remarks.**— The syntypes of “*Megascolex schmardae* Horst, 1883” are housed in the RMNH (RMNH.VER.OL.1818), and the syntypes of “*Perichaeta trityphla* Beddard, 1896” are housed in the NHM (NHMUK 1904.10.5.169) (Reynolds and Cook, 1976, 1981; Supplementary Table 2; E. Sherlock, pers. comm., 29 Aug 2024). However, the syntype of “*Megascolex schmardae* Michaelsen, 1897” at the WNHM (WNHM 3970) (F. Pedro, pers. comm., 22 Oct 2024) with the type locality of “Ceylon, Ratnapura” belongs to the South Asian genus *Megascolex* (Narayanan et al., 2021). Blakemore (2014) pointed out that “since these taxa have not been considered congeneric after 1899, e.g. Michaelsen (1900) had them in separate genera, a replacement name is not required and prevailing usage is maintained (ICZN, 1999: Art. 23.9.5).”

### *Isarogoscolex* James, 2005

*Isarogoscolex* James, 2005: 276–277.

**Type species.**— *Isarogoscolex abiadai* James, 2005, by original designation.

**Other originally included species.**— *Isarogoscolex albayensis* James, 2005

**Diagnosis.**— Pheretimid with male pores superficial; without copulatory pouches or other secondary male pore structure. Clitellum 14–½17. Calciferous glands stalked with vertical or horizontal lamellae in esophageal pouches, opening individually to oesophagus 11–13. Dorso-lateral intestinal caeca two pairs in two consecutive segments starting from 29 or 30. Spermathecal duct without nephridia. Pre-intestinal segments meronephric; intestinal segments one pair astomate megameronephridia only. Holandric.

**Remarks.**— This genus is unique among the pheretimid and Australasian megascolecine genera in having only one pair of astomate megameronephridia per each intestinal segment (James, 2005).

#### 1. *Isarogoscolex abiadai* James, 2005

*Isarogoscolex abiadai* James, 2005: 277–278, fig. 1e, f. Blakemore 2007: 3.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. Male pores superficial on ovate porophores on 18. Clitellum 14–½17. Genital markings paired at 16/17, 19/20 with lenticular centres surrounded by white lips, almost joined at midventral. Oesophagus with vertical calciferous lamellae at ½11, 12–13; lamellae within lateral pouches on oesophagus, pouches opening into

oesophageal lumen independently; blood vessels of lamellae connected to supra-oesophageal, extra-oesophageal vessels. Intestinal origin at 17. Paired intestinal caeca simple, starting from 29, 30. Spermathecae quadrithecate; ampulla ovate, with slender duct about as long as ampulla; diverticulum stalked terminating in club-shaped reservoir.

**Type locality.**— Lower montane forest arboreal habitats on Mt. Isarog, Camarines Sur Province, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 003846), and two paratypes are housed in the KUNHM (Invertebrate Zoology No. 001906) (James, 2005).

#### 2. *Isarogoscolex albayensis* James, 2005

*Isarogoscolex albayensis* James, 2005: 278, fig. 1g–i. Blakemore 2007: 5.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. Male pores superficial on ovate porophores on 18. Clitellum 14–½17. Genital markings paired at 16/17, 19/20 with lenticular centres surrounded by white lips. Oesophagus with calciferous glands with horizontal lamellae at 11–13, glands within lateral pouches on oesophagus, opening into oesophageal lumen independently via broad canal; blood vessels of lamellae connected to supraoesophageal partway down posterior face of glands, extraoesophageal vessels at ventral edges of glands. Intestinal origin at 16. Paired intestinal caeca simple, starting from 30, 31, plus small pockets on 32. Spermathecae quadrithecate; ampulla slender lanceolate, with slender duct about as long as ampulla; diverticulum stalked terminating in club-shaped reservoir.

**Type locality.**— Arboreal habitats in upper montane forest on south ridge of Mt. Malinao, Barangay Jarod, Albay Province, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 003847) (James, 2005).

#### *Manus* Blakemore, 2010

*Manus* Blakemore, 2010a: 95–96. Blakemore 2020: 519.

**Type species.**— *Pheretima koellikeri* Michaelsen, 1928, by original designation.

**Other originally included species.**— None

**Diagnosis.**— Pheretimoid with male pores on penes within copulatory pouches; with secretory diverticulum opening adjacent to prostate gland on male pore with penial seta internally. Clitellum 14–16. Calciferous glands and esophageal pouches absent. Dorso-lateral intestinal caeca one pair, manicate, starting from 27. Spermathecal duct without nephridia. Holandric.

**Remarks.**— Molecular phylogenetic analysis by Sato et al. (2023) revealed that the sole member of this genus, *Manus koellikeri* is closely related to other unidentified Japanese species and *Metaphire communissima* (Goto & Hatai, 1899).

### 1. *Manus koellikeri* (Michaelsen, 1928)

*Pheretima köllikeri* Michaelsen, 1928b: 8–12, figs 1, 2.

*Pheretima* (*Parapheretima*) *koellikeri*—Sims and Easton 1972: 222, 240, 243, 266. Easton 1981: 60.

*Pheretima koellikeri*—Nakamura 1999: 59.

*Metaphire vesiculata* [in part]—Blakemore 2003: 243.

*Pheretima* ? *koellikeri*—Blakemore 2007: 56.

? *Metaphire koellikeri*—Blakemore 2008a: 20, 129–131, fig. 6. Blakemore 2010b: 18.

*Manus koellikeri*—Blakemore 2010a: 96–100, figs 1, 2. Blakemore 2012a: 19. Blakemore 2019: 60. Blakemore 2020: 519–522.

**Diagnosis.**— Spermathecal pores paired on 6/7–7/8. Male pores on penes in copulatory pouches in the setal line of 18. Genital markings absent except for pads around spermathecal pores. Paired intestinal caeca manicate, each with several diverticula, starting from 27. Prostate glands each ducting to penis within copulatory pouch confined to body wall with accessory secretory diverticulum, resembling tubular prostates, extending to 17 or 16, and opening anterior to male pores and associated with penial seta. Spermathecae quadrithecate; ampulla with slightly wavy stalks; diverticula shorter than ampulla and spermathecal duct muscular.

**Type locality.**— Japan.

**Remarks.**— The syntypes are house in the ZMH (ZMH-ANN-V06074) (J. Moore, pers. comm., 8 Aug 2024). See also the comprehensive taxonomic remarks in Blakemore (2010a, 2020).

### *Planapheretima* Michaelsen, 1934

*Pheretima* (*Planapheretima*) Michaelsen, 1934: 15.

*Planapheretima*—Sims and Easton 1972: 208–209, 233. Easton 1979: 64–67. Nguyen et al. 2014: 109. Nguyen et al. 2016: 70. Xiao 2019: 344. Blakemore 2020: 597.

**Type species.**— *Pheretima moultoni* Michaelsen, 1913, by original designation.

**Other originally included species.**— *Pheretima* (*Planapheretima*) *ambulatorix* Michaelsen, 1934 (= *Planapheretima ambulatorix*), *Pheretima* (*Planapheretima*) *frondicola* Michaelsen, 1934 (= *Planapheretima hasselti*), *Pheretima* (*Planapheretima*) *maculata* Ude, 1925 (= *Planapheretima maculata*), *Pheretima* (*Planapheretima*) *nieuwenhusi* [sic] Michaelsen, 1922 (= *Planapheretima nieuwenhuisi*), *Pheretima* (*Planapheretima*) *pallescens* Michaelsen, 1928 (= *Planapheretima pallescens*), *Pheretima* (*Planapheretima*) *scandens* Michaelsen, 1928 (= *Planapheretima maculata*)

**Diagnosis.**— Pheretimoid with male pores superficial, on small penes on porophores, or in shallow copulatory pouches. Clitellum 13, 14–16, 17. Body mainly flattened dorsoventrally forming creeping sole with ventrally crowded setae. Calciferous glands and esophageal pouches absent. Intestinal caeca in most species absent; intestinal walls often with glandular areas. Spermathecal duct without nephridia. Holandric.

**Remarks.**— This taxon was formerly a subgenus of *Pheretima*, and later raised to the specific rank by Sims and Easton (1972).

### 1. *Planapheretima ambulatorix* (Michaelsen, 1934)

*Pheretima* (*Planapheretima*) *ambulatorix* Michaelsen, 1934: 22–25, pl. 1, fig. 3; text-fig. 6.

*Planapheretima ambulatorix*—Sims and Easton 1972: 233, 240. Easton 1979: 71, figs 27e, 29a. Nakamura 1999: 6. Blakemore 2007: 6.

**Diagnosis.**— Spermathecal pores paired on 6/7–7/8. First dorsal pore not recognized. Male pores on minute elongate penes on 18, marked by very slightly prominent, whitish, circular porophores. Clitellum ½13–17. Genital marking not recognized or absent. Body colouration yellowish to yellowish grey without pigmentation in preserved specimen. Intestinal origin at 16. Intestinal caeca absent. Spermathecae quadrithecate; ampulla sack-shaped, more or less longer than broad; duct rather sharply pinched off, about one-third to one-half as wide as the ampulla and about as long as wide; diverticulum as long as or longer than ampulla.

**Type locality.**— Mt. Dulit, Koyan Forest, Sarawak [Malaysia].

**Remarks.**— The syntypes are housed in the NHM (NHMUK 1933.10.6.6) and ZMH (ZMH-ANN-V11955) (Easton, 1979; Supplementary Table 2; J. Moore, pers. comm., 8 Aug 2024).

## 2. *Planapheretima arboricola* (Gates, 1936)

*Pheretima arboricola* Gates, 1936: 399–400. Gates 1972: 169–170. Thai 1997: 5, fig. 3b.

*Planapheretima arboricola*—Sims and Easton 1972: 233, 240. Nakamura 1999: 6–7. Blakemore 2007: 8. Nguyen et al. 2014: 109. Nguyen et al. 2016: 70.

*Planapheretima arboricola* [part]—Easton 1979: 76–77, figs 27j, 30a.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. First dorsal pore 10/11 or 11/12. Male pores minute and superficial on 18, each pore at the centre of a disc-shaped, hemispherical porophore. Clitellum 14–16. Genital marking single transverse median on 18, extending laterally on each side almost to the male porophore, posteriorly to the level of 18/19 and anteriorly to a level about in line with the anterior margins of the male porophores. Body colouration reddish dorsally but fading out gradually on the posterior part. Intestinal origin at 15. Intestinal caeca compound, glove-shaped, the dorsal most secondary caecum the shortest, the ventral most secondary caecum the longest. Spermathecae octothecate; ampulla not clearly demarcated from the slightly shorter spermathecal duct; diverticulum elongate tubular, ectal portion shortly looped, somewhat zigzagged.

**Type locality.**— Karen Hills, Toungoo District [Myanmar].

**Remarks.**— The holotype of this species was destroyed (Easton, 1979). Easton (1979) assumed that this species was the same as *Perionyx arboricola* Rosa, 1890 (type locality: Cobapo village, on the Karin mountains, district of Cheba or Biapo, Myanmar), the type materials of which were deposited in the MGDG (No. 44017) and examined by Easton (1979). Apart from the similarity in setae distribution, prostates, and spermathecal pore positions between the two species, *Pe. arboricola* has a first dorsal pore on 5/6, whereas *Pl. arboricola* has a first dorsal pore on 10/11 or 11/12. In addition, *Pl. arboricola* has manicate intestinal caeca in segment 27 and sessile genital marking glands in segments 17–20, and these characters were not reported in *Pe. arboricola*. Therefore, this species is considered to be distinct from *Pe. arboricola*, unless more specimens from both type localities are collected and examined.

The specimens from Vietnam are different from those in the description of Gates (1936) in having spermathecal pores paired in 6, 7, additional genital markings in 6, and more setae (Nguyen et al., 2016; Thai, 1997).

## 3. *Planapheretima bambophila* (Chen, 1946)

*Pheretima bambophila* Chen, 1946: 86–88, pl. 1, fig. d1–4.

*Planapheretima bambophila* [sic]—Sims and Easton 1972: 233

*Planapheretima bambophila*—Sims and Easton 1972: 241. Easton 1979: 78, fig. 27m. Nakamura 1999: 5. Blakemore 2007: 11. Xiao 2019: 344–345, fig. 314.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 10/11. Male pores minute on 18, each pore on a highly glandular porophore. Clitellum 14–16. Genital marking absent. Body colouration deep purplish or dark chestnut, iridescent dorsally, pale ventrally, paler along ventral glandular zone. Intestinal origin at 15. Intestinal caeca absent; intestinal wall thicker and glandular, distinctly pouched in 22–29, less conspicuous up to 38. Spermathecae quadrithecate; ampulla two lobes; diverticulum club-shaped as long as ampulla, with short and narrow duct.

**Type locality.**— Kiu-Lao-Tung, Mt. Omei [Jiulaodong, Mt. Emei, Sichuan], China.

**Remarks.**— The type materials of this species were destroyed (Xiao, 2019).

## 4. *Planapheretima celebensis* (Michaelsen, 1899)

*Amyntas* [sic] *celebensis* Michaelsen, 1899c: 32–33, fig. 4. Beddard 1900b: 642–643.

*Pheretima celebensis*—Michaelsen 1900: 261–262.

*Planapheretima celebensis*—Sims and Easton 1972: 233, 241. Easton 1979: 70, figs 27d, 28c. Nakamura 1999: 6. Blakemore 2007: 21. Nugroho 2010: 108 (appendix 1).

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. First dorsal pore 6/7. Male pores on 18, each pore on an oval porophore, separated by a transverse furrow. Clitellum 1/3 13, 14–16. Genital markings paired, in lines with male pores, postsetal on 8, on 17/18 and 18/19, and presetal on 19–21. Body colouration bright brownish yellow dorsally, grey ventrally, clitellum dark violet grey in preserved specimen. Intestinal origin not known. Intestinal caeca absent. Spermathecae octothecate; ampulla ovate, duct very short, narrow but not sharply defined; diverticulum slender pear-shaped, 2/3 length of ampulla.

**Type locality.**— Takalekadjo range, central Celebes [Indonesia].

**Remarks.**— The holotype is registered at the ZMH (ZMH-ANN-V05188), but could not be located (Easton, 1979) and currently stated as lost (J. Moore, pers. comm., 8 Aug 2024).

### 5. *Planapheretima continens* (Chen, 1946)

*Pheretima continens* Chen, 1946: 95–97, 139, fig. c1–6.  
*Amyntas continens*—Sims and Easton 1972: 235, 241.  
*Planapheretima continens*—Easton 1979: 75–76, figs 27i, 30b. Nakamura 1999: 5. Blakemore 2007: 23. Xiao 2019: 345–346, fig. 315.

**Diagnosis.**— Spermathecal pores paired on 5/6–7/8 or 4/5–6/7. First dorsal pore 11/12. Male pores on small penes which arise from circular porophores on 18. Clitellum ½13–½17. Genital markings paired, presetal on 9, slightly median to the line of the spermathecal pores. Body colouration grey dorsally, pale ventrally, clitellum light chocolate red. Intestinal origin at 16. Intestinal caeca rudimentary, one segment long, origin not recorded, and with glandular walls posterior to the caeca. Spermathecae sexthecate; ampulla heart-shaped, with a moderately long duct; diverticulum longer than ampulla, with a globular or date-shaped seminal chamber.

**Type locality.**— Mt. Omei, Szechwan [Mt. Emei, Sichuan], China.

**Remarks.**— The type materials of this species were destroyed (Xiao, 2019).

### 6. *Planapheretima hasselti* (Horst, 1883)

*Megascolex hasselti* Horst, 1883: 190–191. Vaillant 1889: 80.  
*Perichaeta hasselti*—Horst 1892: 5–6, fig. 3a–c. Beddard 1895: 426.  
*Amyntas* [sic] *hasselti*—Beddard 1900b: 638.  
*Pheretima hasselti*—Michaelsen 1900: 271.  
*Pheretima (Planapheretima) frondicola* Michaelsen, 1934: 17–22, pl. 1, fig. 2; text-figs 4, 5. Type locality: Mt. Dulit, Sarawak [Malaysia].  
*Planapheretima hasselti*—Sims and Easton 1972: 233, 242. Easton 1979: 71–73, figs 27f, 29b. Nakamura 1999: 6. Blakemore 2007: 45. Nugroho 2010: 108 (appendix 1).  
*Planapheretima frondicola*—Sims and Easton 1972: 233, 242.

**Diagnosis.**— Spermathecal pores paired on 5/6–6/7. First dorsal pore 12/13. Male pores simple, on large,

oval porophores on 18 and extending onto 17 and 19, separated mid-ventrally by a rather narrow space. Clitellum 13–16. Genital marking absent. Body colouration pale yellowish grey or grey with lighter intersegmental furrows in preserved specimen. Intestinal origin at 15. Intestinal caeca absent. Spermathecae quadrithecate; ampulla large, ovate, duct moderately developed; diverticulum narrow, cylindrical reaching nearly half the length of ampulla.

**Type locality.**— Lebong, Sumatra [Indonesia].

**Remarks.**— The syntypes of “*Megascolex hasselti* Horst, 1883” are housed in the RMNH (RMNH.VER.OL.1853), and the syntypes of “*Pheretima (Planapheretima) frondicola* Michaelsen, 1934” are housed in the NHM (NHMUK 1933.10.6.9), and ZMH (ZMH-ANN-V11957) (Easton, 1979; Supplementary Table 2; J. Moore, pers. comm., 8 Aug 2024).

Easton (1979) treated *P. frondicola* as the junior subjective synonym of *P. hasselti* based on the similarity of most morphological characters, except that *P. frondicola* has a longer clitellum and a more fully developed male porophores. However, *P. hasselti* is reported from Sumatra Island, whereas *P. frondicola* is from Borneo Island. Therefore, more data is needed to investigate the status of these two species.

### 7. *Planapheretima lacertina* (Chen, 1946)

*Pheretima lacertina* Chen, 1946: 109–11, pl. 6, fig. a1–5. Thai 1997: 4–5, fig. 3a.  
*Planapheretima lacertina*—Sims and Easton 1972: 233, 243. Easton 1979: 77, figs 27k, 30d. Nakamura 1999: 5. Blakemore 2007: 57. Nguyen et al. 2014: 109. Nguyen et al. 2016: 71. Xiao 2019: 346–347, fig. 316.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. First dorsal pore 10/11. Male pores each in a large glandular depression on 18, its diameter slightly less than segmental length. Clitellum 14–16. Genital marking absent. Body colouration dark chestnut or brownish black pattern on a bluish background; with trapezium presetal and large rhomboid patterns postsetal, and zigzag dorso- and ventrolateral lines. Intestinal origin at 15. Intestinal caeca rudimentary, smooth, ear-like projection confined to 26. Spermathecae octothecate; ampulla heart-shaped, duct with moderately long; diverticulum as long as ampulla, ental 2/3 crooked and whitish serving as seminal chamber.

**Type locality.**— King-Fu-Shan (Mt. King-Fu), [Mt. Jinfo, Chongqing], China.

**Remarks.**— The type materials of this species were destroyed (Xiao, 2019). The specimens from Vietnam are different from those in the description of Chen (1946) in having a smaller body size, fewer setae and spermathecal pores paired in 5/6–7/8 (Nguyen et al., 2016; Thai, 1997).

### 8. *Planapheretima maculata* (Ude, 1925)

*Pheretima maculata* Ude, 1925: 104.

*Pheretima* (*Archipheretima*) *maculata*—Michaelsen 1928a: 18. Ude 1932: 120–121, text-fig. 1.

*Pheretima* (*Archipheretima*) *scandens* Michaelsen, 1928a: 18–22, figs 3, 4. Type locality: Berg Penrissen, West Sarawak [Malaysia].

*Pheretima* (*Planapheretima*) *maculata*—Michaelsen 1934: 15.

*Pheretima* (*Planapheretima*) *scandens*—Michaelsen 1934: 15.

*Planapheretima maculata*—Sims and Easton 1972: 233, 243. Easton 1979: 73–74, fig. 27g, fig. 29c. Nakamura 1999: 5. Blakemore 2007: 61.

*Planapheretima scandens*—Sims and Easton 1972: 233, 245.

**Diagnosis.**— Spermathecal pores paired on 6/7. First dorsal pore 10/11. Male pores simple on 18. Clitellum  $\frac{1}{3}$ 13–16. Genital markings in the form of a light-colored glandular wall, sloping down in a roof-like manner anteriorly to 17/18 and posteriorly to 18/19, surrounding each male pore on 18. Body colouration highly iridescent; yellowish brown dorsally with irregularly arranged rust-red or dark brown spots forming a ring-shaped pattern around each dorsal pore; clitellum violet brown. Intestinal origin at 15. Intestinal caeca absent. Spermathecae bithecate; ampulla ovate, gradually becoming a somewhat longer duct; diverticulum as long as ampulla, swollen and somewhat lobed terminally.

**Type locality.**— Mt. Murud, Borneo [Sarawak, Malaysia].

**Remarks.**— Ude (1925) stated that the specimens he examined belong to the “Sarawak Museum”, which is possibly the Natural History Museum of the Sarawak Museum Department in Kuching, Sarawak, Malaysia, and that the specimens were collected by Dr. Mjöberg. The holotype of “*Pheretima* (*Archipheretima*) *scandens* Michaelsen, 1928” is housed in the ZMH (ZMH-ANN-V10515) (Easton, 1979; J. Moore, pers. comm., 8 Aug 2024). Although the male pore field and the shape of prostatic duct and spermathecal diverticulum of *P. scandens* are different from those of *P. maculata* (Michaelsen, 1928a), Easton (1979)

regarded those differences as infraspecific variation and treated *P. scandens* as the junior subjective synonym of *P. maculata*. As the type locality of *P. maculata* is approximately 650 km far from the type locality of *P. scandens*, more data is needed to investigate the status of these two species.

### 9. *Planapheretima moultoni* (Michaelsen, 1913)

*Pheretima moultoni* Michaelsen, 1913: 90–92. Michaelsen 1914: 59–61, with in-text fig.

*Pheretima* (*Archipheretima*) *moultoni*—Michaelsen 1928a: 14.

*Pheretima* (*Planapheretima*) *moultoni*—Michaelsen 1934: 15.

*Planapheretima moultoni*—Sims and Easton 1972: 209–210, 233, 244. Easton 1979: 68, figs 27a, 28a. Nakamura 1999: 6. Blakemore 2007: 67.

**Diagnosis.**— Spermathecal pores paired on 4/5–6/7. First dorsal pore 9/10. Male pores on slightly raised conical porophores on 18. Clitellum  $\frac{1}{2}$ 13–16. Genital markings paired, pre- and postsetal, slightly median to the male pores on 18. Body colouration light yellowish grey with up to 20 small dark violet-brown or nearly black spots around each dorsal pore, the spots fusing to form a ring with the pore marked by a white spot, the rings fuse to form a median line which becomes larger posteriorly, the number of irregular spots diminish posteriorly. Intestinal origin at 15. Intestinal caeca absent. Spermathecae sexthecate; ampulla ovate or pear-shaped, duct much thinner, but almost as long as ampulla, ending very narrowly; diverticulum slender, club-shaped, slightly thickened and bent over distally, only as long as the ampulla duct in the first pair but almost as long as or somewhat longer than ampulla in the last two pairs.

**Type locality.**— Mt. Poi, Sarawak, North Borneo [Malaysia].

**Remarks.**— The syntypes are housed in the ZMH (ZMH-ANN-V08090) (Easton, 1979; J. Moore, pers. comm., 8 Aug 2024).

### 10. *Planapheretima nieuwenhuisi* (Michaelsen, 1922)

*Pheretima nieuwenhuisi* Michaelsen, 1922: 47–49, figs 15, 16.

*Pheretima* (*Archipheretima*) *nieuwenhuisi* [sic]—Michaelsen 1928a: 22.

*Pheretima* (*Planapheretima*) *nieuwenhuisi* [sic]—Michaelsen 1934: 15.

*Planapheretima nieuwenhuisi*—Sims and Easton 1972: 233, 244. Easton 1979: 74, figs 27h, 29d. Nakamura

1999: 6. Blakemore 2007: 71. Nugroho 2010: 108 (appendix 1).

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 9/10. Male pores each on a small auricle-shaped porophore on 18, extending obliquely backward and almost to 18/19. Clitellum 13–16. Genital marking single, large, median at 17/18, biconvex bordered, moderately convex anterior, very strongly convex posterior. Body colouration intense chestnut brown or maroon becoming more greyish at the anterior and posterior ends, clitellum bright bluish slate-grey. Intestinal origin at 14. Intestinal caeca absent. Spermathecae quadrithecate; ampulla irregular and usually distorted or shriveled, ovate, duct much thinner and shorter, usually sharply separated, distally narrowed; diverticulum pear-shaped, short-stalked, slightly longer than the duct of ampulla.

**Type locality.**— Summit of Berges Damoes, Borneo [near Sambas Regency, West Kalimantan, Indonesia].

**Remarks.**— The syntypes are housed in the RMNH (RMNH.VER.OL.1811) and ZMH (ZMH-ANN-V09306) (Easton, 1979; Supplementary Table 2; J. Moore, pers. comm., 8 Aug 2024).

#### 11. *Planapheretima pallescens* (Michaelsen, 1928)

*Pheretima* (*Archipheretima*) *pallescens* Michaelsen, 1928a: 15–18, fig. 2.

*Pheretima* (*Planapheretima*) *pallescens*—Michaelsen 1934: 15.

*Planapheretima pallescens*—Sims and Easton 1972: 233, 244. Easton 1979: 68–69, fig. 27b. Nakamura 1999: 6. Blakemore 2007: 75.

**Diagnosis.**— Spermathecal pores paired on 4/5–6/7. First dorsal pore 11/12, apparently rudimentary 10/11. Male pores on small porophores at the edge of the median creeping sole on 18. Clitellum not developed. Genital marking not detectable. Body colouration bright yellow with a reddish, mother of pearl lustre and a sparsely developed brown, irregularly defined line on the anterior segments of the body. Intestinal origin unknown. Intestinal caeca absent. Spermathecae sexthecate; ampulla ovate, irregularly shriveled, duct not very sharply defined, short-conical; diverticulum more than twice as long as ampulla, usually not stretched out completely straight, with stalk approximate 1/6 of total length.

**Type locality.**— Berg Penrissen, West Sarawak [Malaysia].

**Remarks.**— As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Easton (1979) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6), and the lectotype is housed in the ZMH (ZMH-ANN-V10522) (J. Moore, pers. comm., 8 Aug 2024). Easton (1979) speculated that this species might be a possible synonym of *Pl. moultoni*.

#### 12. *Planapheretima plumatomusculata* (Thai, 1982)

*Pheretima plumatomusculata* Thai, 1982: 829–830, fig. 3r. Thai 1997: 2–3, fig. 2b.

*Pheretima* (*Terrata*) *plumatomusculata*—Thai 1983: 123.

*Planapheretima plumatomusculata*—Blakemore 2007: 81. Nguyen et al. 2014: 110–111. Nguyen et al. 2016: 71.

**Diagnosis.**— Spermathecal pores paired on 5/6–6/7. First dorsal pore 11/12. Male pores superficial on 18. Clitellum not reported. Genital marking absent. Body colouration with whitish dots scattered on a purple background dorsally, with a longitudinal median-dorsal whitish stripe with purple spots around dorsal pores; on the first 12 segments, the purple spots merge and form a continuous dark purple stripe; pale ventrally. Intestinal origin at 15. Intestinal caeca absent; intestinal wall in 26 thicker. Spermathecae quadrithecate; ampulla and diverticula both ovate with short ducts, diverticula smaller than ampulla.

**Type locality.**— Cuc Phuong, Vietnam.

**Remarks.**— The holotype is housed in the ZMUM (Nguyen et al., 2016). Although Thai (1983) proposed a new subgenus *Terrata* of the genus *Pheretima* for several species including this species, this subgenus is not available because it was proposed in an unpublished thesis (ICZN, 2012: Art. 9.12).

#### 13. *Planapheretima rarus* (Thai, 1997)

*Pheretima rarus* Thai, 1997: 1–2, fig. 2a, a'.

*Planapheretima rarus*—Blakemore 2007: 85. Nguyen et al. 2014: 111.

**Diagnosis.**— Spermathecal pores paired on 5/6–7/8. First dorsal pore 9/10. Male pores on porophores in shallow pouches of parietal invagination on 18. Clitellum 14–16. Genital markings small, oval papillae, ranged in transversal presetal and postsetal lines, 2 on 17, 3+2 on 18, and 2 on 19. Body colouration violet dorsally, pale yellow ventrally. Intestinal origin at 15. Intestinal caeca in 26–27; intestinal wall in 15–26

thicker. Spermathecae sexthecate; ampulla more or less heart-shaped; diverticula as long as or longer than ampulla.

**Type locality.**— Tham Lang village, Muong Long commune, Ky Son District, Nghe An province, Vietnam.

**Remarks.**— The holotype and paratypes are housed in the HNUE (SORC-V.202) (Nguyen et al., 2014).

#### 14. *Planapheretima rufomaculata* (Gates, 1948)

*Pheretima rufomaculata* Gates, 1948: 162–166.

*Planapheretima rufomaculata*—Sims and Easton 1972: 233, 245. Easton 1979: 71, fig. 28d. Nakamura 1999: 5. Blakemore 2007: 87. Nugroho 2010: 108 (appendix 1).

**Diagnosis.**— Spermathecal pores paired on 5/6. First dorsal pore 11/12. Male pores on circular, widely spaced, porophores on 18. Clitellum  $\frac{1}{3}$ 13–16. Genital markings closely paired on 9/10, 16/17 and 19/20, with a clearly marked off, opaque marginal band and a central, slightly depressed area of greyish translucence; slightly median to male pores on 18. Body colouration with pigmentation restricted to three longitudinal, irregular stripes, a median dorsal dark red stripe and two lateral light red stripes. Intestinal origin at 15. Intestinal caeca absent. Spermathecae bithecate; ampulla duct as long as main ampulla; diverticulum tubular, nearly as long as main axis.

**Type locality.**— Rattan Camp and Mist Camp near Idenburg River, West Irian [Papua, Indonesia].

**Remarks.**— The type materials were reported to be deposited in the MZB (Reynolds and Cook, 1976), but could not be located (Easton, 1979; R. M. Marwoto, pers. comm., 18 Sep 2024).

#### 15. *Planapheretima sera* Easton, 1979

*Planapheretima sera* Easton, 1979: 73, fig. 30c, f. Nakamura 1999: 5. Blakemore 2007: 90.

**Diagnosis.**— Spermathecal pores paired on 6/7. First dorsal pore 8/9 or 9/10. Male pores postsetal on large oval posteriorly directed porophores which occupy the whole length of the segment 18. Clitellum  $\frac{3}{4}$ 13–16. Genital markings paired, presetal, in line with male pores on 19, 20. Body colouration yellowish brown with dark brown or red spots dorsally and laterally; clitellum purple. Intestinal origin at 15. Intestinal caeca absent. Spermathecae bithecate; ampulla nearly spherical, with clearly defined duct as long as the main ampulla; diverticulum very long, convoluted, terminating in small spherical seminal chamber.

**Type locality.**— near old campsite, Royal Geographical Society camp 4, ridge top forest, Gunong Mulu, Sarawak [Malaysia].

**Remarks.**— The holotype and paratype are housed in the NHM (NHMUK 1977.21.1 and NHMUK 1977.21.2 for the holotype and paratype, respectively) (Easton, 1979; Supplementary Table 2). Easton (1979) incorrectly provided the voucher specimen numbers to the holotype and paratype.

#### 16. *Planapheretima subulata* (Michaelsen, 1899)

*Amyntas* [sic] *subulatus* Michaelsen, 1899c: 29–31, fig. 3. Beddard 1900b: 641.

*Pheretima subulata*—Michaelsen 1900: 307–308.

*Metapheretima subulata*—Sims and Easton 1972: 233, 246.

*Planapheretima subulata*—Easton 1979: 69–70, figs 27c, 28b. Nakamura 1999: 6. Blakemore 2007: 94. Nugroho 2010: 108 (appendix 1).

**Diagnosis.**— Spermathecal pores paired on 4/5–8/9. First dorsal pore 6/7. Male pores each at the centre of large circular porophores on 18; each porophore covering nearly more than half of the segment length. Clitellum 14–16. Genital markings paired, in line with the male pores, presetal on 19, 20, postsetal on 10, 11 and 17. Body colouration brownish dorsally, light yellowish white ventrally; clitellum yellowish grey in preserved specimen. Intestinal origin at 16. Intestinal caeca absent. Spermathecae decathecate; ampulla nearly spherical, duct about half as long as the main ampulla, not sharply defined; diverticulum large, club-shaped, narrowed at the base, duct about half as long as the total diverticulum length.

**Type locality.**— Hill country in the region of the Kalaena river and southern foothills of Takalekado, Central Celebes [Indonesia].

**Remarks.**— The syntypes are housed in the ZMH (ZMH-ANN-V05192–5193) (Easton, 1979; J. Moore, pers. comm., 8 Aug 2024).

#### 17. *Planapheretima tenebrica* (Chen, 1946)

*Pheretima tenebrica* Chen, 1946: 93–94, pl. 3, fig. a1–5. Thai 1997: 4, fig. 2c.

*Planapheretima tenebrica*—Sims and Easton 1972: 233, 246. Easton 1979: 78, figs 27l, 30e. Nakamura 1999: 5. Blakemore 2007: 97. Nguyen et al. 2014: 111. Nguyen et al. 2016: 72. Xiao 2019: 347–348, fig. 317.

**Diagnosis.**— Spermathecal pores paired on 5/6–8/9. First dorsal pore 9/10. Male pores superficial on 18,

each on lateral side of a depressed area composed of 2 anteroposterior papillae; the region surrounded by a few circular furrows. Clitellum 14–16, encroaching onto 13 and 17. Genital marking absent. Body colouration with three longitudinal reddish brown dorsal stripes on a chocolate-coloured background; clitellum dark chocolate to brick red. Intestinal origin at 15. Intestinal caeca absent; intestinal wall in 26–36 thicker, especially in anterior 4 segments. Spermathecae octothecate; ampulla egg-shaped, duct shorter than the main ampulla; diverticulum short, straight, with small spherical seminal chamber.

**Type locality.**— Mt Omei [Mt. Emei, Sichuan] and Nan-Chuan-Hsein [Nanchuan, Chongqing], China.

**Remarks.**— The type materials of this species were destroyed (Xiao, 2019). The specimens from Vietnam differ from those in the original description of Chen (1946) in having a larger body size, more setae, and simple intestinal caeca (Thai, 1997).

***Pleionogaster* Michaelsen, 1892**

*Pleionogaster* Michaelsen, 1892: 247. Beddard 1895: 433–434. Easton 1979: 114–115. James 2004: 307–308. James 2006: (suppl.) 2.

*Plionogaster* [sic]—Michaelsen 1900: 210. Stephenson 1930: 840. Gates 1943: 105–107.

**Type species.**— *Pleionogaster jagori* Michaelsen, 1892, by subsequent designation in Easton (1979).

**Other originally included species.**— *Pleionogaster samariensis* Michaelsen, 1892

**Diagnosis.**— Pheretimoid with male pores superficial; without copulatory pouches or other secondary male pore structure. Clitellum  $\frac{1}{2}$ 13, 14–16, 17. Reduced esophageal gizzard in 8. Calciferous glands, esophageal pouches and intestinal caeca absent. Intestinal gizzards in 24–32. Spermathecal duct without nephridia. Paired enteric stomate meganephridia and regular ranks of exoic micronephridia in post-clitellate segments. Prostatic ducts united with vasa deferentia near the ental end of the duct. Holandric.

**Remarks.**— *Pleionogaster* was later included in the pheretimoid group by Easton (1979), as this genus was retrieved to be closely related to *Metapheretima* based on numerical analyses. This genus is unique among the pheretimoid genera and deemed to be more closely related to Australasian megascolecine genera (James, 2006).

**1. *Pleionogaster adya* Blakemore, 2016**

*Pleionogaster adya* Blakemore, 2016: 25, fig. 11a–d.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 11/12. Female pores paired on 14. Male pores superficial on 18. Clitellum 14–16. Genital markings weak, crescent-shaped pads paired in 17/18, 18/19 just median to male pore line. Intestinal origin at 19. Intestinal gizzards four in series in 26–32, highly muscularized and each preceded by equisized, flaccid crop. Typhlosolar origin not found. Nephridia eight pairs per segment in anterior, just one pair visible behind 18/19. Testes in 10, 11. Seminal vesicles in 11, 12. Spermathecae quadrithecate; ampulla elongate, undifferentiated from duct; diverticulum stumpy clavate  $\frac{1}{3}$  as long ectally.

**Type locality.**— Kahariam organic farm, Brgy. Adya, Lipa City, Batangas, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the UPV (UPV#S3) (Blakemore, 2016).

**2. *Pleionogaster albayensis* James, 2006**

*Pleionogaster albayensis* James, 2006: 168; (suppl.) 3–4, fig. 1c, d. Blakemore 2007: 5.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore single on 14. Male pores crescentic, paired on porophores on 18. Clitellum 14–17. Genital markings paired presetal 17, 19, 20; paired 17/18, 19/20; paired 18/19 in depression posterior to male pores; unpaired midventral presetal 19. Intestinal origin at 20. Intestinal gizzards four in series in 27–30, highly muscularized. Typhlosolar origin in 47. Micronephridia 12 per segment from 19; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles large, dense, acinous in 11, 12. Spermathecae quadrithecate; ampulla elongate club-shaped; diverticulum simple club-shaped joining duct near body wall on medial side rather than usual lateral side, slightly shorter than ampulla; no differentiation of duct from ampulla within coelom.

**Type locality.**— Montane forest on north ridge of Mt. Malinao, near Tiwi, Albay Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004135) (James, 2006).

**3. *Pleionogaster bicoloris* James, 2006**

*Pleionogaster bicoloris* James, 2006: 168; (suppl.) 4–5, fig. 1e, f. Blakemore 2007: 14.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore single on 14. Male pores paired on porophores tilted posteriorly into sunken male field zone on 18. Clitellum 14–½17. Genital markings paired presetal 17, 19; paired 17/18. Intestinal origin at 19 or 20. Intestinal gizzards four in series in 27–30, highly muscularized. Typhlosole lacking. Micronephridia 12 per segment from 18; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in horseshoe-shaped sacs in 10, 11. Seminal vesicles small, acinous in 11, 12. Spermathecae quadrithecate; ampulla horn-shaped, thinner-walled than stout muscular duct; diverticulum simple club-shaped joining duct near body wall, slightly shorter than spermathecal duct.

**Type locality.**— Upper montane forest on south ridge of Mt. Malinao, Barangay Jarod, Albay Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004136), and two additional adult paratypes are housed in the KUNHM (Invertebrate Zoology No. 002176) and the UPLBMHN (Z-NS-0083) (James, 2006).

**4. *Pleionogaster bulusanensis* James, 2006**

*Pleionogaster bulusanensis* James, 2006: 168; (suppl.) 5–6, fig. 1g, h. Blakemore 2007: 18.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 11/12. Female pore single on 14. Male pores crescentic, paired on small porophores on 18. Clitellum not developed. Genital markings paired presetal and postsetal 17, paired presetal 19–21, all just medial to line of male pores. Intestinal origin at 20. Intestinal gizzards four in series in 27–30, highly muscularized. Typhlosole lacking. Micronephridia 14 per segment from 19; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles arc-shaped in 11, 12. Spermathecae quadrithecate; ampulla blunt lanceolate, duct poorly differentiated; diverticulum narrow digitate, half or less length of main spermathecal axis, joining duct near body wall.

**Type locality.**— Dipterocarp forest at Bulusan Lake, Bulusan National Park, Sorsogon Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004137), and one additional juvenile paratype is housed in the KUNHM (Invertebrate Zoology No. 002179) (James, 2006).

**5. *Pleionogaster caramoanensis* James, 2006**

*Pleionogaster caramoanensis* James, 2006: 170; (suppl.) 11–12, fig. 3c, d. Blakemore 2007: 20.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore single on 14. Male pores crescentic, paired on small flat porophores on 18. Clitellum 14–17. Genital markings paired presetal, lateral to male pores 19, thickened white areas across ventral surface 19–21. Intestinal origin at ½19 or 19. Intestinal gizzards three in series in 26–28 or 27–29, highly muscularized. Typhlosolar origin in 39 or 40. Micronephridia 4–6 per segment from 19; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles loosely acinous in 11, 12. Spermathecae quadrithecate; ampulla blunt cylindrical, muscular duct clearly differentiated; diverticulum simple club-shaped, half or more length of main spermathecal axis, joining duct near body wall via differentiated stalk.

**Type locality.**— Low-elevation forest on karst, Caramoan Peninsula, Camarines Norte Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004145), and one additional adult paratype is housed in the KUNHM (Invertebrate Zoology No. 002194) (James, 2006).

**6. *Pleionogaster castilloi* James, 2006**

*Pleionogaster castilloi* James, 2006: 169–170; (suppl.) 10, fig. 2i, j. Blakemore 2007: 21.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 11/12 or 12/13. Female pores paired on 14. Male pores crescentic, paired on porophores tilted posteriorly, slightly depressed on 18. Clitellum ⅓13–½17. Genital markings broad midventral 17/18, 18/19, 19/20; long shallow indentations in raised areas, somewhat like the fusion of paired indented genital markings; midventral epidermal thickenings on 21, 22. Intestinal origin at 20. Intestinal gizzards 5–7 in series in 25, 26–29, 30, 31, highly muscularized. Typhlosolar origin in 47 or 48. Micronephridia six per segment from 19; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles small, acinous in 11, 12.

Spermathecae quadrithecate; ampulla sagittate thinner-walled than duct; diverticulum simple club-shaped joining duct near body wall, slightly shorter than spermathecal duct.

**Type locality.**— Montane forest on north ridge of Mt. Malinao, Albay Province, near Tiwi, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004143), and one additional adult paratype is housed in the KUNHM (Invertebrate Zoology No. 002191) (James, 2006).

#### 7. *Pleionogaster ffitchae* James, 2006

*Pleionogaster ffitchae* James, 2006: 169; (suppl.) 6–7, fig. 2a, b. Blakemore 2007: 37.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 11/12 or 12/13. Female pore single on 14. Male pores crescentic, paired on small porophores facing posteriorly in sunken male field on 18. Clitellum 14–½17. Genital markings oval, paired, presetal 17; rectangular paired 17/18; oblong, paired presetal 19–21. Intestinal origin at 19. Intestinal gizzards four in series in 27–30, highly muscularized. Typhlosolar origin in 50/51 or 54. Micronephridia 12 per segment from 19; meganephridia stomate, two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles ventral half thick, upper portion slender arc in 11, 12. Spermathecae quadrithecate; ampulla long lanceolate, duct of similar structure; diverticulum short basally-attached.

**Type locality.**— Montane forest on Mt. Isarog, Camarines Sur Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004139), and one additional adult paratype is housed in the KUNHM (Invertebrate Zoology No. 002181) (James, 2006).

#### 8. *Pleionogaster hongii* James, 2006

*Pleionogaster hongii* James, 2006: 168–169; (suppl.) 6, fig. 1i, j. Blakemore 2007: 48.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 11/12. Female pore single on 14. Male pores crescentic, paired on small porophores facing posteriorly in sunken male field on 18. Clitellum 14–½17. Genital markings paired presetal 17, 17/18, 19–21. Intestinal origin at 20. Intestinal gizzards four in series in 27–30, highly muscularized. Typhlosolar

origin in 46. Micronephridia 12 per segment from 19; meganephridia stomate, two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles arc-shaped in 11, 12. Spermathecae quadrithecate; ampulla cylindrical, duct poorly differentiated; diverticulum club-shaped, half or less length of main spermathecal axis joining duct near body wall.

**Type locality.**— Dipterocarp forest at Bulusan Lake, Bulusan National Park, Sorsogon Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004138), and one additional adult paratype is housed in the KUNHM (Invertebrate Zoology No. 002180) (James, 2006).

#### 9. *Pleionogaster horsti* (Beddard, 1886)

*Perichaeta horsti* Beddard, 1886: 300–302.

*Pleionogaster horsti*—Beddard 1895: 434. Michaelsen 1900: 211. Nakamura 1999: 17. Blakemore 2007: 48.

*Pleionogaster ternatae* Michaelsen, 1896: 198–200, pl. 13, fig. 2. Type locality: Possibly Ternate, Batangas, Luzon, the Philippines. Michaelsen 1900: 211.

*Pleionogaster sivickisi* Stephenson, 1933: 923–924. Type locality: Luneta, Manila, Philippine Islands. Nakamura 1999: 17. James 2004: 308.

*Pleionogaster horsti* [in part]—Easton 1979: 115–116, fig. 46a, b.

*Pleionogaster ternate* [sic]—Nakamura 1999: 17.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore not reported. Female pore single on 14. Male pores on 18. Clitellum 14–17. Genital markings paired on 16, 17, 19–22; single median on 18. Intestinal origin at 19. Intestinal gizzards about three in series in 26–28, highly muscularized. Typhlosolar origin, amount of nephridia, testes sacs and seminal vesicles not reported. Spermathecae quadrithecate; ampulla oval or sometimes cylindrical, duct narrow; diverticulum short, tubular, much of the same shape as ampulla.

**Type locality.**— Neighborhood of Manila, the Philippines.

**Remarks.**— James (2004) still retained *P. ternatae* and *P. sivickisi* as synonyms of *P. horsti*, while treated *P. jagori* and *P. samariensis* as valid species. The syntype of “*Perichaeta horsti* Beddard, 1886” is housed in the NHM (NHMUK 1974.1.86–89). The syntype of “*Pleionogaster ternatae* Michaelsen, 1896” is housed in the ZMH (ZMH-ANN-V03838). The syntypes of “*Pleionogaster sivickisi* Stephenson, 1933”

are housed in the NHM (NHMUK 1930.12.26.5–7) (Easton, 1979; James, 2004; Supplementary Table 2; J. Moore, pers. comm., 8 Aug 2024).

#### 10. *Pleionogaster isarogensis* James, 2006

*Pleionogaster isarogensis* James, 2006: 169; (suppl.) 8–9, fig. 2e, f. Blakemore 2007: 51.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore single on 14. Male pores crescentic, paired on small porophores on 18. Clitellum 14–½17. Genital markings oval, midventral, presetal 17, 19, 20; some with additional midventral 18, epidermal thickenings ventral 21, 22. Intestinal origin at 20. Intestinal gizzards four in series in 27–30, highly muscularized. Typhlosolar origin in 41. Micronephridia 6–8 per segment from 19; meganephridia stomate, two per segment from 19 posteriorly. Testes and funnels enclosed in annular sac in 10; U-shaped sac open dorsally in 11. Seminal vesicles loosely acinous in 11, 12. Spermathecae quadrithecate; ampulla ovate; diverticulum short basally-attached.

**Type locality.**— Upper montane forest soils on Mt. Isarog, Camarines Sur Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004141), and three and four additional adult paratypes are housed in the KUNHM (Invertebrate Zoology No. 002184) and the UPLBMHN (ZNS-0088), respectively (James, 2006).

#### 11. *Pleionogaster jagori* Michaelsen, 1892

*Pleionogaster jagori* Michaelsen, 1892: 247–248, fig. 26. Beddard 1895: 434. Michaelsen 1900: 211. Nakamura 1999: 17. Blakemore 2007: 48.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore single on 14. Male pores on 18. Clitellum 14–16, 17. Genital markings paired in front of 17/18, behind 18/19. Intestinal origin not reported. Intestinal gizzards four in series in 27, 29, 31, 33?, highly muscularized. Typhlosolar origin not reported. Nephridia 14 per segment. Testes sacs not reported. Seminal vesicles in 11, 12. Spermathecae quadrithecate; ampulla long, cylindrical, slightly curved, undifferentiated from duct; diverticulum cylindrical, slightly curved, about ½ as long and ⅓ as thick as ampulla.

**Type locality.**— Daraga, Luzon, the Philippines.

**Remarks.**— James (2004) removed this species from the synonymy of *Pl. horsti*. The syntypes of “*Pleionogaster jagori* Michaelsen, 1892” are housed in the ZMH (ZMH-ANN-V00359) (J. Moore, pers. comm., 8 Aug 2024).

#### 12. *Pleionogaster kitangladensis* James, 2004

*Pleionogaster kitangladensis* James, 2004: 310, fig. 4e, f. Blakemore 2007: 55.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore single on 14. Male pores paired on small papillae on 18. Clitellum not developed. Genital markings paired on posterior third of 16; anterior two thirds of 17; paired presetal on 20, 21. Intestinal origin at 19. Intestinal gizzards three in series in 27–29, highly muscularized. Typhlosolar origin in 39/40. Micronephridia eight per segment from 19; meganephridia two per segment from 19 posteriorly. Testes sacs closed laterally but open dorsally in 10; lacking in 11. Seminal vesicles small, acinous in 11, 12. Spermathecae quadrithecate; ampulla sagittate with apical knob, duct short differentiated from ampulla; diverticulum digitate, stalk arising from duct near duct junction with body wall.

**Type locality.**— Mount Kitanglad Range, Bukidnon Province, Mindanao Island, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 003992) (James, 2004).

#### 13. *Pleionogaster malinaoensis* James, 2006

*Pleionogaster malinaoensis* James, 2006: 169; (suppl.) 9, fig. 2g, h. Blakemore 2007: 62.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore single on 14. Male pores crescentic, paired on raised porophores on 18. Clitellum ½13, 14–½17. Genital markings seldom broad midventral in 9; slightly wider than spermathecal pore spacing on 10; seldom midventral round white area on 15; triangular pad on 16; paired presetal in line with male pores on 19–22; less well-developed specimens midventral epidermal thickenings on 22–23. Intestinal origin at 19 or 20. Intestinal gizzards five in series in 25–29, highly muscularized. Typhlosolar origin in 45. Micronephridia 10–12 per segment from 19; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles small, acinous in 11, 12. Spermathecae quadrithecate; ampulla ovate, differentiated from narrower duct; diverticulum simple

club-shaped, joining duct near body wall, slightly longer than spermathecal duct.

**Type locality.**— Montane forest on north ridge of Mt. Malinao, Albay Province, near Tiwi, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004142), and one additional adult paratype is housed in the KUNHM (Invertebrate Zoology No. 002189) (James, 2006).

#### 14. *Pleionogaster miagao* Blakemore, 2016

*Pleionogaster miagao* Blakemore, 2016: 26–27, fig. 12a–h.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 11/12. Female pores paired below crease on 14. Male pores on round porophores as large puckered slits on 18. Clitellum 14–16 ventrally; 14–½17 dorsally. Genital markings mid-ventral, broad V-shaped on pad 16/17 just above setae arc; paired ellipsoid postsetal on 17; paired, broad sunken patches below male pores on 18; paired, corresponding weaker on 19, 20, then weaker in 21–23, tapering as unapillated pads. Intestinal origin at 19. Intestinal gizzards four in series in 27–30, highly muscularized and each preceded by intraseptal crop. Typhlosolar origin about 60. Nephridia eight pairs per segment in anterior. Testes in sacs in 10, 11. Seminal vesicles in 11, 12; last pair in 12 with digitiform diverticulum dorsally. Spermathecae quadrithecate; ampulla elongate on short muscular duct; diverticulum stumpy clavate, ¼ as long ectally.

**Type locality.**— Brgy. Cagbang, Miagao, Iloilo, Panay Island, the Philippines.

**Remarks.**— The holotype is housed in the UPV (UPV#S7) (Blakemore, 2016).

#### 15. *Pleionogaster nautsae* James, 2006

*Pleionogaster nautsae* James, 2006: 170; (suppl.) 12–13, fig. 3g, h. Blakemore 2007: 71.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore single on 14. Male pores crescentic, paired on small porophores on 18. Clitellum 14–½17. Genital markings narrow transverse midventral extending to male pore lines presetal on 17, 19, latter with embedded paired marks; paired indented markings 17/18; broad epidermal thickenings ventral presetal, equatorial annuli of 20, 21; ventral epidermal thickenings presetal ½7, 8–½9, 10. Intestinal origin at

20 or 21. Intestinal gizzards six in series in 24–29, highly muscularized. Typhlosolar origin in 53 or 54. Micronephridia eight per segment from 19; meganephridia stomate, two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles slender arcs with large dorsal block in 11, 12. Spermathecae quadrithecate; ampulla club-shaped, duct not differentiated; diverticulum similar shape, short basally-attached.

**Type locality.**— Lower riparian forest near Barangay San Miguel, Pangabinan, Catanduanes Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004147), and two additional adult paratypes are housed in the KUNHM (Invertebrate Zoology No. 002196) (James, 2006).

#### 16. *Pleionogaster nillosae* James, 2006

*Pleionogaster nillosae* James, 2006: 170; (suppl.) 10–11, fig. 3a, b. Blakemore 2007: 71.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13. Female pore invisible. Male pores crescentic, paired on small flat porophores on 18. Clitellum unknown. Genital markings faint, paired presetal 17, 19; slight thickening of epidermis over ventral surface of 7–9. Intestinal origin at 20. Intestinal gizzards six in series in 24–29, highly muscularized. Typhlosole lacking. Micronephridia 8–10 per segment from 19; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles slender arches in 11, 12. Spermathecae quadrithecate; ampulla elongate horn-shaped, duct muscular; diverticulum simple club-shaped joining duct near body wall, much shorter than ampulla.

**Type locality.**— Low-elevation forest on karst, Caramoan Peninsula, Camarines Norte Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004144), and one additional juvenile paratype is housed in the KUNHM (Invertebrate Zoology No. 002193) (James, 2006).

#### 17. *Pleionogaster samariensis* Michaelsen, 1892

*Pleionogaster samariensis* Michaelsen, 1892: 248–249, fig. 27. Beddard 1895: 434–435. Michaelsen 1900: 211. Nakamura 1999: 17. Blakemore 2007: 48.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore not reported. Female pore single on 14. Male pores on 18. Clitellum not developed. Genital markings paired 17, 19. Intestinal origin not reported. Intestinal gizzards three in unknown segments. Typhlosolar origin not reported. Nephridia 6 or 10 per segment. Testes sacs not reported. Seminal vesicles in 11, 12. Spermathecae quadrithecate; ampulla long, cylindrical, but bent over in the shape of a horseshoe; diverticulum slightly curved, cylindrical, about half as long and half as thick as ampulla.

**Type locality.**— Loquilocun, Samar, the Philippines.

**Remarks.**— James (2004) removed this species from the synonymy of *Pl. horsti*. The syntype of “*Pleionogaster samariensis* Michaelsen, 1892” is housed in the ZMB (No. 567) (Easton, 1979; Reynolds and Cook, 1976; Supplementary Table 2).

#### 18. *Pleionogaster sorsogonensis* James, 2006

*Pleionogaster sorsogonensis* James, 2006: 170; (suppl.) 12, fig. 3e, f. Blakemore 2007: 93.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 13/14. Female pore invisible. Male pores crescentic, paired on small porophores on 18. Clitellum not developed. Genital markings midventral 10/11, 11/12, 16, 20–22; paired 17, 19. Intestinal origin at 19. Intestinal gizzards five in series in 25–29, highly muscularized. Typhlosolar origin in 40. Micronephridia four per segment from 19; meganephridia clearly stomate, two per segment from 19 posteriorly. Testes and funnels enclosed in annular? or ventrally separated? sacs in 10, 11. Seminal vesicles loosely acinous in 11, 12. Spermathecae quadrithecate; ampulla club-shaped, duct poorly differentiated; diverticulum simple club-shaped, half or more length of main spermathecal axis, joining duct near body wall.

**Type locality.**— Dipterocarp forest at Bulusan Lake, Bulusan National Park, Sorsogon Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004146) (James, 2006).

#### 19. *Pleionogaster tiwiensis* James, 2006

*Pleionogaster tiwiensis* James, 2006: 168; (suppl.) 3, fig. 1a, b. Blakemore 2007: 98.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 11/12 or 12/13. Female pore single on 14. Male pores crescentic paired on raised porophores

on 18. Clitellum  $\frac{1}{2}$ 13, 14– $\frac{1}{2}$ 17. Genital markings midventral broad pad on 17; paired presetal in line with male pores on 18; narrow elongate midventral over equator, presetal portion of 20, 21; midventral epidermal thickenings of 22–24. Intestinal origin at 19. Intestinal gizzards four in series in 25–28 or 27–30, highly muscularized. Typhlosolar origin in 47. Micronephridia 6–10 per segment from 19; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles small, acinous in 11, 12. Spermathecae quadrithecate; ampulla club-shaped; ampulla not sharply demarked from duct; diverticulum simple club-shaped joining duct near body wall.

**Type locality.**— Montane forest on north ridge of Mt. Malinao, near Tiwi, Albay Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004134), and four additional adult paratypes are housed in the KUNHM (Invertebrate Zoology No. 002175) (James, 2006).

#### 20. *Pleionogaster valida* James, 2004

*Pleionogaster valida* James, 2004: 309, fig. 4c, d. Blakemore 2007: 103.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 12/13 or 13/14. Female pores closely paired on 14. Male pores on 18. Clitellum 14– $\frac{2}{3}$ 17. Genital markings paired on 17/18; anterior portion of 18, paired anterior to and surrounding male pores; paired 18/19; broad single 19/20– $\frac{2}{3}$ 20; shorter unpaired anterior  $\frac{2}{3}$  of 21, sometimes 22. Intestinal origin at 19. Intestinal gizzards four in series in 27–30 or 26, 28–29, highly muscularized. Typhlosolar origin in 49. Micronephridia ten per segment from 19; meganephridia two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles small, acinous in 11, 12. Spermathecae quadrithecate; ampulla elongate bearing apical knob, ampulla not sharply demarked from duct; diverticulum simple sac-shaped joining duct near body wall.

**Type locality.**— Mount Kitanglad Range, Bukidnon Province, Mindanao, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 003990) (James, 2004).

#### 21. *Pleionogaster viracensis* James, 2006

*Pleionogaster viracensis* James, 2006: 169; (suppl.) 7–8, fig. 2c, d. Blakemore 2007: 104.

**Diagnosis.**— Spermathecal pores paired on 7/8–8/9. First dorsal pore 11/12. Female pore single on 14. Male pores crescentic, paired on small porophores facing posteriorly in sunken male field on 18. Clitellum 14–½17. Genital markings oval, paired, presetal 17; rectangular paired 17/18; oblong, paired presetal 19–21; midventral at equator 18. Intestinal origin at 19. Intestinal gizzards four in series in 27–30, highly muscularized. Typhlosolar origin in 52. Micronephridia ten per segment from 19; meganephridia stomate, two per segment from 19 posteriorly. Testes and funnels enclosed in annular sacs in 10, 11. Seminal vesicles slender arcuate in 11, 12. Spermathecae quadrithecate; ampulla broad club-shaped, muscular duct very short, slightly differentiated; diverticulum short basally-attached.

**Type locality.**— Low-elevation forest near Barangay Summit, Buradan, Catanduanes Province, Luzon, the Philippines.

**Remarks.**— The holotype is housed in the NMA (NMA 004140), and one additional adult paratype is housed in the KUNHM (Invertebrate Zoology No. 002183) (James, 2006).

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