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Journal

Annals of the Entomological Society of America, 110(2)

ISSN

0013-8746

Authors

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Publication Date

2017

DOI

10.1093/aesa/saw071

Peer reviewed

Research

Ovoviviparity in the Tropical Earwig Species *Spongovostox semiflavus* (Dermaptera: Spongiphoridae), With Potential Convergent Elongation of Male Genitalia

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Received 21 July 2016; Accepted 20 September 2016

Abstract

Ovoviviparity and viviparity have evolved independently multiple times in animals. Although females exhibit extensive parental care of their eggs, (ovo)viviparity has only been reported in a few species of free-living, non-epizoic earwigs. In contrast, to date, all the studied members of families Arixeniidae and Hemimeridae, which live on mammals, are viviparous. We herein report ovoviviparity in the tropical earwig species, *Spongovostox semiflavus* (Bormans, 1894) (Forficuloidea: Spongiphoridae: Spongiphorinae). We observed that females of this species retain well-developed embryos within the ovaries and then lay them with complete egg envelopes just before hatching. An average of 9.4 embryos concurrently developed in a female's body. A similar condition has been reported for only one other species *Marava arachidis* (Yarsin, 1860), in the subfamily Spongiphorinae. Without additional mating, *Spo. semiflavus* females produced at least three clutches, consisting of an average of nine offspring within a period of 14–27 d. Both *Spo. semiflavus* and *M. arachidis* males are characterized by elongated male genitalia that are more than twice as long as their body lengths. Interestingly, elongated male genitalia are also present in the two other spongiphorids for which (ovo)viviparity has been reported. We discuss the causes of the potential convergence of the evolution of the male genital structure and the development of (ovo)viviparity in females.

Key words: genital evolution, ovarian fertilization, ovoviviparity, spongiphoridae, viviparity

Although females of most insect species deposit eggs, vivi- or ovoviviparity has been reported in >10 insect orders, indicating their multiple evolutionary origins (Hagan 1951, Meier et al. 1999, Heming 2003, Benoit et al. 2015). Pseudoplacental viviparity has been reported for the earwig (Insecta: Dermaptera) families Hemimeridae and Arixeniidae, members of which live on mammals (on hamster rats [*Cricetomys* Waterhouse, 1840 spp. and *Beamys* Thomas, 1909 spp.] in Africa, and bats [especially, *Cheiromeles torquatus* Horsfield, 1824] in Asia, respectively; Heymons 1912, Hagan 1951, Nakata and Maa 1974). A recent study revealed that embryos of *Arixenia esau* Jordan, 1909 (Arixeniidae) were likely to be nourished within the uterus after their initial growth in the terminal ovarian follicles (pseudoplacental–uterotrophic viviparity; Tworzyllo et al. 2013a). The remaining earwig families are typical free-living earwigs. Morphological and molecular phylogenetic studies have shown that both Hemimeridae and Arixeniidae are specialized in-group members of the superfamily Forficuloidea (Klass 2001, Haas and Klass 2003, Jarvis et al. 2005, Tworzyllo et al. 2013b, Kocarek et al. 2013, Naegle et al. 2016). Although female free-living earwigs exhibit parental care of their eggs (and young nymphs in some species; Günther and Herter 1974, Costa 2006), most species are

oviparous, and (ovo)viviparity has been reported for three species in the family Spongiphoridae (Forficuloidea). Females of *Marava arachidis* (Yarsin, 1860) (Spongiphorinae; we follow the subfamilial classification system of Steinmann 1990 in this study, as suggested by Kamimura et al. 2016a) retain well-developed embryos, which are enclosed in thin but complete egg envelopes until several minutes before hatching (Herter 1943 1965, Patel and Habib 1978). Because the birth product of this species is eggs, some authors have categorized this species as oviparous (e.g., Hagan 1951). However, nymphs of *M. arachidis* hatch within a few minutes after egg deposition (Herter 1943), compared with the usual oviparous species in which the maternal care of eggs generally lasts from one to several weeks (Günther and Herter 1974, Costa 2006). Based on previous findings (Herter 1943, 1965; Patel and Habib 1978; Costa 2006; Kočárek 2009; Kamimura et al. 2016b), *M. arachidis* is considered ovoviviparous for the purpose of this study. Kočárek (2009) found developed embryos in the abdomen of fixed samples of *Chaetospania borneensis* (Dubrony, 1879) (Spongiphoridae: Labiinae). The most developed embryo lacked a chorion, which indicates viviparity (Kočárek 2009). Similarly, Matzke (2011) observed fully developed embryos within the

bodies of female *Sphingolabis hawaiiensis* (de Bormans, 1882) (Labiinae).

During a faunal and ecological study of earwigs on Penang Island, Peninsular Malaysia (Kamimura et al. 2016a), we discovered that *Spongovostox semiflavus* (Bormans) (Spongiphorinae) is ovoviviparous. Ovoviviparity and viviparity require adaptations in females to accommodate developing embryos within their bodies for a prolonged time period, which likely influence the evolution of the male genitalia (see Kamimura et al. 2016b and references therein). Our preliminary literature search revealed that all known (ovo)viviparous, free-living earwigs are characterized by elongated male genitalia (Borelli 1932, Ramamurthi 1958, Steinmann 1990, Kamimura et al. 2016b). However, taxonomists usually examine and describe only the terminal portion of the male genital organs. Based on our own observations, we herein report the entire structure of the male genital organs for all known species of (ovo)viviparous, free-living earwigs, and discuss the possible convergence of the evolution of male genital morphology and changes in female reproductive mode from oviparity to (ovo)viviparity.

Materials and Methods

Insect Rearing and Morphology

Two male and two female specimens of *Spo. semiflavus*, collected in March 2015 from forested areas of Bukit Jambul and Bukit Kukus, Penang Island (05° 30' N, 100° 28' E), Malaysia, and their offspring (Fig. 1) were used for this study. The insects were kept in plastic containers (55 mm in diameter, 38 mm in height) with plaster of Paris at the base. They were maintained at $26 \pm 1^\circ\text{C}$ under a photoperiod of 12:12 (L:D) h, and provided with water and unlimited amounts of commercial cat food. Cultures were checked and food changed every 3 d. All of the following experiments were conducted under the same laboratory conditions.

For the morphological observations, male genitalia or spermatheca (the sperm storage organ in females) were dissected from

samples prepared in insect Ringer solution (0.9 g NaCl, 0.02 g CaCl_2 , 0.02 g KCl, and 0.02 g NaHCO_3 in 100 ml water), mounted on a slide, and then observed and photographed under a differential interference contrast (DIC) microscope ($\times 100$ to $\times 400$, BX53; Olympus, Tokyo, Japan).

Mating Behavior

To observe mating behavior, five pairs of virgin males and females ("v" in Fig. 1; age: 7–12 d after imaginal eclosion) were placed in separate plastic containers (55 mm in diameter, 38 mm in height) with plaster of Paris at the base. Virgins of both sexes were obtained by separating newly emerged adults from stock cultures every 3 d. In earwigs, female adults collected using this method usually have no sperm in the spermatheca (Kamimura 2006; Kamimura and Lee 2014a,b; Kamimura et al. 2016b). Using time-lapse recordings made with a video camera (GZ-MG980S; Victor, Kanagawa, Japan), behavior was recorded for 3 h and 20 min for two pairs, and for 8 h for three pairs during the light phase. These pairs were later kept for 6 d before the male was removed from the container. Females were released into the pairing vessel 30 min prior to the start of recording for acclimation; the males were introduced immediately before observation was initiated.

Embryogenesis Observation

At various times after pairing and/or the deposition of the previous batch of offspring (Fig. 1), eight females were deeply anaesthetized with carbon dioxide gas for ~ 1 min. The abdomen was removed from these females and was fixed in FAA (formalin: 95% ethanol: glacial acetic acid = 6:16:1). Later, the ovaries were removed from the abdomen and observed under a fluorescence microscope (ECLIPSE 80i; Nikon, Tokyo, Japan) with an ultraviolet filter set (excitation, 360–370 nm; dichroic mirror, >400 nm; absorbance filter, >400 nm) after staining in $2 \mu\text{g/ml}$ 4', 6-diamidino-2-phenylindole (DAPI) solution (Kamimura et al. 2016b).

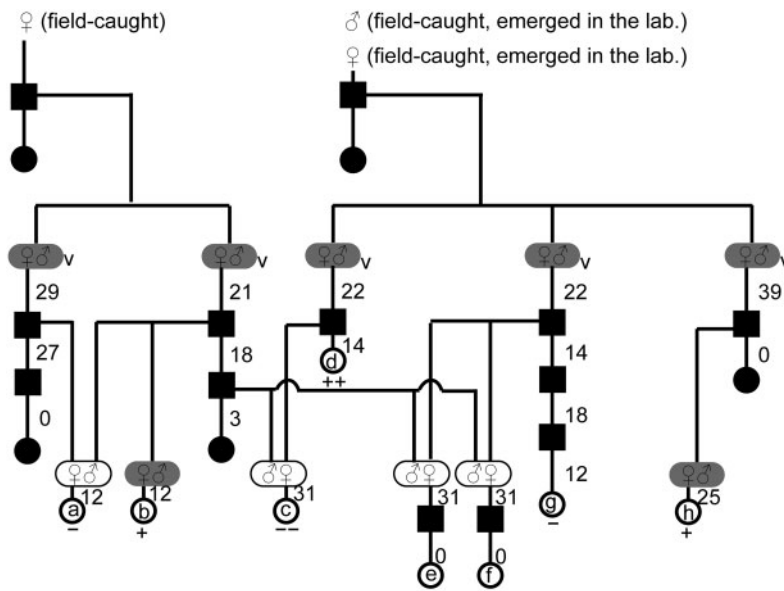


Fig. 1. Pedigree of *Spongovostox semiflavus* used in this study. The solid squares and solid circles represent the appearance of offspring and the death of a female, respectively. Sib- and nonsib pairings are indicated by gray and open ovals, respectively, and those marked with "v" were video-recorded. The open circles, a–h, represent females fixed with FAA, with an indication of ovarian status: --, ovaries could not be detected (possibly because of atrophy); -, with only undeveloped eggs; +, with developed embryos; and ++, with well-developed embryos possessing pigmented eyes. The numerals show the time (in days) between respective events.

Comparison of Male Genitalia

We examined the male genital structures of all four known (ovo)viviparous species of free-living earwigs: *Spo. semiflavus* ($n=3$), *M. arachidis* ($n=1$; see Kamimura et al. 2016b), *C. borneensis* ($n=1$, dried specimen, collected in Brinchang, Cameron Highlands, Pahang, Malaysia, between 7 and 9 April 2012), and *Sph. hawaiiensis* ($n=2$, dried specimens, collected from Amok, Malekula, Vanuatu, on 17 September 1958, and from Bougainville Island, Papua New Guinea, on 13 June 1956). Because the male genitalia of *Spo. semiflavus* are extremely long (see Results), a curvimeter (COMCURVE-8, KOIZUMI, Tokyo, Japan) was used to measure the entire length from an enlarged copy of photographs taken under the DIC microscope (to the nearest 8.7–11.1 μm , depending on the magnification; see Kamimura 2000 for details).

For comparative purposes, we also examined the male genitalia of *Chaetospania anderssoni* Brindle, 1971 ($n=2$, dried specimens, offspring of a female collected from Sungai Nipah, Penang Island, 2012), which is an oviparous congener of *C. borneensis* (Kamimura et al. 2016a).

Results

Mating Behavior

We observed four complete mating sequences for three pairs of *Spo. semiflavus*. *Marava arachidis* males always grab a female's antenna or mouthparts with their mouthparts to coerce the female into mating (Herter 1943; Kamimura et al. 2016a,b). This type of behavior was not observed in *Spo. semiflavus*. Instead, as is commonly observed in other earwig species (see Kamimura 2014 for a review), when a male detected a female with his antennae, he rotated his abdomen nearly 180° around the anteroposterior axis and walked backward to establish an end-to-end copulation posture (Fig. 2A). Mating lasted 75.0 ± 44.9 min (mean \pm SD; range: 24–128 min). One pair mated twice, at 56 and 92 min, within an interval of 227 min during 8 h of video recording.

Birth Products

During the maintenance of our cultures every 3 d, we observed the sudden appearance of first-instar nymphs in our rearing vessels containing females ($n=13$ cases). In 10 cases, the number of nymphs varied from 2 to 14 (average = 9.4 nymphs). Because it takes one to several weeks for earwig eggs to hatch (Günther and Herter 1974, Costa 2006), this indicates that either the egg period of *Spo. semiflavus* is exceptionally short, or that females deposit first-instar nymphs as the birth product. We successfully observed females with a newly deposited egg that contained a fully developed nymph in complete egg envelopes, together with nymphs, some of which were at a stage preceding full body pigmentation ($n=2$; Fig. 2G, H). Thus, although we could not directly observe the hatching of the deposited eggs, this clearly indicates that *Spo. semiflavus* females deposit eggs that contain a fully developed nymph. One female gave birth three times and two females gave birth twice within a period of 14–27 d (Fig. 1).

Female Reproductive Systems and Embryonic Development

As described by Schneider and Klass (2013), the spermatheca of this species consists of an extremely long, thin, blind duct lacking a capsule at the distal end (Fig. 2B). The spermathecal orifice opens onto a well-developed sclerite, upon which fingerprint-like circular folds surround the spermathecal opening (Fig. 2B, C). Each of the paired

ovaries consisted of about six short ovarioles attached to a highly elongated lateral oviduct (Fig. 2D). Among seven females for which the ovaries were examined, seemingly developing eggs were found in three that were fixed 12–25 d after the initiation of cohabitation with males (= possible occurrence of the first mating) or the deposition of the previous clutch (Fig. 1). The developmental stages of the embryos varied among the females, but not within an individual female, and spanned those with only cleavage nuclei beneath the egg surface to those with already pigmented compound eyes (Fig. 2E). However, there was no apparent relationship between the estimated incubation period and the stage of embryonic development: a female fixed 14 d after giving birth had embryos with fully pigmented eyes in the ovaries (Fig. 2E), whereas a female 25 d after the initiation of pairing with males had embryos with only appendage primordia (Fig. 2F). Similarly, two females that were fixed 12 d after depositing their previous clutch had only undeveloped eggs in the ovaries, as did two females fixed just after deposition of the previous batch of offspring (Fig. 2D). These results indicate high variation in the timing of insemination relative to mating and the deposition of the previous clutch.

Morphology of (Ovo)viviparous and Oviparous Earwig Genitalia

Spongovostox semiflavus male genitalia are greatly elongated, and are ~ 2.3 times the length of the body excluding the forceps (mean length = 16.2 mm, range: 15.8–16.3, $n=3$; Fig. 3A). The virga, which is a heavily sclerotized process containing the terminal part of the ejaculatory duct with the gonopore at the tip, was also elongated along almost the entire length of the genitalia. A similar condition was reported for *M. arachidis* (Fig. 3B; Ramamurthi 1958, Kamimura et al. 2016b). The penis lobe of *M. arachidis* encloses an elongated sclerite, called a virgal guide, which functions as a guiding sheath for the virga to facilitate insertion into the female spermatheca during copulation (Fig. 3G; vgg; Kamimura et al. 2016b). A similarly elongated sclerite with a sharply pointed tip was also found in the penis of *Spo. semiflavus* (Fig. 3F; vgg?). The penis lobe of *M. arachidis* also encloses a pair of triangular sclerites, called genital hooks (Fig. 3G; gh), which securely clamp the opening region of the spermatheca during copulation (Kamimura et al. 2016b). However, only one larger triangular sclerite was detected in the penis lobe of *Spo. semiflavus* (Fig. 3F; gh?). As previously described by Borelli (1932), the parameres (= external parameres) of *Spo. semiflavus* were conspicuously sinuated (Fig. 3F), whereas this structure was simple with a rounded tip in *M. arachidis* (Fig. 3G; Kamimura et al. 2016b).

The male genitalia of *C. borneensis* and *Sph. hawaiiensis* were much shorter than those of *Spo. semiflavus* and *M. arachidis*, which were ~ 33 and 30% of the body length excluding the forceps, respectively (Fig. 3C, D). Nevertheless, the middle part of the genitalia was apparently elongated, as evidenced by the long and slender virga enclosed within the genitalia (Fig. 3H, J). As in *Spo. semiflavus* and *M. arachidis*, the penis lobe of *C. borneensis* encloses an elongated sclerite, which also likely functions as a guiding structure for the elongated virga. However, the tip of the potential virgal guide did not taper but was instead broad (Fig. 3J; vgg?), and was accompanied by a similarly shaped rectangular sclerite (Fig. 3J; rsc). The virga of this species was thin and extremely long with a weakly expanded tip structure (Fig. 3J). In contrast, the elongated virga itself had an enlarged triangular tip with a sharply pointed apex in *Sph. hawaiiensis* (Fig. 3H, I; vg + vgg?). In addition, the penis lobe of *Sph. hawaiiensis* encloses

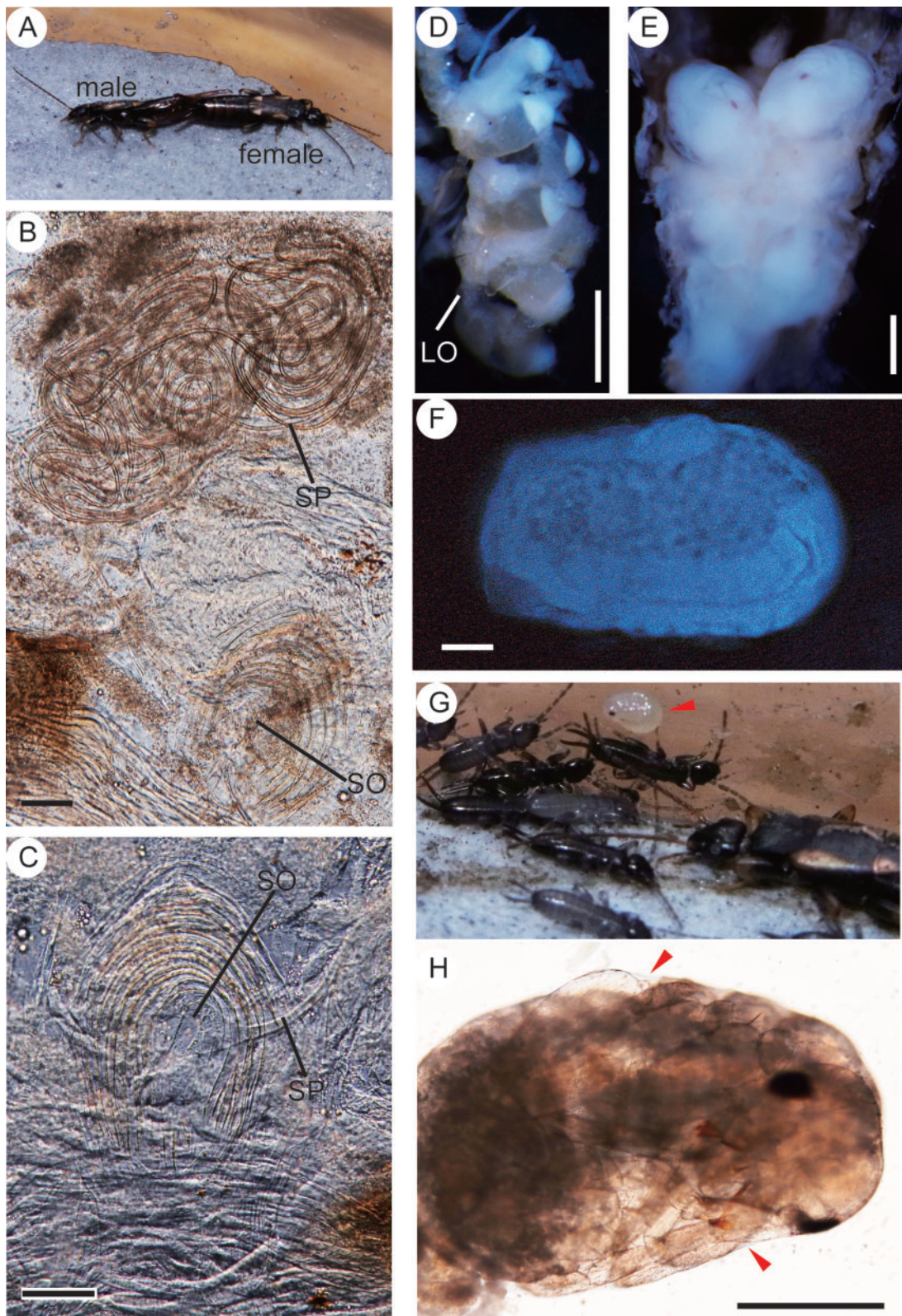


Fig. 2. Mating postures (A), spermatheca (B), spermathecal opening (C), undeveloped eggs (D), and developing embryos (E–F) in the ovaries, a deposited egg surrounded by hatchlings (G), and a fully developed nymph in a deposited egg (H) of *Spongovostox semiflavus*. An egg and the egg envelopes are indicated by red arrowheads in G and H, respectively. Abbreviations: LO, lateral oviduct; SO, spermathecal opening; SP, spermatheca. Scale bars: 500 μ m in D, E, and H; 100 μ m in B, C, and F.

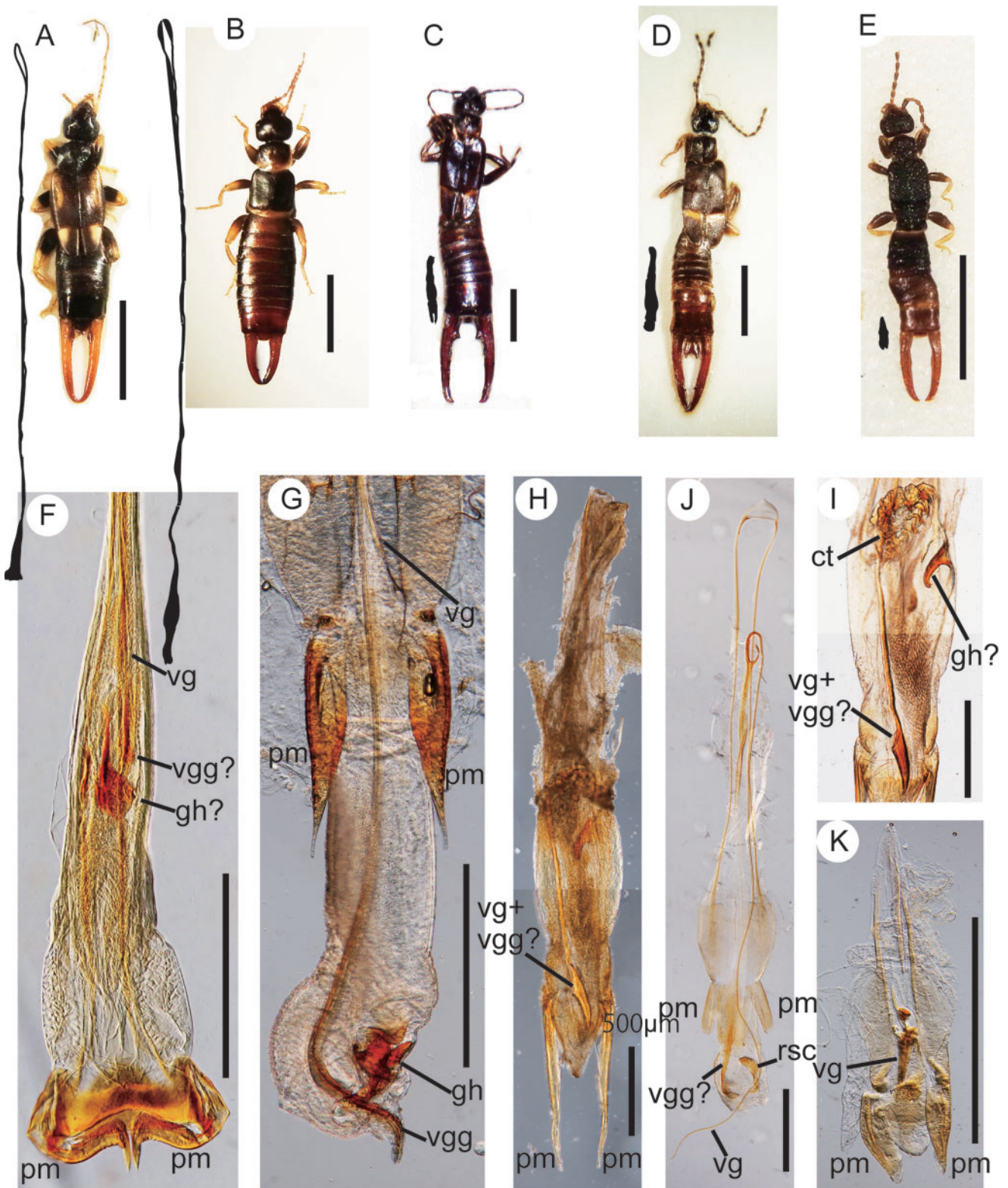


Fig. 3. Male habitus, male genitalia (shown as a silhouette), and an enlarged view of the distal part of the male genitalia of *Spongovostox semiflavus* (A, F), *Marava arachidis* (B, G), *Sphingolabis hawaiiensis* (C, H-I), *Chaetospania borneensis* (D, J), and *Chaetospania anderssoni* (E, K). Abbreviations: ct, crest-like structure; gh, genital hook; pm, paramere; rsc, rectangular sclerite; vg, virga; vgg, virgal guide. Scale bars: 3 mm in A-E, 500 μ m in F-K.

a conspicuous hook-like sclerite (Fig. 3I: gh?) and a crest-like structure that consists of sharply pointed tooth (Fig. 3I: ct). As in *M. arachidis* (Kamimura et al. 2016b), these structures likely function to hold a mate when the penis lobe is everted during

copulation. Interestingly, except for the short virga and simple parameres, we failed to detect any similarly heavily sclerotized structures in the genitalia of the oviparous *C. anderssoni*, which were only about 12% of the body length (Fig. 3E, K).

Discussion

The reproductive biology of *M. arachidis* is the most extensively studied among the (ovo)viviparous free-living earwigs (Herter 1943, Ramamurthi 1956, Patel and Habib 1978, Kamimura et al. 2016b). Although our observations were preliminary and fragmentary, the present study revealed the following characteristics shared by *M. arachidis* and *Spo. semiflavus*. First, in both species, females deposit eggs that contain a fully developed embryo as the birth product. Fully developed eggs are apparently larger than undeveloped eggs (Fig. 2D, E; for *M. arachidis*, compare Fig. 3E and F of Kamimura et al. 2016b). Because such changes in egg dimensions also occur in oviparous earwigs (e.g., Knabke and Grigarick 1971, Shepard et al. 1973, Rankin et al. 1995), this does not mean that continuous nourishment of the eggs after fertilization occurs in the ovaries. The clutch size of these ovoviviparous species is small (fewer than 20; for *M. arachidis*, see Herter 1943) compared with that of oviparous species of a similar body size [for example, in *Nala lividipes* (Dufour, 1829), generally >30 (Situmorang and Gabriel 1988) and in *Euborellia* Burr, 1910 spp., at least 20 and usually >30 (Knabke and Grigarick 1971, Situmorang and Gabriel 1988, Jamet and Caussanel 1995, Rankin et al. 1995, Kamimura 2003)], possibly to enable the retention of large eggs within the body. Females of *Sph. hawaiiensis* also show a reduced fecundity, but deposit offspring one at a time over a prolonged time period (37 nymphs over 72 d, Marucci 1955; 26 nymphs over 28 d, Matzke 2011). Although embryos of varying developmental stages were observed in a single female of both *C. borneensis* (Kočárek 2009) and *Sph. hawaiiensis* (Matzke 2011), synchronized development of offspring seems to be the norm in *M. arachidis* (Kamimura et al. 2016b) and *Spo. semiflavus* (this study). This results in the deposition of the whole batch of fully deposited eggs within a relatively short time frame. In *Spo. semiflavus*, ovarioles are greatly shortened and contain only one developing egg in the basal-most part at a time. Similar conditions were reported for *C. borneensis* (Bilinski et al. 2014). For *M. arachidis*, Ramamurthi (1956) reported that each ovary has a single ovariole. However, we observed that the ovaries of this species are essentially configured like those of *Spo. semiflavus* and *C. borneensis* (Y. K., unpublished data). Bilinski et al. (2014) found the opposite ovarian structure (i.e., longer ovarioles attached to shorter lateral oviducts) in *Irdex chapmani* Brindle, 1980 (Spongiphoridae: Spongiphorinae). The discovery of *C. borneensis*-type ovaries in two ovoviviparous spongiphorine earwigs strongly supports their apparent adaptation for the retention of large-sized eggs and ovarian fertilization, similar to a specialized lateral oviduct wall for the passing of large, fully developed eggs (Tworzydło 2015).

The spermathecal structure, which consists of a long blind tube that lacks internal branches and a terminal sclerotized capsule (Fig. 2B), and fingerprint-like, concentric circular folds around the spermathecal opening (Fig. 2C), are also shared by *Spo. semiflavus* and *M. arachidis* (Schneider and Klass 2013, Kamimura et al. 2016b). This indicates a very close relationship between these two spongiphorine earwigs. Similar folds around the spermathecal opening have also been reported for *Spo. mucronatus* (Stål, 1860), a congener of *Spo. semiflavus* (Kamimura et al. 2016a). However, males of this species possess relatively short genitalia (Steinmann 1990, Sakai 1992, Y. Kamimura, unpublished data), and the birth product is presently unknown for this species and the subfamily Spongiphorinae in general. Further studies of the reproductive biology and phylogeny of this group are needed.

Females of *M. arachidis* remove the egg envelopes of newly deposited eggs using their mouthparts (Herter 1943, Patel and Habib

1978). It is presently unclear whether this maternal assistance is required for nymphs to hatch (Costa 2006). For *Sph. hawaiiensis*, Marucci (1955) observed "a round object" that was expelled from a female's body. The female picked it up with her mouthparts, apparently removing "a very thin membrane" surrounding the nymph. Matzke (2011) also observed that females immediately treat newly deposited nymphs with their mouthparts so that curled nymphs are stretched out. Therefore, maternal hatching assistance is likely also shared by this species, which belongs to the subfamily Labiinae. In this study, we were not able to observe the hatching process of *Spo. semiflavus*, including that of the eggs that were removed from the mother for observation.

Spongovostox semiflavus and *M. arachidis* differ in courtship and mating initiation behaviors. Males of *M. arachidis* coerce females into mating by grabbing the female's antenna with their mouthparts (Herter 1943, Kamimura et al. 2016b). A similar mating sequence has been reported for only one other related earwig species, *Pseudomarava prominens* Steinmann, 1990 (Briceno and Eberhard 1995). In contrast, male *Spo. semiflavus* did not exhibit any signs of this type of behavior. In *Spo. semiflavus*, as in many other earwig species, female quiescence seems to be necessary for males to establish genital coupling (Kamimura 2014). During *M. arachidis* copulation, a pair of sclerites (genital hooks) in the male penis lobe pinches the membranous region near the spermathecal opening, frequently resulting in copulatory wounding (Kamimura et al. 2016b). In *Spo. semiflavus*, the male genitalia contain a single, but larger, triangular sclerite. Together with the conspicuously sinuated parameres, this structure likely functions to hold the female during mating. Examination of additional female samples is required to determine whether these structures also cause copulatory wounding. An elongated sclerite, which possibly functions like a virgal guide of *M. arachidis*, is also present in *Spo. semiflavus* and *C. borneensis*, but not in *Sph. hawaiiensis*. Interestingly, the tip of the virga itself seems to be enlarged (or completely fused with a large sclerite) in *Sph. hawaiiensis*. The lack of spermatheca in the females of this species (see below) may be the cause of this difference in the male genitalia.

Despite these species-specific differences, all four species are characterized by elongated male genitalia, which are ~30–250% of the body length. The families Spongiphoridae, Chelisochidae, and Forficulidae are characterized by a single intromittent organ (= single virga), and the male genitalia are generally short. In contrast, males possess elongated virgae in many species within the family Anisolabididae (e.g., Kamimura 2000, van Lieshout and Elgar 2011). In this group the virgae are paired, and thus one of them can be used as a spare intromittent organ if the other is broken during copulation (Kamimura and Matsuo 2001). The long and thin virga of *M. arachidis* also sometimes breaks during copulation, but remains functional even after the loss of the tip structure (Kamimura et al. 2016b). These features indicate a strong selection pressure for genital elongation associated with the evolution of (ovo)viviparity. One possible explanation for this is that the elongated male genitalia are directly inserted into the ovaries (or oviducts) to deliver sperm. However, in *M. arachidis*, the elongated virga was observed being inserted into the long spermatheca instead of the ovaries (Kamimura et al. 2016b). Surgical removal of the spermatheca resulted in failed offspring production in this species, which clearly demonstrates that sperm migrate from the spermatheca to the ovaries, where egg fertilization occurs (Kamimura et al. 2016b). The insemination and fertilization processes for *Spo. semiflavus* are presently unknown, although fertilization apparently occurs in the ovaries as in

M. arachidis, *C. borneensis*, and *Sph. hawaiiensis*. However, the retention of a well-developed spermatheca in *Spo. semiflavus* suggests that this organ is used to store sperm until needed for fertilization. In contrast, *Sph. hawaiiensis* females completely lack a spermatheca (Schneider and Klass 2013), which indicates the direct deposition of sperm into the ovaries or oviducts in this species. The spermathecal structure is presently unknown for *C. borneensis*. Thus, delivering sperm to the ovaries cannot be the sole explanatory factor for genital elongation in (ovo)viviparous earwigs.

Alternatively, (ovo)viviparous females are thought to have greater opportunity and potential mechanisms for biasing paternity after mating with multiple males, because of the prolonged interaction between a mother and the developing embryos within the mother's body (cryptic female choice: Eberhard 1996, Zeh and Zeh 2001). Males may use their elongated genitalia to stimulate their mate to increase the likelihood of successful paternity. However, the available literature indicates that the male genitalia of both Arixeniidae and Hemimeridae, which show elaborate adaptations for viviparity (see Introduction), are not very elongated (Nakata and Maa 1974). Unfortunately, no information is presently available for the birth products of any congeners of *Spo. semiflavus*, *Sph. hawaiiensis*, and *M. arachidis*. In addition, only one oviparous species of genus *Chaetospania* was available for the present study, which renders our comparison quite preliminary. Additional reproductive biology studies are clearly warranted for many more species of earwigs.

Acknowledgments

This study was partially supported by a Keio Gijuku Academic Development Fund grant from Keio University and JSPS KAKENHI Grant 15K07133 to Y.K. We thank M. Nishikawa for specimen identification, D.V. Logunov for allowing us to examine specimens of *Sphingolabis hawaiiensis* preserved in the Manchester Museum, D. Matzke for providing valuable information on the biology of *Sph. hawaiiensis*, and two anonymous reviewers for useful comments on a previous version of the manuscript.

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