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Chih-Han Chang^a & Jiun-Hong Chen^a

^a Institute of Zoology

^b Department of Life Science, National Taiwan University, Taipei, Taiwan, ROC

^c Institute of Zoology, National Taiwan University, No. 1, Roosevelt Road, Section 4, Taipei 106, Taiwan, ROC E-mail:

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Three new species of octothecate pheretimoid earthworms from Taiwan, with discussion on the biogeography of related species

CHIH-HAN CHANG¹ & JIUN-HONG CHEN^{1,2}

¹Institute of Zoology, and ²Department of Life Science, National Taiwan University, Taipei, Taiwan, ROC

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Abstract

Three new species of octothecate *Metaphire* pheretimoid earthworms are described from Taiwan. They have close phylogenetic relationships with five described species, *Metaphire paiwana*, *Metaphire bununa*, *Metaphire riukiensis*, *Metaphire taiwanensis*, and *Amyntas formosae*. These eight species are all octothecate. They have similar body size, colour, prostate glands and caeca, and the seven species belonging to the genus *Metaphire* have C-shaped male pores. Excluding *M. riukiensis*, which has been found only in the Ryukyu Islands, the other seven species are endemic species in Taiwan. Each of them has a distinct geographical distribution. Accordingly, we inferred that the ancestor of these eight species, including *M. riukiensis*, came to Taiwan from the continent of East Asia during the Pleistocene. A few of their descendants went northward to the Ryukyu Islands and were isolated. The others remained in Taiwan, dispersed, and were isolated by geographical barriers such as mountains and rivers. Subsequent allopatric speciation events in Taiwan and in the Ryukyu Islands then generated these eight species.

Keywords: *Biogeography, earthworm, Metaphire, phylogenetic relationship, Taiwan*

Introduction

Taiwan, a continental island on the west edge of the Pacific Ocean, is separated by the 170-km wide Taiwan Strait from the mainland of China. Most of the area of Taiwan is occupied by mountains: the Central Mountain Area, which is composed of the Central Mountain Range, Shei-Shan Mountain Range, Yu-Shan Mountain Range, and Ali-Shan Mountain Range, lies in central Taiwan, with 258 mountain peaks over 3000 m. Near the east coast lies the Coastal Mountain Range, in which the majority of the mountain peaks are about 1000 m (Figure 1).

During the period between 1964 and 1999, research on the earthworm fauna of Taiwan was suspended. In 1999, 26 earthworm species were reviewed (Shih et al. 1999). However, 29 more species were reported in the next 5 years (Tsai CF et al. 1999, 2000a, 2000b, 2000c, 2001, 2002, 2003, 2004; Tsai SC et al. 2000; Chang et al. 2001; Chuang and Chen

Correspondence: Jiun-Hong Chen, Institute of Zoology, National Taiwan University, No. 1, Roosevelt Road, Section 4, Taipei 106, Taiwan, ROC. E-mail: chenjh@ntu.edu.tw

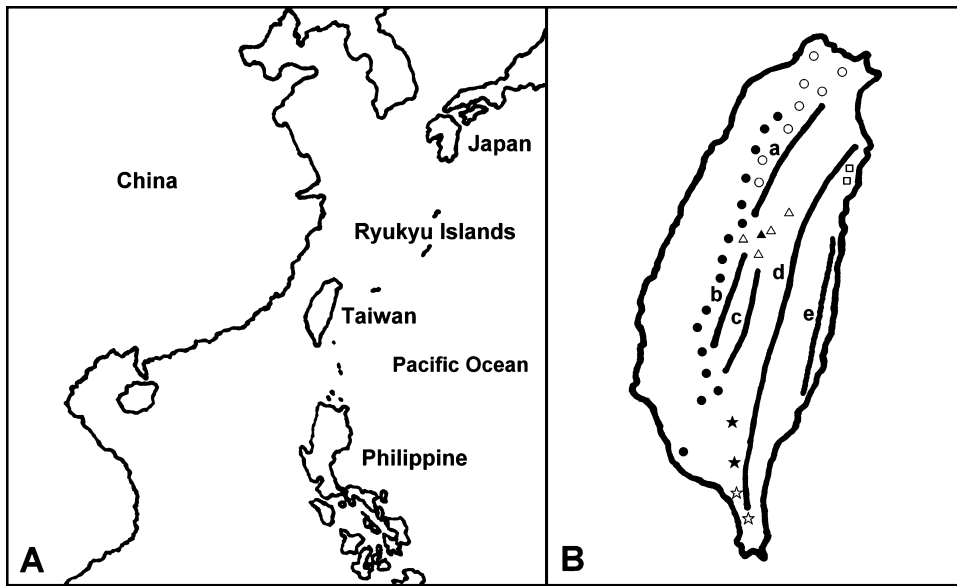


Figure 1. The map of Taiwan and surrounding areas. (A) The location of Taiwan in East Asia. (B) The map of the major mountain ranges and the distributions of the earthworm species discussed in this paper in Taiwan. Shei-Shan Mountain Range (a), Ali-Shan Mountain Range (b), Yu-Shan Mountain Range (c), Central Mountain Range (d), and Coastal Mountain Range (e) are the five major mountain ranges in Taiwan. Earthworm species, *Amyntas formosae* (solid circle), *Metaphire bununa* (open triangle), *Metaphire paiwannana* (open star), *Metaphire yuanpowa* (open circle), *Metaphire nanaoensis* (open square), *Metaphire taiwanensis* (solid triangle), and *Metaphire tahanmonta* (solid star), showed different distributions in Taiwan.

2002; Chuang et al. 2002; Shen and Tsai 2002; Shen et al. 2002, 2003; Chen and Chuang 2003). Among these species, endemism is about 52.7%, including 29 species. Comparing the endemism of the earthworm fauna of China and Japan, which are about 78.1% and 65.0%, respectively (Tsai CF et al. 2000a), the endemism of the earthworm fauna is much lower in Taiwan. However, we strongly believed that this result should be continuously promoted by programmed survey in the future.

This paper reports three new species from Taiwan. All of them are large earthworms, with length greater than 300 mm and diameter wider than 10 mm.

The collected earthworms were anaesthetized in 10% ethanol solution, fixed in 5% formalin solution, and preserved in 70% ethanol solution. They are deposited at the Department of Life Science, National Taiwan University, Taipei, Taiwan.

***Metaphire yuanpowa* sp. nov.**
(Figure 2)

Type material

Holotype: a mature (clitellate) specimen (dissected) collected 1 August 1999 from Wulia, Taipei County, north-west of the Shei-Shan Mountain Range, in the north region of Taiwan (Figure 1) by S. P. Wu (coll. no. 14-02577). Paratype: a mature (clitellate) specimen (dissected) collected 9 June 2000 from same collection site of holotype by C. E. Li (coll. no. 14-02576), and a mature (clitellate) specimen (dissected) collected 18 March 1995 from Pinglin, Taipei County by H. T. Shih (coll. no. 14-00015).

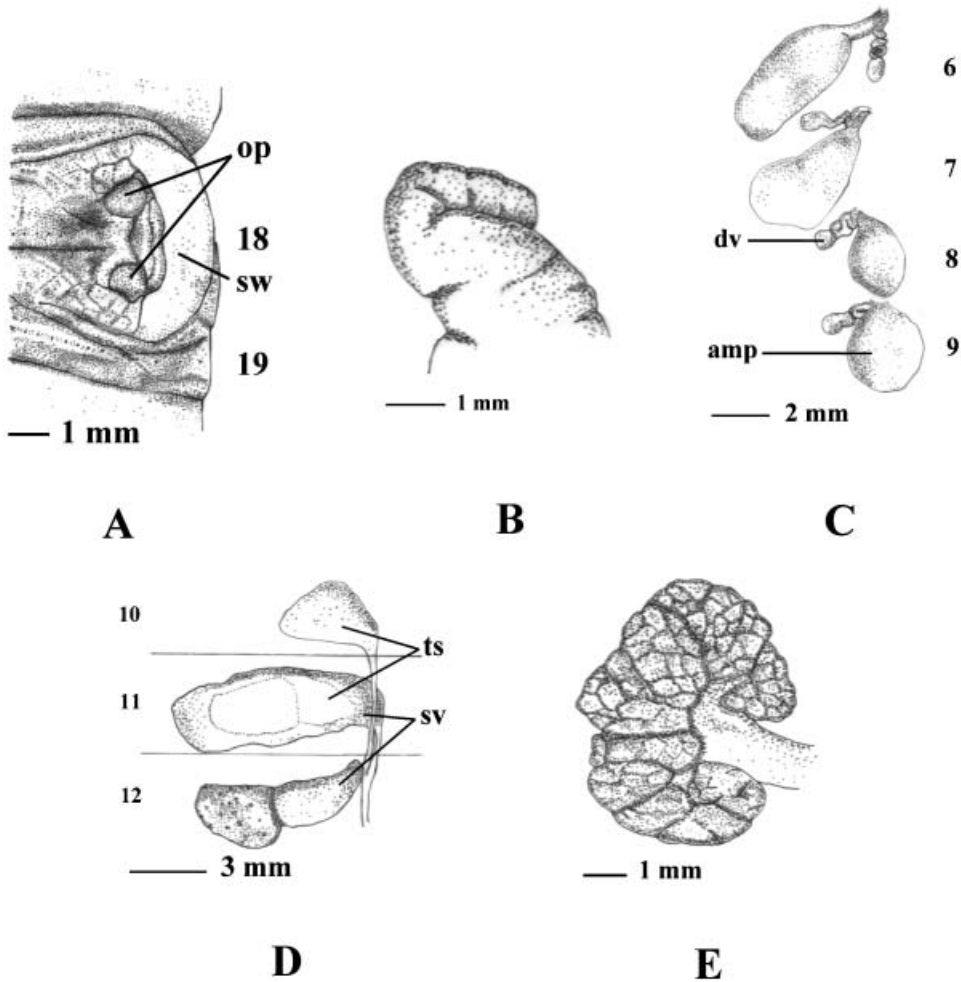


Figure 2. *Metaphire yuanpoza*. (A) Male pore region (op, oval pad; sw, skin wall); (B) caecum; (C) spermathecae (dv, diverticulum; amp, ampulla); (D) testis sacs and seminal vesicles (ts, testis sacs; sv, seminal vesicles); (E) prostate gland.

Other material

A mature (clitellate) specimen collected 15 June 1999 from Wulia, Taipei County by J. H. Wu (coll. no. 14-00125); and a mature (clitellate) specimen collected 17 November 2000 from Shindian, Taipei County by S. P. Wu (coll. no. 14-02571).

External characters

Length (mature) 215–425 mm, clitellum width 13.9–15.6 mm, segment number 129–189. Number of annulets (secondary segmentation) per segment three in 5–9, five in 10–13, and three in body segments behind 17. Prostomium epilobous. Setae 114–122 in 7, 126–162 in 20, 30–35 between male pores. First dorsal pore in 12/13. Clitellum 14–16, smooth, saddle-shaped, length 9.8–14.1 mm, dorsal pore absent, setae absent. Spermathecal pores four pairs in 5/6–8/9, lateral, distance between the paired pores about 0.5 body

circumference ventrally apart. No genital papillae in the spermathecal region. Female pore single, situated on the medio-ventral in 14. Male pore paired, situated on setal line close to lateral border of 18. Each male pore area is C-shaped, with the opening of the C facing the ventral setal line, bordered by a thick skin wall, which has several folds on its lateral side. The male pore area is enlarged, with length about twice the length of 18, extending to the setal line of 17 and 19. The male aperture is situated on the end of the ventral setal line, with one oval pad on each side. The two oval pads are linked by a vertical bar-shaped structure extending from the male aperture. These structures are sometimes partially covered by the skin wall bordering the male pore area. Genital papillae absent in the male pore area.

Live specimens bluish brown or dark purplish grey with metallic lustre on dorsum, reddish brown on ventral. Preserved specimens purplish brown on dorsum, light greyish brown on ventral.

Internal characters

Septa 5/6–7/8 thickened, 8/9 thin, 9/10 absent, 10/11–13/14 greatly thickened. Gizzard in 8–10. Intestine enlarged from 15. Intestinal caeca paired in 27, simple, extending anteriorly to 23. Lateral hearts enlarged in 10–13.

Spermathecae four pairs in 6–9. Ampulla large, about 3.5–6.2 mm in length, with a stalk about 0.5–1.3 mm in length. The spermathecal diverticulum is short, beyond the middle of spermathecae, with a small oval seminal chamber on the tip. Nephridia tufted, attached to the post-segmental septa, surrounding the segmental chambers anterior to the 6/7 septum. Ovaries paired in 13, medio-ventral, close to the 12/13 septum.

Testis sacs paired in 10 and 11, the anterior pair oval, smooth, medio-ventral in front of 10/11, the posterior pair is much larger than the anterior one, filling the space between septa. Sperm ducts meeting in 12. Seminal vesicles paired in 11 and 12, the anterior pair included in the posterior testis sac, both pairs moderate in size. Prostate glands paired in 18, large, lobular, extending to 17.

Habitat and behaviour

This species lives in the mountains below the altitude of 2000 m, where the vegetation is evergreen broadleaf forest, deciduous broadleaf forest or mixed coniferous–broadleaf forest, according to the altitude. Because it can be found both in virgin forest and secondary forest, it might tolerate low levels of human activity. This species is an anecic species, having permanent vertical burrows. It is active around the upper layer of soil or on the ground at night. Although it is occasionally active after rain, it usually stays in the soil at day. When resting, it is usually found more than 30 cm deep below the ground, and the deepest case we found this species is in 80 cm.

Remarks

Metaphire yuanpowa is a common species in the mountain area of northern Taiwan. It is usually found moving across the road at night, or at early morning after rain. This species resembles the other two sympatric species, *Amyntas aspergillum* and *A. formosae*, in body size, shape and colour, but it is easily distinguished by external characters in the field. The male pore area of *M. yuanpowa* is enlarged, with an obvious oval pad on each side of the male pore, while the other two species do not have these characters. The spermathecal

pores of *A. formosae* are medio-dorsal in 5/6–8/9, and the pores are evident with the naked eye through the lighter colour of the pore borders (Michaelsen 1922). *Amyntas aspergillum* has many papillae on the male pore area. Furthermore, *A. aspergillum* was recognized as a peregrine species in Taiwan (Tsai CF et al. 2000a) and is usually found in cultivated soil, especially in the grassland of public parks (personal observation), while *M. yuanpowa* and *A. formosae* are often found on the mountain slope, where the soil is less disturbed.

Metaphire yuanpowa shares most of its characters with *M. paiwana* and *M. bumuna*, including body size, colour, number of spermathecae, and the position and morphology of prostate gland and intestinal caeca (Tsai CF et al. 2000c). However, the male pore area of *M. paiwana* and *M. bumuna* has only one oval pad between the male aperture and the anterior end of the male pore area, and the male pore area of *M. paiwana* also has a horizontal ridge (Tsai CF et al. 2000c). Moreover, *M. yuanpowa* has testis sacs paired in 10 and 11, while both *M. paiwana* and *M. bumuna* have testis sacs paired only in 10.

Except for number of spermathecae, *M. yuanpowa* is similar to *M. trutina*, which has only three pairs of spermathecae (Tsai et al. 2003) and belongs to the *houletti*-group in the genus *Metaphire* (Sims and Easton 1972). It is not yet known if the two species are distantly related due to the difference in the number of spermathecae or closely related due to the similarity of other characters. According to our field survey, *M. yuanpowa* is restricted to the west edge of the Shei-Shan Mountain Range, but *M. trutina* is found only in the east edge of the Shei-Shan Mountain Range. Although they seem to be allopatric, the detailed distribution pattern of the two species is still unknown. A comparative study based on cytochrome *c* oxidase subunit I gene sequence is now underway to unravel the phylogenetic relationship of these two species.

The species name “*yuanpowa*” is given to describe the male pore area of this species. The male pore area of this species is like the Chinese “yuanpau”, which is a kind of currency in the past in China.

***Metaphire nanaoensis* sp. nov.**

(Figure 3)

Type material

Holotype: a mature (clitellate) specimen (dissected) collected 11 August 2002 from Nanao, Ilan County, north-east of the Central Mountain Range in the north region of Taiwan (Figure 1) by Y. H. Chen and C. H. Chang (coll. no. 14-04354). Paratypes: a mature (clitellate) specimen (dissected) with the same collection data as holotype (coll. no. 14-04355), and a mature (clitellate) specimen (dissected) collected 20 November 2002 from Nanao, Ilan County by Y. H. Chen (coll. no. 14-05024).

Other material

Three mature (clitellate) specimens collected 20 November 2002 from Nanao, Ilan County by Y. H. Chen (coll. no. 14-05423, 14-05426, 14-05427).

External characters

Length (mature) 335–429 mm, clitellum width 10.1–14.9 mm, segment number 132–177. Number of annulets (secondary segmentation) per segment three in 5–9, five in 10–13, and

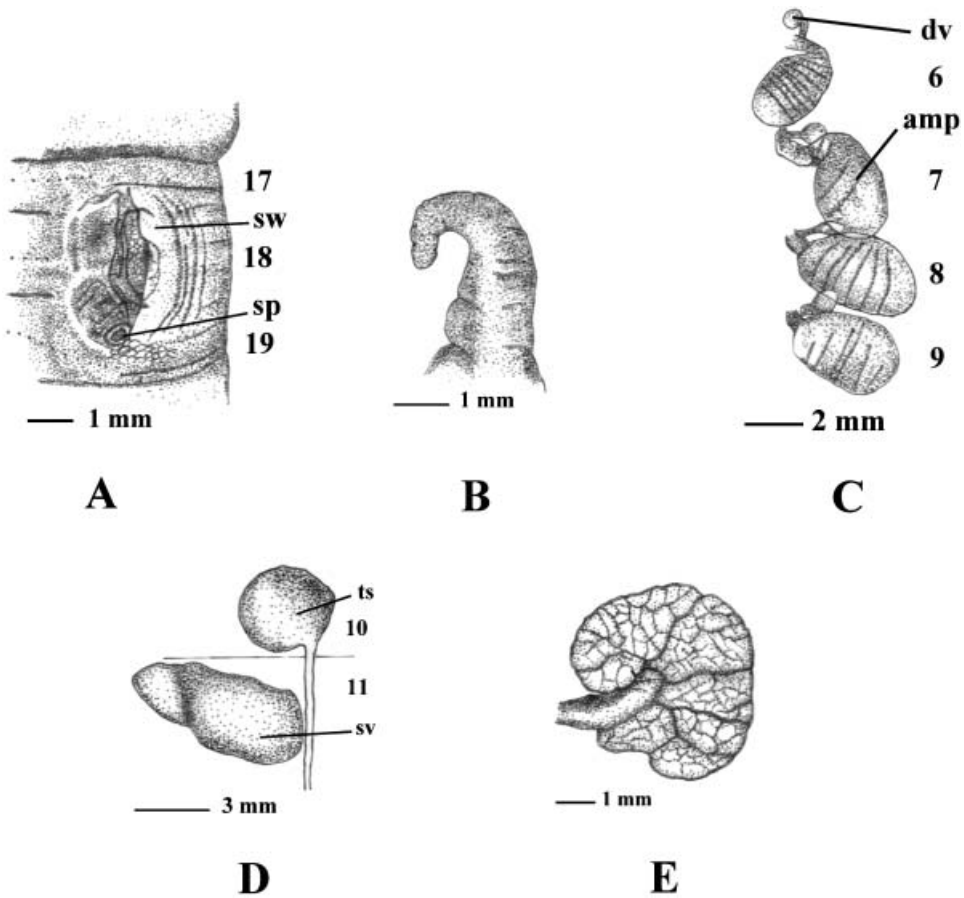


Figure 3. *Metaphire nanaoensis*. (A) Male pore region (sw, skin wall; sp, small pad); (B) caecum; (C) spermathecae (dv, diverticulum; amp, ampulla); (D) testis sacs and seminal vesicles (ts, testis sacs; sv, seminal vesicles); (E) prostate gland.

three in body segments behind 17. Prostomium prolobous. Setae 103–114 in 7, 120–131 in 20, 19–23 between male pores. First dorsal pore in 12/13. Clitellum 14–16, smooth, saddle-shaped, length 13.8–14.4 mm, dorsal pore absent, setae absent. Spermathecal pores four pairs in 5/6–8/9, ventral, distance between the paired pores about 0.4 body circumference ventrally apart. No genital papillae in the spermathecal region. Female pore single, situated on the medio-ventral in 14. Male pore paired, situated on setal line close to lateral border of 18. Each male pore area is C-shaped, with the opening of the C facing the ventral setal line, bordered by a thick skin wall, which has several folds on its lateral side. The male pore area is enlarged, with length about twice the length of 18, extending to the setal line of 17 and 19. The male aperture is situated on the end of the ventral setal line, partially covered by the skin wall bordering the male pore area. The region covered by the skin wall is swollen, forming a smooth appearance. A very small pad presents on the posterior end of the male pore area. Genital papillae absent in the male pore area.

Live specimens bluish brown or dark purplish grey with metallic lustre on dorsum, reddish brown on ventral. Preserved specimens purplish brown on dorsum, light greyish brown on ventral.

Internal characters

Septa 5/6–7/8 thickened, 8/9 thin, 9/10 absent, 10/11–13/14 greatly thickened. Gizzard in 8–10. Intestine enlarged from 15. Intestinal caeca paired in 27, simple, extending anteriorly to 23. Lateral hearts enlarged in 10–13.

Spermathecae four pairs in 6–9. Ampulla large, about 3.5–5.5 mm in length, with a stalk about 0.5–1.4 mm in length. The spermathecal diverticulum is short, beyond the middle of spermathecae, with a small oval seminal chamber on the tip. Nephridia tufted, attached to the post-segmental septa, surrounding the segmental chambers anterior to the 6/7 septum. Ovaries paired in 13, medio-ventral, close to the 12/13 septum.

Testis sacs paired in 10, oval, smooth, medio-ventral in front of 10/11. Seminal vesicles paired in 11, filling the space between septa. Some specimens have a pair of very small vestiges of seminal vesicles in 12. Prostate glands paired in 18, large, lobular, extending to 17.

Habitat and behaviour

This species lives in the mountains below the altitude of 1500 m, where the vegetation is evergreen broadleaf forest or deciduous broadleaf forest. Because it can be found both in virgin forest and secondary forest, it might tolerate low levels of human activity. This species is an anecic species, having permanent vertical burrows. It is active around the upper layer of soil or on the ground at night. Although it is occasionally active after rain, it usually stays in the soil during the day. When resting, it is usually found more than 30 cm deep below the ground.

Remarks

The male pore area of *M. nanaoensis* is C-shaped, and with respect to body size, colour, number of spermathecae, and position and shape of prostate gland and intestinal caeca, *M. nanaoensis* resembles *M. yuanpowa*, *M. paiwannana* and *M. bununa*. However, the male pore area of *M. yuanpowa* has an oval pad on each side of the male aperture, and the width between the paired spermathecal pores of *M. yuanpowa*, which is about 0.5 body circumference apart, is wider than that of *M. nanaoensis*. The major difference between the two species is that *M. yuanpowa* is holandric, while *M. nanaoensis* is protandric. *Metaphire paiwannana* and *M. bununa* are also protandric species, but the male pore areas of these two species are different from that of *M. nanaoensis*. The male pore area of *M. paiwannana* and *M. bununa* has an oval pad between the male aperture and the anterior end of the male pore area, and the male pore area of *M. paiwannana* also has a horizontal ridge (Tsai CF et al. 2000c). These differences are easily seen under a dissection microscope, or even with the naked eye.

The species name “*nanaoensis*” is given referring to Nanao in Ilan County in Taiwan, where the species was first collected.

***Metaphire tahanmonta* sp. nov.**

(Figure 4)

Type material

Holotype: a mature (clitellate) specimen (dissected) collected 3 June 2002 from Mt Tahan, Pingtung County, south-west of the Central Mountain Range, in the south region of

Taiwan (Figure 1) by S. P. Wu (coll. no. 14-03993). Paratypes: a mature (clitellate) specimen (undissected) collected 5 May 2003 from Paoshan, Kaohsiung County by C. H. Chang (coll. no. 14-05898), and a mature (clitellate) specimen (dissected) collected 5 May 2003 from Ernchituan, Kaohsiung County by C. H. Chang (coll. no. 14-05899).

External characters

Length (mature) 291–408 mm, clitellum width 12.9–14.7 mm, segment number 122–191. Number of annulets (secondary segmentation) per segment three in 5–9, five in 10–13, and three in body segments behind 17. Prostomium prolobous. Setae 122–144 in 7, 134–156 in

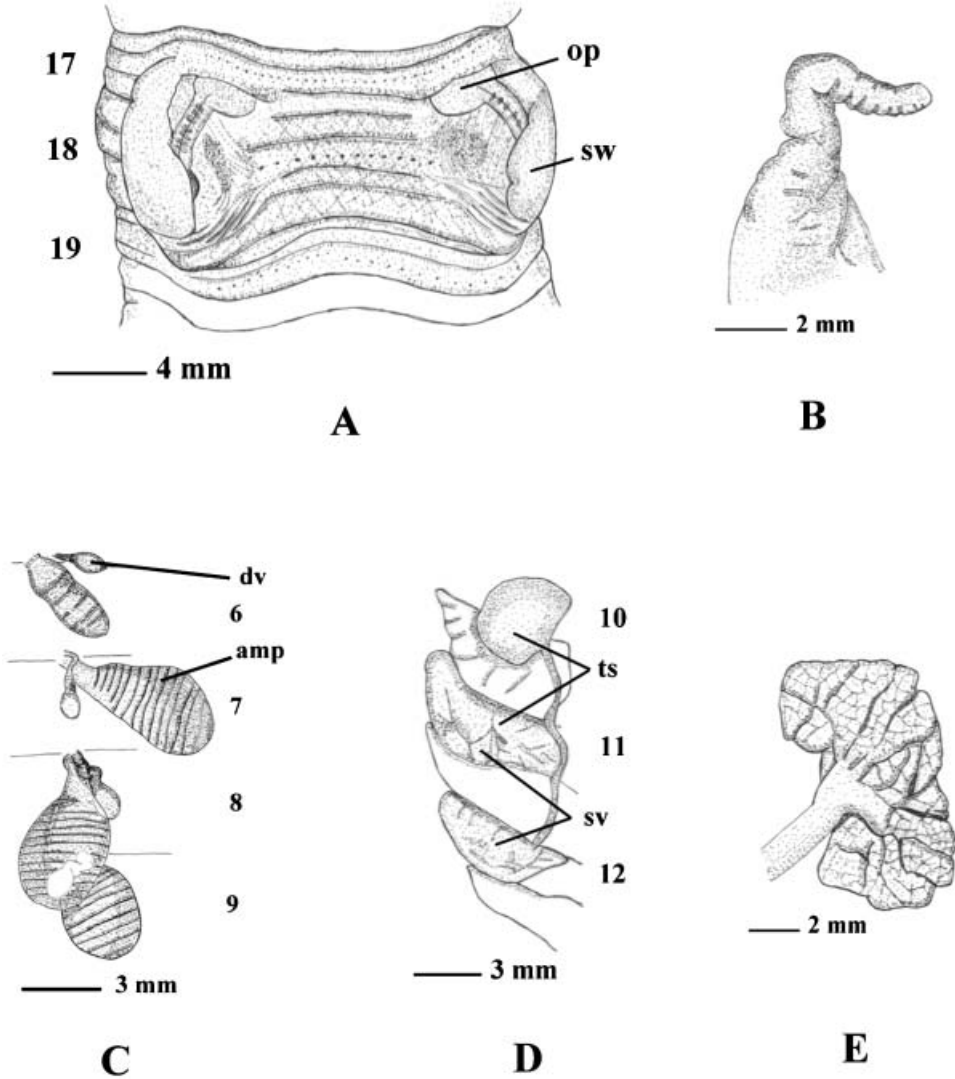


Figure 4. *Metaphire tahanmonta*. (A) Male pore region (op, oval pad; sw, skin wall); (B) caecum; (C) spermathecae (dv, diverticulum; amp, ampulla); (D) testis sacs and seminal vesicles (ts, testis sacs; sv, seminal vesicles), seminal vesicles in 11 are embedded in the testis sacs and are not shown in this figure; (E) prostate gland.

20, 24–30 between male pores. First dorsal pore in 12/13. Clitellum 14–16, smooth, saddle-shaped, length 12.8–15.5 mm, dorsal pore absent, setae absent. Spermathecal pores four pairs in 5/6–8/9, lateral, situated above the lateral-midline, distance between the paired pores about 0.55 body circumference ventrally apart. No genital papillae in the spermathecal region. Female pore single, situated on the medio-ventral in 14. Male pore paired, situated on setal line close to lateral border of 18. Each male pore area is slightly C-shaped, with the opening of the C facing the ventral setal line, bordered by a thick skin wall. The appearance of the anterior part of the skin wall is tubercular. The male pore area is enlarged, with length about twice the length of 18, extending to the setal line of 17 and 19, surrounded by circular folds. The male aperture is situated on the extended line of the ventral setal line, slightly posterior to the middle of the male pore area. A horizontal ridge extends from the setal line, backward to the male aperture. An oval pad is situated behind the setal line of 17, close to the anterior end of the male pore area. The oval pad is linked to the male aperture through a seminal groove. Genital papillae absent in the male pore area.

Live specimens dark purplish grey with metallic lustre on dorsum, reddish brown on ventral. Preserved specimens purplish brown on dorsum, light greyish brown on ventral.

Internal characters

Septa 5/6–7/8 thickened, 8/9 and 9/10 absent, 10/11–13/14 greatly thickened. Gizzard in 8–10. Intestine enlarged from 15. Intestinal caeca paired in 27, simple, extending anteriorly to 23. Lateral hearts enlarged in 10–13.

Spermathecae four pairs in 6–9. Ampulla large, about 3.6–5.6 mm in length, with a stalk about 1.2–1.9 mm in length. The spermathecal diverticulum is short, usually shorter than one-third of spermathecae length, with a small oval seminal chamber on the tip. Nephridia tufted, attached to the post-segmental septa, surrounding the segmental chambers anterior to the 6/7 septum. Ovaries paired in 13, medio-ventral, close to the 12/13 septum.

Testis sacs paired in 10 and 11, the anterior pair oval, smooth, medio-ventral in front of 10/11, the posterior pair is much larger than the anterior one, filling the space between septa. Sperm ducts meeting in 12. Seminal vesicles paired in 11 and 12, the anterior pair included in the posterior testis sac, both pairs moderate in size. Prostate glands paired in 18, large, lobular, extending to 17.

Habitat and behaviour

This species lives in the mountains between the altitudes of 500 and 2000 m, where the vegetation is evergreen broadleaf forest or deciduous broadleaf forest, according to the altitude and latitude. Because it can be found both in virgin forest and secondary forest, it might tolerate low levels of human activity. This species is an anecic species, having permanent vertical burrows. It is active around the upper layer of soil or on the ground at night. Although it is occasionally active after rain, it usually stays in the soil during the day. When resting, it is usually found more than 30 cm deep below the ground.

Remarks

Metaphire tahanmonta has a length greater than 300 mm, width over 10 mm, four pairs of spermathecae, and C-shaped male pores with an oval pad and a horizontal ridge. These characters are shared with *M. paiwannana*. However, *M. paiwannana* is protandric (Tsai CF

et al. 2000c), while *M. tahanmonta* is holandric. In pheretimoid earthworms, most species have a holandric condition, while rare species have a protandric condition (Sims and Easton 1972; Easton 1979; Tsai CF et al. 2000c). Accordingly, it is reasonable to regard the holandric specimens as a different species.

Regarding body size, position of seminal vesicles, number of spermathecae, and holandry, *M. tahanmonta* shares the same characters with *M. yuanpowa*. However, the male pores of the two species are very different. The male pore of *M. tahanmonta* has a horizontal ridge and only one oval pad, while that of *M. yuanpowa* has no horizontal ridge and two oval pads on each side of the male aperture. Therefore, they are easily distinguished by their external characters.

The species name “*tahanmonta*” is given referring to Mt Tahan in Pingtung County, Taiwan, where this species was collected.

Discussion

The five earthworms, *Metaphire yuanpowa*, *M. nanaoensis*, *M. tahanmonta*, *M. paiwannana*, and *M. bumuna* are all octothecate. Among them, *M. paiwannana* and *M. bumuna* have been inferred to have close phylogenetic relationships with *M. riukiuiensis* from the Ryukyu Islands, Japan (Tsai CF et al. 2000c) and with *M. taiwanensis*, a gigantic earthworm from Taiwan (Tsai et al. 2004). The close resemblance in external characters between *M. riukiuiensis* and *A. formosae* has also been mentioned (Ohfuchi 1957). These eight species present several common characters (Table I). They have similar body size and colour, their lateral hearts are enlarged in 10–13, and the position and morphology of prostate glands and caeca of these eight species are similar. Besides this, their habitats, burrows, casts, and behaviour are also similar. Excepting *A. formosae*, the other seven species have C-shaped male pores (copulatory pouches). Most of them have oval pads or vestiges of oval pads in their male pore area, and their male pores are covered with lateral skin folds. Due to the difference in male pore area and the absence of copulatory pouches, *A. formosae* belongs to the genus *Amyntas*, while the other seven species belong to the genus *Metaphire*. The close resemblance in morphological characters in the eight species implies their close phylogenetic relationship. This implication was preliminarily supported by our phylogenetic analysis based on mitochondrial 16S rRNA gene sequence data (Chang and Chen 2003). This result suggests that the presence or absence of copulatory pouches, which so far is the key character between *Amyntas* and *Metaphire* (Sims and Easton 1972), may be due to convergent evolution. If it is the case, the grouping of species into *Amyntas* and *Metaphire* does not relate to their phylogenetic relationships, and *Amyntas* and *Metaphire* may not be monophyletic groups.

According to Sims and Easton's (1972) grouping, *M. yuanpowa* and *M. tahanmonta*, like *M. riukiuiensis*, belong to the octothecate holandric *ignobilis*-group within the genus *Metaphire*. On the other hand, *M. nanaoensis*, which should be grouped with *M. paiwannana*, *M. bumuna* and *M. taiwanensis*, belongs to the octothecate protandric *stephensoni*-group (Tsai et al. 2004) within the genus *Metaphire*. However, comparing the morphology of the eight species, including *M. riukiuiensis*, *M. yuanpowa*, *M. tahanmonta*, *M. paiwannana*, *M. bumuna*, *M. taiwanensis*, *M. nanaoensis*, and *A. formosae*, we strongly suggest that they are more closely related to each other than to con-group earthworm species. For this reason, Sims and Easton's (1972) grouping is considered inapplicable in the discussion on the phylogeny and biogeography of these eight closely related species.

Excluding *M. riukiuiensis*, the other seven species are all endemic to Taiwan. For this reason, the speciation events generating these species must have occurred in Taiwan.

Table I. A comparison of the eight closely related earthworm species, *Amyntas formosae*, *Metaphire paiwanina*, *M. bununa*, *M. yuanpoowa*, *M. nanaoensis*, *M. taiwanensis*, *M. tahanmonta*, and *M. riukiensis* (spermathecae paired in 6–9).

Character	<i>A. formosae</i>	<i>M. paiwanina</i>	<i>M. bununa</i>	<i>M. yuanpoowa</i>	<i>M. nanaoensis</i>	<i>M. taiwanensis</i>	<i>M. tahanmonta</i>	<i>M. riukiensis</i>
Locality	West of Central Mountain Area, Taiwan	South-west of Central Mountain Range, Taiwan	Middle of Central Mountain Range, Taiwan	North of Shei-Shan Mountain Range, Taiwan	North-east of Central Mountain Range, Taiwan	Middle west of Central Mountain Range, Taiwan	South-west of Central Mountain Range, Taiwan	Ryukyu Island
Length (mm)	173	292–293	255–352	215–425	335–429	637–655	408	219–270
Segment number	144	132–140	124–221	129–189	132–177	185–228	185	135–138
Setae between male pores	22–28	22–26	6–29	30–35	19–23	24	24	5–6
Male pores	Round	C-shaped	C-shaped	C-shaped	C-shaped	L- or C-shaped	C-shaped	C-shaped
Number of oval pad	0	1	1	2	1 ^a	1	1	0
Distance between paired spermathecal pores through ventral side	0.875 body circumference	0.5 body circumference	0.36 body circumference	0.5 body circumference	0.4 body circumference	–	0.55 body circumference	–
Testis sacs in 11	Absent	Absent	Absent	Present	Absent	Absent	Present	Present
Seminal vesicles in 12	Vestigial or absent	Absent	Vestigial or absent	Present	Vestigial or absent	Vestigial	Present	Present

^aA vestige between the male aperture and the posterior end of the male pore area presents.

Because Taiwan emerged from the West Pacific Ocean near the continent of East Asia about 5 million years ago (Lin and Wu 1997), the ancestor of these species probably came to Taiwan during the Pleistocene (2,000,000~10,000 B.P.), when Taiwan was linked several times with the continent of East Asia through land bridges formed by sea-level alterations due to glaciations (Voris 2000; Lin et al. 2002). This is the only period in the past in which Taiwan was connected with the continent of East Asia by closure of the Taiwan Strait (Lin and Wu 1997). Such inference has been similarly drawn in mammals (Lai 1989; Hsu et al. 2000, 2001; Horng et al. 2003), birds (Yan 1989), reptiles (Lu and Chen 1989; Lin et al. 2002), amphibians (Lu and Chen 1989), and insects (Lin and Wu 1997), and is also proposed by Tsai CF et al. (2000a) in earthworms. So far, it is reasonable to propose that the ancestor of these species might have come from south-east China during glaciations. According to this hypothesis, the sister group of these eight earthworm species should be found in south-east China if it is not extinct. However, the sister group of the eight species remains unrecognized in this study for two reasons. First, we examined all species reported from China in closely related groups proposed by Sims and Easton (1972). Some species of *ignobilis*-group and *bucculenta*-group (Sims and Easton 1972) within the genus *Metaphire*, such as *M. bucculenta*, *M. bipapillata* and *M. ignobilis*, were found in China (Gates 1935; Chen 1936). These species could be candidates as the sister group of the eight species. But none of them has large body size and has male pore areas similar to the latter. Second, till now, only a few samples have been recorded from the mountains in those south-eastern provinces of China such as Fu-Chan or Can-Ton. Such results give little information on the sister group. Therefore, no Chinese earthworms can be the reasonable sister group in this study. More phylogenetic studies with extensive sampling of the Chinese *Metaphire* earthworm species are necessary to find the sister group of these eight species.

Accordingly, the allopatric speciation origins of the seven earthworm species in Taiwan result from dispersal of the ancestor species. Except for *M. bununa*, all the other six species in Taiwan are distributed below 3000 m in altitude. Because the high mountains run north to south in Taiwan, they provide several geographical barriers to animal dispersal from west to east and vice versa, and for gene flows between west and east populations. This pattern allows allopatric speciation to occur, resulting in closely related species occupying different areas in Taiwan (Lue and Lai 1997; Lin et al. 2002). The situation is much the same in the seven earthworm species. *Amyntas formosae* is restricted to the western hills of the Central Mountain Area, *M. yuanpowa* is restricted to the west edge of the Shei-Shan Mountain Range and *M. nanaoensis* is restricted to the north tip of the Central Mountain Range. Besides high mountains as geographical barriers, a large river is another barrier that earthworms will not be able to cross. This is also the pattern in the seven earthworm species in Taiwan. The southern boundary of *M. nanaoensis* is He-Ping River; and the northern boundary of *M. tahanmonta* is Lau-Nong River.

Except for the Ryukyu Islands, *M. riukiuiensis* or related species have not been found in Japan. *Metaphire riukiuiensis* has only been found in the southernmost island group of the Ryukyu Islands, Sakishima group (Ohfuchi 1957). These islands are separated from the northern parts of the Ryukyu Islands by Kerama Gap, and have never been linked with them by land bridges in the past (Lin et al. 2002). The geographical distribution of these species implies that the ancestor of *M. riukiuiensis* came northward from Taiwan, rather than southward from Japan, though the land bridge between Taiwan and the Ryukyu Islands formed several times in the Pleistocene. This hypothesis is well supported by Ohfuchi (1957). He recognized that the earthworm species in the two southernmost groups, Sakishima group and Okinawa group, have intestinal caeca similar to those of the

species in the Oriental region, in which South China and Taiwan are included (Hikida and Ota 1997; Lin and Wu 1997; Tzeng et al. 1997; Tsai CF et al. 2000a), rather than those of the species in the Palaeartic region, in which Japan is included (Cox and Moore 2000).

The eight earthworm species in Taiwan and Ryukyu Islands do not show any geographical trends in their character states. The character states of these species are mosaic, and concordance of state-shift does not occur among these species. Besides this, we are not able to recognize enough synapomorphic characters for cladistical analysis. All these phenomena impede the understanding of phylogenetic relationships among these eight earthworm species through morphological characters. For these reasons, further phylogenetic analyses based on molecular data are now being conducted.

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