

# Genital morphology and mating behaviour of *Allostethus* (Dermaptera), an earwig genus of enigmatic phylogenetic position

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## Abstract

In the suborder Forficulina (order Dermaptera; earwigs), the families Apachyidae, Anisolabididae, and Labiduridae form a possibly paraphyletic assemblage Mesodermaptera, which is characterized by laterally paired penes that point in opposite directions (anterior and posterior) when in repose. A previous study of a labidurid species, *Labidura riparia* (Pallas, 1773), revealed that males predominantly use the right penis for insemination, although both penes are functional. This result suggests that labidurids may have retained handedness in penis use, leading eventually to the loss of the less frequently used left penis in the common ancestor of the Eudermaptera, estimated to be the sister clade of Labiduridae. However, HAAS & KUKALOVA-PECK (2001: European Journal of Entomology 98: 445–509) included another representative of Labiduridae, *Allostethus indicum* (Burmeister, 1838) (Allostethinae) in their extensive phylogenetic analysis, and found that hindwing structures of this species showed multiple plesiomorphic characteristics, making Labiduridae (sensu lato) a polyphyletic assemblage. The aim of the present study was to describe the genital structures and copulation of *A. indicum* in detail. The genital morphologies of a congener and other labidurid genera (*Nala*, *Labidura*, *Forcipula*) were also examined for comparison. Male *A. indicum* predominantly used (or were ready to use) the right penis for insemination, as in *L. riparia*. However, the possible female genital structure responsible for this handedness differed between the two species: the base of the spermatheca showed a striking spiral in *L. riparia*, while the spermatheca opened to an asymmetrically arranged vagina in *Allostethus*. Female *Allostethus* also possessed a pair of elongated thin tubes, which have to date been reported only for the basal groups of earwigs, as well as the vagina and the internally branched spermatheca. The developmental origin of an ovipositor-like structure also differs between *Allostethus* and the other labidurids examined, lending support to the polyphyly of Labiduridae sensu lato.

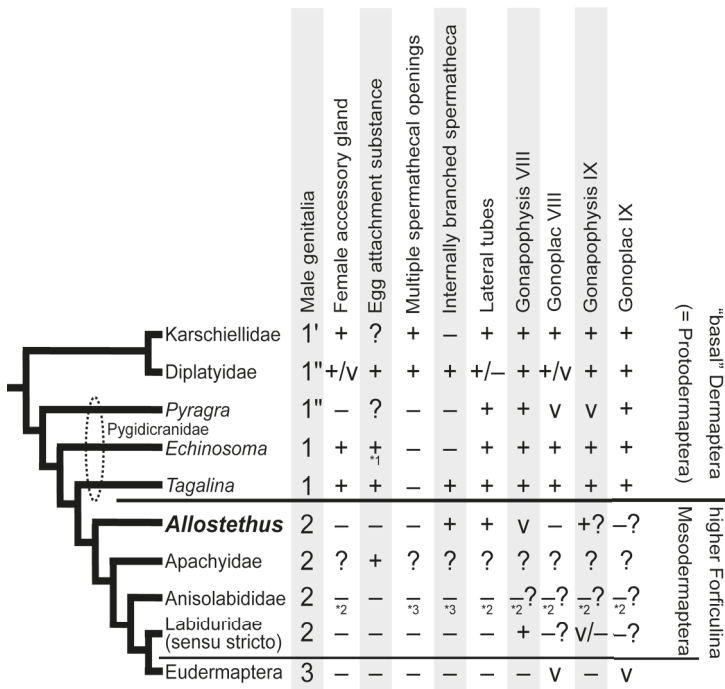
## Key words

Labiduridae, evolution of laterality, dermapteran phylogeny, genital evolution, mating behaviour, cryptic female choice.

## 1. Introduction

Dermaptera (earwigs) is a polyneopteran insect order with ~2200 described species from mainly tropical and warm temperate regions (POPHAM 2000; GRIMALDI & ENGEL 2005; HAAS et al. 2012). The order is generally and conveniently subdivided into three taxa: Hemimerina, Arixeniina, and Forficulina. Forficulina comprises typical free-living earwigs, while members of the former two taxa live on mammals [hamster rats (*Cricetomys* spp.)

in Africa and bats (*Cheiromeles torquatus* Horsfield) in Asia, respectively] and show many adaptations to their phoretic-epizoic lifestyle (NAKATA & MAA 1974). Several studies have suggested that both Hemimerina and Arixeniina are in-group members of Forficulina (KLASS 2001; HAAS & KLASS 2003; JARVIS et al. 2005; TWORZYDLO et al. 2012; KOCAREK et al. 2013). Their phylogenetic placements in Forficulina are not settled, but a recent study sug-



**Fig. 1.** The most elaborate phylogenetic hypothesis for the Forficulina (modified from HAAS & KUKALOVÁ-PECK 2001 and HAAS & KLASS 2003) with the characteristics of the reproductive morphologies of each group. Although HAAS & KUKALOVÁ-PECK (2001) originally proposed that Karschiellidae is the first offshoot of the present Dermaptera, while paraphyletic Diplatyidae is basal-most to the other extant Forficulina, subsequent detailed examination of female genitalia by KLASS (2003) supported the monophyly of two taxa, Diplatyidae (*Haplodiplatys* and *Diplatys*) and Karschiellidae + Diplatyidae (HAAS & KLASS 2003). For Pygidicranidae, only genera with estimated phylogenetic positions are shown. Information of the character states is from the results of the present study and the following references: KLASS (2003); KAMIMURA (2004a, 2007); MATZKE & KLASS (2005); COSTA (2006); SHIMIZU & MACHIDA (2011a,b); SCHNEIDER & KLASS (2013); KAMIMURA & LEE (2014). \*1, Y. Kamimura, pers. obs. for *Echinosophoma denticulatum*. \*2, Y. Kamimura, pers. obs. for *Anisolabis maritima* (Bonelli, 1832) and *Euborellia plebeja* (Dohrn, 1863). \*3, cf. POPHAM (1965a), see text for details.

gests that Hemimerina and Arixeniina are sister groups of Forficulidae and Chelisochidae, respectively (KOCAREK et al. 2013). STEINMANN (1986, 1989a,b, 1990, 1993) further divided Forficulina into three groups: Protodermaptera (families Pygidicranidae, Diplatyidae, and Karschiellidae), Mesodermaptera (families Anisolabididae, Apachyidae, and Labiduridae), and Eudermaptera (families Spongiphoridae, Chelisochidae, and Forficulidae). Protodermaptera is more often referred to as the “basal” Dermaptera, and members retain many primitive characteristics, such as blattoid-type necks, segmented cerci in nymphal stages of some groups, and well-developed ovipositor components in the female genitalia (GILES 1963; POPHAM 1965a; KLASS 2003; SHIMIZU & MACHIDA 2011b; HAAS et al. 2012). Mesodermaptera and Eudermaptera comprise the “higher Forficulina”. Although the phylogenetic relationships among forficuline families have not been resolved, previous studies based on morphological and/or molecular traits support the monophyly of Eudermaptera (SAKAI 1987; HAAS 1995; HAAS & KUKALOVÁ-PECK 2001; HAAS & KLASS 2003; COLGAN et al. 2003; KAMIMURA 2004b; cf. JARVIS et al. 2005; KOCAREK et al. 2013) and higher Forficulina (SAKAI 1987; POPHAM 1985; HAAS 1995; HAAS & KUKALOVÁ-PECK 2001; HAAS & KLASS 2003; JARVIS et al. 2005; KOCAREK et al. 2013), while the “basal” Dermaptera and Mesodermaptera are likely paraphyletic (Fig. 1).

One major problem in estimating the phylogenetic relationships among taxonomic assemblages is insufficient sampling of representative species from each group. Increases in the number of sampled taxa often reveal polyphyly or paraphyly of an assemblage that had previously been believed to be monophyletic. Inclusion of the genus *Allostethus* Verhoeff, 1904 in their extensive cladistic analysis by HAAS & KUKALOVÁ-PECK (2001) is such an

example. *Allostethus* is a relatively small genus with only about 10 named species of medium-sized to large earwigs from the Oriental region (STEINMANN 1989a). With two other genera, *Gonolabidura* Zacher, 1910 and *Allostethella* Zacher, 1910, this genus comprises Allostethinae, a subfamily of the family Labiduridae (BRINDLE 1965; POPHAM 1965b; SAKAI 1982; STEINMANN 1989a). The subfamily Allostethinae is defined by the peculiarly shaped thoracic mesosternum, which is normal in the anterior portion, but towards the metasternum distinctively narrows to about one-half of the width of its anterior end (BRINDLE 1965; POPHAM 1965b; STEINMANN 1989a). Before HAAS & KUKALOVÁ-PECK (2001) included *Allostethus indicum* (Burmeister, 1838) in their phylogenetic analysis, the general characteristics of Labiduridae were used to reconstruct dermapteran phylogeny (e.g., SAKAI 1987; HAAS 1995; POPHAM 2000). Moreover, more recent studies based on molecular and/or morphological data included only one to several members of two other subfamilies as representatives of Labiduridae: Nalinae (genus *Nala*) and Labidurinae (genera *Labidura* and *Forcipula*) (e.g., KAMIMURA 2004b; COLGAN et al. 2004; JARVIS et al. 2005; KOCAREK et al. 2013). However, based on their detailed examination of wing structures, HAAS & KUKALOVÁ-PECK (2001) revealed that hindwing structures of *A. indicum* show multiple plesiomorphic characteristics (such as the anojugal fulcalare with an almost elliptical head, a narrow neck and a broad and weakly sclerotized tail, and the third anal anterior positioned far from the anal anterior 1+2 basivenale), resulting in the placement of this genus as the basal-most taxon of paraphyletic Mesodermaptera. In the phylogeny estimated by HAAS & KUKALOVÁ-PECK (2001), Apachyidae and Anisolabididae are the second and third offshoots of Mesodermaptera, respectively, while “Labiduridae” except for *Allostethus* (henceforth,

Labiduridae sensu stricto, including *Forcipula*, *Labidura*, and *Nala*) is the sister clade of monophyletic Eudermaptera (Fig. 1). Thus, “Labiduridae” sensu BRINDLE (1965), POPHAM (1965b), SAKAI (1982), and STEINMANN (1989a), which includes Allostethinae (henceforth, Labiduridae sensu lato), is likely a polyphyletic assemblage (Fig. 1). In HAAS & KUKALOVÁ-PECK’S (2001) analysis, only two traits – bidirectionally pointing penes in repose and the anterior margin of hindwing fustis with embayment – support the monophyly of Mesodermaptera + Eudermaptera. These character states change again at the base of the monophyletic Eudermaptera, showing that Mesodermaptera can be only defined as a paraphyletic assemblage by plesiomorphic character states (HAAS & KUKALOVÁ-PECK 2001).

In taxonomic studies of insects, male genital traits usually receive special attention because of their extremely rapid divergence among species (EBERHARD 1985). Dermaptera is no exception: male genital traits are used not only in diagnoses among closely related species but also in the higher classification of this order. Males of all Dermaptera have a genital (phallic) organ placed, at the midline of the body, in the reflected membrane above the coxosternum of abdominal segment IX (subgenital plate). In six families, the genitalic organ includes a pair of penes, with few exceptions (in this paper, the terminologies of KLASS 2003 and KAMIMURA 2014 are followed for female and male genital structures, respectively). Among the “basal” dermapteran families (Karschiellidae, Pygidicranidae, and Diplatyidae), the right and left penes are symmetrical in Pygidicranidae and Diplatyidae, both pointing to the head when not in copulation, whereas in Karschiellidae the left penis is strongly reduced (e.g., STEINMANN 1986). In Mesodermaptera, penes are asymmetric when in repose: the left and right penes point in opposite directions (e.g., POPHAM 1965a; STEINMANN 1989a; KAMIMURA & MATSUI 2001; KAMIMURA 2006). The members of Eudermaptera have only one penis without exception (STEINMANN 1990, 1993), as do the phoretic earwigs (Hemimerina and Arixeniina; NAKATA & MAA 1974). Importantly, however, in these taxa (Eudermaptera, Hemimerina, and Arixeniina) either the ejaculatory ducts and gonopores are still paired, or there is at least some reminiscence of a formerly paired condition with the presence of a vestigial ejaculatory duct on the non-functional side (e.g., SNODGRASS 1959: fig. 4H,I; POPHAM 1965a: fig. 4; KAMIMURA 2006: fig. 3C, table 4).

In contrast, taxonomists rarely include the morphology of female genitalia in descriptions of earwig species. However, female genital characteristics are being increasingly recognized to contain important information for phylogenetic studies of earwigs (KLASS 2001, 2003; SCHNEIDER & KLASS 2013). Female and male genital structures of animals often coevolve, and various forms of sexual selection (including sexual conflict) have been proposed as the underlying driving force(s) of the coevolution (see KAMIMURA 2014 for a review of studies on Dermaptera). Female genital structures, in-

cluding the components of ovipositors and accessory glands, also likely coevolve with the site and mode of oviposition. Despite their potential importance for determining the phylogeny of earwigs, the female genital structures and related reproductive biology of any member of the subfamily Allostethinae have not been studied.

In this study, we describe the genital structures and copulation of *Allostethus indicum* in detail for the first time. Based on additional samples, the male and female genitalia of *Allostethus burri* Brindle, 1965 are also reported. For comparative purposes, the female genitalic regions of three other labidurids are described briefly. Based on the results, we discuss the placement of this enigmatic genus in dermapteran phylogeny.

## 2. Materials and methods

### 2.1. Insects, rearing, and morphological observations

One male, 8 females, and about 30 nymphs of *A. indicum* were collected from forest areas of various locations in Penang Island (05°30'N 100°28'E), Malaysia, during April–November 2012. Field-collected adults were placed individually in separate plastic vessels (60 mm diameter, 40 mm height) with plaster of Paris at the base and stored at 26±1°C (12 h photoperiod). All animals were provided with water, unlimited amounts of commercial cat food, and a small piece of peeled tree bark for harbourage. Nymphs (field-collected and laboratory-raised) were kept in groups in larger vessels (110 mm diameter, 100 mm height) of a similar style, and checked for imaginal eclosion every 3 days. Laboratory-raised virgins of both sexes (3–40 days old; including F1 generation) were used for the various types of observation and experiments described below. All of the following observations and experiments were conducted under the same laboratory conditions. For later observations of male and female genital morphologies, the samples used in the following experiments or that died during rearing were preserved in a freezer (–20°C).

As additional samples for morphological observations, frozen-preserved specimens (four males and four females) of *A. indicum*, collected in Tapah Hill, Perak, Malaysia in February 2012, were obtained from a dealer in insect specimens. A male and a female of *Allostethus burri*, which were collected in Gunung Bringcahng, Cameron Highlands, Pahang, Malaysia on April 8, 2012, and Tanah Rata, Cameron Highlands, Pahang, Malaysia on July 11, 2012, respectively, were also examined regarding genital morphology.

For morphological observations, genitalia were dissected from male and female individuals in insect Ringer solution (0.9 g NaCl, 0.02 g CaCl<sub>2</sub>, 0.02 g KCl and 0.02 g NaHCO<sub>3</sub> in 100 ml water) under a stereomicroscope (EZ

vision, Saxon, Guangzhou, China), and then examined under light microscopes (BX53 and CX21, Olympus, Tokyo;  $\times 40$ –400). Several samples of the female genitalia were also observed using fluorescence microscopy (ECLIPSE 80i; Nikon, Tokyo, Japan) with a UV filter set (excitation, 330–385 nm; dichroic mirror,  $> 400$  nm; absorbance filter,  $> 420$  nm) without staining.

For comparison, the female genitalia were examined under the light and stereo microscopes for following three labidurid species belonging to two other subfamilies of Labiduridae: *Labidura riparia* (Pallas, 1773) (Labidurinae:  $n = 11$ , Penang Island, Malaysia, May–November, 2012;  $n = 17$ , Malacca, Malaysia, August 2012;  $n = 12$ , Cameron Highlands, Malaysia, April–July, 2012;  $n = 12$ , Ishikari, Japan, June 2005;  $n = 13$ , Miyazaki, Japan, October 2005), *Forcipula quadrispinosa* (Dohrn, 1863) (Labidurinae:  $n = 1$ , Chiang Mai, Thailand, November 2004;  $n = 1$ , Doi Inthanon, Thailand, February 2005), and *Nala lidivipes* (Dufour, 1829) (Nalinae:  $n = 3$ , offspring of two females collected at Ishigaki Island, Japan, June 2005). The samples of *L. riparia* were also examined under the fluorescence microscope (for the Malaysian populations) or a confocal laser-scanning microscope (LSM-410 CLSM, Zeiss, Oberkochen, Germany; for the Japanese populations).

## 2.2. Courtship and mating behaviour

To observe courtship and mating behaviour, a virgin male (but in one case, a field-collected male of unknown age) and a virgin female were introduced into a mating arena (identical to the small rearing vessel but without harbourage) with a transparent plastic lid. To avoid possible detrimental effects of inbreeding, pairing of a male and a female derived from the same female was carefully avoided. Their behaviour was recorded for 2.25–49 hours with a video camera (GZ-MG980S; Victor, Kanagawa, Japan) using a time-lapse recording function (one frame per 2 s). Observations in dark periods (19:00–07:00 hours) were conducted under a dim red light. One or two pairs were observed simultaneously. Because of the limitation in the number of video recorders, the starting time, ending time, and duration of video recording varied according to the schedule of other experiments. After video recording, the males were euthanized by placing them in a freezer, and then dissected under the stereo microscope to record the asymmetry in the bidirectionally pointing penes: R-ready, the right penis is directed posteriorly and the left penis is deflected to the anterior, or L-ready, the opposite condition. The females were reared individually for 2 months to produce offspring, and then preserved in the freezer for later examination of insemination status. In total, 11 pairs were observed, of which one pair with no mating was removed from the subsequent analyses. Because the forceps are located at the caudal end and male and female genitalia are located on the ventral side of the abdomen, male earwigs usually rotate their abdo-

men nearly 180° around the anterior-posterior axis, and walk backwards to establish an end-to-end copulation posture. The direction of this abdominal rotation was recorded for each copulation following the definition of KAMIMURA (2006) and KAMIMURA & LEE (2014): clockwise (CW) or counterclockwise (CCW), as viewed from the head of the male (see Fig. 2A for an example of CCW rotation).

## 2.3. Genital coupling

To study the genital coupling during copulation, adult pairs were released into a mating arena (see 2.2.). Then, 10 min after the initiation of copulation, the mating pairs were fixed instantaneously by pouring liquid nitrogen into the vessel. These samples were later dissected to observe the genital coupling and to determine which penis had been used for insemination. The male mating posture (direction of abdominal rotation: see 2.2.) was also recorded. All statistical analyses of the data were conducted using the 'R' software (Version 3.0.1; R CORE TEAM 2013).

## 3. Results

### 3.1. Male genitalia

In male earwigs, sperm are produced in a pair of testes and then transferred to a spherical seminal vesicle for storage. In the groups with paired penes, two independent ejaculatory ducts lead from the seminal vesicle to the male genitalia (sensu stricto: phallic organs), which are located in the reflected membrane above the coxosternum of abdominal segment IX (subgenital plate). These features, shared by members of Mesodermaptera, as well as bidirectionally pointing penes (the definitive characteristic of this assemblage: STEINMANN 1989a), were also observed for *A. indicum* and *A. burri* (Table 1). As an exception, one male of *A. indicum* had two penes both reflected to the anterior (see 3.3.). As described in STEINMANN (1989a), each penis bears a club-shaped virga, which is a heavily sclerotized process containing the terminal part of the ejaculatory duct and has the gonopore on its tip (Fig. 2C). Overall, males were significantly biased towards R-ready (Table 1), despite the lack of any apparent morphological difference between the right and left penis lobes or virgae. This trend was observed for each locality (Tapah Hill and Penang), although the trend was not significant for the former locality because of the small sample size (Table 1). In *L. riparia*, which predominantly use the right penis for copulation, damaged right penes or virgae were observed frequently in irregularly left-handed males (KAMIMURA 2006). In this study, no such genital damage was noted in our *Allostethus* samples.

**Table 1.** Laterality of paired penes in male *Allostethus* spp. \*Binomial test with the null hypothesis that the ratio of R-ready to L-ready males is 1 : 1.

Species	Locality	R-used/R-ready	L-used/L-ready	P*
<i>Allostethus indicum</i>	Penang	13	4	0.0490
	Tapah	3	1	—
	Subtotal	16	5	0.0266
<i>Allostethus burri</i>	Gunung Brinchang	1	0	—
	Total	17	5	0.0169

### 3.2. Female genitalia

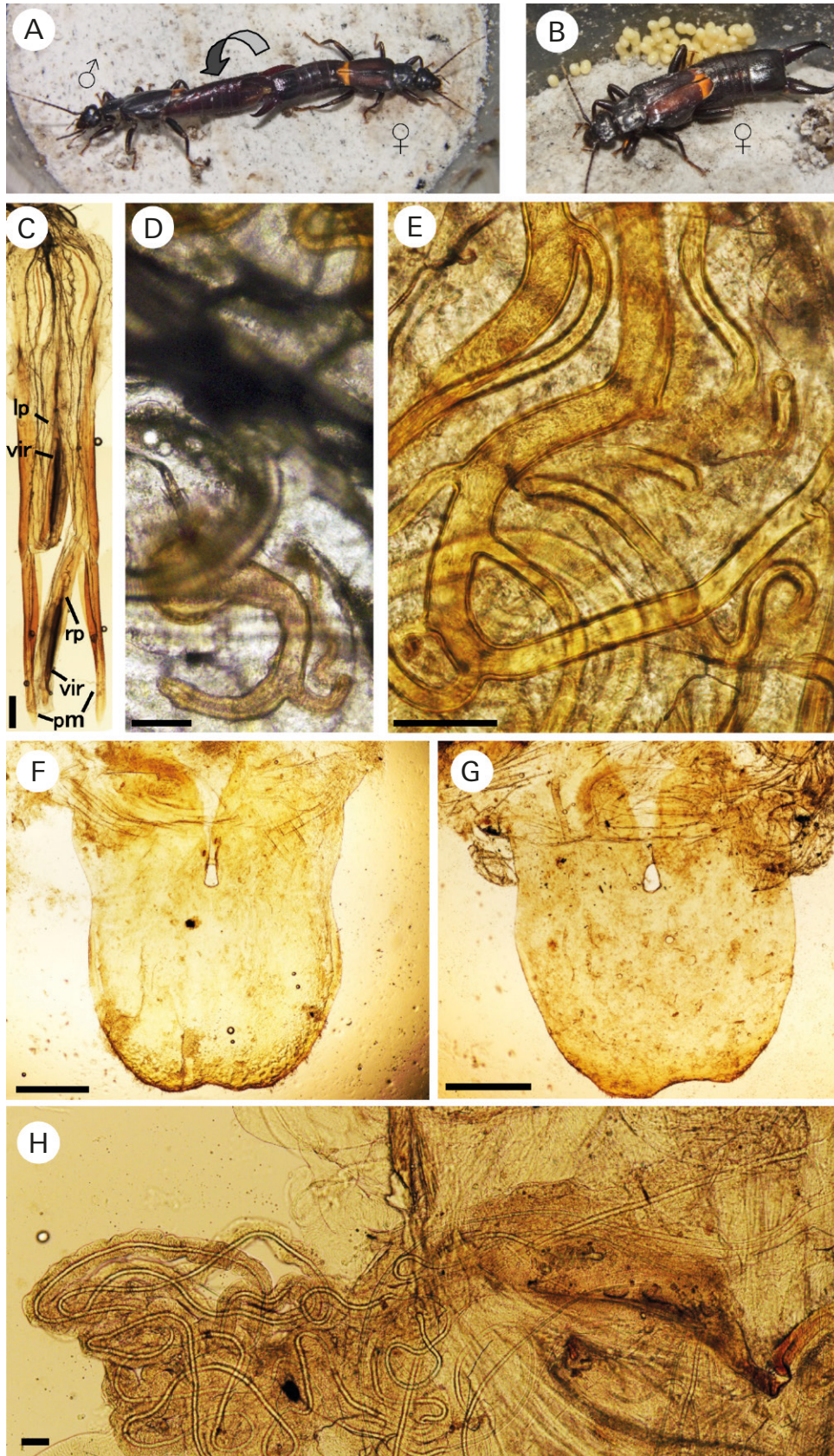
The female genitalia of *Allostethus* spp. were characterized by a large, conspicuous, posteriorly pointing lobe, of which both the dorsal and ventral surfaces were heavily sclerotized (referred to as the ovipositor-like projection). This lobe was located dorsal to the subgenital plate, with its tip almost reaching the anus (Fig. 3A). Usually, a small hole or a slit penetrates the entire lobe from dorsal to ventral at the midline (Figs. 2F,G, 3A), indicating that this structure is generated by fusion of the distal part of laterally paired primordia. The base of the plate was located upon abdominal segment IX. Gonoplacs [= coxal lobes] (gl) and gonapophyses (gp) of abdominal segments VIII and IX represent the major components of the ovipositor in many insect taxa, including basal Dermaptera (KLASS 2003). Judging from the location, the ovipositor-like projection is likely derived from the ninth segmental gonoplacs (gl9) and/or gonapophysis (gp9). Females of the other labidurid species (sensu lato) examined in this study (*Nala*, *Labidura*, and *Forcipula*) also possessed a well-developed ovipositor-like projection consisting of a pair of triangular lobes (Figs. 3B–D, 4C). In *Nala* and *Forcipula*, the paired lobes were close together but not fused (Fig. 3B,D). In *Labidura* the inner edges of the left and right lobes were fused together for almost their entire length, and a groove extends along the ventral midline of projection and reaches the spermathecal opening anteriorly (Figs. 3C, 4C); the larger posterior part of the groove may represent the fusion line of the lobes of the two sides. However, the ovipositor-like projections of these genera are located at the hind margin of abdominal segment VIII. The outer margin of the lobe was well-pigmented, indicating heavy sclerotization, and the pigmented area continued brokenly to under the laterally adjoining sclerites (3B–D, 4C). These structures are directly comparable to the eighth segmental gonapophysis (gp8) and laterocoxa IX (LC9) of the basal Dermaptera (for example, compare Fig. 3B–D with fig. 2 of KLASS 2003). In *Labidura*, many muscles originated from the laterally adjoining sclerite like LC9 of *Dacnodes* sp. (Pygidicranidae) studied by KLASS 2003 (Y. Kamimura, personal observation). However, this assignment is tentative and coxa VIII (CX8) is a likely alternative. At the hind margin of the segment VIII, similar structures with conspicuous pigmentation were also observed in the females of *Allostethus* (Figs. 3A, 4A), but possible gp8 was much reduced and vestigial. This finding supports the

view that the ovipositor-like projection of *Allostethus*, as a component of ninth segment, is not homologous to the eighth segmental ovipositor-like projection of the other labidurids. Interestingly, in *Nala* and *Labidura*, a pair of tiny, unpigmented, but distinctive projections were found hidden dorsally under gp8 (Fig. 3B,C). These structures likely represent the vestiges of gp9.

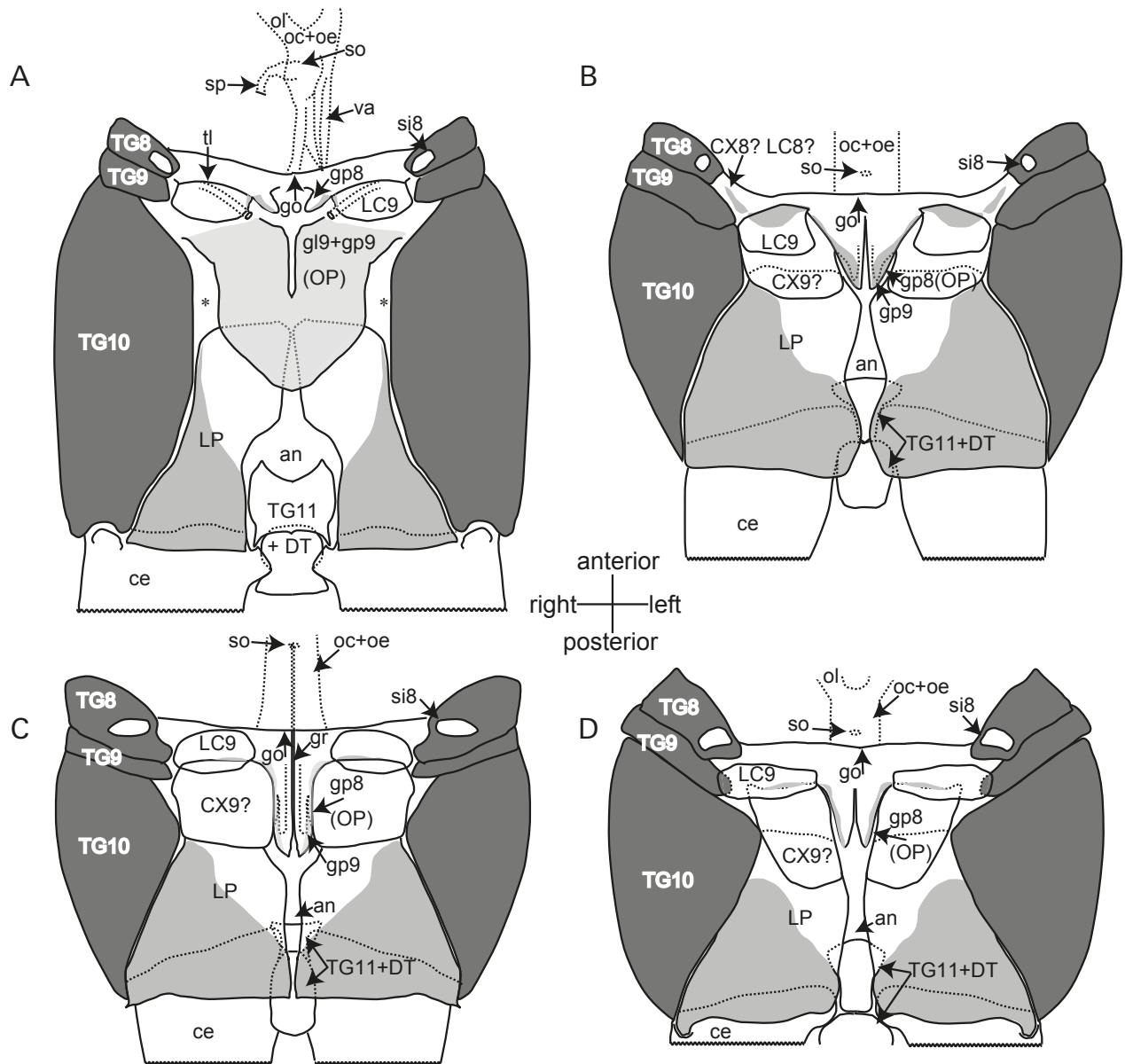
Except for two samples from Penang in poor condition, the females of *Allostethus* spp. examined in this study possessed a pair of very long, delicate blind tubes at the base of the ovipositor-like projection ( $n = 24$  in total; Figs. 2H, 3A). Based on the morphological characteristics and their locations relative to the other female genital components, these tubes were identified as the lateral tubes, which have been reported for almost all members of the basal Dermaptera studied to date (KLASS 2003; see Discussion). The lateral tubes of *Allostethus* spp. usually lacked internal branching. Of 23 samples of *A. indicum* examined for this aspect, in only four (two from Penang and two from Tapah Hill) we detected that one of the paired lateral tubes was bifurcated.

The observed position of the gonopore and the spermatheca did not vary among the members of Labiduridae sensu stricto: the ventral lip of the gonopore represents the opening of the gonoduct at the hind margin of the segment VII, while the spermathecae are located at the dorsal side of the gonoduct in the middle of segment VII (Figs. 3B–D, 4C). The spermatheca is genuinely an element of segment VIII, and thus this observed condition suggests expansion of the area bearing the spermathecal opening towards the anterior to form the dorsal wall of the gonoduct. In contrast, the membrane flanking the intersegmental region VII–VIII (apparently of ectodermal origin) of *Allostethus* invaginates into the segment VII to form a vagina (enlarged terminal part of the gonoduct), which has the spermathecal opening and the opening of the common oviduct at the latero-dorsal and anterior sides, respectively. The vagina of *Allostethus* is located at left side of the midline of the body with some conspicuous folding (Figs. 3A, 4A,B).

The morphology of the spermatheca itself also varies between *Allostethus* and the other labidurids (sensu stricto) studied here. Although the sample sizes for *Nala* and *Forcipula* were small ( $n = 3$  and 2, respectively), females of these genera had a single, tubular spermatheca without internal branching, as in *Labidura*. The proximal part of the spermatheca of *Labidura* showed a characteristic sinistral spiral (Fig. 4C; among 65 females examined in



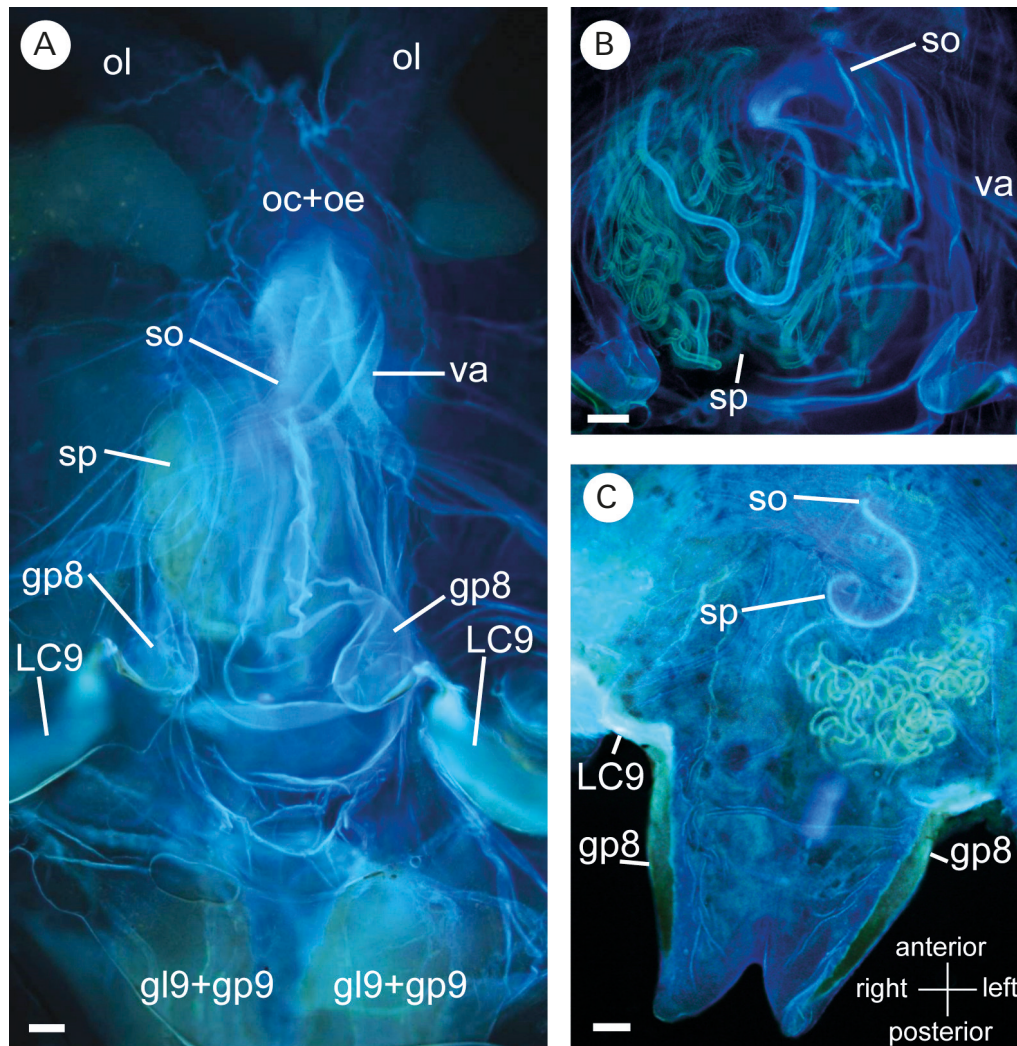
**Fig. 2.** Mating posture (A), a female caring for eggs (B), male genitalia (C) and female genital structures (D–H) of *Allostethus indicum*. (A) Mating posture. The male (left) has the abdomen twisted in a counterclockwise (CCW) direction (indicated by the gray curved arrow) to establish genital coupling with the female (right). (B) A female caring her for eggs. Females sometime relocate eggs. (C) Male genitalia, entire view dorsally; right penis (rp) points posteriorly. (D) A spermatheca-like structure, possibly formed by malformation. (E) Part of the spermatheca with many branches. (F,G) Examples of the ovipositor-like projection. (H) Lateral tubes (tl). — Abbreviations: lp, left penis; pm, paramere; rp, right penis; vir, virga. Scale bars: 400  $\mu$ m in C, F, G, 50  $\mu$ m in D, E, H.



**Fig. 3.** Schematic drawings of the female genitalia of Labiduridae sensu lato. (A) *Allostethus indicum*. (B) *Nala livivipes*. (C) *Labidura riparia*. (D) *Forcipula quadrispinosa*. Cerci, lateral tubes, lateral or common oviducts cut near the base. Whole spermatheca removed (B–D) or cut near the base (A). Pigmented parts are shown in grey (terga in dark grey) except for cerci and tergum XI + dorsal sclerite of telson. — Abbreviations: an, anus; ce, cercus; CX8? LC8?, coxa VIII or laterocoxa VIII; CX9?, coxa IX?; gl9 + gp9 (OP), gonoplares IX and/or gonapophysis IX forming ovipositor-like projection; go, ventral lip of gonopore; gp8, gonapophysis VIII; gp8 (OP), gonapophyses VIII forming ovipositor-like projection; gp9, gonapophysis IX; gr, groove on the ovipositor-like projection; LC9, laterocoxa IX; LP, lateral plate; oc, common oviduct; oe, extended oviduct; ol, lateral oviduct; si8, spiracle VIII; so, spermathecal opening; sp, spermatheca; TG8–10, tergum VIII–X; TG11 + DT, tergum XI + dorsal sclerite of telson; tl, lateral tubes; va, vagina. For the regions with the asterisk, see main text (3.3.).

total, this condition was observed for 62 females, the 3 others being ambiguous cases). “Sinistral” following the terminology used in gastropods (e.g., SCHILTHUIZEN & DAVISON 2005). This feature could not be confirmed for *Nala* and *Forcipula* because of the small sample sizes. Except for two samples from Penang and one sample from Tapah Hill in poor condition, the females of *Allostethus* spp. examined in this study consistently possessed a single, elongated, tubular spermatheca with its opening on the right-dorsal side of the vagina (Fig. 4B).

Internal branching occurred frequently in the thin tubular part of the spermatheca (Fig. 2E): at least one internal branching was detected in 17 of 19 females from Penang (*A. indicum*), all three females from Tapah Hill (*A. indicum*), and a single sample of *A. burri*. Although internal branching was frequent, the female samples of *Allostethus* spp. possessed only one spermathecal opening. As a possible exception, in one female (caught as a nymph in the field and emerged in the laboratory) a small, branching, spermatheca-like structure was observed in addi-



**Fig. 4.** Fluorescence micrographs of the female genitalia of *Allostethus indicum* (A, B) and *Labidura riparia* (C). All photographs are shown in the direction indicated in (C). — For abbreviations, see Figure 3. Scale bars: 100  $\mu$ m.

tion to an apparently normal spermatheca (Fig. 2D). Although we could not determine whether this structure had an opening to receive sperm, this tiny structure was likely non-functional. Female *Diplatys flavicollis* Shiraki 1907 (Diplatyidae) sometimes possess spermathecal capsules lacking a duct and an opening, termed satellite spermathecae (11 cases among 60 females examined; KAMIMURA 2004a). If the observed spermatheca-like structure in *Allostethus* lacks an opening, this would be the second report of this type of malformation for female earwigs.

### 3.3. Courtship, mating behaviour, and genital coupling

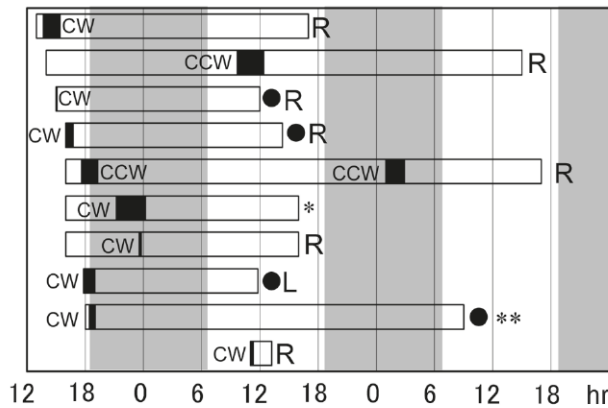
When a virgin female and a virgin male of *Allostethus indicum* were placed in an observation stage, the male actively courted the female, by directing his abdomen and forceps to the female abdomen, simultaneously twisting the abdomen 180° around the anterior-posterior axis and retreating to establish genital contact. The duration between introduction of a pair and occurrence of the first

mating varied extensively among pairs:  $214 \pm 374$  min (mean  $\pm$  SD,  $n = 10$ ) with a range of 0–1183 min (Fig. 5), and a duration of the first mating of  $71.4 \pm 62.2$  (range, 8–180) min. Although the males continued to court the female frequently after the first mating, the females usually escaped from the courting male, and repeated mating was observed between the same pairs in only one case. In this pair, the second mating, which lasted 116 min, occurred at 1782 min after the first mating, which lasted 98 min.

Among the 10 females observed, four laid fertile eggs within 2 months after copulation. Eggs were deposited on the substrate of the rearing vessel as a pile (Fig. 2B). During the field survey, a similar egg batch of *A. indicum* was accidentally found in a small cavity in a decaying log. Thus, although several members of basal Dermaptera have been reported to attach eggs to the substrate with adhesive substances (MATZKE & KLASS 2005; SHIMIZU & MACHIDA 2009, 2011b), this species apparently does not show this habit.

The four inseminated females had mated only once for 8–61 min, indicating that sperm transfer initiates within 8 min (at least in some cases). However, the other six





**Fig. 5.** Copulation durations and frequencies in 10 pairs of *Allostethus indicum*. Each rectangle represents the time window of video recording for each pair, in which the filled parts indicate copulation. Later dissection revealed that seven males were R-ready (R), one was L-ready (L), one had both penes pointing to the head (\*), and one other male could not be examined because of cannibalism (\*\*). Dark periods are indicated by gray shading. CW and CCW indicate the direction of male abdominal rotation recorded at the initiation of each copulation (see text for details). Filled circles indicate females that laid fertile eggs.

females laid no fertile eggs and had no detectable sperm in the spermathecae when they were dissected 2 months after mating. These uninseminated females copulated with males for  $114.2 \pm 86.1$  min (in total, including one female that mated twice), suggesting frequent infertile matings. Interestingly, the inseminated females accepted male mating attempts more rapidly than those remaining uninseminated (latency to the first copulation,  $10.5 \pm 12.2$  vs.  $349.3 \pm 443.2$  min; Mood's median test,  $P = 0.048$ ), while there was no significant differences in the duration of the first copulation ( $36.3 \pm 21.9$  vs.  $94.8 \pm 70.9$  min; Mood's median test,  $P = 0.52$ ).

In the freeze-fixation experiment of mating pairs ( $n = 5$ ), three males used the right penis. In these males, the right penis was directed posteriorly for genital coupling, while the left penis pointed toward the head as when in repose. For the other two males, the opposite condition was observed. The penes used were dilated (endophallic sac evaginated, possibly caused by increased hemolymph pressure) and the virga was exposed. When the right (left) penis was used, its tip was inserted into the female vagina, while its base lay on the ventral side of the base of the ovipositor-like projection and the membranous region on the right (left) side of the projection (\* in Fig. 3A; because of the end-to-end mating posture and nearly  $180^\circ$  rotation of the male abdomen, the right side of the male contacts the right side of the female). Although the male penis was separated readily after thawing of the samples, in the frozen samples, the virga was inserted directly into the spermatheca. Of the three males that used the right penis for copulation, one and two twisted the abdomen in the CW or CCW direction, respectively. The other two males used the left penis while rotating the abdomen in CW direction.

Although the video-recorded pairs were not fixed during copulation, dissection after the video session revealed laterality in penes as follows: eight males twisted the abdomen in the CW direction, of which one and five males were L-ready and R-ready, respectively, while one male had both the right and left penes pointing anteriorly. The other one was cannibalized by the partner female after mating, and thus could not be examined for his genitalia. The other two males that rotated the abdomen in CCW direction (including one consistently rotated the abdomen in the CCW direction for two matings) were R-ready. As an overall trend, male *A. indicum* rotated the abdomen more often in CW direction than in CCW direction (11:4; in a total of 15 males observed in the two experiments), but this trend was not significantly different from even (binomial test,  $P = 0.12$ ) and unrelated to the laterality of penis use (Fisher's exact probability test;  $P = 0.50$ ).

## 4. Discussion

### 4.1. Male genitalia and genital coupling

Male *Allostethus indicum* predominantly use (or are ready to use) the right penis for insemination, although both penes are likely functional without any detectable morphological differentiation between them (Table 1). The usage pattern of paired penes has been investigated for a few representative species of earwigs. In Diplatyidae (*Diplatys flavicollis*; KAMIMURA 2004a), Pygidicraniidae (*Echinosoma denticulatum* Hincks, 1954; KAMIMURA & LEE 2014), and Anisolabididae (*Anisolabis littorea* (White, 1846), *A. maritima* and *Euborellia plebeja*; GILES 1961a; KAMIMURA & MATSUI 2001; KAMIMURA & IWASE 2010; cf. KAMIMURA 2003), males use or are ready to use the right or left penes without great bias. In contrast, males of *Labidura riparia* predominantly use the right penis for insemination, although both penes are functional with no detectable morphological differentiation between them (KAMIMURA 2006). Considering the sister-group relationship between the Labiduridae (sensu stricto) and Eudermaptera proposed in multiple studies (SAKAI 1987; HAAS 1995; WIRTH et al. 1999; HAAS & KUKALOVÁ-PECK 2001; HAAS & KLASS 2003; COLGAN et al. 2003; KAMIMURA 2004b; JARVIS et al. 2005; KOCAREK et al. 2013; Fig. 1), extant labidurids may have retained morphological and/or behavioural characters that resulted eventually in the loss of the less frequently used left penis in the common ancestor of the Eudermaptera (KAMIMURA 2006, 2007). There are several possible causes of the right-handedness in penis use of *Allostethus*. In many insect taxa, the evolution of asymmetric genitalia is associated with asymmetric copulatory positions (LUDWIG 1970; HUBER et al. 2007; HUBER 2010). Thus, one possibility is that the direction of abdominal rotation is related to the laterality of penis use; that is, one penis

for CW and the other for CCW rotation of the male abdomen (KAMIMURA 2003). However, in male *L. riparia*, no consistent correlation was observed between the two asymmetric traits (KAMIMURA 2006), as in the two other species of earwigs studied to date (*Euborellia plebeja*, KAMIMURA 2003; *Echinosoma denticulatum*, KAMIMURA & LEE 2014). The present study also failed to detect any significant relationships between the two traits in *A. indicum* (see 3.3.).

Structural asymmetries in female genitalia also likely cause coevolutionary changes in male genital asymmetries and laterality of mating behaviours (HUBER et al. 2007). In *L. riparia*, the spiral-shaped basal part of the spermatheca (Fig. 4C), which directly contacts with a male virga during copulation, is the most plausible cause of the right-handed use of the male genitalia. No such spiral of the spermathecal opening region was observed for *Allostethus*. Instead, the locations of the vagina (left side of the midline of the body) and the spermathecal opening (right-dorsal side of the vagina) in female *Allostethus* would seem to receive a right penis more smoothly than a left penis. This finding supports the view that the observed right-handedness in *Allostethus* and *Labidura* is homoplasy. Female genital morphologies likely impose selection on male genital structures and mating behaviours even after copulation has begun (cryptic female choice; THORNHILL 1983; EBERHARD 1996). The observed frequent infertile matings and their relationship to the latency to the first mating in *Allostethus* are also suggestive of cryptic female choice.

## 4.2. Female genitalia

Regarding the female genitalia of *Allostethus* spp., the present study revealed four characteristics: (1) presence of a well-developed, ovipositor-like lobe and plate upon segment IX, (2) presence of a pair of elongated thin tubes, which originate from near the base of the ovipositor-like projection, (3) frequent internal branching of a single, tubular spermatheca, and (4) formation of a vagina. Among these features, (2)–(4) have not been reported for the members of higher Forficulina (Mesodermaptera + Eudermaptera), while shared by (at least some) representatives of ‘basal’ Dermaptera (Fig. 1).

The basal dermapterans studied to date possess an ovipositor, although reduction of some of the major projections (gl8, gp8, gl9, or gp9) and sclerites (LC8, CX8, LC9, CX9, and others) is frequently, and in various combinations, found in many groups (KLASS 2003). The projections of the ovipositor are reduced to short lobes in Anisolabididae (GILES 1961b), Spongiphoridae, Chelisochidae, and Forficulidae (SCHNEIDER & KLASS 2013; including lacking differentiation of the gonapophyseal projections, gp, from the coxal projections, gl). Labiduridae sensu lato is unique among the higher Forficulina in having discrete gonapophyses gp8 and gp9, although the latter were not detected in *Forcipula* (BHATNAGAR 1964; this study).

Judging from the apparent morphology, it seems likely that the ovipositor-like projection of *Allostethus* is formed by median fusion of the paired gl9 and/or gp9 (or of undifferentiated gl9+gp9). This type of morphogenesis, that is, fusion of the distal (but not all basal) parts of individual projections, is rare in external structures of insects, and has been reported only for medioventral thoracic formations of some chrysomelid beetles (KLASS et al. 2011). In *Allostethus*, gp8 are also distinct (but vestigial). In contrast, the main components of the ovipositor-like projections of the other labidurids apparently originate from the abdominal segment VIII (Fig. 3). They are without conflict interpreted as the gonapophyses gp8; in *L. riparia* the left and right gp8 are fused almost up to their tips, which appears as an apomorphy. In these species belonging to Labidurinae and Nalinae, possible gp9 are much reduced (*L. riparia* and *N. livivipes*) or totally absent (*F. quadrispinosa*). Thus, the ovipositor-like projection of *Allostethus* is evidently non-homologous to those of the other subfamilies. To our knowledge, a well-developed gp9 is unique to female *Allostethus* among the higher Forficulina.

The ovipositor-like structures of Labiduridae (sensu lato, including *Allostethus*), which is rather short and completely hidden in the genital chamber, seems unlikely to function as a device for oviposition. Like other earwigs lacking an ovipositor (Eudermaptera and Anisolabididae), the females of Labiduridae sensu lato deposit free eggs as a pile (*Nala*, SITUMORANG & GABRIEL 1988; *Labidura*, reviewed in COSTA 2006; *Allostethus*; this study). In *Labidura*, the median groove of the ovipositor plate (the distal part of which may represent the median fusion line of the gp8 of the two sides) leads directly to the opening of the spermatheca (Figs. 3C, 4C) indicating that it functions as a guide for the male penis during copulation.

KLASS (2003) found a large unpaired gland in nearly all of the basal dermapterans studied. Associated with this gland, which opens on the midline of the body on segment IX, a pair of thin, very long cuticular tubes was found in the basal dermapterans except for *Diplatys*; they have been referred to as the lateral tubes (lt in KLASS 2003). KLASS (2003) discussed that no similar organ has been recorded in other insect taxa, and thus the lateral tubes are likely autapomorphic for Dermaptera or a subgroup thereof. Laterally paired, thin, elongated tubes of *Allostethus* are located at the base of the ovipositor-like projection. With the interpretation that the ovipositor-like projection consists of gl9 and/or gp9, the thin tubes are likely homologous to the lateral tubes, which have to date been reported only for the basal dermapterans.

Although KLASS (2003) found that the lateral tubes were frequently associated with a large, unpaired accessory gland, no such gland was detected in *Allostethus* spp., as in other labidurids examined in this study. Among the basal Dermaptera, female *Esphalmenus* completely lack the unpaired gland but possess well-developed lateral tubes, similar to *Allostethus*. Regarding the unpaired accessory gland, KLASS (2003) hypothesized se-

cretive functions. Like many other members of the higher Forficulina, female *Allostethus* was found to lay free eggs as a batch with no adhesive structure. In contrast, many basal dermapterans, including diplatyids that lack lateral tubes, have been reported to deposit eggs with an egg stalk, made of adhesive substances (MATZKE & KLASS 2005; SHIMIZU & MACHIDA 2011b). The only example of the higher Forficulina with eggs deposited with adhesive substances is *Apachyus chartaceus* (de Haan, 1842) (SHIMIZU & MACHIDA 2011a). Female *Apachyus* has a homologous IX<sup>th</sup>-segmental accessory gland (J. Kaidel & K.-D. Klass, unpubl. data).

The anterior border of the female genital opening is not homologous among the various earwigs. It is the ventral lip of a primary gonopore (the opening of the common oviduct) on segment VII in *Esphalmenus* and in Eudermaptera (Condition 1; KLASS 2003; SCHNEIDER & KLASS 2013). The dorsal side of the common oviduct extends posteriorly to segment VIII in *Diplatys*, *Haplodiplatys*, *Karschiella*, *Pyragra*, and possibly *Bormansia* (forming an extended oviduct; Condition 2) or the oviductal opening and the spermathecal opening together sink into an invagination termed a vagina in *Echinosoma*, *Dacnodes*, *Tagalina*, and *Anataelia* (Condition 3; KLASS 2003). As revealed in the present study (see 3.2.), the gonopore of labidurids sensu stricto corresponds to (1), but the VIII<sup>th</sup>-segmental area bearing the spermatheca has expanded far anteriorly to form the roof of the gonoduct (there is, so to speak, a dorsal-only vagina). A vagina is formed in *Allostethus*, making it comparable to the basal dermapterans of (3). Considering the deep invagination of vagina into segment VII with the spermatheca in this segment (Figs. 3A, 4A), the condition of *Allostethus* is especially comparable with those of *Tagalina*, and *Anataelia* (KLASS 2003), but the spermatheca opened on the latero-dorsal wall instead of the dorsal side. The exact homology of the vagina between *Allostethus* and basal dermapterans is at present unknown. Both the conditions found in *Allostethus* and Labiduridae sensu stricto may be unique in Dermaptera. It should be noted that a loss of the vagina (transition from (3) to (1)) might occur easily (and thus plausibly several times independently) by pedomorphosis (i.e., arrested ontogenetic development of gonoducts; KLASS 2003; SCHNEIDER & KLASS 2013).

The morphology of the spermatheca itself of *Allostethus* also differs from those of Labiduridae sensu stricto in branching propensity. Females in other families of the higher Forficulina and Arixeniina studied so far have a single unbranched spermatheca with or without a sclerotized capsule at the distal end, as well as some pygidicranids (POPHAM 1965a; HUDSON 1973; MARIANI 1994; KLASS 2003; KAMIMURA 2004a; SCHNEIDER & KLASS 2013). For higher Forficulina, internal branching has been reported as uncertain cases or as malformations induced by stress. POPHAM (1965a) noted that female *Epilabis penicillata* (Borelli, 1911) (= *Carcinophora penicillata* in POPHAM 1965a; Anisolabididae) have two independent spermathecae or a bifid one (indeterminable from the description). KAMIMURA (2007) reported the occurrence of

multiple or branched spermathecae in gamma-irradiated samples of two earwig species, *E. plebeja* (Anisolabididae) and *Proreus simulans* (Stål, 1860) (Chelisochidae), which normally have a single, unbranched spermatheca. In contrast, spermathecae with a single opening and internal branching have been reported for the pygidicranids *Tagalina* (KLASS 2003), *Challia* (KAMIMURA 2004b), and *Gonolabina* (MARIANI 1994). Such internal branching was also found for the lateral tubes of *Allostethus*, but much less frequently ( $n = 4$ ), indicating that the developmental process of female genitalia is unstable in this species.

Overall, in contrast to the right-handedness of penis use, these plesiomorphic characteristics of the female genitalia lend support to the view that *Allostethus* represents the basal-most clade among higher Forficulina (though with *Apachyus* as a plausible alternative candidate for this position), making Labiduridae sensu lato polyphyletic.

### 4.3. Conclusions

Even excluding *Allostethus*, no single synapomorphic characteristic has been shown to define Labiduridae. Among the three families of Mesodermaptera, the members of Apachyidae are well characterized with multiple features, such as the carinate femur of legs (HAAS 1995), the conspicuously dilated tenth abdominal segment (STEINMANN 1989a), and the anojugal cell of the hindwing being smaller than the jugal cell (HAAS & KUKALOVÁ-PECK 2001). However, except for five traits of hindwings identified by HAAS & KUKALOVÁ-PECK (2001), there is no single diagnostic character for discriminating the members of Labiduridae (sensu stricto) from anisolabidids (most species are apterous). The presence of a basal vesicle at the base of a virga is sometimes used as a diagnostic characteristic of Labiduridae from Anisolabididae (e.g., STEINMANN 1989a). Some anisolabidids, however, possess conspicuous basal vesicles (KAMIMURA 2014). Accordingly, HAAS & KUKALOVÁ-PECK (2001) found weak support for the monophyly of Labiduridae sensu stricto. The retention of gp8 together with reduction of almost all other ovipositor components may be a diagnostic feature of this group.

Among the 43 traits examined by HAAS & KUKALOVÁ-PECK (2001), no single characteristic is shared by only *Allostethus* and other Labidurids [*Forcipula clavata* Liu, 1946 (Labidurinae), *L. riparia* (Labidurinae), *N. lividipes* (Nalinae)]. Accordingly, given that the observed right-handedness in penis use is homoplasy, there is no positive reason for placing *Allostethus* in Labiduridae among Mesodermaptera. Instead, *Allostethus* likely represents one of the most primitive taxa that evolved Mesodermapteran-type, laterally asymmetric male genitalia. This genus is characterized by a unique combination of presumably plesiomorphic (basal dermapteran) and apomorphic (higher forficulian) character states (Fig. 1), as well as own apomorphies. Labiduridae sensu lato is evidently a polyphyletic assemblage, and according to the view-

point that approves only monophyletic groups as taxonomic units, Allostethinae would be more appropriately treated as an independent family Allostethidae (sensu ZACHER 1911). Further comparative studies including the other members of Allostethinae (*Gonolabidura* and *Allostethella*) are clearly needed.

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