Journal of Helminthology

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Review Article

Cite this article: Malysheva SV and Sokolova EA (2024). Redescription of *Meteterakis striatura* Oshmarin & Demshin, 1972 (Heterakidae: Meteterakinae) from a geoemydid tortoise in China with comments on the genus. *Journal of Helminthology*, **98**, e87, 1–15
https://doi.org/10.1017/S0022149X24000634

Received: 22 June 2024
Revised: 30 August 2024
Accepted: 01 September 2024

Key words:
Geoemyda spengleri; *Meteterakis*; nematoda; parasites; phylogeny; Reptilia; taxonomy

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Redescription of *Meteterakis striatura* Oshmarin & Demshin, 1972 (Heterakidae: Meteterakinae) from a geoemydid tortoise in China with comments on the genus

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Abstract

Meteterakis striatura Oshmarin & Demshin, 1972 is redescribed from the posterior intestine of tropical tortoise *Geoemyda spengleri* (Gmelin, 1789) (Testudines: Geoemydidae) from China. Some characteristic features of the male reproductive system not reported previously are now reported for the present species. These include the presence of two blind diverticula near the mid-region of the seminal vesicle and a small cuticular structure near the opening of the cloaca – which we propose to name the 'scutum.' The morphological function and diagnostic value of these characters as well as presence of gubernaculum or 'gubernacular mass' in examined representatives of the genus, including paratype specimens of *M. amamiensis* Hasegawa, 1990 and *M. ishikawanae* Hasegawa, 1987 is discussed. Illustrative material is supplemented with scanning electron microscope and light microscope images of adult males and females. The molecular characterization of the species is inferred from 18S and 28S rDNA. The taxonomic composition of the genus *Meteterakis* is discussed and the full list of species with taxonomic remarks is updated.

Introduction

The *Meteterakis* genus was proposed by Karve (1930) for nematodes *Meteterakis govindi* Karve, 1930 described from the intestine of *Duttaphrynus melanostictus* (Schneider, 1799) (as *Bufo melanostictus* Schneider, 1799) (Anura: Bufonidae) and placed in Heteterakinae (Nematoda: Heterakidae). Later, the genus was moved to *Heterakis* (Baylis, 1936; Koo, 1939), and then transferred into subfamily Spinicaudinae (López-Neyra, 1947) or considered as a junior synonym for *Ganguleterakis* Lane, 1914 (Skrjabin & Schikhobalova, 1949). Freitas (1956) reinstated *Meteterakis* and included it in the family Heterakidae, whereas Inglis (1957a) established the subfamily Meteterakinae.

Inglis (1958) made a significant revision of the *Meteterakis* genus having included in it eight species that previously considered as members of the following genera: *Spinicauda* Travassos, 1920 (i.e., *M. cophotis* [Baylis, 1935] Inglis, 1958, *M. japonica* [Wilkie, 1930] Inglis, 1958 and *M. longispiculata* [Baylis, 1929] Inglis, 1958); *Africana* Travassos, 1920 (*M. mabuyi* [Chakravarty, 1944]) *Africana varani* (Chakravarty, 1944) and *A. howardi* Li, 1933 were considered as synonyms of *M. govindi* and *M. japonica*, respectively) and *Ganguleterakis* (*M. triaculeata* [Kreis, 1933] Inglis, 1958). This taxonomic decision significantly expanded the morphological scope of the genus by adding species with spicules of different sizes and morphology, as well as the number of genital papillae in the males. Inglis (1958) considers one of the key characteristics of the genus to be the presence of indefinite gubernacular mass developed from the cloacal walls and present in all species (except *M. triaculeata*). Baker (1984) analyzed the composition and geographic distribution of the studied genus and noted 16 species and their synonyms. In his work, Baker (1984) does not attempt to resolve taxonomic issues of the genus and points out additional problems related to the outdated classification of host species. In the latest study of the genus by Junker *et al.* (2015), the authors mention 23 species and divide *Meteterakis* species into four morphological groups based on the size and the ratio of spicule lengths. The present study provides new morphological and molecular data for *Meteterakis striatura* Oshmarin & Demshin, 1972, originally described from the intestine of *Mauremys mutica* (Cantor, 1842) (as *Clemmys mutica* Boettger, 1888) (Testudines: Geoemydidae) in Vietnam; composition of the genus *Meteterakis* is discussed following the analysis of the literature and the newly received data.

Materials and methods

Morphological observations

Nematodes were recovered from intestine of a female specimen of *Geoemyda spengleri* (Gmelin, 1789) (Geoemydae), which was kept in the Moscow Zoo Exotarium and originated from Guangxi Province (China). The exact locality is unknown. A post-mortem examination and dissection were done by Professor A.V. Tchesunov from Moscow State University. The nematode material obtained was passed to the Laboratory of Systematics and Evolution of Parasites of A.N. Severtsov Institute of Ecology and Evolution RAS for further study. Fourteen specimens were fixed in 4% formaldehyde, and 10 of them were processed to anhydrous glycerin (Seinhorst, 1959) for permanent mounts on glass slides and further observation at Nikon Eclipse 90i microscope (Nikon, Tokyo, Japan). Two male and two female specimens were processed for scanning electron microscopy (SEM) by serial dehydrations utilizing ethanol and acetone and then dried in a Hitachi Critical Point Dryer HCP-1 (Hitachi Ltd., Japan). Nematodes were placed on aluminum stubs, and sputter-coated with gold in a S150A Sputter Coater (Edwards, UK). Specimens were viewed with a JSM-6380LA (JEOL) SEM (JEOL, Peabody, USA).

Molecular profiles

Two males and the single female specimen were fixed in 95% ethanol and stored at −18°C before DNA extraction. The DNA was extracted with the aid of QiAamp Micro Kit (Qiagen, Germantown, USA) according to manufacturer's instructions. Polymerase chain reaction (PCR) was performed using the Encyclo Plus PCR kit (Evrogen, Moscow, Russia) according to the manufacturer's instructions. Primer pairs LSU391F (5′-AGC GGA GGA AAA GAA ACT AA-3′) and LSU501R (5′-TCG GAA GGA ACC AGC TAC TA-3′) were used to amplify the D2-D3 expansion segment of the 28S rDNA fragment (Nadler *et al.*, 2006). PCR cycling parameters included primary denaturation at 94°C for 3 minutes followed by 34 cycles at 94°C for 30 s, 52°C for 30 s, and 72°C for 1 minute, followed by post-amplification extension at 72°C for 7 minutes. A pair of nematode-specific primers designated as nem18SF (5′-CGC GAA TRG CTC ATT ACA ACA GC-3′) and nem18SR (5′-GGG CGG TAT CTG ATC GCC-3′) were used to amplify the 5′ portion of 18S rDNA (Floyd *et al.*, 2005). PCR cycling parameters included primary denaturation at 95°C for 5 minutes followed by 5 cycles at 94°C for 30 s, 47°C for 30 s and 72°C for 40 s and 35 cycles at 94°C for 25 s, 54°C for 30 s and 72°C for 40 s, followed by post-amplification extension at 72°C for 5 minutes. Another primer pair designated as 24F (5′-AGR GGT GAA ATY CGT GGA CC-3′) and Q39 (5′-TAA TGA TCC WTC YGC AGG TTC ACC TAC-3′) were used to obtain the remaining 3′ end of 18S rDNA (Blaxter *et al.*, 1998). PCR cycling parameters included primary denaturation at 95°C for 5 minutes followed by 35 cycles at 94°C for 60 s, 53°C for 90 s and 72°C for 90 s, followed by post-amplification extension at 72°C for 6 minutes.

PCR reaction products were visualized in an agarose gel and bands were excised for DNA extraction and cleaned with the Wizard SV Gel and PCR Clean-Up System (Promega, Madison, USA). Ethanol precipitation was used to purify and concentrate obtained DNA. Samples were directly sequenced using the same primers as used for primary PCR reactions. Nematode sequences obtained during this study have been deposited in GenBank (National Center for Biotechnology Information) (https://www.ncbi.nlm.nih.gov/) as PP571902-PP571904 for 18S and PP571899-PP571901 for 28S rDNA.

For comparative purposes and phylogeny construction 28S rDNA sequences from the National Center for Biotechnology Information GenBank database were also used (GenBank accession numbers are given in the phylogram). Sequence alignments were generated using Clustal_X (Thompson *et al.*, 1997) under default values for gap opening and gap extension penalties. MEGA 5.2 (Tamura *et al.*, 2011) was used to select the best evolution model (J2+G) and to infer the phylogeny based on maximum likelihood method. Support for the clades of the maximum likelihood tree was assessed using bootstrap analysis with 1,000 pseudo-replicates.

Results

Family Heterakidae Railliet & Henry, 1912
Subfamily Meteterakinae Inglis, 1957
***Meteterakis* Karve, 1930**
Syn. *Cometeterakis* Cruz & Ching, 1975
Heterakoides Teixeira de Freitas, 1956
Pareterakis Teixeira de Freitas, 1956

Diagnosis (*sensu* Inglis, 1958, amended): Meteterakinae. Medium-sized nematodes with well-defined cuticular annulation of the body. Multiple somatic papillae dispersed throughout the body. Head end is rounded, slightly dimorphic in males and females; oral opening tri-radiate surrounded with three lips, each having a prominent cuticular flange projecting anteriorly above the lip. Three anteriorly directed pharyngeal teeth present. Six tiny papillae of inner circle and four large submedian papillae present, located as two on dorsal and one on each subventral lips. Amphid openings are slit-like and locate at oval amphidial plates. Pharynx divided into short anterior procorpus separated from the long posterior corpus by valves, isthmus and a pear-like basal bulb. The intestine is wider in its anterior part then gradually narrows posteriorly where joins the rectum. Lateral alae present; in males, it terminates at the level of the precloacal sucker, and in females continues to the end of the tail tip. The nerve ring encircles the oesophageal corpus anterior to excretory pore which opens ventrally and leads to a large excretory vesicle. Males possess precloacal ventral sucker surrounded by a well cuticularized rim and caudal alae supported by three or four large fleshy papillae. Of these papillae, two or three pairs lie about the level of the precloacal sucker and the remaining pair is lateral to the cloacal opening. Genital papillae significantly vary in number (from 6 to 23 pairs). Spicules paired, equal or subequal, alate or non-alate, usually well tessellated. Gubernaculum present. Unpaired accessory cuticular structure (the 'scutum'), present at the cloacal aperture (see Discussion). Tail conical with narrow distal tip. In females, the vulva is located at the middle of the body and opens on its ventral side; vulval flap developed from anterior vulval lip may present or absent. Genital tract didelphic, opistodelphic. Vulva leads to a short *vagina vera* which turns posteriorly and runs into a long *vagina uterina*, which in turn continues posteriorly as a common uterus and splits into two parallel uteri. Tail long, conical, sharply pointed. Mature eggs are oval with thick and smooth shells.

Type species:
Meteterakis govindi Karve, 1930
syn. *Africana varani* Maplestone, 1931
Spinicauda bufonis Yamaguti, 1935
Heterakis govindi Baylis, 1936
Ganguleterakis govindi Skrjabin, 1949

Meteterakis gambhiri Zhang & Zhang, 2011 (see Comments section in current paper)

Meteterakis bufonis Gambhir *et al*., 2006 (see Comments section in current paper)

Other species:

Meteterakis amamiensis Hasegawa, 1990
Meteterakis asansolensis Sou, 2019
Meteterakis andamanensis Soota & Chaturvedi, 1972
Meteterakis aurangabadensis Deshmukh & Choudhari, 1980
Meteterakis baylisi Inglis, 1958
Meteterakis formosensis Sata, 2018
Meteterakis guptai Gupta & Naiyer, 1993
Meteterakis hurawensis Bursey *et al*., 2017
Meteterakis ishikawanae Hasegawa, 1987
Meteterakis japonica (Wilkie, 1930) Inglis, 1958
syn. *Spinicauda japonica* Wilkie, 1930
Africana howardi Li, 1933
Pareterakis howardi (Li, 1933) Freitas, 1956
Meteterakis howardi (Li, 1933) Skrjabin, Schikhobalova & Lagodovskaja, 1961 (see Comments section in current paper)
Meteterakis karvei Naidu & Thakare, 1981
Meteterakis lombokensis Purwaningsih, Dewi & Nugroho, 2016
Meteterakis longispiculata (Baylis, 1929)
syn. *Spinicauda longispiculata* Baylis, 1929
Meteterakis louisi Inglis, 1958
Meteterakis occidentalis Sata, 2018
Meteterakis paucipapillosa Wang, 1980
Meteterakis pursatensis Bursey, Goldberg & Grismer, 2019
Meteterakis saotomensis Junker, Mariaux, Measey & Mutafchiev, 2015
Meteterakis singaporensis (Sandosham, 1954)
Meteterakis striatura Oshmarin & Demshin, 1972
Meteterakis vaucheri Adamson, 1986
Meteterakis wangi Zhang & Zhang, 2011
Meteterakis wonosoboensis Purwaningsih, Dewi & Hasegawa, 2015

Species inquirendae:

Meteterakis crombiei Bursey Goldberg & Kraus, 2005
Meteterakis lyriocephali (Crusz & Ching, 1975)
Meteterakis mabuyi (Chakravarty, 1944)
syn. *Africana mabuyae* Chakravarty, 1944
Meteterakis sinharajensis (Crusz & Ching, 1975)
Meteterakis triaculeata (Kreis, 1933)
syn. *Ganguleterakis triaculeatus* Kreis, 1933

Species incertae sedis:

Africana bufonis Biswas & Chakravarty, 1963
Meteterakis bufonis (Biswas & Charkavarty, 1963) Baker, 1984
syn. *Heterakis bufonis* Biswas & Charkavarty, 1963

Comments:

Meteterakis gambhiri Zhang & Zhang, 2011 is a replacement name for *Meteterakis bufonis* Gambhir *et al*., 2006, which, according to the International Code of Zoological Nomenclature (ICZN), was a junior secondary homonym of *Meteterakis bufonis* (Biswas & Charkavarty, 1963) Baker, 1984 (see Baker; 1984; ICZN, 1999 Articles 57.3 and 72.7; Zhang & Zhang, 2011).

Meteterakis howardi (Li, 1933) was accepted by Skrjabin *et al.* (1961) as an independent representative of *Meteterakis* described as *Africana howardi* by Li (1933), while Inglis (1958) recognized this species as a junior synonym for *Meteterakis japonica* (Wilkie, 1930). Inglis's opinion has become established in the literature, and the name combination *Meteterakis howardi* has never been mentioned in further revisions of the genus (Baker, 1984; Junker *et al*., 2015).

Meteterakis (Spinicauda) mathevossianae (Skarbilovich, 1950) was mentioned in the description of *M. bufonis* (Gambhir *et al.*, 2006), however, it is still considered a valid species of the genus *Spinicauda* (Nematoda: Heterakidae) (see Jamdar, 2021; Gambhir *et al*., 2006; Skarbilovich, 1950).

Meteterakis rodriguesi Vicente & Corrêa Gomes, 1971 has been accepted as *Bufonerakis rodriguesi* (Vicente & Corrêa Gomes, 1971) (see Baker, 1980).

Hosts and habitat:

Gastrointestinal tract of reptiles and amphibians.

Geographical distribution:

India, Sri Lanca, Myanmar, Vietnam, China, Japan, East Indies, and Afrotropics.

Meteterakis striatura Oshmarin & Demshin, 1972 (Figures 1–7)

Measurements

See Table 1.

General

Body cuticle with fine striation beginning just posterior the cephalic papillae and continuing nearly to the end of tail (Figure 3D). Tiny somatic papillae are scattered throughout the body. Prominent lateral alae present. Distal edges of the alae are bifid in transverse section. Cephalic extremity rounded with tri-radiate oral opening, surrounded with three well-developed lips each with prominent cuticular flange projecting anteriorly (Figure 3A; Figure 5A, B). Six tiny papillae of inner circle present as two on each lip closely to oral opening. Dorsal lip is wider and bears two large double cephalic papillae, each subventral lip with one large double cephalic papilla present; slit-like amphid opening located at oval amphidial plates, and three small papillae located posterior to each amphid (Figure 3C, E, F). Anterior end of pharynx is divided into three lobes, one dorsal and two subventral; each bears anteriorly directed pharyngeal tooth, where the dorsal is the largest. Pharynx is long, and muscular, separated from the cylindrical part of the oesophagus by valves, isthmus, and a basal bulb (Figure 1A–C; Figure 2A). Isthmus is narrow, well defined from the corpus. Basal bulb pear-like, consisting of three well-defined lobes with strongly developed valves; cardia are moderately developed. The intestine is narrow at its junction with the basal bulb, expands rapidly forming a short wide part then gradually narrowing to adjoin the rectum. The nerve ring is in the mid-level of pharyngeal corpus (Figure 1A, B). Excretory pore opens on the ventral body side posterior to nerve ring and leads into the large vesicle (Figure 2B; Figure 5E, F).

Male

Lateral alae commencing from the nerve ring level extending posteriorly becoming indistinct anterior to ventral sucker. Testis forming a loop anterior to mid-body level then extends posteriorly to seminal vesicle. Two blind diverticula present, opening in the middle region of seminal vesicle (Figure 1A; Figure 5C). *Vas deferens* comparatively short, occupying one-fifth of reproductive system total length. Ventral sucker rounded, supported by prominent cuticular rim (Figure 4B). Small rounded swelling leading to an elongated vesicle with granular content present between the body of the sucker and posterior side of the rim. Prominent caudal alae present (Figure 4E). Genital papillae vary in size and shape but are always larger then somatic papillae. Two pairs of large pedunculate papillae situated at the level of ventral sucker and support the anterior end of caudal alae; three papillae pairs present at

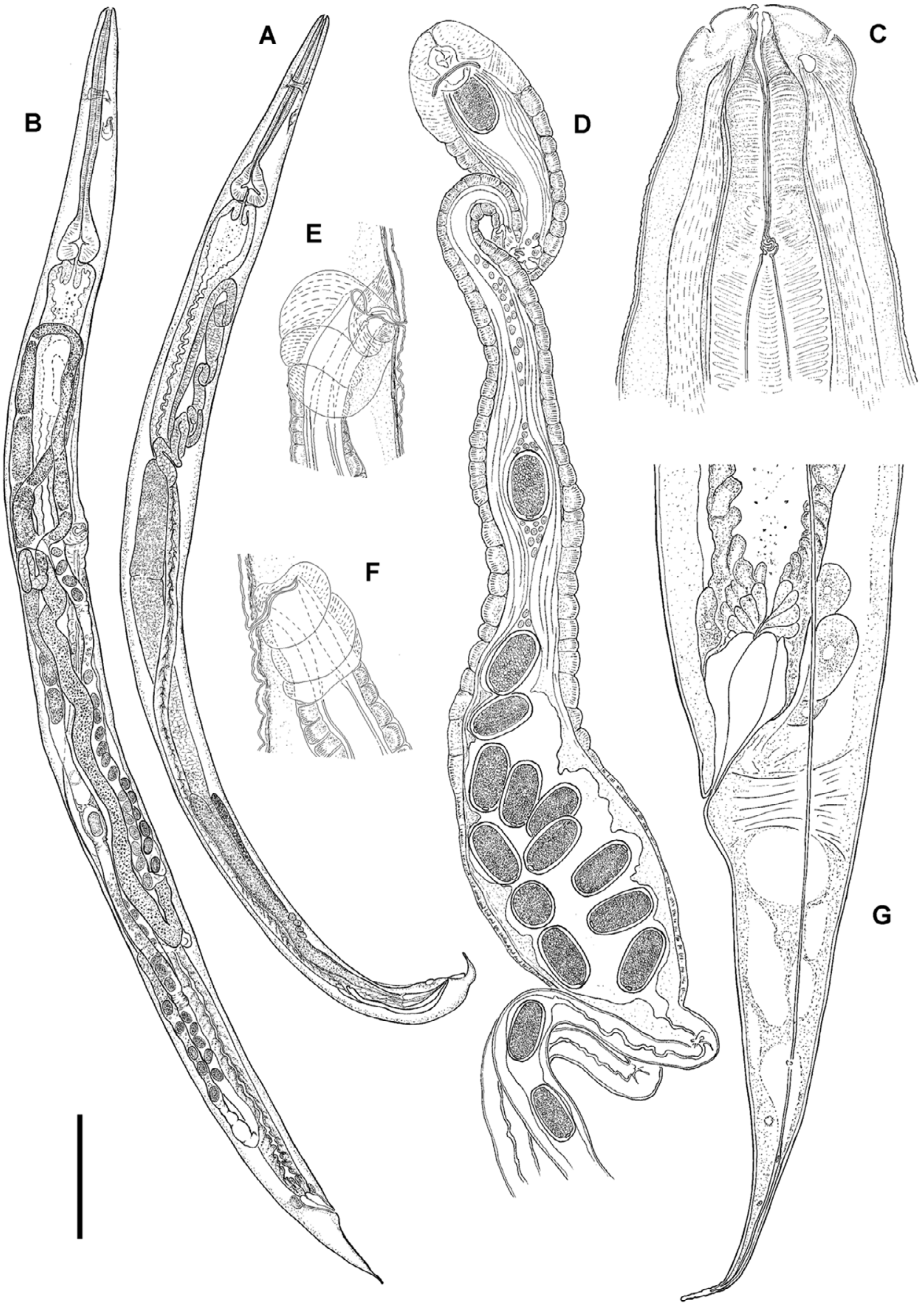

Figure 1. Line drawings of *Meteterakis striatura* Oshmarin & Demshin, 1972. (A) male, entire view; (B) female, entire view; (C) female anterior end, lateral view; (D) vulva and anterior part of female genital tract, ventral view; (E, F) vulva, lateral view (right and left sides, respectively); (G) female posterior region, lateral view. (Scale bars for A = 35 µm, B = 600 µm, C = 150 µm, D = 135 µm, E = 100 µm, F = 125 µm, G=85 µm.)

cloacal level: one preanal pair, one closely spaced adanal pair and one tiny postanal pair seated slightly laterally to the cloacal aperture; one large pedunculate sublateral pair supporting the posterior part of caudal alae; five pairs postcloacal: one large subventral pair just posterior to cloacal aperture, one sublateral pair, two subdorsal pairs and one subventral closest to tail tip (Figure 5; Figure 7A). Multiple somatic papillae present anterior to ventral sucker as well as pre and postcloacal area. Spicules are long, subequal, alate, tessellated along most of their length with spirally twisted distal tips (Figure 2D–G; Figure 4D; Figure 6B, D). Proximal ends of spicules are widened, forming well-defined heads slightly irregular in size and turned towards the ventral side of the body (Figure 2F; Figure 6A). On the second third of their length, the spicules bend ventrally. Gubernaculum developed as a thickening of the dorsal cloaca wall with lateral ventrally pointed processes flanking the spicules and probably closing above them. A small accessory structure – the 'scutum' – is near the cloacal opening (see Discussion). The scutum has the form of a bent plate attached to the dorsal wall of the cloaca with the free end directed dorsally (Figure 2C, E, F, G; Figure 4C; Figure 6E (black arrowhead). Tail short, conical, curved ventrally with pronounced cuticular striation and long distal tip.

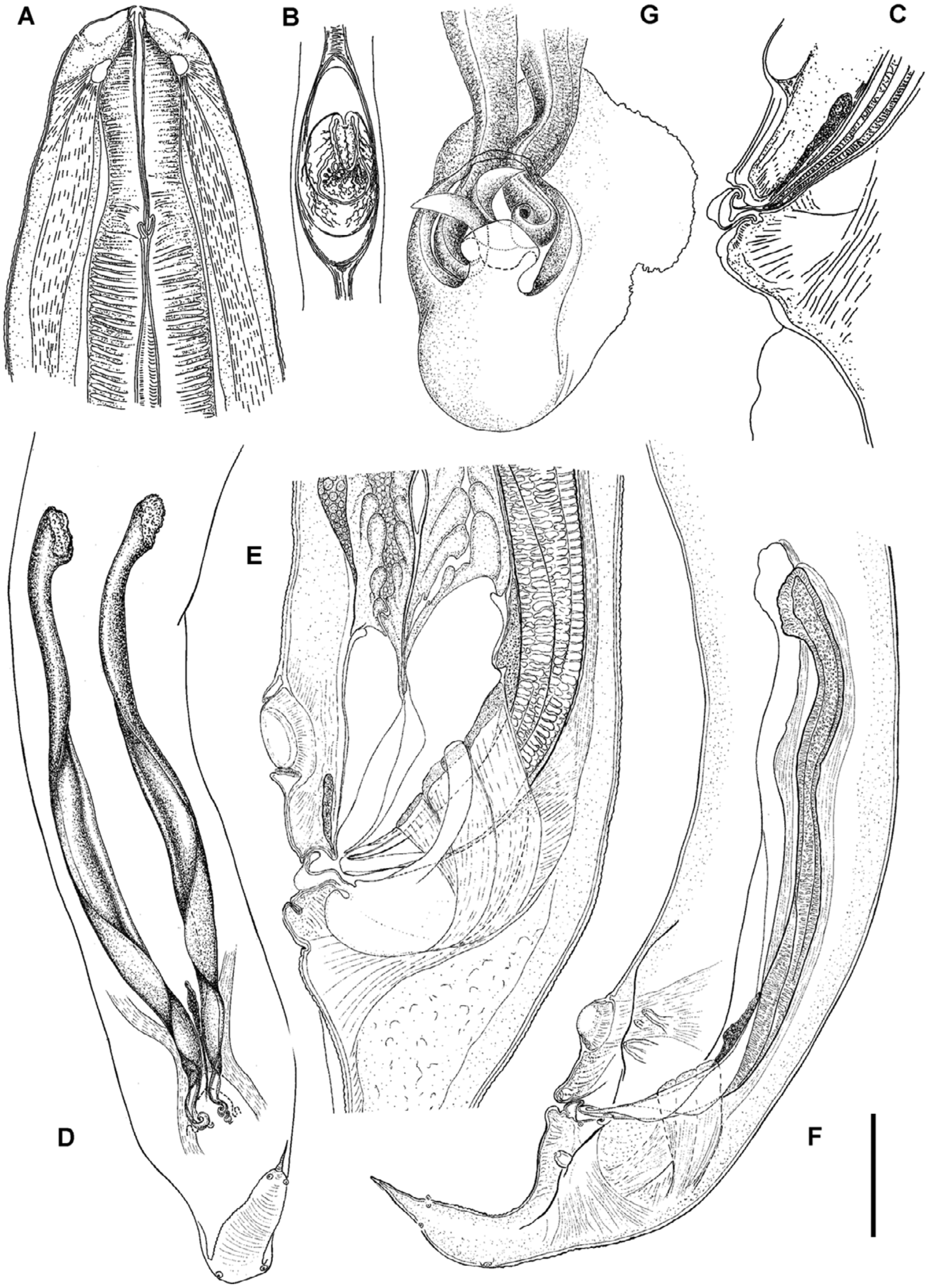

Figure 2. Line drawings of *Meteterakis striatura* Oshmarin & Demshin, 1972, male. (A) anterior end, lateral view; (B) excretory pore, ventral view; (C) cloaca region with protruding scutum, lateral view; (D) posterior end, ventral view; (E) optical section trough cloaca region, spicules and gubernaculum disposition can be observed, lateral view; (F) posterior end, lateral view; (G) spicules distal ends and gubernaculum, ventral view. (Scale bars for A = 750 μm, B = 60 μm, C = 35 μm, D = 120 μm, E, F = 100 μm, G = 65 μm.)

Female

Lateral alae starts soon after oral opening anterior to nerve ring level and is continuous posteriorly, becoming indistinct at phasmid level close to tail tip. Vulva is slit-like without a flap (Figure 1E, F). *Vagina vera* is short, muscular, posteriorly directed, densely braided with muscular sphincter and bended ventrally before opening into the vulva. *Vagina uterina* long, posteriorly directed adjoining common uterus which divides posteriorly into two uteri filled with mature eggs (Figure 1D). Uteri run posteriorly joining oviducts close to anal level and then turn anteriorly joining ovaries placed anterior to vulva level (Figure 1B). Ovaries long, anteriorly directed, flexing posteriorly at basal bulb level, and ending at vulva level. Eggs oval with thick, smooth shells, embryonated at morula stage. Small oval polar body can be observed on one of the poles of the eggs (Figure 5G, H). Eggs, occupying the *vagina uterina*, are orientated by the polar body towards the vulva opening. Anal opening slit-like; rectum elongated, with thick cuticular lining (Figure 3B). Tail long, conical, gradually passing into cuticular tip.

Host and locality

Intestine of *Geoemyda spengleri* (Gmelin, 1789) (Geoemydae) collected from Guangxi Province of China and kept in captivity in Moscow Zoo, Russian Federation.

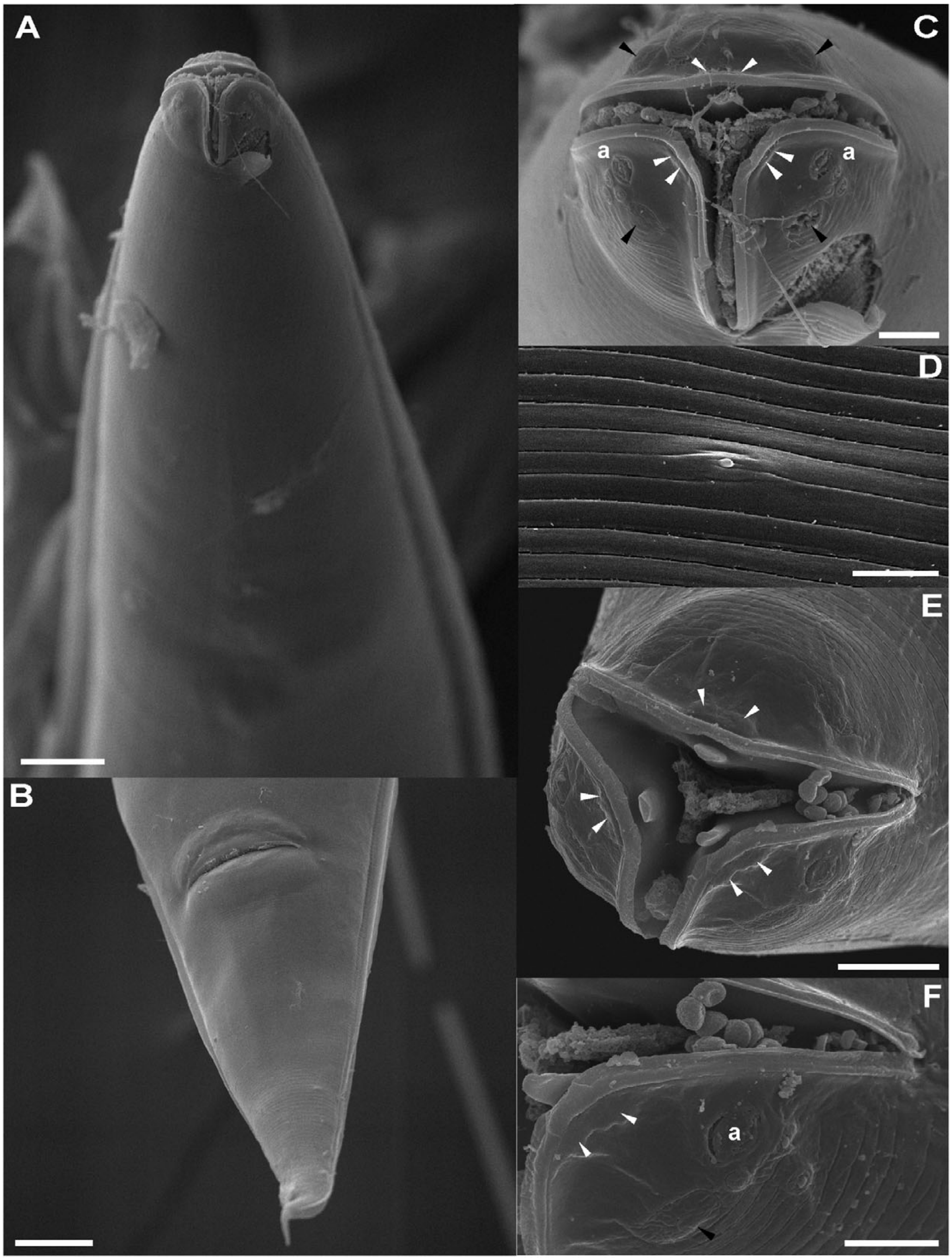

Figure 3. SEM images of *Meteterakis striatura* Oshmarin & Demshin, 1972 (A) female anterior end, ventral view; (B) female posterior end, ventral view; (C) female head end, enface view; (D) cuticular annulation and somatic papilla, female mid-body region; (E) male head end, enface view; (F) male's subventral lip (a – amphidial plate, white arrowhead – inner circle papillae; black arrowhead – cephalic double papilla). (Scale bars for A = 30 µm, B, C = 30 µm, D = 5 µm, E = 20 µm, F = 10 µm.)

Deposited material

Single male and two females voucher specimens are deposited in the National Nematode Collection of New Zealand under the following numbers: 3500-3503. A male voucher specimen No. 14351 is deposited in the Centre of Parasitology, Institute of Ecology and Evolution, Russian Academy of Sciences, collection.

Remarks

Meteterakis striatura was discovered during a scientific expedition to Vietnam conducted by the Pacific Research Institute of Fisheries and Oceanography (now Russian Federal Research Institute of Fisheries and Oceanography) from December 1959 to December 1960 and then from April to September 1961. The host and parasite material were collected by P.G. Oshmarin, Yu.L. Mamaev and A.M. Parukhin. During the expedition, 10 specimens of tortoise *Mauremys mutica* (Cantor, 1842) (as *Clemmys mutica* Boettger, 1888) were collected from two localities: the vicinity of the Tam Dao village and nearby Haiphong City. Although the collection site for the nematode species' host is not specified in the description, the collection date aligns with the collections in Tam Dao village. The original description does not provide deposition numbers of type slides or the location of the deposited material. Differential diagnosis given in the original description states that *M. striatura* can be distinguished from the other representatives by the morphology of

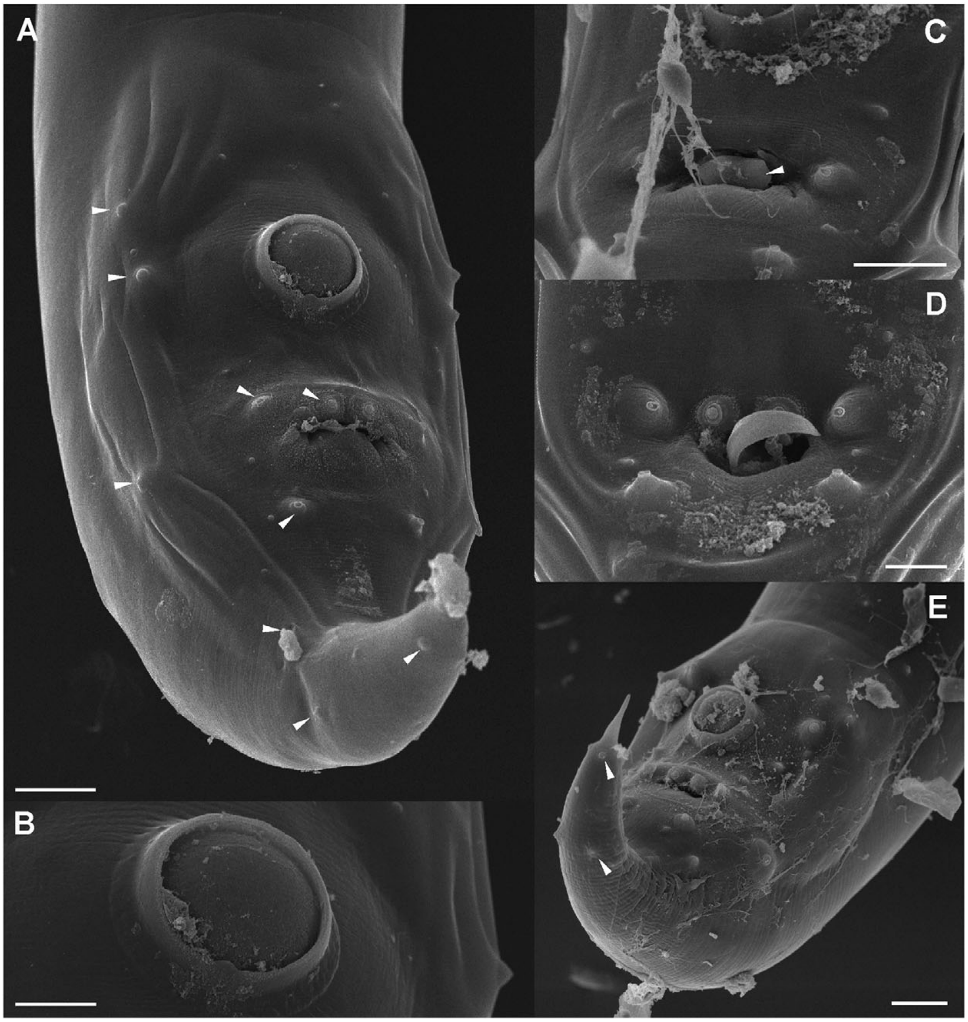

Figure 4. SEM images of *Meteterakis striatura* Oshmarin & Demshin, 1972, male posterior end. (A) ventral view (white arrowheads indicate genital papillae); (B) ventral sucker, (C) cloaca area (white arrowhead indicates scutum); (D) spicule tip protruding through cloaca aperture, ventral view; (E) anteroventral view (white arrowhead indicates genital papillae). (Scale bars for A = 20 μm, B = 40 μm, C, D = 20 μm, E = 15 μm.) SEM, scanning electron microscopy.

the basal bulb, the presence of a striated cuticle on the ventral side of the tail, and lateral rows of large cells within the hypodermis. Due to the lack of a full differential diagnosis in the main description, we give it below in the present paper. Despite the poor taxonomic value of listed morphological peculiarities (see Discussion), such morphological characteristics as male and female body sizes, number of genital papillae in males, and general spicule morphology, illustrated in the main description, let us conclude that the species studied herein is conspecific with *M. striatura.*

Differential diagnosis

Meteterakis striatura is characterized by long alate spicule with a distinct tessellation in males and the absence of a vulval flap in females. Spicules exceeding 500 μm in length make *M. striatura* closer to the following congeners: *M. amamiensis* Hasegawa, 1990, *M. aurangabadensis* Deshmukh & Choudhari, 1980, *M. formosensis* Sata, 2018, *M. ishikawanae* Hasegawa, 1987, *M. japonica* (Wilkie, 1930), *M. karvei* Naidu & Thakare, 1981, *M. lombokensis* Purwaningsih, Dewi & Nugroho, 2016, *M. longispiculata* (Baylis, 1929), *M. louisi* Inglis, 1958, *M. occidentalis* Sata, 2018, *M. pursatensis* Bursey, Goldberg & Grismer, 2019, *M. singaporensis* (Sandosham, 1953), *M. vaucheri* Adamson, 1986, *M. wangi* Zhang & Zhang, 2011 and *M. wonosoboensis* Purwaningsih, Dewi & Hasegawa, 2015. Males of *M. striatura* can be distinguished from *M. louisi*, *M. singaporensis*, *M. vaucheri*, and *M. wangi* by having smaller spicule size (678–688 μm *vs* 970–1100 μm, 740–960 μm, 1057–1242 μm and 740–930 μm, respectively). Discussed species has alate spicules which makes it different from *M. aurangabadensis* and *M. longispiculata*, which possess non-alate spicules. *Meteterakis striatura* varies significantly from *M. amamiensis*, *M. formosensis*, *M. japonica*, *M. karvei*, and *M. occidentalis* by having slender spicules with moderately developed heads. In contrast, in listed species, spicules are robust with funnel-shaped proximal ends. Compared with *M. wonosoboensis*, whose males also have slender alate spicules, *M. striatura* can be differentiated by the absence *vs* presence of vulvar flap in females. *Meteterakis striatura* is closest to *M. lombokensis*, *M. pursatensis*and *M. ishikawanae* in having close body dimensions in males and females, absence of vulva flap and general spicule morphology with well-developed ala and moderately developed proximal ends. However, all four species can be differentiated by the specific spicule shape. In *M. lombokensis*, proximal ends of spicules are strongly curved ventrally, making a C-shaped

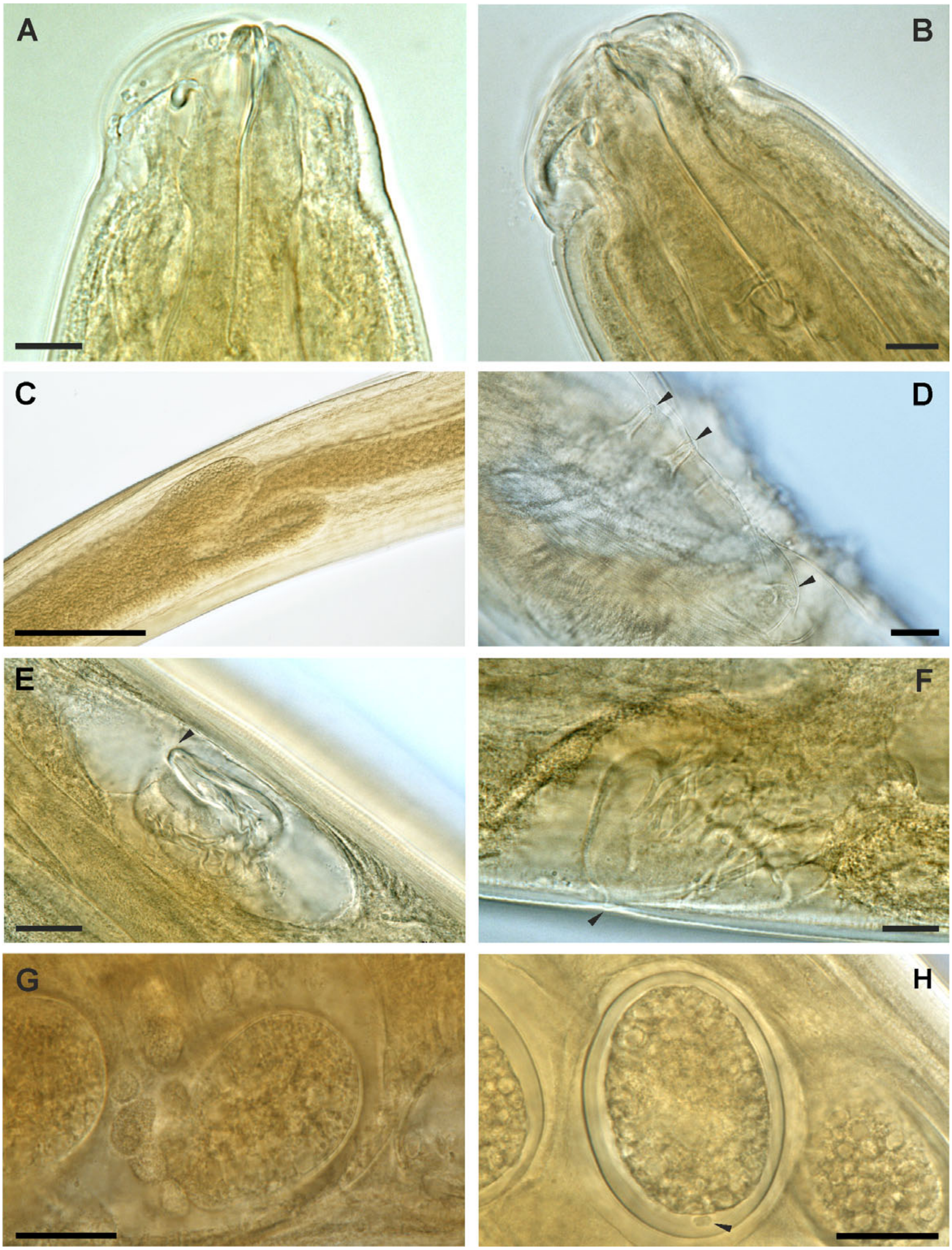

Figure 5. Light microscope images of *Meteterakis striatura* Oshmarin & Demshin, 1972. (A) male head end, sublateral view; (B) female head end, sublateral view; (C) blind diverticula, opening in the middle region of seminal vesicle; (D) caudal ala supported by three pedunculate papillae (black arrowheads); (E, F) excretory pore in male, ventral and lateral views, correspondingly (black arrowhead indicate excretory pore orifice); (G) immature eggs surrounded with spermia; (H) mature egg with oval polar body marked with black arrowhead. (Scale bars for A = 25 μm, B = 20 μm, C = 200 μm, D-F = 25 μm, G, H = 50 μm.)

appearance in the lateral position, whereas in *M. striatura* spicules, distal ends are straighter. *Meteterakis pursatensis*, in contrast, has straighter proximal ends of spicules than observed in *M. striatura*. In addition, in *M. pursatensis* spicules, their distal third bends under 90 degrees towards the ventral body wall when smoothly bent in *M. striatura*. In its morphological and morphometric characteristics, *M. striatura* is undoubtedly closest to *M. ishikawanae* described from *Odorrana ishikawae* (Stejneger, 1901) (as *Rana ishikawae* [Stejneger, 1901]) of Okinawa Island, Japan (Hasegawa, 1987). Both species have very similar body measurements in males and females, spicule size and morphology, number and distribution of genital papillae in males, and females lack vulval flap. However, males of *M. striatura*

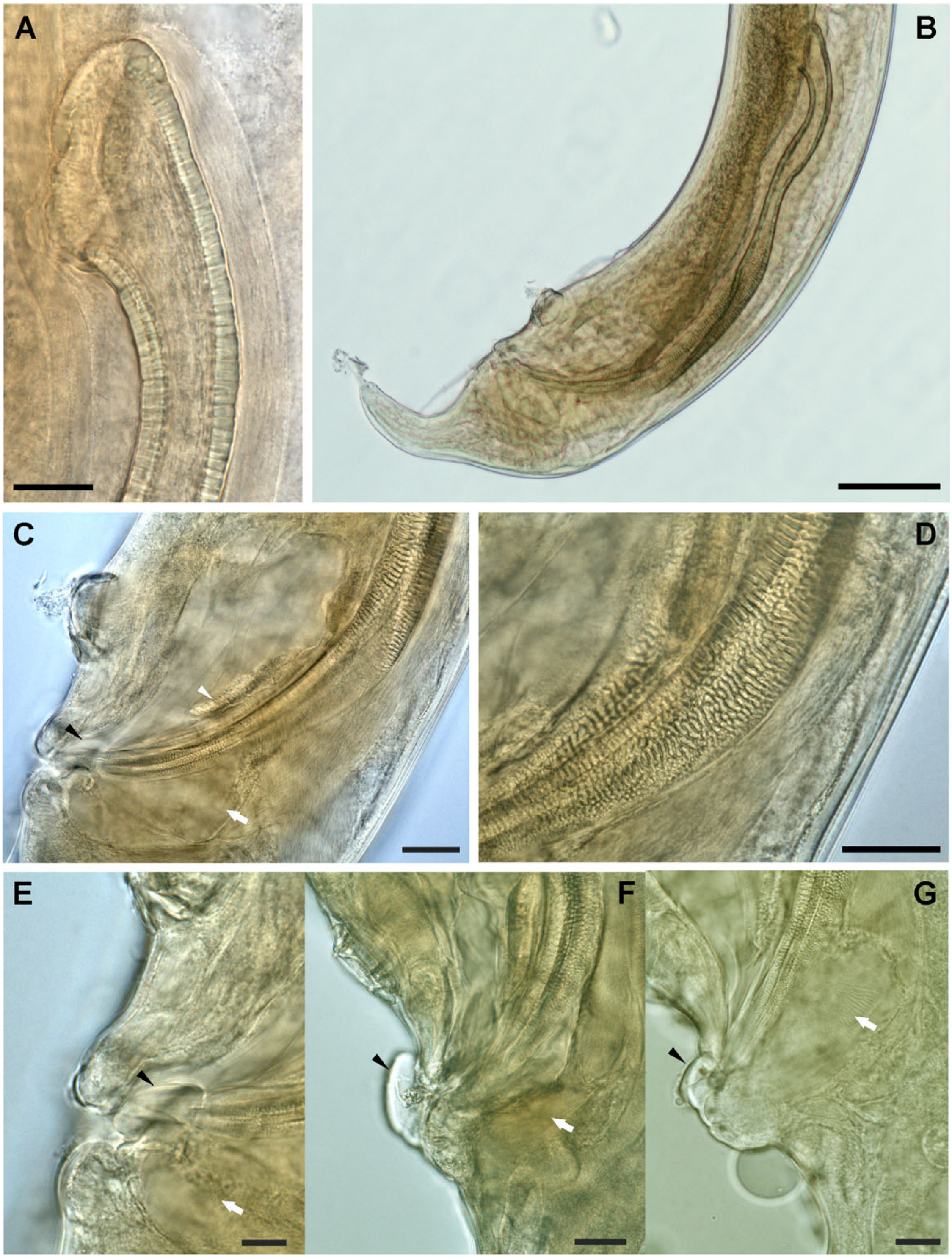

Figure 6. Light microscope images of males of *Meteterakis striatura* Oshmarin & Demshin, 1972. (A-E) *Meteterakis amamiensis* Hasegawa, 1990 (F) and *Meteterakis ishikawanae* Hasegawa, 1987 (G). (A) Left spicule proximal end; (B) posterior body end; (C) cloaca region showing muscle cords braiding spicules (white arrowhead), gubernaculum (white arrow) and scutum (black arrowhead), lateral view; (D-F) cloaca region of *M. striatura*, *M. amamiensis*, and *M. Ishikawanae*, consequently, showing scutum (black arrowhead) and gubernaculum (white arrow), lateral view. (Scale bars for A, C, D = 25 μm, B = 200 μm, E-G = 10 μm.)

can be differentiated by the narrower proximal parts of spicules blades bending in an S-shape, while in *M. ishikawanae*, proximal parts of spicules smoothly bend posteriorly to spicules heads' which are less prominent than in *M. striatura*.

Molecular characterization

The 18S and 28S rDNA sequences obtained for three nematode specimens were identical. Molecular phylogenetic analysis of the

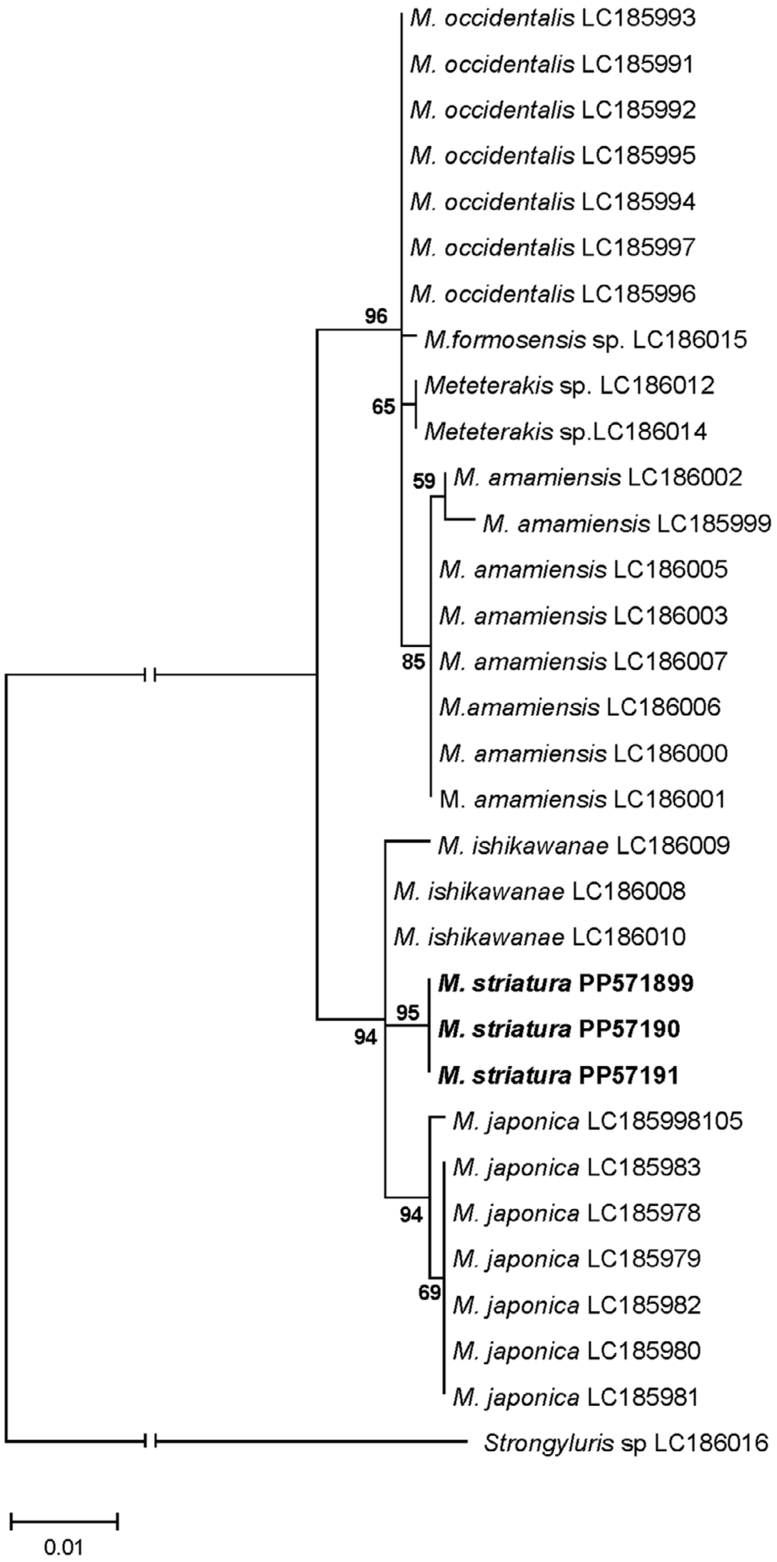

Figure 7. A maximum likelihood tree based on 28S rDNA of *Meteterakis* spp. Bootstrap values of 50% or higher are shown above the branches. Newly obtained sequences are indicated in bold.

28S rDNA sequence (D2-D3 expansion segment, alignment length 735 bp) based on the newly obtained data and sequences available for the genus *Meteterakis* shows the presence of two well-separated clades with good support (Figure 7). *Meteterakis striatura* joins the same clade with *M. japonica* and *M. ishikawanae* while another clade is represented by *M. occidentalis*, *M. formosensis*, *M. amamiensis* and *Meteterakis* spp., the latter obtained from *Plestiodon stimpsonii* (Thompson, 1912) (from Okinawa, Ishigaki, and Mihara locations). The inter-specific relationships are resolved only for representatives of *M. japonica*. The level of nucleotide difference between

Table 1. Morphometrics (in µm unless otherwise stated) of *Meteterakis striatura* Oshmarin & Demshin, 1972 (present study and the original description) and *Meteterakis ishikawanae* Hasegawa, 1987; mean ± standard deviation (range), except for de Man ratios

Species	*M. striatura* Oshmarin & Demshin, 1972 (present study)		*M. striatura* Oshmarin & Demshin, 1972*		*M. ishikawanae* Hasegawa, 1987**	
Character	Males	Females	Males	Females	Males	Females
n	4	6	–	2	Holotype and 12 paratypes	Allotype and 20 paratypes
L (mm)	4.29 ± 0.68 (3.3–4.83)	4.44 ± 0.75 (3.39–5.09)	4.2–6.2	**5.440**; 4.84	5.08 (4.13–6.27)	5.57 (4.53–6.43)
L′ (mm)	4.03 ± 0.7 (3.18–4.6)	4.05 ± 0.7 (3.06–4.31)	5.65	**5.14**; 4.45	4.888	5.22 (4.27–6.01)
Basal bulb height	202 ± 4.5 (198–208)	215.5 ± 12.8 (199–228)		**195**; 170	160 (143–180)	185 (175–213)
Basal bulb diam.	176 ± 20.5 (159–200)	196 ± 13.5 (180–212)		**130**; 115	153 (118–150)	158 (133–175)
Pharynx	69.5 ± 4.2 (65–75)	65 ± 4.8 (55–73)	60	**50**	58 (53–63)	60 (53–70)
Oesophagus	665 ± 22.4 (652–675)	684 ± 24.6 (650–720)	705 (622–735)	**680**; 665	680 (590–700)	720 (680–800)
Nerve ring	390.6 ± 24.0 (356–414)	388 ± 26.6 (365–426)	–	–	260 (240–290)	290 (260–320)
Excretory pore	564.2 ± 34 (543–614)	546.7 ± 18.8 (530–568)	–	**510**; 430	450 (410–510)	460 (410–490)
Head to vulva (mm)	–	2.177 ± 0.32 (1.87–2.71)	–		–	2.240 (1.930–2.590)
Max. body diam.	323 ± 21.2 (311–355)	306 ± 54.3 (253–370)	170–225	**280**; 225	180 (150–230)	210 (180–240)
Anal/cloacal body diam.	167.3 ± 22.1 (148–193)	140.7 ± 10.4 (130–152)	–	–	–	–
Tail length	249 ± 15.6 (228–263)	394.2 ± 53.3 (330–480)	250	**300**; 385	192 (168–230)	350 (260–420)
Left spicule	684.3 ± 5.5 (678–688)	–	(560–680)	–	590 (520–650)	–
Right spicule	652 ± 9.2 (642–660)	–				
Eggs	–	69.5 ± 4.3 (55–65) × 48.5 ± 5 (43–54)	–	67–74×42	–	61–78×40–48
a	13.2 ± 2.1 (10.5–15.5)	9.7 ± 2.8 (13–19.3)				
b	4.2 ± 0.6 (3.2–4.45)	4.2 ± 0.2 (3.9–4.44)				
c	17.1 ± 2.0 (14.5–19.45)	11.7 ± 0.9 (10.6–12.8)				
c′	1.5 ± 0.2 (1.2–1.75)	2.9 ± 0.3 (2.7–3.2)				
V, %	–	43.36 ± 9.0 (37.6–56.7)	–		–	
V′, %	–	47.4 ± 9.9 (41.3–62.1)	–		–	

[a] total body length divided by maximum body diameter;
[b] total body length divided by pharyngeal length (the pharynx is defined as head end to the pharyngo-intestinal junction);
[c] total body length divided by tail length;
[c′] tail length divided by body diameter at the anal/ cloacal aperture;
[L] total body length (head to tail tip);
[L′] body length from head to anal/ cloacal aperture; n, number of specimens examined;
[V] position of vulva from anterior end expressed as percentage of body length;
[V′] position of vulva from anterior end expressed as percentage of distance from head to anal aperture; data for holotype specimen of *M. striatura* is given in bold.
*Six nematode specimens have been studied from the same host; however, the exact number of measured male specimens is not in the main description. The holotype female and one paratype female specimens containing mature eggs have been measured.
**Measurements holotype male and allotype female are not given separately.

M. striatura and *M. japonica* group is 6 bp, and 3 bp between the studied species and *M. ishikawanae.* Within the species *M. japonica* and *M. ishikawanae*, differences are 2 and 3 bp, respectively. The nucleotide differences between *M. striatura* and representatives of the other clade reach 13 and 17 bp (*M. occidentalis* and *M. amamiensis*, respectively), but within the clade do not exceed 22 bp (*Meteterakis* spp. and *M. amamiensis*). Comparison of data for 18S rDNA sequences (alignment length 845 bp) showed complete identity of sequences for *M. striatura* and *M. japonica* and 2 bp difference with *M. amamiensis.*

Discussion

The distinguishing characteristics of *M. striatura*, as outlined in the primary description by the authors, encompass several key features, including the shape of the basal bulb, notably the anterior portion resembling a truncated cone (see Figure 58, 2 after Oshmarin & Demshin, 1972); the presence of striated cuticle on the ventral side of the tail, lateral rows of large cells within the hypodermis and a transverse fold situated on the ventral aspect of the body, observed immediately posterior to the lips. The present authors consider that the presence of the transverse fold and the unique structure of the basal bulb may be attributable to muscular contraction during specimen fixation. Some male specimens examined in the present study exhibited all described features, including protrusion of the cloacal region, as depicted in the original description; however, our molecular analyses conducted on three distinct individuals provide evidence supporting their conspecificity. Moreover, groups of 4–5 cells resembling the ones described by Oshmarin & Demshin (1972) were identified within the pseudocoelom in studied male specimens and probably represent pseudocoelomocytes.

Observation of the type material of *M. amamiensis* and *M. ishikawanae*, kindly provided by Meguro Parasitological Museum (Tokyo, Japan), confirmed the high morphological similarity between the latter species and studied herein *M. striatura.* Hasegawa (1987) does not mention *M. striatura* in the differential diagnosis, although he gives a bibliographic reference for the latter species. Such morphological similarity probably gave rise to some suspicions about the co-specificity of these nematodes. The present study revealed some morphological differences in the shape of spicules and position of scutum between *M. striatura* and *M. ishikawanae*, given previously in the differential diagnosis. Based on Inglis's (1958) statement that spicule shape is of primary importance in distinguishing the species within *Meteterakis* and our molecular analysis that did not determine the relationships between the discussed species, we recognize *M. striatura* and *M. ishikawanae* as non-co-specific. Hasegawa (1990) notes that he supposed *M. ishikawanae* to be specific to *Rana ishikawae* (Anura: Ranidae); however, later, it was discovered by his colleague in the tortoises *Geoemyda japonica* Fan, 1931 (given as *Geoemyda spengleri japonica* Fan, 1931) (Testudines: Geoemydidae) on Okinawa Island (Nakachi, personal communication; author's note). We assume that the monophyletic origin of *G. spengleri* and *G. japonica* and the discovery of a fossil species, *Geoemyda amamiensis* from Tokunoshima Island, closely related to *G. japonica*, support Hasegawa's earlier suggestion that *Meteterakis* spp. could be introduced to Okinawa Island from continental China by some reptiles (Hasegawa, 1987; 1990; Yasukawa *et al.*, 2001; Takahashi *et al.*, 2007; Yasukawa & Ota, 2008).

According to Inglis (1958), disagreements regarding the position and independence of the genus *Meteterakis* were caused by an underestimation of the importance of such morphological characters as gubernacular mass and the number of male caudal papillae. The term 'gubernacular mass', which later became confusing and ignored by some authors, was proposed by Inglis (1958) to describe the cuticularized structure located in the cloacal region and surrounding spicules. According to Inglis (1958), the gubernacular mass is a characteristic feature for the present genus which can be more or less developed in all its representatives; this mass is a thickening of the cuticular lining of the walls of the cloaca more developed on the dorsal and ventral side and less pronounced laterally. Inglis (1958) emphasizes that the true dimensions of a given structure are often difficult to determine and highlights it in his illustrations for the genus revision with a dotted line. According to Inglis (1958), authors often mistakenly determine its size and shape; thus, in the description of *Spinicauda bufonis* (Yamaguti, 1935), the author depicts only the ventral part of this structure, denoting it as a 'gub' (apparently implying the gubernaculum). In the technique section of his article, Inglis (1958) states that the confusion that takes place in the literature associated with the presence or absence of a gubernaculum in *Meterakis* representatives initially arose because of the incorrect application of clearing techniques when specimens had been cleared with lactophenol, and further over-cleared with creosote, causing the internal cuticular structures including spicules to become indistinguishable – especially in small representatives of the genus. In further descriptions and revisions of the *Meteterakis* genus, the term 'gubernacular mass' was neither frequently used (Cruz & Ching, 1975; Junker *et al.*, 2015; Purwaningsih *et al.*, 2016) nor discussed. However, some authors (Oshmarin & Demshin, 1972; Hasegawa, 1987) highlighted the area at cloacal opening with a dotted line without further discussion. Oshmarin and Demshin (1972) in their description of *M. striatura* do not use the term 'gubernacular mass', although they highlight some dotted outlines in the illustration of the posterior end of the male, while drawing attention to another cuticular structure near the cloaca opening, suggesting that it may be a gubernaculum.

Observation of present material, including paratype specimens of *M. amamiensis* and *M. ishikawanae*, revealed the presence of massive sclerotization of the dorsal cloaca wall soon after the cloaca opening in the area of passage of the distal ends of spicules. It is tightly woven with muscles and hard to observe. Present sclerotization is approximately 100–110 μm in length, has a saddle shape when observed laterally, and has muscle attachment along its proximal edge. The distal end of the discussed structure has a swelling resting against the lower cloacal lip. In *M. striatura*, at the anterior part of the sclerotization, we observed lateral, ventrally pointed processes flanking the spicules and closing above them. In addition, in all studied representatives of the genus, we observed a small cuticularized structure immediately near the cloaca opening (Figure 2C, E, F) resembling a thin plate of subtriangular or hastate shape with the free edge directed deep into the cloaca. In *M. striatura*, this structure is very small, translucent, and poorly visible in a light microscope. However, as observed from our material, in some cases, it can protrude outward and is visible on SEM images (Figure 5D). The exact structure protruding outside the cloaca aperture was observed in *M. amamiensis* and *M. ishikawanae* (Figure 6F, G). An analysis of the literature has shown that this structure can also be observed in SEM images of *M. japonica* (see Figure 33 in Purwaningsih *et al.*, 2015), *M. lombokensis* (see Figure 2S in Purwaningsih *et al.*, 2016), and *M. wangi* (Figure 2E in Zhang & Zhang, 2011). In the illustrations for *M. wangi* there is an image of a partially damaged structure, which is designated as the gubernaculum (see Figure 1H in Zhang & Zhang, 2011), but unfortunately it is not shown in association with the spicules in the drawing of the male posterior end, and it is difficult to identify its origin. Adamson (1986) in the description of *M. vaucheri* has illustrated a small subtriangular detail of male genital cone (see Figure 1N in Adamson, 1986). We believe that same structure is marked as the gubernaculum in the following species: *M. asansolensis* (see Figures 1E and 1G in Sou, 2019), *M. guptai* (Gupta & Naiyer, 1993), *M. hurawensis* (Bursey *et al.*, 2017), *M. japonica* (in the original description by Wilkie [1930]), *M. wonosoboensis* (Fig. 8 in Purwaningsih *et al.*, 2015) and illustrated on the drawings for *M. formosensis* and *M. occidentalis* and marked as posterior cloacal lip (see Figure 2F, G; Figure 3F, G in Sata, 2018).

A characteristic feature of the male reproductive system in nematodes is the presence of such cuticular structures as spicules, gubernaculum and telamon. Based on the definitions given by different authors (Lee, 2010; Mehlhorn, 2016) the gubernaculum is formed from a dorsal thickening of a dorsal wall of the spicular pouch. It is essentially a curved plate forming a groove in which the spicules can move. The term 'telamon' was proposed by Hall (1921) to describe a small cuticular structure found in males of *Hyostrongylus rubidus* (Hassall & Stiles, 1892). The telamon is developed from the ventral wall of the cloaca near its aperture. It extends laterally into the lateral walls and then anteriorly as flattened curved plates in the lateral walls of the cloaca. Both the gubernaculum and telamon appear to be protective structures developed to support the walls of the cloaca and its aperture from the passage of spicules; they also support and guide spicules when extruded. According to Hall (1921), the term 'gubernaculum' should be restricted to the longitudinal structure in the dorsal wall of the cloaca toward its anterior end, and the term 'telamon' should be used for the supporting structure of variable form near the cloacal aperture. Hall assumed the presence of telamon in some Oxyurida, Spiruroidea, and Filarioidea. However, the term is mainly used to describe the accessory cuticular structure in the Strongyloidea (Hall, 1921; Lee, 2010).

Based on these definitions and our observations, the term 'gubernacular mass' refers to the massive cuticular sclerotization of the dorsal wall of the cloaca, which corresponds to the definition of the gubernaculum. We consider that small cuticular formation observed near the cloaca opening is associated with the gubernaculum and most probably serves is an accessory piece of the latter. To avoid further confusion about the mentioned structure, we propose using the term 'scutum' from the Latin word meaning 'shield' relating to form and partially to function, namely the reflection/direction of spicule blades. Apparently, the scutum plays the function of a guiding organ and perhaps serves for anchoring with a female's vulval flap during copulation. As observed, the scutum is better developed in *M. amamiensis*, possessing a well-developed vulval flap. In contrast, in *M. striatura* and *M. ishikawanae*, where females lack a vulval flap, the scutum is less pronounced. We believe this structure is present in all representatives of the genus but is often overlooked because it resembles the cloaca lip.

Another important morphological feature found in males of *M. striatura* and marked for *M. amamiensis* and *M. ishikawanae* (present study) and perhaps overlooked in other species is the presence of blind diverticula in the male reproductive system. Previously, a single blind diverticulum was noted only for *M. vaucheri* (Adamson, 1986). The purpose of such a morphological formation is not entirely clear; diverticula originate at the same level and are outgrowths of the wall of the seminal vesicle filled with sperm. The sizes of diverticula differ slightly from each other.

Adamson (1986) pointed that such important morphological and taxonomic feature as number and disposition of caudal papillae in males of *Meteterakis* causes difficulties because of the presence of a large number of somatic papillae that can be easily confused with genital papillae; and also, with the fact that the number of genital papillae can vary within a species. There is no doubt that the number of papillae is certainly an important diagnostic feature, and re-examination of type materials of previously described species is highly desirable, but this was not considered within the scope of present work. For this reason, in the diagnosis of the genus, we indicate the range within the change in the number of indicated genital papillae for species of the genus that are valid in our opinion.

Baker (1984) in the analysis of Meteterakinae and Spinicaudinae accepts the synonymy of *M. longispiculata* and *Heterakis* (*Spinicauda*) *cophotis* Baylis, 1936 proposed by Crusz and Sanmugasunderam (1973) and lists 16 nominal species of *Meteterakis* genus including *Meteterakis bufonis* (Biswas & Chakravarty, 1963), as a new combination for *Heterakis bufonis* Biswas & Chakravarty, 1963 from *B. melanostictus* (Calcutta, India). The authors of the present study disagree with Baker's (1984) assumptions regarding the inclusion of *Heterakis bufonis* Biswas & Charkavarty, 1963 as a representative of the genus *Meteterakis* due to the absence of the lateral alae in females, which is the strong diagnostic character of the genus. We place this species as species *insertae sedis* together with *Africana bufonis* Biswas & Chakravarty, 1963, as proposed by Baker (1984).

Meteterakis sinharajensis (Crusz & Ching, 1975) and *M. lyriocephali* (Crusz & Ching, 1975), which were referred to *Meteterakis* by Chabaud (1978), also raise some doubts about the validity of these species. Both species (see Crusz & Ching, 1975) have been described from the same host specimen of *Lyriocephalus scutatus* (Linnaeus, 1758) (Squamata: Agamidae) from Sri Lanka, where 3 males and 30 females were identified as representatives of *Meteterakis* spp. and remaining 33 males and 44 females were referred to a new genus named *Cometeterakis* because of distinctly unequal in size spicules. Crusz & Ching (1975) also note that they found representatives of *M. sinharajensis* in *Pseudotyphlops philippinus* as well and give measurements that do not overlap either in the sizes of males and females, or the sizes of male spicules. In the description of *C. lyriocephali*, the authors of the species indicate a large variation in the sizes of the right and left spicules, as well as varying positions and numbers of sessile papillae. However, illustrations by Crusz and Ching (1975) show that the number of large papillae also varies, suggesting the presence of more than two species in a single host. Given these inaccuracies, we place both species as *species inquirendum.*

Inglis (1957b, 1958) points out the morphological isolation of two representatives of the genus: *M. mabuyi* and *M. triaculeata.* Both species are distinguished by the insufficient degree of development of the anterior cuticular flange of the lips; females of *M. mabuyi* lack the lateral alae (present morphological character is not mentioned in the description of *M. triaculeata*). Inglis (1958) could not confirm the presence of the gubernacular mass in *M. mabuyi* since only a single female was observed; in males of *M. triaculeata*, gubernacular mass was not observed. Inglis (1958) considered all three mentioned characters essential in determining the genus but left both species within *Meteterakis* due to the restricted amount of studied material. However, the situation with the 'gubernacular mass' has been clarified (present study), and the absence of the lateral alae, which plays an essential role in species identification (Sata, 2019), makes the authors place both species as *species inquirendae* until the next morphological revision of the type material.

Based on the similarity of morphometric parameters of *M. gambhiri* (Gambhir *et al.*, 2006) (described as *M. bufonis* and later renamed by Zhang & Zhang [2011]) and the type species *M. govindi*, we place *M. gambhiri* as a junior synonym of the latter species. Also, special attention deserves to be given to *M. crombiei*, described from *Sphenomorphus jobiensis* (Meyer, 1874) (Sauria: Scincidae) from Fergusson Island, Papua New Guinea (Bursey *et al.*, 2005). This is the only species of the genus for which eggs with a tuberculate shell surface are described, while in all other congeners the eggs have a smooth shell. The absence of a differential diagnosis in the description of the species, as well as a special morphology that matches the description of eggs in some representatives of the genus *Spinicauda*, made by the same authors force us to place this species to the *species inquirenda* until clarifying the diagnosis and morphological features of the eggs.

Unfortunately, no reliable data regarding the life cycle of *Meteterakis* is available; Sata (2019) inclines to Anderson's (2000) assumption that they may be similar to Spinicaudinae when infection of the definitive host occurs through the eggs containing a third-stage larva. The high dispersion of the present parasitic group and lack of host specificity may also suggest the involvement of paratenic invertebrate hosts, such as lumbricids or terrestrial mollusks, which tend to be a common food source for most of *Meteterakis* hosts.

The molecular research of *Meteterakis* spp. performed by Sata (2018) for the East Asian islands, has revealed the presence of two genetically diverse lineages within the studied genus, namely J and A groups, which demonstrate different patterns of speciation. Thus, diversification within the J group (includes *M. japonica* and *M. ishikawanae*) correlates with the host biogeography and suggests co-divergence with vicariance event of the host fauna. However, in the A group (which includes *M. amamiensis*, *M. occidentalis*, *M. formosensis* and two undescribed species from Iriomotejima and Ishigakijima Islands, respectively) phylogenetic diversity does not correspond to the host biogeography and implies diversification by repeated colonization. Based on an analysis of data performed by Sata (2018), he concluded that any continental lineage close to the J group (including *M. japonica* and *M. ishikawana*) was expected to be relictual or absent. Our data refute the present assumption since the species studied herein and reported by the authors in this current paper species join Sata's J group in all analyses conducted. However, the relationships within the group remain unresolved. All *Meteterakis* species studied using molecular techniques have very similar spicule morphology and, according to the division of Junker (Junker *et al.*, 2015), belong to the same group: a group whose spicules are equal and intermediate in length. However, there is a significant difference in the spicules morphology: in the A group, spicules are robust with funnel-shaped proximal ends, while in the J group, spicules are more slender with moderately developed heads. In addition, lateral alae are better developed in the J group, while narrow or absent in A-group species.

More sampling of *Meteterakis* spp. from the mainland belonging to different morphological groups differing in the spicules' morphology would be desirable to obtain a more reliable picture of the genus phylogeny.

Acknowledgements. The present research was conducted within the framework of the Biological Diversity program No. 0109-2018-0075, 'Ecology and diversity of parasitic organisms'. The authors are very grateful to Dr. Toshiaki Kuramochi and Dr. Hiroshi Saito from Meguro Parasitological Museum (Tokyo, Japan) and National Museum of Science and Nature (Amakubo, Japan), respectively, for providing the paratype material for *M. amamiensis* and *M. ishikawana* for comparative purposes. The authors also thank Dr. Devanshu Gupta, Officer-in-Charge of Coleoptera Section and Publication Division in Zoological Survey of India (Kolkata, India), Jamie Blackman, Fernandes Opook and Tithi Gandi from Manaaki Whenua Landcare Research (Auckland, New Zealand) for their help with finding the rare literature sources and Professor Alexey V. Tchesunov from Moscow State University (Moscow, Russia) for providing of nematode material.

Financial support. The Ministry of Business, Innovation and Employment (MBIE) in New Zealand partially funded the research through Strategic Science Investment Funding (SSIF) for Nationally Significant Collections and Databases.

Competing interest. None

Ethical standard. Not applicable

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