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Revision of the earthworm genus *Archipheretima* Michaelsen (Clitellata: Megascolecidae), with descriptions of new species from Luzon and Catanduanes Islands, Philippines

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Abstract

A revision of Archipheretima (Clitellata: Megascolecidae) based on all available type material and the description of five new species modifies the genus diagnosis in the following points: Archipheretima have calciferous lamellar regions of the esophagus in the region of segments xi–xiii, paired supraesophageal vessels with connectives to the calciferous lamellae, hearts of xiii attached post-septally, multiple paired dorsolateral intestinal caeca, and usually very sparse dorsal setae. Blue coloration is common to all the species described, and probably to the other known species. Non-Philippine species previously assigned to the genus are excluded by this diagnosis; as a result, the new combinations Polypheretima picta (Michaelsen, 1892) and P. beccarii (Cognetti, 1909) are proposed. The new species are named Archipheretima gritzae, A. middletoni, A. ricei, A. cofini, and A. pandanophila. They were collected only on Luzon Island, except A. gritzae which also occurs on Catanduanes. The redefined Archipheretima is a biogeographically and morphologically homogenous taxon.

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Introduction

Archipheretima Michaelsen, 1928 is a very interesting genus of earthworms, from ecological, esthetical and biogeographical points of view. From what little is known of their ecology, it appears that some of them could be categorized as errant earthworms, much as certain Polychaeta are so described. While some errant polychaetes are free-swimming or crawling, rather than inhabiting burrows or interstitial spaces in the substrate, these earthworms are often found crawling about in

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plain sight in daylight hours on the forest floor (Michaelsen 1929, 1930). Local people warned that these wandering worms are capable of spraying toxic fluids from their backs when irritated, which would be about the only defense available to an errant earthworm. My experience in the Philippines was similar. Men who work in the forests reported seeing bright blue worms freely moving about during the rainy season, and some mentioned the spray.

Some species are apparently arboreal, at least facultatively or during early juvenile stages. We encountered juveniles and adults in plant leaf axils, including those of *Pandanus* and *Freycinetia* (Pandanacae) and ferns. Some were in palmate-fronded climbing ferns, in which a basal portion of the frond is modified as a cup

filled with adventitious roots and decaying organic matter. Many of our specimens were found in leaf litter layers, and only a very few actually in soil.

Many species are intensely colored in hues not commonly seen in earthworms, in this case tending towards deep blues and turquoise, with bright greenish cuticular iridescence. *Archipheretima ophiodes* Michaelsen, 1929 has irregularly scattered white flecks on the dorsal surface, and one species described here goes even further, adding yellow anterior bars and yellow centers to the white spots.

To date the genus is only known to occur on the central and northern islands of the Philippines and on Borneo (Easton 1979; but see the remarks on Archipheretima zonata below). Other Borneo-Philippines faunal connections are mainly manifested in the western Philippine Palawan archipelago, in which the southern outlier islands Balabac and Bugsuk are very close to Borneo and probably were part of a Palawan-Borneo-Sundaland land mass at Pleistocene low water (Heaney 1985, 1993). Our two collection expeditions on Palawan did not find Archipheretima there. Considering the isolation of Palawan from the rest of the Philippines, its geological origins in eastern China (Hall 1996, 1998), and the wide, though spotty, distribution of Archipheretima in the Luzon region and the Visayas, it seems unlikely that this genus arrived in Luzon via Palawan.

The material studied in the present paper was collected as part of a comprehensive effort to discover and document the earthworms of the Philippines. Prior to this undertaking, there had never been an organized effort to collect earthworm specimens from that country. In early 2001 we set out to begin collections in the entire country; during the next three years we made collections throughout Luzon Island and neighboring areas, including Catanduanes, Mindoro, the Batanes archipelago and the islands of Romblon Province. In our work *Archipheretima* were only found on Luzon and Catanduanes, but they have also been reported in the Philippines from Samar Is. (Michaelsen 1892) and Marinduque Is. (Rosa 1894; Gates 1970).

Material and methods

Collection effort was focused on the primary forest vegetation, because this is where one is most likely to find the endemic species of earthworms. *Archipheretima* were obtained by wandering around looking at the ground, scratching through the forest litter, searching under and on top of fallen tree trunks, and searching within the leaf axils and root mats of vascular epiphytes, the leaf axils of ferns and Pandanaceae, and under

mats of mosses on rocks and tree limbs. Live photographs were taken of all distinguishable morpho-species in the field. Specimens were fixed in 10% formalin for at least 24 hours, then transferred to 80% ethanol. Where numbers of specimens of a species allowed, duplicate sets were preserved in 95% ethanol for DNA extraction. Holotype material is deposited in the National Museum of the Philippines Annelida collection (NMA), other material in the Kansas University Natural History Museum (KUNHM). Collection station numbers in locality data (PTAGS000: Philippine Terrestrial Annelid and Gastropod Survey) are in chronological order.

In order to evaluate the status of the genus Archipheretima and to review the corresponding taxonomic decisions of earlier workers, type material for as many potentially relevant species names as possible was examined through loans from museums. Those names include Megascolex iris Michaelsen, 1892, the type species of Archipheretima, as well as M. margaritaceus Michaelsen, 1892, Pheretima beccarii Cognetti de Martiis, 1909, P. ophiodes Michaelsen, 1929, and P. zonata Michaelsen, 1922. None of the material obtained for P. ophiodes was useful, however, as it had been drastically dissected and virtually destroyed. For Megascolex mazarredi Rosa, 1894, M. pictus Michaelsen, 1892, and Pheretima penrisseni Michaelsen, 1928, no material could be located for this study.

Descriptions are based on observations of dorsal dissections. Except where noted, dimensions and segment counts are from clitellate adult specimens. Conventional notation for earthworms was used: lower case Roman numerals indicate segment numbers, Arabic numerals separated by slashes (e.g. 6/7) indicate segmental furrows or septa, and upper case letters denote intersetal distances and ratios (e.g. AB:YZ = 1:1). Illustrations were prepared with a drawing tube mounted on a Wild M5 stereomicroscope, scanned and edited as digital images. Photographs of live material were also scanned and edited as digital images.

Locality names in the Philippines include the province, the municipality and the barangay whenever known to us, unless the site is in a protected area or is quite remote from habitations. A barangay is like an extended neighborhood, and is the smallest political division in the Philippines; a municipality is the next higher political unit, between the barangay and province levels.

Taxonomic section

Clitellata: Megascolecidae Rosa, 1891

Archipheretima Michaelsen, 1928

Megascolex Templeton (part). – Beddard (1895, p. 370).

Amynthas Kinberg (part). – Beddard (1900, p. 612). Pheretima Kinberg (part). – Michaelsen (1900, p. 234). Pheretima (Archipheretima) Michaelsen. – Michaelsen (1928, p. 7).

Pheretima (*Archipheretima*) Michaelsen (part). – Michaelsen (1934, p. 15).

Archipheretima Michaelsen. – Sims and Easton (1972, p. 200, 232); Easton (1979, p. 21).

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

Diagnosis. Perichaetine Megascolecidae with combined male and prostatic pores on xviii, no copulatory bursa or other secondary male pore structure; testes and funnels of x, xi free or in sacs; prostates racemose xviii; spermathecal diverticula multilocular; esophageal gizzard in viii, vertical calciferous lamellae in lateral esophageal pouches xi–xiii; three to six pairs short dorso-lateral intestinal caeca or pouches in region of xxix–xxxv; all anterior septa present; hearts x–xiii latero-esophageal, hearts of xiii attached to supra-esophageal vessels usually just behind septum 12/13, doubled supraesophageal vessel in x–xiii; micronephric throughout, and nephridia extremely small; peptonephridia in paired dense clusters within some or all of iv–vi.

Archipheretima iris (Michaelsen, 1892)

Megascolex iris Michaelsen. – Michaelsen (1892, p. 244); Beddard (1895, p. 383).

Amynthas iris (Michaelsen). – Michaelsen (1899, p. 15); Beddard (1900, p. 647).

Pheretima (Archipheretima) iris (Michaelsen). – Michaelsen (1900, p. 276).

Archipheretima iris (Michaelsen). – Sims and Easton (1972, p. 200, 232); Easton (1979, p. 26).

Material examined. Syntypes (565, Museum für Naturkunde Berlin): Samar, Loquilocun, Philippines, Jagor coll.

Diagnosis. Archipheretima with spermathecal pores paired 6/7/8/9, 0.04 circumference apart; female pore single in xiv; male pores at peaks of conical porophores in xviii, pores between 2nd and 3rd setal lines, 0.04 circumference apart, 0 setae between male pores, porophores with smooth darkened surfaces. Clitellum annular xiii— xvii; genital markings broad midventral oval on 17/18, but mainly on presetal half of xviii, similar marking 18/19 mainly on postsetal xviii, oval midventral 19/20, 20/21. Esophagus with calciferous glands containing vertical lamellae xi—xiii; intestinal origin 1/2 xvi, simple dorso-lateral caeca originating

xxxi–xxxii, xxxiii, each confined to segment of origin. Nephridia in dense tufts in v on 5/6. Each spermatheca with ovate ampulla, narrow duct shorter than ampulla; single shortly stalked diverticulum terminating in ovate receptacle with one internal chamber; diverticulum-duct junction within body wall.

Description. Dull tan to light brown pigment preserved, faded blue pigment ventrally on clitellate individual. Prostomium epilobous; body 200 × 10 mm (x), 9 mm (xxv), 115 segments; body circular in crosssection. First dorsal pore 12/13; spermathecal pores paired 6/7/8/9, 0.04 circumference apart; female pore single in xiv; male pores at peaks of conical porophores in xviii, pores between 2nd-3rd setal lines, 0.04 circumference apart, 0 setae between male pores, porophores with smooth darkened surfaces. Dorsal setae sparse, setal rings more crowded ventrally, AB:YZ = 2.5-3.0:1, dorsal gaps ZZ:YZ = 3:1; 40 setae on vii, 49 on xxv; ventral gap = 3:2. Clitellum annular xiii-1/2 xvii; genital markings broad midventral oval on 17/18, but mainly on presetal half of xviii, similar marking 18/19 mainly on postsetal xviii, oval midventral 19/20, 20/21.

Anterior septa all present, 8/9–13/14 transparent, slightly muscular. Nephridia in dense tufts in v on 5/6.

Long gizzard in viii displacing septa posteriorly, muscular proventriculus in vii; esophagus with calciferous glands containing vertical lamellae xi–xiii; intestinal origin xvi, simple dorso-lateral caeca originating xxxi–xxxii, xxxiii, each confined to segment of origin; typhlosole lacking.

Hearts x-xiii latero-esophageal, xiii attached post-septally to supra-esophageal vessel, commissural vessels vi-ix lateral.

Ovaries and funnels free in xiii; spermathecae paired vii–ix; each spermatheca with ovate ampulla, narrow duct shorter than ampulla; single shortly stalked diverticulum terminating in ovate receptacle with one internal chamber; diverticulum-duct junction within body wall. Male sexual system holandric, small seminal vesicles xi, xii arcuate; each prostate a single lobed racemose mass within xviii, with short straight duct; genital marking glands lacking.

Remarks. Archipheretima iris being the type species of the genus, it was particularly important to have good data on this species. The syntypes of A. iris were in relatively good condition, but the internal organs were soft and transparent from inadequate preservation at some point. Both worms examined clearly have intestinal caeca in segments xxxi and xxxii, and the clitellate individual had another very small pair of intestinal pouches in xxxiii. The previously dissected aclitellate individual, the one on which all past accounts of internal organs in this species had been based, very clearly has esophageal lamellae in lateral pouches of the esophagus in xi–xiii. The pouches in xi are small and could

be overlooked easily, but the others are large and only required slight movement of the hearts to become obvious. I did not look at the clitellate individual in this region, in order to avoid further damage to the limited material available. It is conceivable that the species could be found at additional collection locations on Samar Island, Philippines. Samar has extensive forest cover in the interior, and relatively little elevational relief. Therefore it is likely that there is habitat close enough to the type locality, Loquilocun, in which a population of this species could be found.

Archipheretima margaritacea (Michaelsen, 1892)

Megascolex margaritaceus Michaelsen. – Michaelsen (1892, p. 245); Beddard (1895, p. 383).

Amynthas margaritaceus (Michaelsen). – Michaelsen (1899, p. 16); Beddard (1900, p. 647).

Pheretima (Archipheretima) margaritacea (Michaelsen). – Michaelsen (1900, p. 282).

Archipheretima margaritacea (Michaelsen). – Sims and Easton (1972, p. 232); Easton (1979, p. 25).

Material examined. Syntype (V361, Typus, Zoologisches Museum Hamburg): Samar, Loquilocun, Philippines.

Diagnosis. Spermathecal pores paired 6/7/8/9. One midventral genital marking at 10/11, composed of oval field with numerous small dark flecks; paired genital markings almost fused over 18/19, similar in appearance to other genital markings; dorsal setae of post-clitellate segments sparse, irregularly distributed, many gaps. Lamellar pouches of esophagus in xi?, xii, xiii, xiv?.

Remarks. No further information beyond that reported in Easton (1979) could be derived from the Hamburg type material of A. margaritacea. The specimen consists of the body wall with the intestine in segments behind the dissected section, the gizzard, and the gut and male organs of segments x–xx. However, the intestine is quite delicate and nearly transparent from poor preservation. With staining and careful observation the lamellae were detected in the loose fragment containing some of the anterior organs.

Archipheretima mazarredi (Rosa, 1894)

Megascolex mazarredi Rosa. - Rosa (1894, p. 6).

Amynthas mazarredoi (Rosa); incorrect subsequent spelling of species epithet. – Michaelsen (1899, p. 15); Beddard (1900, p. 644).

Pheretima mazarredoi (Rosa). – Michaelsen (1900, p. 283); Gates (1970, p 155).

Archipheretima mazarredoi (Rosa). – Sims and Easton (1972, p. 232).

Archipheretima mazarredi (Rosa). – Easton (1979, p. 22).

Remarks. The only information available on this species derives from the original description (Rosa 1894) and from some large aclitellates examined by Gates (1970). Until the present study it was the only octothecal species known, and it was described with the body size much larger than in the two octothecal species newly described below. The material examined by Gates could not be located in the US National Museum of Natural History (Washington, DC), the Museum of Comparative Zoology (Cambridge, MA), or the Canadian Museum of Nature (Ottawa; ON), the known current locations of other elements of Gates' collection. The natural range of the species, Marinduque Island, Philippines, has probably undergone substantial habitat alteration in the last 35 years, so persistence of the species is not certain.

Polypheretima picta (Michaelsen, 1892) comb. n.

Megascolex pictus Michaelsen. – Michaelsen (1892,

p. 246); Beddard (1895, p. 384).

Amynthas pictus (Michaelsen). – Michaelsen (1899, p. 83); Beddard (1900, p. 623).

Pheretima picta (Michaelsen). – Michaelsen (1900, p. 294).

Pheretima (*Archipheretima*) picta (Michaelsen). – Michaelsen (1928, p. 10; 1934, p. 15).

Archipheretima picta (Michaelsen). – Sims and Easton (1972, p. 230).

Archipheretima picta (Michaelsen) (part). – Easton (1979, p. 26).

Remarks. The type material for Megascolex pictus is registered as lost ("perditus") in the Museum für Naturkunde, Berlin (catalog number 554). It was unavailable to Easton (1979) already; thus, his decision to place Archipheretima beccarii (Cognetti de Martiis, 1909) in synonymy with A. picta (Michaelsen) was based on comparison of material in the former name to the published descriptions in the latter. That synonymy is considered as unreliable at this point, and M. pictus as a nomen dubium, since no material for the latter could be examined. However, the information available justifies placing both species names in Polypheretima.

Polypheretima beccarii (Cognetti, 1909) comb. n.

Pheretima beccarii Cognetti. – Cognetti de Martiis (1909, p. 331).

Pheretima (Archipheretima) beccarii Cognetti. – Michaelsen (1928, p. 11).

Archipheretima beccarii (Cognetti). – Sims and Easton (1972, p. 230).

Archipheretima picta (Michaelsen) (part). – Easton (1979, p. 26).

Material examined. Holotype (C.E. 44045, Ann. M.C. 44.1909, Museo Civico di Storia Naturale Giacomo

Doria, Genova): Borneo, Sarawak, viaggio Doria and Beccari.

Diagnosis. Polypheretima with spermathecal pores paired 5/6/7/8/9, 0.16 circumference apart between 13th and 14th setal lines; male pores at centers of flat circular porophores in xviii, pores in 16th setal line, 0.2 circumference apart, 24 setae between male pores. Clitellum annular xii–xvii; genital markings small half-circles anterior to male porophores in xviii, discrete circles just behind each spermathecal pore vi–ix. Septum 8/9 lacking, long gizzard in viii–ix displacing septa posteriorly; esophagus with lateral pouches containing vertical lamellae xi–1/2 xiv; intestinal origin xv, caeca lacking; typhlosole from xxiii, complex structure, with densely crowded vertical flaps.

Hearts x-xiii esophageal, commissural vessels vii, ix lateral, vii to gizzard only; supraesophageal vessel doubled x-xiii; extraesophageal vessels join ventral esophageal surface near 10/11. Ovaries and funnels free in xiii; spermathecae paired vi-ix; each spermatheca with irregular round ampulla, narrow duct shorter than ampulla; single shortly stalked diverticulum terminating in ovate receptacle with one (5 spermathecae) or two internal chambers (3 spermathecae); diverticulum-duct junction coelomic. Male sexual system holandric; testes, funnels, other contents of x, xi enclosed in annular sacs formed from close insertion of septa 9/10/11/12 on body wall.

Description. Unpigmented or pigment lost in preservative; prostomium epilobous; body 250 × 9 mm (x), 8 mm (xxv), 145 segments; body circular in cross-section. First dorsal pore 12/13; spermathecal pores paired 5/6/7/8/9, 0.16 circumference apart between 13th–14th setal lines; female pore single in xiv; male pores at centers of flat circular porophores in xviii, pores in 16th setal line, 0.2 circumference apart, 24 setae between male pores. Setae more crowded ventrally, AB:YZ = 1:2, dorsal gaps ZZ:YZ = 3:1; 74 setae on vii, 78 on xxv; no ventral gaps. Clitellum annular xii–xvii; genital markings small half-circles anterior to male porophores in xviii, discrete circles just behind each spermathecal pore vi–ix.

Septum 8/9 lacking, 9/10/11–13/14 transparent, slightly muscular. Nephridia preseptal in dense tufts on 5/6, 6/7; carpeting body wall in vii–ix, very small elsewhere, generally not seen.

Long gizzard in viii–ix displacing septa posteriorly; esophagus with lateral pouches containing vertical lamellae xi–1/2 xiv; intestinal origin xv, caeca lacking; intestine deeply sacculated xvi–xxviii, segmental constrictions with thick corrugated surface diminishing in extent after xxxiii, absent after xxviii; typhlosole from xxiii, complex structure, with densely crowded vertical flaps.

Hearts x-xiii esophageal, commissural vessels vii, ix lateral, vii to gizzard only; supraesophageal vessel

doubled x-xiii; extraesophageal vessels join ventral esophageal surface near 10/11.

Ovaries and funnels free in xiii; spermathecae paired vi–ix; each spermatheca with irregular round ampulla, narrow duct shorter than ampulla; single shortly stalked diverticulum terminating in ovate receptacle with one (5 spermathecae) or two internal chambers (3 spermathecae); diverticulum-duct junction coelomic. Male sexual system holandric, testes, funnels, other contents of x, xi enclosed in annular sacs formed from close insertion of septa 9/10/11/12 on body wall; large seminal vesicles xi, xii blocky main section with small dorsal lobe; each prostate a single lobed racemose mass within xviii, with short straight duct; genital marking glands lacking.

Remarks. This entirely acaecate specimen has a complex typhlosole and modified portions of the intestinal lining at segmental constrictions in the anterior intestine. Other Archipheretima have two or more pairs of caeca, no typhlosole, and no such modified intestinal lining. The Borneo worm has esophageal rather than latero-esophageal hearts, no trace of septum 8/9 (though a much-examined specimen such as this could have lost it in dissection), no ovisacs, and does have dorsal lobes of the seminal vesicles. All of these characteristics are in contrast to Philippine Archipheretima. Ingesta included much mineral soil, including large sand grains, plus finely divided organic matter. The typical Philippine Archipheretima diet is mainly coarse to medium organic matter, and rarely mineral soil. Characteristics shared among P. beccarii, P. picta and the Philippine species are the esophageal lamellar pouches and doubled supraesophageal vessels in xi-xiv, and a clitellum extending over xiii-xvii. The doubled supraesophageal vessels are much farther apart in the Philippine material seen so far.

The genus diagnosis proposed above is based on examination of the type species and other Philippine species, and excludes P. beccarii and P. picta from Archipheretima. Provisionally I place the two species names in Polypheretima Easton as defined in Easton (1979, p. 28), where the examined specimen's acaecate condition, circular male porophores, numerous discrete genital markings, annular testes sacs and spermathecal structure fit well. Borneo is within the known range of Polypheretima, whereas it is not part of the known range of Metapheretima Michaelsen, a potential alternative placement. Segmental coverage of the clitellum beyond xiv-xvi could occur in Polypheretima as it does in Metapheretima (see Easton 1979). Easton (1979), in a footnote to his key to *Polypheretima*, notes that *A. picta* will key to choice three of triplet 7, and states that "The male pores and genital markings of this species closely resemble those of *Polypheretima*, and confusion may occur when dealing with individuals lacking fully developed clitella and spermathecal diverticula." His

figure of the spermatheca of *A. picta* (Easton 1979, p. 23, fig. 10e) shows a bilobed diverticulum, which is representative of 3 of the 8 diverticula in the only known material, the one also examined here. *Polyphere-tima* spermathecal diverticula are said to be simple (Easton 1979), a proposition which, though generally true, may not be universal.

? Archipheretima zonata (Michaelsen, 1922)

Pheretima zonata Michaelsen. – Michaelsen (1922, p. 42).

Pheretima (Archipheretima) zonata (Michaelsen). – Michaelsen (1928, p. 11); Michaelsen (1934, p. 15).

Archipheretima zonata (Michaelsen). – Sims and Easton (1972, p. 181, 232).

Archipheretima zonata (Michaelsen) (part). – Easton (1979, p. 23).

Material examined. Holotype (1816, Rijksmuseum Natural History, Leiden): Borneo, Nanga Raoen, May 1894, J. Büttikofer coll.

Diagnosis. Archipheretima(?) with pigment absent from segmental equators, present between them, spermathecal pores paired 5/6/7/8/9; male pores xviii, 0.03 circumference apart; clitellum annular xiii—xvii; anterior septa all present, nephridia preseptal in dense tufts on 5/6, 6/7; esophagus with low vertical lamellae xi—xiii; intestinal origin xvi.

Spermathecae paired vi–ix; each spermatheca with ovate ampulla, narrow duct shorter than ampulla; single shortly stalked diverticulum terminating in ovate receptacle with 2–4 externally demarcated chambers. Male sexual system holandric, testes, funnels, other contents of x, xi enclosed in annular sacs formed from close insertion of septa 9/10/11/12 on body wall but free within the coelomic spaces of x, xi.

Description. Pigment absent from segmental equators, present between them, appearance striped; body 360×15 mm (xv); body circular in cross-section. Spermathecal pores paired 5/6/7/8/9; female pores paired in xiv; male pores xviii, 0.03 circumference apart. Setae very slightly more crowded ventrally, AB:YZ = 4:5, about 100 setae on vii, 80 on xxv. Clitellum annular xiii–xvii.

Anterior septa all present, 10/11–13/14 transparent, slightly muscular. Nephridia preseptal in dense tufts on 5/6, 6/7; carpeting body wall in vii–ix, very small elsewhere, generally not seen.

Gizzard viii; esophagus with low vertical lamellae xi–xiii; intestinal origin xvi.

Hearts x-xii esophageal, commissural vessels vii, ix lateral, vii to gizzard only; supraesophageal vessel doubled xi-xii.

Spermathecae paired vi–ix; each spermatheca with ovate ampulla, narrow duct shorter than ampulla; single

shortly stalked diverticulum terminating in ovate receptacle with 2–4 externally demarcated chambers. Male sexual system holandric, testes, funnels, other contents of x, xi enclosed in annular sacs formed from close insertion of septa 9/10/11/12 on body wall but free within the coelomic spaces of x, xi; each prostate a single racemose mass within xviii, with non-muscular duct.

Remarks. The intestinal tissues were too macerated to allow any decision on the presence or absence of caeca, a typhlosole, or other intestinal wall differentiation. Consequently, this species cannot be placed confidently in any genus. Features suggesting that it does not belong in Archipheretima as defined here are: striped pigmentation throughout, hearts esophageal, and last hearts in xii. Michaelsen (1922) noted that the lack of caeca was not certain, and gave no further details of intestinal features.

Easton's (1979) placement of *Pheretima penrisseni* Michaelsen, 1928 in synonymy with A. zonata is questionable, because (A) his description of A. zonata differs from Michaelsen's (1928) original description of P. penrisseni in several important points, and (B) the type material for P. penrisseni could not be found, neither for Easton's nor for the present study. The contrasting character states (presented here as ?Archipheretima zonata/?A. penrisseni) are: (1) female pores paired/unpaired; (2) all anterior septa present/ septa 8/9/10 absent; (3) testes and funnels free within segments, the septa of which meet at the body wall/testes and funnels within thin-walled sacs that may be joined ventrally and in segment xi include seminal vesicles; (4) seminal vesicles of xi clearly separate from testes and funnels/apparently within or united to testes sacs; (5) spermathecal duct partially free of body wall/ entirely within body wall; (6) spermathecal diverticula with externally marked chambers/divided internally; (7) pigmentation striped/unstriped. Easton (1979) dismissed differences in genital markings as due to the stage of maturity, but the immature material examined by Michaelsen (1928) had slight traces of genital markings. The A. zonata holotype is clitellate but entirely lacks genital markings. Michaelsen stated that there is no trace of any caeca in A. penrisseni, and that it belongs to a small species group also including A. zonata, A. picta and A. beccarii. The question remains whether that group was based on an overall view of the species, not just on the form of the spermathecae. Resolution of the issue, as well as conclusive generic placement of *Polypheretima picta* and ?*Archipheretima* penrisseni, is impossible in the absence of type material for these species names, thus depends on finding new material in Borneo.

Of the species once placed in *Archipheretima*, only those of Philippine origin clearly remain in the genus as now defined. Judgment must be reserved on those species for which type material was unavailable or

insufficient to provide the necessary data. This casts doubt on the biogeographical problem mentioned in the present paper's introduction, the disjunct distribution comprising Borneo and the northern and eastern Philippines. As things stand, this disjunction would be true if *Archipheretima* were the appropriate placement for *A. penrisseni* and *A. zonata* as well as *A. beccarii* and *A. picta*, or it would be false, should all these species be transferred to one or more other genera.

? Archipheretima penrisseni (Michaelsen, 1928)

Pheretima (Archipheretima) penrisseni Michaelsen. – Michaelsen (1928, p. 11; 1934, p. 15).

Archipheretima penrisseni (Michaelsen). – Sims and Easton (1972, p. 232).

Archipheretima zonata (Michaelsen) (part). – Easton (1979, p. 23).

Remarks. Treated as a nomen dubium here, rather than as a synonym of ?A. zonata, for the reasons explained above in the remarks on the latter species.

Archipheretima ophiodes (Michaelsen, 1929)

Pheretima (Archipheretima) ophiodes Michaelsen. – Michaelsen (1929, p. 85); Michaelsen (1930, p. 273); Michaelsen (1934, p. 15).

Archipheretima ophiodes (Michaelsen). – Sims and Easton (1972, p. 230); Easton (1979, p. 27).

Material examined. Syntype (V10418, Zoologisches Museum Hamburg): Mt. Azapan, Luzon, Philippines.

Diagnosis. Impossible at this time, see the remarks below.

Description. Length 245–300 mm, diameter 13–20 mm. 106–118 segments. Clitellum xii–xvii, firts dorsal pores 12.13. Setae approximately 60 on vii, 67 on xxvi, 72 on xxx; setae more crowded ventrally, dorsal gaps large (zz = 0.25 circumference). Male pores superficial on raised porophores extending from xviii to xx, female pores paired on xiv. Spermathecal pores paired in 4/5/6/7, 0.33 circumference apart, no genital markings.

All anterior septa present and non-muscular. Hearts in x-xiii, Holandric, testes sacs in x, xi; seminal vesicles in xi, xii, simple, thin. Spermathecae pyriform to sac-like, not differentiated into ampulla and duct; diverticula small, globular.

Remarks. The above description is given after Easton (1979). The material available for examination was even less than what Easton had seen, and no additional information could be derived from it. Archipheretima ophiodes was collected in northern Luzon, at about 1400 m elevation on Mt. Azapan in the province then called Vizcaya. The latter has since been divided in two provinces, the east now being Nueva Vizcaya, the west Quirino. I have been unable to locate Mt. Azapan

(or several possible alternative spellings) on any extant map or in old gazetteers of Philippine place names. The only useful clue to the location is the mention in Michaelsen (1929) of the tribe of men accompanying the collector that is now known as the Aeta or Agta people. According to D. Balete (pers. comm. 2001), who has traveled extensively in all parts of the Philippines, these people are more likely to have been present in modern Quirino Province. In any case, this is well within the documentable range of the genus, and is not far from the Aurora Province sites visited in the course of the present study.

Archipheretima gritzae sp. n. (Fig. 1A, B)

Etymology. At the request of her brother, this species is named in honor of Alison Gritz of Fairfield, Iowa, on the occasion of her 16th birthday.

Material examined. Holotype (NMA 004174): PTAGS069, Philippines, Catanduanes Province, low elevation forest north of Barangay Summit, Buradan, 13°46′N, 124°16′E, 275 m asl, 22 May 2001. S.W. James, P. James, J. James, K. James, J. ffitch, A. Castillo colls. Three adult paratypes (KUNHM Invertebrate Zoology 002355): same data as holotype.

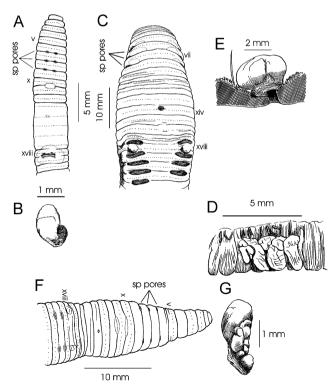


Fig. 1. Morphological structures in *Archipheretima* species. (A, B) *A. gritzae* sp. n.; (C–E) *A. middletoni* sp. n.; (F-G) *A. ricei* sp. n., Kalinga material. (A, C, F) Ventral view; sp pores = spermathecal pores. (B, E, G) Spermatheca. (D) Caeca of juvenile from PTAGS047.

Additional material. One preclitellate (KUNHM Invertebrate Zoology 002356): PTAGS068, Catanduanes Province, low elevation forest near Barangay Summit, Buradan, 13°43.60N, 124°17.14E, 250 m asl, 21 May 2001. S.W. James, P. James, J. James, K. James, J. ffitch, A. Castillo colls.; one juvenile (KUNHM Invertebrate Zoology 002357): PTAGS071, Catanduanes Province, lower riparian forest near Barangay San Miguel, Pangabinan, 13°54.50N, 124°11E, 212 m asl, 23 May 2001, S.W. James, J. ffitch, A. Castillo colls.; one adult, one preclitellate (KUNHM Invertebrate Zoology 002350): PTAGS056, Albay Province, Barangay Jarod, upper montane forest on south ridge of Mt. Malinao, 13°23.96 N, 123°37.16E, 1030 m asl, 11 May 2001. S.W. James and A. Castillo colls.

Diagnosis. Archipheretima with spermathecal pores paired 6/7/8/9, 0.09 circumference apart, male pores on porophores, pores between 3rd and 4th setal lines, 0.09 circumference apart, 0–2 setae between male pores. Dorsal setal rings complete ii–xxii, xxiv, but with wide irregular dorsal gaps thereafter, dorsal setae sparse, sporadic; 30–38 setae on vii, 34–36 setae on x, 20–28 on xxv; ventral gap = 3:2. Genital markings paired concavities with smooth, slightly darker surface posterior to male pores within xviii, broad midventral oval on 19/20 (2), midventral oval post-setal ix to presetal edge of x, or 10/11 (Fig. 1A).

Esophagus with calciferous glands containing vertical lamellae xi–xiii, glands opening by common large duct into esophageal lumen in xii; blood vessels of lamellae connected to supra-esophageal, extra-esophageal vessels.

Description. In life dusky blue-green, dull greenishgray or dusky light brown pigment preserved, sometimes with rosy tinge on segments i-vi, pigment slightly fainter ventrally. Prostomium epilobous; body 68–101 × 3.2–4.3 mm (x), 3.2–4.6 mm (clitellum), 3.0–4.4 mm (xxv), 86–107 segments; body circular in cross-section. First dorsal pore 12/13 or 13/14; spermathecal pores paired 6/7/8/9, 0.09 circumference apart, pores deep in furrows; female pores paired in xiv just lateral to first setal line; male pores transverse slits superficial on xviii on ovate low conical porophores, pores between 3rd-4th setal lines, 0.09 circumference apart, 0–2 setae between male pores. Dorsal setal rings complete ii-xxii, xxiv but with wide irregular dorsal gaps thereafter, dorsal setae sparse, sporadic; 30–38 setae on vii, 34–36 setae on x, 20–28 on xxv; ventral gap = 3:2. Clitellum annular 1/2xiii, xiv-1/2 xvii; genital markings paired concavities with smooth, slightly darker surface posterior to male pores within xviii, broad midventral oval on 19/20 (2), midventral oval post-setal ix to presetal edge of x, or 10/11 (Fig. 1A).

Anterior septa all present, 9/10–13/14 slightly muscular, junctions of 9/10–11/12 with body wall close together. Nephridia in dense tufts on pharynx in v;

nephridia of pre-intestinal segments numerous, small; nephridia of intestinal segments extremely small, hardly protruding into coelomic cavity, on pre- and post-septal arcs on body wall.

Large gizzard in viii, esophagus with calciferous glands containing vertical lamellae xi–xiii, glands opening by common large duct into esophageal lumen in xii; blood vessels of lamellae connected to supra-esophageal, extra-esophageal vessels; intestinal origin 1/2 xvi (2), xvii (5), simple dorso-lateral caeca originating xxix–xxxii (5), xxx–xxxiii (2) each confined to segment of origin; typhlosole lacking. Intestinal texture xvii–xxviii circumferential grooves within segments, smoother thereafter.

Hearts x-xiii latero-esophageal, xiii attached post-septally to supra-esophageal vessel, commissural vessels vi-ix lateral; supra-esophageal vessel doubled x-xiii, connected to calciferous glands; extra-esophageal vessels to ventral esophageal wall near 10/11, connected to calciferous gland ventral margins; efferent parieto-esophageal vessels from extra-esophageals in xiii.

Ovaries and funnels free in xiii, small ovisacs xiv; spermathecae paired vii–ix; each spermatheca with ovate ampulla, broad duct shorter than ampulla; single shortly stalked or sessile diverticulum terminating in ovate receptacle with 2–4 internal chambers (Fig. 1B). Male sexual system holandric, testes of x in open forward ventral pocket of septum 9/10, funnels free; testes, funnels of xi free; seminal vesicles xi, xii arcuate with broader ventral portion; vasa deferentia very delicate, free from body wall en route to ental end of prostatic ducts; each prostate 1–3 lobed racemose mass within xviii, with muscular straight duct; genital marking glands lacking.

Remarks. Archpheretima gritzae keys to A. margaritacea in Easton (1979), the similarities including the same numbers, locations and spacing of spermathecal pores, the presence of broad pre- and post-clitellar genital markings, and the body length. In contrast, A. gritzae is more slender, has only one preclitellar genital marking at 9/10 or 10/11, paired genital markings posterior to the male pores in xviii, and one postclitellar midventral marking at 19/20, and the last is not present in all specimens. Setal numbers are greater by about 50% in A. gritzae. Archipheretima margaritacea is said to lack male porophores, but A. gritzae clearly has them. However, the available specimens of A. margaritacea are immature. Internal characters were not recorded in the original description of A. margaritacea; type material is either missing or lacking the organs necessary for a more complete description of the species (Easton 1979), and hence for a thorough comparison with A. gritzae.

There were two distinct color variants present in the lot from PTAG069, after preservation. Some specimens were distinctly light brown in the main, while others, the minority, were greenish to bluish gray. No other internal or external characters were found to be correlated with

this color difference. The presence of a roseate brown tint of segments i—vi in most specimens, including the greenish ones, and the pink color of apparent regenerated segments on greenish worms further argue against taxonomic separation of the two color forms. The two specimens from Mt. Malinao were larger, had the caeca set back one segment, the intestinal origin slightly forward, and the preclitellar midventral genital marking one segment back compared to the Catanduanes material. Otherwise they were virtually identical.

The many caeca were of two types. The anterior two pairs had longer pockets, with distinct apertures when viewed from the inside, while the following two or three pairs were more like extensions of the dorsal anterior intestinal wall of the corresponding segments. The intestine of the following segments had the usual smooth, unexpanded appearance.

The three calciferous glands, viewed in a horizontal section, look like one three-lobed gland with vertical lamellae, with the common opening in xii. Blood circulation is arranged segmentally, with connections from the esophageal vessels to the dorsal and ventral edges of the glands, a fact which suggests that the structure has resulted from union of three glands rather than from division of a single gland.

The final remarkable feature is the extremely small size of the nephridia in the intestinal segments. At first inspection there do not appear to be any, and viewing some specimens at 25x magnification the presence of nephridia could not be ascertained. In *Dendropheretima* James, in which the disposition of the nephridia is similar, the individual organs are much larger and quite conspicuous. In *Archipheretima* these small nephridia may be so close to, or under, mesenteries that they are hard to see without examining sections.

The specimens were found in superficial locations, in one case under the bark of a prostrate dead tree trunk, in another in soil accumulated in pockets of bedrock adjacent to a small stream, and in the third at the soil-litter interface. Except at the stream site (PTAG 069), it was very difficult to find these worms.

Archipheretima middletoni sp. n. (Figs. 1C–E; 2)

Etymology. The species is named after the late Robert Hunter Middleton, a Chicago calligrapher and designer. Material examined. Holotype (NMA 004171): PTAGS048, Philippines, Aurora Province, Maria Aurora National Park, old growth remnant forest, 15°41′N 121°22′E, 725 m asl, 14 April 2001, S. James, P. Nillos and A. Castillo colls. Two adult paratypes (NMA 004172): same data as holotype; five adult paratypes (KUNHM Invertebrate Zoology 002349): same data as holotype.

Additional material. (KUNHM Invertebrate Zoology 002348): four juveniles from PTAGS047, Aurora Province, Maria Aurora National Park, secondary forest, 15°41.39′N, 121°22.27E, 635 m asl, 13 April 2001, S. James, D. James colls.

Diagnosis. Archipheretima colored deep indigo blue with scattered dorsal spots; preclitellate spots pure bright yellow, closely grouped in anterior segments, in some of iv-xi; postclitellar spots pure white with vellow centers: blue pigment confined to epidermis. not in circular muscle layer. Spermathecal pores paired 6/7/8/9, 0.30–0.34 circumference apart, flanked by postsetal oblong genital markings in vi-viii encroaching on 6/7/8/9; one GM missing from vi in some specimens; female pores paired in xiv; male pores on porophores, 0.19-0.21 circumference apart, 12-26 setae between male pores, male field strongly concave. Clitellum annular xii-xvii, 1/2 xviii; genital markings intersegmental paired oval to lanceolate in line with male pores on 17/18/19/20, 20/21 (some), 21/22 (some); those of 17/18/19 curved around porophores. Anterior septa all present, weakly muscular. Nephridia in dense preseptal tufts on 5/6.

Large gizzard in 1/2 vii, viii; esophagus with vertical lamellae in pouched expansions of esophageal walls xi–xiii, lamellar zones opening separately into esophageal lumen; blood vessels of lamellar expansions connected dorsally to supra-esophageal, ventrally to extra-esophageal vessels; paired simple dorso-lateral caeca originating xxix–xxxii (1), xxx–xxxiii (2), xxx–xxxiv (2), xxxi–xxxiv (1), each confined to segment of origin typhlosole lacking. Spermathecae paired vii–ix; each spermatheca with spherical ampulla, broad duct shorter than ampulla, duct fluted internally, confined to body wall; diverticulum mostly or wholly intramural, simple.

Description. In life deep indigo blue with scattered dorsal spots; preclitellate spots pure bright yellow, closely grouped in anterior segments, in some of iv-xi; postclitellar spots pure white with yellow centers (Fig. 2), some spots joined by slender equatorial white stripes to wider ventral white stripes; spots may be confined to one side, paired or singly, or forming bars from joined spots, or grouped in adjacent segments forming broad white areas with multiple yellow spots; these are probably fused simple spots; ventral intersegmental furrows tinted blue; in head, tail segments ventral side solid deep blue. Preserved color dusky blue, yellow absent, white stained with blue pigment; pigment confined to epidermis, not in circular muscle layer. Prostomium epilobous; body $208-264 \times 15-20 \,\mathrm{mm}$ (x), 18–23 mm (clitellum), 16–24 mm (xxv), 98–124 segments, mean 112; body circular in cross-section. First dorsal pore 12/13; spermathecal pores paired 6/7/8/9, 0.30-0.34 circumference apart, pores deep in furrows, flanked by postsetal oblong genital markings in vi-viii



Fig. 2. Archipheretima middletoni sp. n. on forest floor at collection site. Photograph by S.W. James.

encroaching on 6/7/8/9; one GM missing from vi in some specimens; female pores paired in xiv; male pores transverse slits superficial on xviii on ovate to hemispheric porophores, 0.19–0.21 circumference apart, 12-26 setae between male pores, male field strongly concave. Clitellum annular xii-xvii, 1/2 xviii; genital markings intersegmental paired oval to lanceolate in line with male pores on 17/18/19/20, 20/21 (some), 21/22 (some); those of 17/18/19 curved around porophores (Fig. 1C). Dorsal, lateral setae confined to white spots or narrow white equatorial stripes, ventral unpigmented segmental equators with closely spaced setae about 25 per cm, total setal counts 52 setae on vii, 49 setae on x, 48-60 on xxv; numbers dependent on presence of dorsal spots, spot-free post-clitellar segments with about 50-56 setae: ventral gap AA:AB = 2:1

Anterior septa all present, weakly muscular. Nephridia in dense preseptal tufts on 5/6; nephridia of clitellum segments carpeting body wall; nephridia of intestinal segments extremely small, hardly protruding into coelomic cavity, on pre- and post-septal arcs on body wall.

Large gizzard in 1/2 vii, viii, esophagus with vertical lamellae in pouched expansions of esophageal walls xi-xiii, lamellar zones opening separately into esophageal lumen; blood vessels of lamellar expansions connected dorsally to supra-esophageal, ventrally to extra-esophageal vessels; intestinal origin xvi (5), xvii (1), paired simple dorso-lateral caeca originating xxix-xxxii (1), xxx-xxxiii (2), xxx-xxxiv (2) xxxi-xxxiv (1), each confined to segment of origin (Fig. 1D); typhlosole lacking. Caecal lining thick, villous, whiter in contrast to general intestine.

Hearts x-xiii latero-esophageal, esophageal connective of x penetrating septum 10/11 to reach supra-esophageal in xi; heart xiii attached to middle of supra-esophageal vessel of xiii, commissural vessels vi-ix lateral; supra-esophageal vessel usually doubled xi-xiii, connected to calciferous glands; extra-esophageal vessels to ventral

esophageal wall near 10/11, connected to calciferous gland ventral margins; efferent parieto-esophageal vessels from extra-esophageals in xiii.

Ovaries and funnels free in xiii; spermathecae paired vii—ix; each spermatheca with spherical ampulla, broad duct shorter than ampulla, duct fluted internally, confined to body wall; diverticulum mostly or wholly intramural, simple (Fig. 1E). Male sexual system holandric; testes, funnels of x, xi free; seminal vesicles xi, xii elongate with narrow dorsal end; vasa deferentia very small, obscured in body wall; each prostate single dense racemose mass within xviii, tightly bound to body wall by membranes, gland almost sessile on muscular short duct; genital marking glands lacking.

Remarks. The closest in external appearance is A. ophiodes, which lacks the vellow spots according to the report by its collector. The yellow pigment is entirely lost after preservation, and the pure white of the spots, equatorial bands, and ventral side is stained slightly with the blue. Regardless of color differences, the male porophore shape of the new species is circular rather than elongate over three segments, it has many genital markings rather than none, the location of spermathecae is more posterior in A. middletoni, and the spermathecal diverticula are mostly intramural. By spermathecal location and numbers A. middletoni resembles A. gritzae and A. margaritacea, from which it can be distinguished by size, color, spermathecal anatomy, genital marking pattern, number and distribution of setae, configuration of the esophageal lamellae, and the situation of the testes in segment x, among other characteristics. Coelomic spaces of formalin-fixed worms were nearly filled with dense, coagulated body fluids, which had to be carefully removed in order to see the internal organs. Only segments ii-iv, x, and xi lacked this material.

The remarkable coloration may be cryptic and/or disruptive, the former because the spots tend to resemble small patches of light reflecting from dead leaves on the

forest floor, the latter because spots may break up the earthworm's body outline. Regardless of which of these effects is more significant in the eyes of vertebrate earthworm predators, including earthworm collectors, these worms are surprisingly hard to see from distances over several meters.

All adults were found in the open on the forest floor, during intermittent heavy rains. Local guides insisted that this was normal behavior for these worms, and that they did not burrow. Our guides related the local belief that these large worms travel to river banks, where they enter the water and metamorphose into the large spotted eels inhabiting the river. Juvenile A. middletoni have the same coloration as the adults. We found them in one size class only (about 50-70 mm), and exclusively in above-ground locations such as arboreal ferns and leaf axils of *Pandanus* sp. In marked contrast to our collecting experience before and since, each plant from which a juvenile was collected contained only the one juvenile, never more, and no other earthworms of any kind. Ordinarily, a plant may contain several to twenty or more individual earthworms of two or more species, including other species of Archipheretima.

Another unusual feature of *A. middletoni* was the calm behavior at the moment of capture, and in captivity until fixation. They could be handled without any attempt to escape, or set on the ground for photography sessions, during which they would remain as placed for several minutes before starting to move off.

Archipheretima ricei sp. n. (Figs. 1F, G; 3A, B)

Etymology. The Rev. Dilbert Rice is an American missionary (retired) who, while serving the people of Imugan, established the Kalahan Foundation and some forest preserves in the area. The Rev. Rice deserves great credit for protecting some of the last remnants of the forest of the Caraballo Mountains, a transverse range crossing northern Luzon. This species is named in his honor.

Material examined. Holotype. (NMA004169): PTAGS-045, Philippines, Nueva Vizcaya Province, Barangay Imugan of Santa Fe, montane forest on Mt. Akbab, Kalahan Foundation land, 16°11.44′N, 120°52.21′E, 1675 m asl, 11 April 2001, S. James, P. Nillos colls.

Additional material. Three juveniles (NMA 004170): same data as holotype. One adult (KUNMH Invertebrate Zoology 002341): PTAGS022, Kalinga Province, Barangay Balbalasang, sitio Magdalao, montane forest, 17°27.31′N, 121°04.32′E, 1600 m asl, 15 March 2001, K. Daley, S. James colls. One adult (KUNMH Invertebrate Zoology 002342): PTAGS023, Kalinga Province, Balbalasang, sitio Am-likao, montane forest,

17°26.31′N, 121°04.21′E, 1800 m asl, K. Daley, S. James colls.

Diagnosis. Archipheretima with spermathecal pores three pairs 6/7/8/9, 0.16–0.28 circumference apart increasing posteriorly, male pores face posteriorly on low rounded porophores xviii with deep indentations anterior, posterior to porophores, pores in 6th–8th setal lines, 0.18 circumference apart, 0, 5 or 10–16 setae between male pores. Genital markings paired and midventral before clitellum, paired behind clitellum; dorsal setae sparse, dorsal 1/3 nearly asetal, setae twice as crowded ventrally; dorsal gap variable 7–10:1, ventral gap = 5:3; 32–50 setae on vii, 26–40 setae on x, 26–36 on xxv. Nephridia in dense tufts ventral, preseptal on 4/5, 5/6.

Large gizzard in 1/2 vii–viii, viii only; esophagus with vertical calciferous lamellae xi–xiii but mainly xii, xiii; lamellar pouches opening by common large aperture into esophageal lumen in xii or independently; shallow paired dorso-lateral caeca xxx–xxxiii or xxxi–xxxiii.

Description. In life brilliant indigo blue to green, with green iridescence, dusky turquoise to tan preserved, ventral side pale, some juveniles (Imugan material) burgundy when preserved. Prostomium epilobous; body $95-104 \times 6-8 \,\mathrm{mm}$ (x), $8-10 \,\mathrm{mm}$ (xxv), 79, 90-96 segments; body circular in cross-section but ventrum flat. First dorsal pore 11/12 (1), 12/13 (4), 13/14 (1, but in this specimen all pores closed); spermathecal pores three pairs 6/7/8/9, 0.16-0.28 circumference apart increasing posteriorly, pores with small half-lenticular lips on anterior side, deep in furrows; female pores paired in

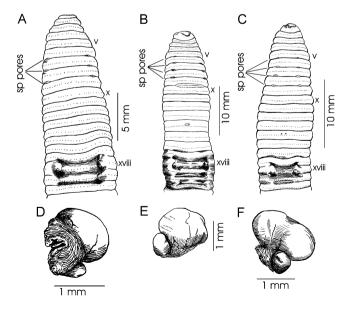


Fig. 3. Morphological structures in *Archipheretima* species. (A, B) *A. ricei* sp. n., Nueva Vizcaya material; (C, D) *A. cofini* sp. n.; (E, F) *A. pandanophila* sp. n. (A, C, E) Ventral view; sp pores = spermathecal pores. (B, D, F) Spermatheca.

xiv; male pores face posteriorly on low rounded porophores xviii with deep indentations anterior, posterior to porophores, pores in 6th to 8th setal lines, 0.18 circumference apart, 0, 5 or 10–16 setae between male pores. Male field sunken, surrounded by lateral ridges. Clitellum annular xiii–xv, incompletely developed; genital markings paired ovals on 9/10, 19/20 (4 individuals) 19/20/21 (2), L 21/22 (1) or R 21/22 (1) (Fig. 3A); broad midventral (Kalinga material only) 10/11/12 (1), 10/11 (1) (Fig. 1F). Dorsal setae sparse, dorsal 1/3 nearly asetal, setae twice as crowded ventrally; dorsal gap variable 7–10:1, ventral gap = 5:3; 32–50 setae on vii, 26–40 setae on x, 26–36 on xxv.

Anterior septa all present, 7/8–15/16 slightly muscular. Nephridia in dense tufts ventral, preseptal on 4/5, 5/6; nephridia of pre-intestinal segments numerous, carpeting body wall; nephridia of intestinal segments small, on pre- and post-septal arcs on body wall.

Large gizzard in 1/2 vii–viii, viii only, esophagus with vertical calciferous lamellae xi–xiii but mainly xii, xiii; lamellar pouches opening by common large aperture into esophageal lumen in xii (Kalinga), or independently (Imugan); blood vessels of lamellae connected to supraesophageal, extra-esophageal vessels; intestinal origin xvi (2), xvii (4), shallow paired dorso-lateral caeca xxx–xxxiii or xxxi–xxxiii; typhlosole lacking.

Hearts x-xiii latero-esophageal, xiii attached post-septally to supra-esophageal vessel, commissural vessels vi-ix lateral; supra-esophageal vessel doubled xi-xiii, with transverse connective between supra-esophageal vessels in xii; supra-esophageals connected to calciferous glands; extra-esophageal vessels to ventral esophageal wall near 10/11, connected to calciferous gland ventral margins; efferent parieto-esophageal vessels from extra-esophageals in xiv.

Ovaries and funnels free in xiii; spermathecae paired vii–ix; each spermatheca with ovate to knobby ampulla, broad duct shorter than ampulla; single shortly stalked or sessile diverticulum terminating in ovate receptacle with 2–4 internal chambers (Fig. 1G); duct and diverticulum attachment largely within body wall (Fig. 3B). Male sexual system holandric, testes, funnels free; seminal vesicles xi, xii broad acinous crescents; vasa deferentia very delicate, free from body wall en route to ental end of prostatic ducts; each prostate dense racemose mass within xviii, with very short muscular straight duct; genital marking glands lacking.

Remarks. Archipheretima ricei has the same location and number of spermathecae as A. gritzae, A. margaritacea, A. iris, and A. middletoni. In A. ricei worms are broader and longer than in the first of those other species, much smaller than in the last, have a nearly asetal dorsal surface, more widely spaced male and spermathecal pores than in the first three species, but more narrowly spaced than in A. middletoni. They have only paired post-clitellar genital markings as in

A. middletoni, whereas the other species have midventral post-clitellar genital markings. Archipheretima ricei preclitellar genital markings are midventral, unlike in A. middletoni and A. iris, but as in A. margaritacea and A. gritzae. Internal differences are few. Specimens of A. ricei do not show testes in low forward pouches of septum 9/10 as in A. gritzae.

The two Kalinga specimens were collected in very different places, one in nearly saturated soil adjacent to a watercourse, the other in a well-drained area of forest at a higher elevation. Small juvenile blue worms probably belonging to the genus were collected at a Magdalao forest site just above station PTAGS022, but it cannot be determined whether these belong to the same or a different species. Local men report the presence of larger worms of the same color as the juveniles during the rainy season, when the worms are seen roaming about on the forest floor.

Differences between the Nueva Vizcaya and Kalinga specimens are few, the latter having a common duct for the sections of the esophageal lamellae pouches of a side, and somewhat fewer setae per segment. Given the small numbers of individuals from both sites, and the lack of fully mature specimens, I propose to place all in the same species. A representative from each site is figured to show the external differences.

Archipheretima cofini sp. n. (Fig. 3C, D)

Etymology. Romeo Cofin, then the Captain of Barangay Lias, was our host and chief guide during the collecting in his region. The species is named after him

Material examined. Holotype (NMA 004168): PTAGS034, Philippines, Mountain Province, Mt. Lamagan, Barangay Lias of Barlig, lower montane forest in climbing ferns, 17°07.34′N, 121°10.20′E, 1675 m asl, 4 April 2001, S. James, A. Castillo, R. Cofin colls.

Additional material. One juvenile (KUNHM Invertebrate Zoology 002344): same data as holotype.

Diagnosis. Archipheretima with four pairs spermathecal pores in 5/6/7/8/9, 0.23–0.28 circumference apart increasing posteriorly, male pores face posteriorly on low rounded porophores xviii, pores in 15th setal line, 0.25 circumference apart, 18 or 26 setae between male pores. Dorsal setae sparse, setae twice as crowded ventrally; dorsal gap variable 5 or 6:1, ventral gap = 5:2; 32 setae on vii, 40 setae on x, 80 on xxv. Clitellum annular xiii–xvi, dorsal only xvii; genital markings paired ovals on 19/20, broad midventral 9/10, 20/21– 1/2 xxi; deep smooth-surfaced indentations flanking porophores 17/18, 18/19.

Esophagus with vertical calciferous lamellae xi-1/2 xiv but mainly xii, xiii; esophagus showing pouches only

in xii, xiii; lamellar pouches opening independently into esophageal lumen; intestinal origin 1/2 xvi, paired dorso-lateral pocket-shaped caeca xxx–xxxii, shallower in xxxiii–xxxvi; all caeca lined with white villous corrugations unlike general intestinal lining.

Description. In life brilliant indigo blue with green iridescence, duller blue preserved, ventral side pale. Prostomium epilobous; body $149 \times 8.5 \,\mathrm{mm}$ (x), $8 \,\mathrm{mm}$ (clitellum), 9 mm (xxv), 108–119 segments; body circular in cross-section. First dorsal pore 12/13; spermathecal pores four pairs 5/6/7/8/9, 0.23-0.28 circumference apart increasing posteriorly, pores with small halflenticular lips on anterior side, deep in furrows; female pores paired in xiv; male pores face posteriorly on low rounded porophores xviii, pores in 15th setal line, 0.25 circumference apart, 18 or 26 setae between male pores. Male field sunken, surrounded by lateral ridges. Dorsal setae sparse, setae twice as crowded ventrally; dorsal gap variable 5 or 6:1, ventral gap = 5:2; 32 setae on vii, 40 setae on x, 80 on xxv. Clitellum annular xiii-xvi, dorsal only xvii; genital markings paired ovals on 19/20, broad midventral 9/10, 20/21-1/2 xxi; deep smooth-surfaced indentations flanking porophores 17/18, 18/19 (Fig. 3C).

Anterior septa all present, 7/8–15/16 slightly muscular. Nephridia in dense tufts preseptal on 4/5, 5/6; nephridia of pre-intestinal segments numerous, carpeting body wall; nephridia of intestinal segments small, on pre- and post-septal arcs on body wall.

Large gizzard in viii, esophagus with vertical calciferous lamellae xi-1/2 xiv but mainly xii, xiii; esophagus showing pouches only in xii, xiii; lamellar pouches opening independently into esophageal lumen; blood vessels of lamellae connected to supra-esophageal, extra-esophageal vessels; intestinal origin 1/2 xvi, paired dorso-lateral pocket-shaped caecae xxx-xxxii, shallower in xxxiii-xxxvi; all caeca lined with white villous corrugations unlike general intestinal lining; typhlosole lacking.

Hearts x-xiii latero-esophageal, xiii attached post-septally to supra-esophageal vessel, commissural vessels vi-ix lateral; supra-esophageal vessel doubled xi-xiii; extra-esophageal vessels to ventral esophageal wall near 10/11, connected to calciferous gland ventral margins; efferent parieto-esophageal vessels not seen.

Ovaries and funnels free in xiii; spermathecae paired vi–ix; each spermatheca with irregular ovate ampulla, broad duct shorter than ampulla, confined to body wall; single shortly stalked or sessile diverticulum transversely placed ovate receptacle with 2–3 internal chambers (Fig. 3D); diverticulum attachment largely within body wall but receptacle not. Male sexual system holandric, testes, funnels free; seminal vesicles xi, xii broad acinous crescents; vasa deferentia very delicate, obscured in body wall en route to ental end of prostatic ducts; each prostate dense fine-textured racemose mass within xviii,

with very short muscular straight duct; genital marking glands lacking.

Remarks. With four pairs of spermathecae, A. cofini is similar to A. mazarredi in the number, location and spacing of spermathecal pores. Compared to the latter species, A. cofini has fewer than half as many setae in the anterior segments, prominent rather than indistinct male pores, pre-and post-clitellar midventral genital markings rather than only paired GMs, and an intestinal origin in xvi rather than in xvii.

Gates (1970) gave a preliminary account of a taxon possibly related to *A. mazarredi*, without stating explicitly how many pairs of spermathecae it has. This undescribed taxon also differs from *A. cofini* in several respects, including in genital markings and intestinal origin.

Archipheretima pandanophila sp. n.

(Fig. 3E, F)

Etymology. The specific epithet means 'fond of Pandanus', as the specimens were collected in the leaf axils of Pandanus sp. It is to be treated as adjectical for the purposes of nomenclature. Locally, the Pandanus spp. are known as pandan, so the new species name is also intelligible to people using the Philippine common name for the plant.

Material examined. Holotype (NMA 004173): PTAGS230, Philippines, Nueva Vizcaya Province, Solano, Mt. Palali, lower montane forest in pandan plants, 16°27.03′N, 121°13.06′E, 1274 m asl, 19 November 2003, S. James coll. Paratype (KUNHM Invertebrate Zoology 002354): same data as holotype.

Diagnosis. Archipheretima with four pairs relatively closely spaced spermathecal pores in 5/6/7/8/9, 0.15–0.17 circumference apart increasing posteriorly, in 10th setal line, pores with slightly tumid lips on either side; female pores paired in xiv in 2nd setal line; male pores face posteriorly on low hemispheric porophores xviii, pores in 11th setal line, 0.13 circumference apart, 13 setae between male pores. Male field sunken xvii–xx, surrounded by lateral ridges. Dorsal setae sparse, irregular, setae twice as crowded ventrally; dorsal gap variable: $YZ = 0.2-0.9 \,\text{mm}$, $ZZ = 0.6-4.0 \,\text{mm}$; ventral gap = 1:1 or 2:1; setae of ventralmost surface about 10/mm; 54 setae on vii, 48-54 setae on x, 64-72 on xxv. Clitellum annular xiii-xvii; genital markings indistinct paired smooth-surfaced dark indentations flanking porophores 17/18, 18/19.

Calciferous glands with vertical lamellae xi-xiii, glands of xi, xii opening together into esophageal lumen in xii, glands of xiii join esophageal lumen in xiii; blood vessels of lamellae connected to supra-esophageal; intestinal origin xvi, intestine deeply pouched xvi-xxx, paired dorso-lateral pocket-shaped caecae xxx,

xxxi–xxxv; all caeca lined with white villous corrugations unlike general intestinal lining; typhlosole mere wrinkle xxx, xxxi–xlii, xlvi. Extensive vascularization of intestine xvi–xx; circumferential intestinal wall blood vessels present elsewhere.

Description. In life brilliant blue-green, duller bluegreen preserved, ventral side paler. Prostomium epilobous, tongue closed; body 120, $126 \times 8 \,\mathrm{mm}$ (x), $8 \,\mathrm{mm}$ (clitellum), 9 mm (xxv), 110, 115 segments; body circular in cross-section. First dorsal pore 12/13: spermathecal pores four pairs 5/6/7/8/9, 0.15-0.17 circumference apart increasing posteriorly, in 10th setal line, pores with slightly tumid lips on either side; female pores paired in xiv in 2nd setal line; male pores face posteriorly on low hemispheric porophores xviii, pores in 11th setal line, 0.13 circumference apart, 13 setae between male pores. Male field sunken 1/2 xvii–1/2 xx, surrounded by lateral ridges. Dorsal setae sparse, setae twice as crowded ventrally; dorsal gap variable: $YZ = 0.2-0.9 \,\text{mm}$, $ZZ = 0.6-4.0 \,\text{mm}$; ventral gap = 1:1 or 2:1; setae of ventralmost surface about 10/mm; 54 setae on vii, 48–54 setae on x, 64–72 on xxv. Clitellum annular xiii-xvii; genital markings paired smoothsurfaced dark indentations flanking porophores 17/18, 18/19 (Fig. 3E).

Anterior septa all present, 7/8–15/16 slightly muscular, maximum muscularity at 12/13/14. Nephridia in dense tufts preseptal on 4/5/6; nephridia of pre-intestinal segments numerous, carpeting body wall; nephridia of intestinal segments small, on pre- and post-septal arcs on body wall.

Large gizzard in vii–viii, calciferous glands with vertical lamellae xi–xiii, glands of xi, xii opening together into esophageal lumen in xii, glands of xiii join esophageal lumen in xiii; blood vessels of lamellae connected to supra-esophageal; intestinal origin xvi, intestine deeply pouched xvi–xxx, paired dorso-lateral pocket-shaped caecae xxx, xxxi–xxxv; all caeca lined with white villous corrugations unlike general intestinal lining; typhlosole mere wrinkle xxx, xxxi–xlii, xlvi. Extensive vascularization of intestine xvi–xx; circumferential intestinal wall blood vessels present elsewhere.

Hearts x–xiii latero-esophageal, xiii attached post-septally to supra-esophageal vessel, commissural vessels vi–ix lateral; supra-esophageal vessel doubled xi–xiii; extra-esophageal vessels not seen; efferent parieto-esophageal vessels from xiii via septum 13/14 to body wall xiv–xviii.

Ovaries and funnels free in xiii; spermathecae paired vi–ix; each spermatheca with cordate to ovate ampulla, broad duct shorter than ampulla, duct nearly confined to body wall; single sessile diverticulum transversely placed trangular receptacle with 3–4 internal chambers (Fig. 3F); diverticulum attachment largely within body wall but receptacle not. Male sexual system holandric, testes, funnels free; septa adjacent to testicular segments not closely placed

on body wall; seminal vesicles xi, xii broad crescents; vasa deferentia very delicate, obscured in body wall en route to ental end of prostatic ducts; each prostate dense fine-textured racemose mass within xviii, with very short muscular straight duct; genital marking glands lacking.

Remarks. Archipheretima pandanophila is octothecal, as are A. cofini and A. mazarredi, but the spacing of the pores is much closer, and it shows only the indistinct genital markings flanking the male porophores. Compared to A. cofini, there are fewer setae in the anterior segments, the dorsal setal spacing is more irregular and the ventral gap much narrower. The calciferous lamellae are not separated from the esophageal lumen in A. cofini, and there is no typhlosole. The forms of the spermathecae and spermathecal diverticula are also distinct.

Archipheretima sp.

Material examined. (KUNHM 002352): PTAGS186, Philippines, Luzon Island, Maconacon, Northern Sierra Madre Natural Park, secondary riparian forest under logs, 17°23.81′N, 122°12.92′E, 57 m asl, 11 March 2003, N. Aspe, S. James colls.

Remarks. Two small juveniles (50, 71 mm long) with no sign of reproductive characters were found at this location. The characters of the gut and circulatory systems were consistent with the other *Archipheretima* described here. Local men here and elsewhere in the northern Sierra Madre range reported seeing blue earthworms during the rainy season, but we were unable to locate any adults. This record is included here, as it extends the known range of *Archipheretima* to northeastern Luzon.

Discussion

The genus definitions given in Sims and Easton (1972) and Easton (1979) make no mention of lamellar structures in the esophagus, intestinal caeca, or duplicated supraesophageal vessels, except to state that the first and second are absent. Gates (1970) did notice the lamellae in segments xi–xiii in A. mazarredi, but did not report intestinal caeca. Because all other features of the new species described above match the characteristics of Archipheretima, I choose to place these species in this genus. Based on the data presented above for the type and other included species, I am emending the generic diagnosis to include intestinal caeca, calciferous lamellae, and related properties of the circulatory system. Archipheretima can no longer be considered acaecate as in Sims and Easton (1972) and Easton (1979).

The somatic characters of the species described here support the new diagnosis for the genus. All have intestinal caeca of the same form, lined with a thick villous layer not equal to the lining of adjacent internal surfaces of the intestine. All have some form of

esophageal lamellae arranged vertically (circumferentially) in xi–xiii, sometimes extending into xiv, and sometimes missing from xi. In some species these lamellae are in expansions of the esophageal wall, not divided from the esophageal lumen; in others the lamellar surfaces are pinched off into separate sacs with ducts to the esophagus. Regardless of the disposition of the lamellae, the lamellar blood circulation is connected dorsally to supra-esophageal vessels that are doubled, and ventrally to the normally (in related genera) paired extra-esophageal vessels. There is interspecific variation in the supra-esophageal vessels, with the doubling complete only in some of the species.

Another unusual feature is the post-septal attachment of the hearts in xiii to the supra-esophageal vessels. Megascolecid hearts are normally attached pre-septally at the posterior of a segment, and this is the case in segments x-xii of *Archipheretima*. Nephridia of the intestinal segments are extremely small, hardly protruding into the coelomic cavity, but farther forward they are somewhat more conspicuous. They are found in pre- and post-septal arcs on the body wall. Peptonephridia, rather than being located on the anterior faces of anterior septa, are crowded in dense clusters along the pharynx.

The testes of segment x are either wholly free or tucked into a forward pocket of septum 9/10, which is open to the rest of the segment, thus is not a testes sac in the strict sense. In this case, coagulated sperm material is present throughout segment x, rather than confined to a sac as in most of the *Pheretima* complex of genera. No such pocket exists in segment xi. Annular testes sacs are present in *A. mazarredi* (sometimes), *A. beccarii*, *A. iris*, and ?*A. zonata*. Testes sacs are present in *A. ophiodes*, but were not characterized.

Archipheretima is similar to Dendropheretima James and Isarogoscolex James in the general structure of the calciferous lamellae and the blood vessels in segments x-xiii. The calciferous region has vertically oriented lamellae in xi-xiii, just as in the other two genera. However, in Archipheretima the lamellae may be in lateral pouches of the esophageal lumen or in separate glands opening to the esophagus by a common duct in xii, rather than by individual segmental ducts (*Isarogoscolex*) or by either segmental ducts or a combined opening in xiv via paired channels (Dendropheretima). All three genera show paired supra-esophageal vessels connecting to the dorsal edges of the lamellar pouches, and paired extra-esophageal vessels connected to the ventral edges of the pouches. In the new Archipheretima species there are greater numbers of caeca, although the posteriormost one or two pairs are quite shallow and appear to be little more than slight extensions of the intestinal wall. Nevertheless, the linings of these proto-caeca are distinct in appearance from the intestinal walls of preceding and following segments. Finally, all three genera are found primarily in microhabitats with organic material.

Previous records from the Philippines were from Samar, Marinduque and eastern Luzon. Our collections found the genus in southern Luzon, Catanduanes, and northern Luzon. In addition to the records reported here, our guides from a small community near Tuguegarao reported seeing blue worms in the Mt. Cetaceo area (17°43'N, 121°59'E), which is in NE Luzon. One of our collecting teams found a single Archipheretima in Kalbaryo-Patapat, a forest reserve in extreme NW Luzon. So far our work in Mindoro. Sibuyan, Tablas, Palawan and Mindanao has failed to find members of this genus. For the time being, the known distribution range is the greater Luzon faunal region, which includes Catanduanes and Marinduque, plus Samar. Archipheretima will probably be found on Leyte, which was united with Samar at Pleistocene low water (Heaney 1985). As Samar and Leyte were also joined to Dinagat, Siargao and Mindanao at low water levels, the genus could also be present on these three islands. Perhaps the Mindanao distribution will be only the NE portion of that large island. We have collections from throughout, but no Archipheretima have been found.

At this point it is premature to do more than suggest that Archipheretima may share some biogeographic history with Dendropheretima and Isarogoscolex. The latter two genera are known only from southern Luzon, a section of the island that arrived late in the geological evolution of the Philippines (Hall 1996, 1998), possibly in conjunction with the Samar area. One working hypothesis might be that the three genera arrived on that late-arriving land fragment, and spread from there. In this scenario, Archipheretima has been much more successful at colonizing new areas than the other two genera. This may be a consequence of the errant habits of several species. Archipheretima ricei or the adults of a very similar species in the same place are known by local men to wander on the forest floor during the rainy season. This being among the most northerly records, it suggests that range expansion has favored errant species more than those found in soils, such as A. gritzae. Future collections from other locations in the known and predicted ranges may tell us more about the role of species ecology in dispersal.

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