

Right-Handed Penises of the Earwig *Labidura riparia* (Insecta, Dermaptera, Labiduridae): Evolutionary Relationships Between Structural and Behavioral Asymmetries

Y. Kamimura^{1,2*}

¹Department of Environmental Systems, Risho University, Kumagaya, Saitama 360-0194, Japan

²Department of Ecology and Systematics, Graduate School of Agriculture, Hokkaido University, Kita-ku, Sapporo 060-8589, Japan

ABSTRACT The number of penises vary in the insect suborder Forficulina (order Dermaptera; earwigs). Males of the families Diplatyidae, Pigidicranidae, Anisolabididae, Apachyidae, and Labiduridae have two penises (right and left), while those of the Spongipohridae, Chelisoichidae, and Forficulidae have a single penis. The proposed phylogenetic relationships among these families suggest that the single-penis families evolved from an ancestor possessing two penises. To date, examinations of double-penis earwig species have found that only a single penis is used per single copulation. These diversities in structural and behavioral aspects of genitalia raises the following intriguing questions: How are the two penises used? Why did a penis degenerate in several earwig families, and which one was lost? To address these questions, structural and behavioral asymmetries were examined in detail for a representative species *Labidura riparia* (Labiduridae). Although there was no detectable morphological differentiation between the right and left penises, male *L. riparia* predominantly used the right one for insemination. This significant “right-handedness” developed without any experience of mating and was also manifested in the resting postures of the two penises when not engaged in copulation. However, surgical ablation of the right penis did not influence the insemination capacity of males. In wild-caught males, only about 10% were left-handed; within this group, abnormalities were frequently observed in the right penis. These lines of evidence indicate that the left penis is merely a spare intromittent organ, which most *L. riparia* males are likely never to use. Additional observations of five species of single-penis families revealed that the left penis degenerated in the common ancestor of this group. Considering the proposed sister relationship between the Labiduridae and the single-penis families, it is possible that such behavioral asymmetries in penis’ use, as observed in *L. riparia*, are parental to the evolutionary degeneration of the infrequently used left penis. *J. Morphol.* 267:1381–1389, 2006. © 2006 Wiley-Liss, Inc.

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Behavioral asymmetry, i.e., the biased use of laterally paired organs, is a fascinating problem in evolutionary and developmental biology. Although vol-

umes of reports have detailed the development, genetics, evolution, and physiological backgrounds of behavioral asymmetries in vertebrates, especially right-handedness in humans (e.g., Ludwig, 1970; Neville, 1976; Rogers and Andrew, 2002; and references therein), studies of invertebrates are rare. This is especially true for cases in which behavioral asymmetries are not associated with morphological differentiation of the left and right organs, the so-called structural asymmetry (Byrne et al., 2002, 2004).

Palmer (1996) classified conspicuous asymmetry in animals into two major categories: directional asymmetry (DA) and antisymmetry (AS). In the former case, most individuals of a population are behaviorally or structurally asymmetrical toward one side (either right-handed or left-handed). In populations with AS, “right-handed” and “left-handed” individuals are equally frequent. Based on phylogenetic analysis of asymmetry variation among animals, Palmer (1996) pointed out the evolutionary trend by which AS tends to precede DA in the asymmetrical traits expressed in postlarval phases. For example, phylogenetic patterns of flatfishes suggest that DA has evolved multiple times from an AS ancestor, which was characterized by polymorphism in the direction of ocular migration (Policansky, 1982; Chapleau, 1993). In populations exhibiting AS, the handedness of each individual can be determined by environmental factors rather than genetic factors. Peculiarly, no significant response to a particular direction has been reported for artificial selection of traits showing AS. This finding indicates the significance of

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*Correspondence to: Yoshitaka Kamimura, Laboratory of Animal Ecology, Department of Ecology and Systematics, Graduate School of Agriculture, Hokkaido University, Kita 9, Nishi 9, Kita-ku, Sapporo 060-8589, Japan. E-mail: kamimu@res.agr.hokudai.ac.jp

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epigenetic factors in controlling handedness in AS traits. In contrast, the expression of handedness in DA traits is likely to be genetically determined. Therefore, the evolutionary transition AS → DA would be accompanied by a genetic assimilation process, i.e., the replacement of an external environmental trigger of handedness determination by a genetic trigger (Palmer, 1996). Although Palmer's (1996) arguments are focused on structural asymmetries, behavioral traits are also likely to show the same trend of AS preceding DA. In relation to the interplay between behavioral and structural laterality, this possible trend is fascinating because an AS → DA transition in behavior would promote the evolution of DA in the morphology from the ancestral state of lateral symmetry. For example, consider laterally paired organs such as the right and left hand. When one hand is rarely used for some reason (i.e., the development of behavioral asymmetry) that infrequently used organ may degenerate and so a structural asymmetry is established. Such a scenario of interplay between behavioral and structural asymmetries is characterized by usage bias of paired organs preceding morphological differentiation. To my knowledge, no empirical examples of such transitional states have been reported.

Earwig Genitalia as a Model Case

Male genital organs and their use patterns in earwigs (Insecta: Dermaptera) provide a rare opportunity to analyze the evolutionary relationship between behavioral and structural asymmetries. The Dermaptera is usually divided into three suborders: Hemimerina, Arixeniina, and Forficulina. Members of the former two suborders live on mammals and show special modifications adapted to phoretic habits (Nakata and Maa, 1974). According to the system of Sakai (1982), the Forficulina consist of eight families of free-living typical earwigs: Pygidicranidae (including Karschellidae (Popham, 1965b) as Karschellinae), Diplatyidae (= Diplatyinae of Pygidicranidae (Steinmann, 1989)), Anisolabididae (= Carcinophoridae (Popham, 1965b; Steinmann, 1989)), Apachyidae, Labiduridae, Spongiphoridae (= Labiidae (Popham, 1965b; Steinmann, 1989)), Chelisochidae, and Forficulidae. Although a recent study has suggested that the Hemimerina, which are phoretic on rodents, are an in-group member of the Forficulina (Jarvis et al., 2005), I adopted the strict definition of Forficulina in this article. Among the Forficulina, males of the families Pygidicranidae, Diplatyidae, Anisolabididae, Apachyidae, and Labiduridae have two intromittent organs (right and left penises), with few exceptions (e.g., Karschellinae in which the left penis is greatly reduced). The Spongiphoridae, Chelisochidae, and Forficulidae (Eudermaptera) are characterized by a single penis (Burr, 1915a,b, 1916; Popham, 1965a). A virga is the sclerotized end part of an ejaculatory duct and functions as a sperm transfer

organ (Fig. 1A). Membranous penis lobes surround each virga (Fig. 1). In this article, a penis lobe and the virga wrapped in it are collectively referred to as a penis. In Diplatyidae and two subfamilies of Pygidicranidae (Pyragrinae and Esphalmeninae) two or bifurcated virgae are present in each of two penis lobes, resulting in four gonopores per males, while a single virga with a gonopore per each penis lobe is present in the remaining earwigs (e.g., Popham, 1965a). Sperm produced in paired testes and stored in a seminal vesicle are transferred via a virga directly into a female sperm storage organ (spermatheca) during mating (Popham, 1965a; Kamimura, 2000, 2004a; Fig. 1A). To establish genital contact, males twist their abdomen in a clockwise (CW; viewed from the head of the male) or in the counterclockwise (CCW) direction (Fig. 1A). To date, only a handful of species of Diplatyidae and Anisolabididae have been examined in regard to the use patterns of their two penises. In the Diplatyidae and Pygidicranidae (so-called "basal Dermaptera") both the right and left penises point toward the anterior of the body when not in copulation (Fig. 1A for the definition of the left-right and anterior-posterior axes). Hereafter, the term "resting state" is used to address such conditions of the penises when not in copulation. In a previous study, I found that male *Diplatys flavicollis* (Diplatyidae) used either the right ($n = 3$) or left ($n = 6$) penis for insemination (Kamimura, 2004a). Although the sample size of that study was small, this species can be characterized by its symmetrical morphology and possible AS in penis-use behavior. In the Apachyidae, Anisolabisidae, and Labiduridae the left and right penises point in opposite directions when resting (Popham, 1965a; Fig. 1B,C). Because a penis should point straight posteriorly during mating (Fig. 1A), organs pointing posteriorly while resting can be considered ready for mating (R-ready, Fig. 1B or L-ready, Fig. 1C). For the Anisolabididae, no significant bias has been reported for the resting state of *Euborellia plebeja* ($n = 29$; Kamimura and Matsuo, 2001), *Anisolabis maritima* ($n = 242$; Kamimura and Matsuo, 2001), and *A. littorea* ($n = 32$; Giles, 1961). In *E. plebeja*, the actual use pattern of the penises was only weekly, but significantly biased toward the left (11 R: 25 L; Kamimura, 2003b). In these studies, males were fixed before or during mating, and thus each individual was scored only once. Preliminary observations however indicate that each male preferentially uses a specific one of the two penises for multiple matings (behavioral AS) rather than random or alternative use of the two penises (Y. Kamimura, unpublished data).

Among families with two penises, the Labiduridae are of particular interest for studies of the use patterns and structural asymmetry of paired genitalia because recent studies of molecular phylogeny have suggested a sister-group relationship between the Labiduridae and the Eudermaptera, which is

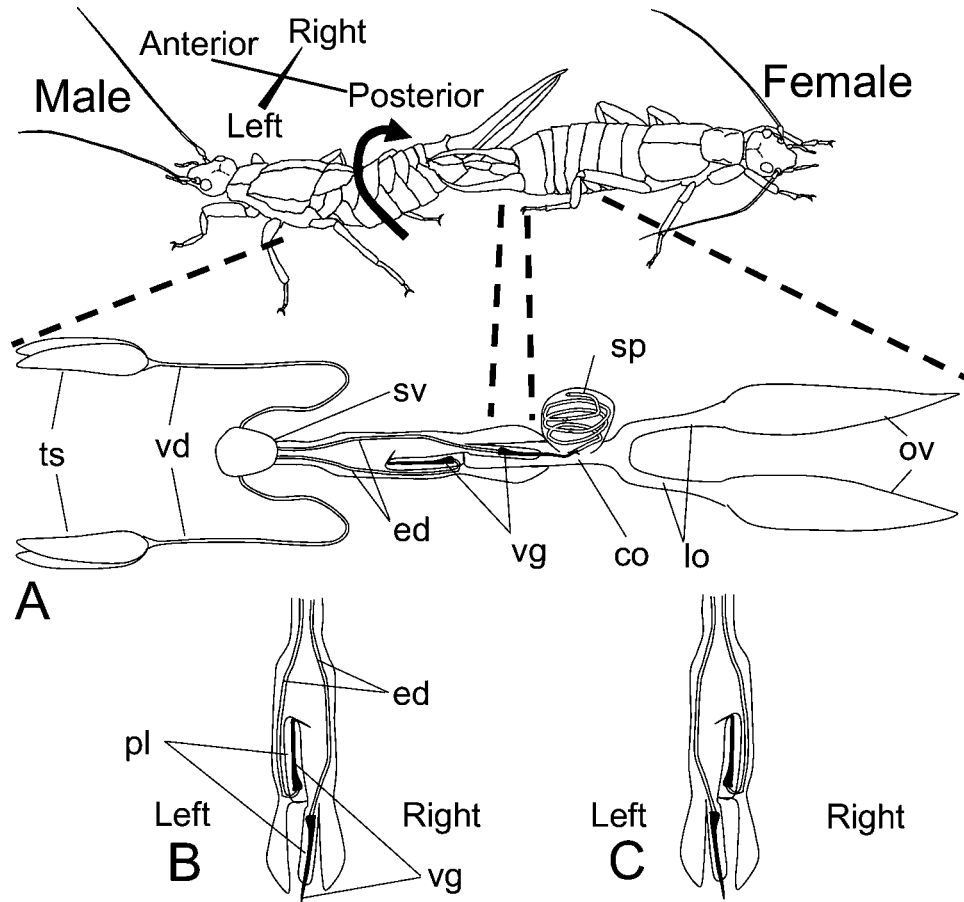


Fig. 1. **A**: Schematic drawings of a mating pair of *Labidura riparia* with male and female reproductive organs, showing the male twisting his abdomen in a counter-clockwise (CCW) direction. **B–C**: Two resting states of male genitalia, R-ready (**B**) and L-ready (**C**). See text for details of resting states. ts, testis; vd, vas deferens; sv, seminal vesicle; ed, ejaculatory duct; vg, virga; sp, spermatheca; co, common oviduct; lo, lateral oviduct; ov, ovary; pl, penis lobe.

characterized by a single penis (Wirth et al., 1999; Colgan et al., 2003; Kamimura, 2004b; Jarvis et al., 2005: note that Jarvis et al. (2005) conducted phylogenetic analyses of combined datasets of molecular and morphological data, which resulted in the inclusion of the Hemimerina and Anisolabididae within this clade). Cladistic analyses of morphological datasets also support this relationship (Sakai, 1987; Haas, 1995; Haas and Kukulová-Peck, 2001; Haas and Klass, 2003). Therefore, it is possible that extant labidurids retain morphological or behavioral characters that eventually lead to the loss of one penis in the common ancestor of the Eudermaptera. Although many authors have described mating behaviors (Weidner, 1941; Schlinger et al., 1959; Joshi, 1960; Arora and Bhatnagar, 1961; Herter, 1963; Vancassel and Caussanel, 1968; Caussanel, 1970; Tawfik et al., 1972; Shepard et al., 1973; Ammar and Farrag, 1974; Singh et al., 1982; Situmorang and Gabriel, 1988) and genital morphology (Bhatnagar, 1964; Bhatnagar and Singh, 1965; Brindle, 1966; Hudson, 1973; Steinmann, 1979; Sakai, 1984) of the cosmopolitan labidurid *Labidura riparia*, to my knowledge, no

studies have used a sufficient sample number to examine the structural and behavioral genital asymmetries of any labidurids. Arora and Bhatnagar (1961), and Singh et al. (1982) described the insertion of a virga into a spermatheca during *L. riparia* mating but they did not mention the laterality of penis use. Bhatnagar (1964) described the resting state of genitalia, in which the left penis points anteriorly and the right penis points posteriorly, without explicit declaration of the sample size observed.

Using *Labidura riparia* as a representative of the Labiduridae, the present study was conducted to answer the following questions: 1) Does AS or DA occur in the resting state and use pattern of two penises? 2) Are both penises functional? 3) Is there any morphological differentiation between the right and left penises? Furthermore, I investigated the laterality of degenerated ejaculatory organs for five representative species of single-virga earwigs. For two members of this clade (*Marava arachidis* [Spongipholidae] and *Forficula auricularia* [Forficulidae]), Ramamurthi (1959) reported the presence of a closed rudimentary ejaculatory duct, which indicates that

the single-penis families derived from double-penis earwigs after losing one of two ejaculatory organs. Popham(1965a) reported that only the right ejaculatory duct is functional in *F. auricularia*, suggesting the degeneration of the left penis in this species. However, his report did not reveal the sample size observed. It is important to compile information of the laterality of degenerated ejaculatory organs in single-penis earwigs to discuss their evolutionary origin. Based on these prior studies and the present research, I have discussed possible evolutionary transitions in the behavioral and structural asymmetries of earwig genitalia.

MATERIALS AND METHODS

Laterality of Male Genitalia

Adults and nymphs of *Labidura riparia* (Pallas, 1773) were collected from five populations (IK, Ishikari, Hokkaido Prefecture; KG, Kumagaya, Saitama Prefecture; IM, Ichinomiya, Chiba Prefecture; KS, Kurashiki, Okayama Prefecture, and MZ, Miyazaki Prefecture) in Japan from September 2003 to October 2005 (Fig. 2) throughout the reproductive season of this species. Genital asymmetries of the resting state were investigated for males ($n = 22-90$) from each of the five populations. Among these, nine specimens from IM were collected as nymphs, reared in the laboratory (for rearing methods, see below), and dissected at >3 days after their imaginal eclosion. From frozen fixed samples, male genitalia were carefully dissected in phosphate buffered saline (PBS), and the asymmetry in the resting state (R- or L-ready; Fig. 1B,C) was immediately scored. The genitalia were then mounted on a slide with Eukitt[®] mounting medium (O. Kindler, Freiburg, Germany). Virga length was measured using a binocular eyepiece on an Olympus CH40 (for KG and IM populations; to the nearest 25 μm) or Olympus BH2 (for the other populations; to the nearest

8 μm) light microscope. Any abnormalities of the genitalia, such as damage or abnormal coloration, were carefully checked.

Development of Genital Laterality

To determine the developmental stage when any asymmetries appeared in the genitalia, newly emerged male adults were fixed at various stages. Field-collected or F1 generation nymphs of the IM population were reared in plastic vessels (8 cm in diameter) with a floor made of plaster, at $(25 \pm 1)^\circ\text{C}$ and 14 h light:10 h dark. They were provided with water and unlimited amounts of commercial cat food. Imaginal eclosion was checked daily at 11:00 a.m., and newly emerged males were individually separated. The males were randomly assigned into one of the four treatments for fixing by freezing immediately or 1-3 days later. This procedure yielded males fixed 0-24, 24-48, 48-72, or 72-96 h after imaginal eclosion. These samples were later dissected to check the resting state as described above. For the samples fixed 0-48 h after eclosion the lengths of both the right and left virgae were also measured. Scanning electron microscope (SEM) observations were also used for several of these samples that were processed with sublimation drying and coating with gold.

Genital Use Patterns and Surgical Experiment

Two mating experiments were conducted to examine the use pattern and the insemination potential of the two penises of *Labidura riparia*. Experiments were conducted at $(25 \pm 1)^\circ\text{C}$ using individuals derived from the KG and IM populations.

In the first experiment, adult pairs were released into a mating arena (identical to the rearing vessel). One minute after the initiation of copulation, the mating pairs were instantaneously fixed using flash-freezing spray (SPOT FREEZE-S, Fine Chemical Japan Co., Tokyo, Japan). These samples were later dissected to determine which penis had been used for insemination. The male mating posture (direction of abdominal twisting; Fig. 1A) was also recorded.

For the second experiment, either the right or left penis, randomly determined, was ablated with fine forceps from males anesthetized with ice-cold water ($n = 32$ in total). After at least 5 days following the surgery, the males were each paired with a virgin female for 24 h and their behaviors were recorded with a video camera (Panasonic NV-GS50K; Matsushita Electric Industrial Co., Osaka, Japan) and a time-lapse digital video recorder (W-DVR-400; Wireless Tsukamoto Co., Suzuka, Mie Prefecture, Japan). The males and females were then fixed and dissected to check the success of the surgical treatment and of insemination, respectively. When viable sperms were detectable in the spermathecae, those trials were designated as "insemination successful." In the other cases, the video records were checked for the occurrence of mating.

Degeneration of Ejaculatory Organs in Single-Penis Earwigs

To gather supplementary information on the evolutionary degeneration of penises, observations were made of the male reproductive organs of five earwig species belonging to the single-virga families: *Paralabelula curvicauda* (Motschulsky, 1863) (= *Metalabela carvicauda* in Sakai, 1982; Spongiphoridae), *Proreus simulans* (Stål, 1860) (Chelisochidae), *Forficula scudderi* Bormans, 1880, *F. mikado* Burr 1904, and *Anechura harmandi* (Burr, 1907) (Forficulidae). From frozen-stored male samples, the seminal vesicle and ejaculatory ducts were dissected in PBS with the genitalia and mounted on a slide. In the process of dissection, the right and left sides of the reproductive-genital systems were stained with a small amount of neutral red and Nile blue sulfate dye powders, respectively. This staining procedure enabled rapid and precise determination of the lateral axis in the mounted samples. I determined whether the right or left side of the two ejaculatory ducts had degenerated based on the lateral positions of the rudimentary (closed) and intact ejaculatory ducts.

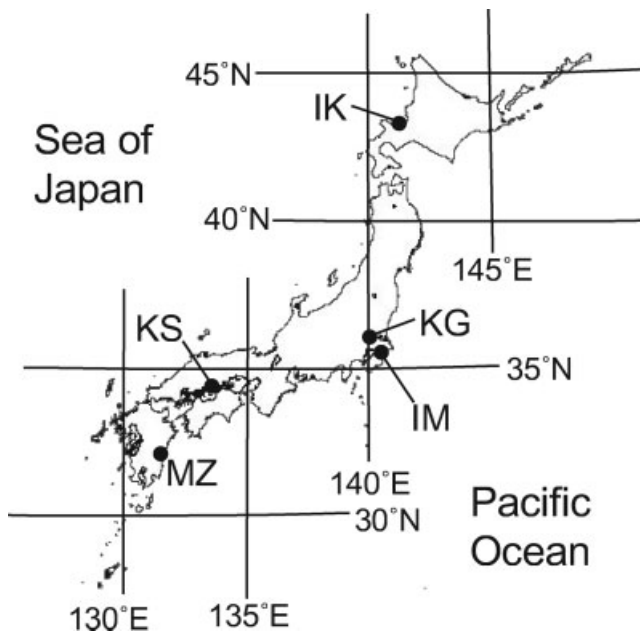


Fig. 2. Collection localities of *Labidura riparia* in Japan: IK, Ishikari, Hokkaido Prefecture; KG, Kumagaya, Saitama Prefecture; IM, Ichinomiya, Chiba Prefecture; KS, Kurashiki, Okayama Prefecture, and MZ, Miyazaki, Miyazaki Prefecture.

TABLE 1. Resting state of the male genitalia for five *Labidura riparia* populations

Population (n)	Collection Dates	R-ready	L-ready	P*
IK (90)	Jun.–Aug. 2005	86 (0, 0)	4 (1, 1)	<0.001
KG (35)	Jun.–Jul. 2004	31 (0, 0)	4 (1, 0)	<0.001
IM (33)	May 2004	29 (1, 0)	4 (1, 0)	<0.001
KS (22)	Sept. 2005	19 (0, 2)	3 (1, 1)	<0.001
MZ (32)	Oct. 2005	29 (0, 0)	3 (0, 0)	<0.001

The numbers inside parentheses indicate no. of samples with genital damage, no. of samples with abnormal pigmentation in the opposite, not-readied penis.

*Binomial test with the null hypothesis that the ratio of R-ready to L-ready males is 1:1.

RESULTS

When resting, most male *Labidura riparia* (86.4%–95.6% of samples) had the right penis pointing posteriorly and the left penis flexed anteriorly (R-ready; Fig. 1B). In the remaining samples, the reverse condition (L-ready; Fig. 1C) occurred. The resting state was highly biased toward R-ready, irrespective of the populations (Table 1). In a total of nine samples out of the 212 examined, damage (n = 5) or abnormal pigmentation (n = 4) of the virgae and/or penis lobes were detected (Fig. 3A; Table 1).

In abnormally pigmented samples, penis lobes were black, indicating a melanization response caused by injury. Organs with apparent injury were designated as “damaged.” Damaged or abnormally pigmented organs seemed to be nonfunctional. Such abnormalities exclusively occurred on the flexed (not readied) side of the genitalia. These abnormalities occurred on the right side in six out of 18 L-ready samples, and on the left side in three of 197 R-ready samples observed. The Fisher exact probability test revealed that abnormalities occurred at a much higher rate in L-ready samples than in R-ready samples (P < 0.0001).

Time-course sampling of newly emerged adults revealed that both the right and left penises point posteriorly immediately after imaginal eclosion (Fig. 4). Without any mating experience, asymmetry in the resting state developed from 48–96 h after imaginal eclosion, resulting in a majority of R-ready males and only one example of an L-ready male (Fig. 4).

No significant difference was detected between the length of the right and left virgae in all five populations examined (IK, paired-sample t-test, $t_{86} = 1.29, P = 0.20$; KG, $t_{30} = 0.95, P = 0.34$; IM, $t_{28} = 0.39, P = 0.70$; KS, $t_{20} = 1.71, P = 0.10$; MZ, $t_{31} = 0.51, P = 0.62$). The same applied to the case when

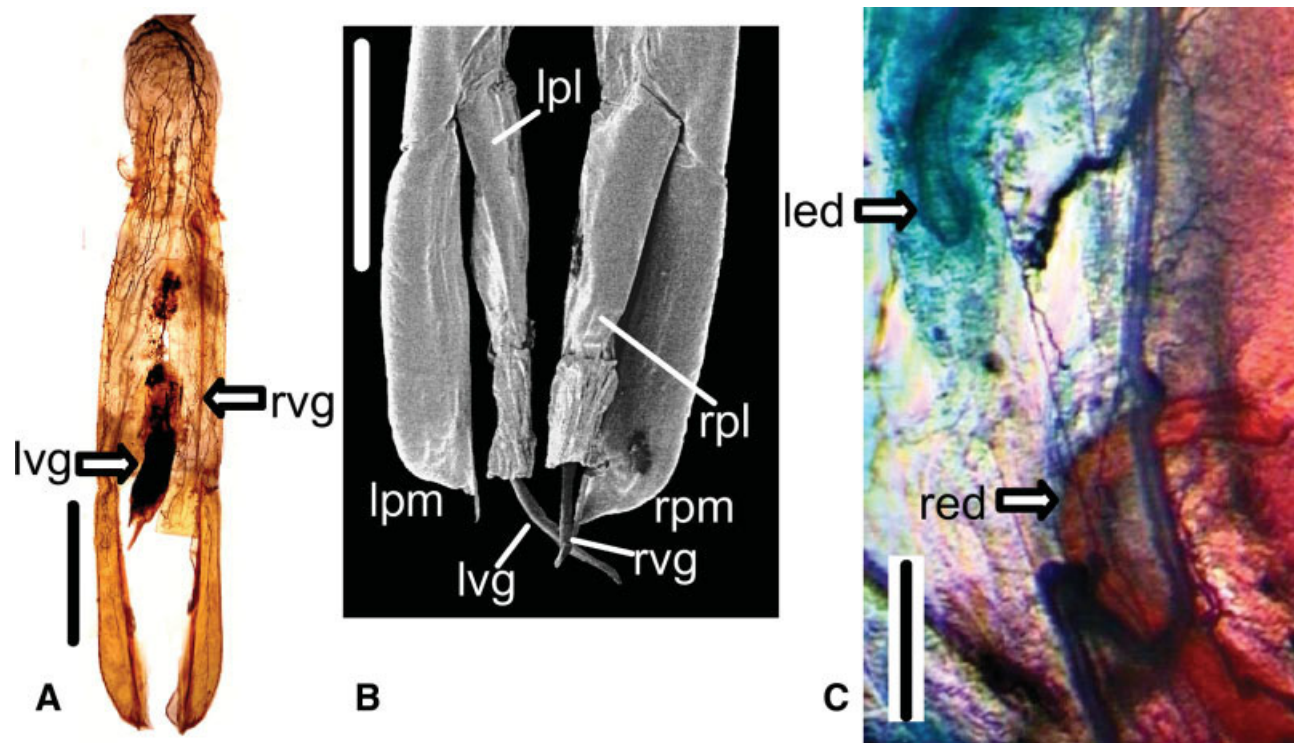


Fig. 3. A: Genitalia of *Labidura riparia* with an intact right virga pointing backward (rvg) and a necrotic left virga in a necrotic and flexed penis lobe (lvg). B: SEM photograph of genitalia of *Labidura riparia* showing a case in which no lateral differentiation has been developed. Both the left and right virgae (lvg and rvg, respectively), each in the left and right penis lobes (lpl and rpl), point posteriorly. The left and right parameres (lpm and rpm) are also laterally symmetrical. C: Ejaculatory ducts of *Forficula scudderii* stained with neutral red (right side) and Nile blue sulfate (left side). The left ejaculatory duct (led) ends, forming a cul-de-sac structure, while the right duct (red) is intact, continuing to the right virga. Scale bars: 1 mm in A, 500 μm in B, and 100 μm in C.

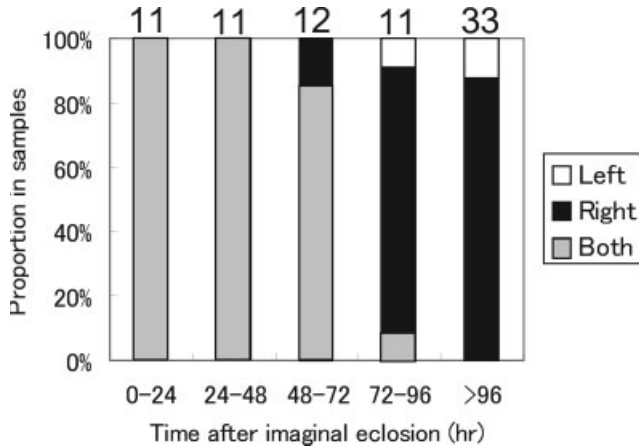


Fig. 4. Development of laterality in the resting state of genitalia of *Labidura riparia*: Both, both the right and left penes point straight backward (symmetrical state); Left (right), the left (right) penis points straight posteriorly, while the right (left) penis is flexed pointing anteriorly (antisymmetrical state). The numerals above the columns indicate the sample size. Note that the data for >96 h were the same as those shown in Table 1 (IM population).

asymmetry in the resting state had not been developed, i.e., when both virgae were pointing backward (Fig. 5). This result confirms that the resting postures of virgae (i.e., pointing anteriorly or posteriorly) did not skew the measurements. Other than length, I noticed no morphological differences between the right and left virgae and penis lobes (Fig. 3B).

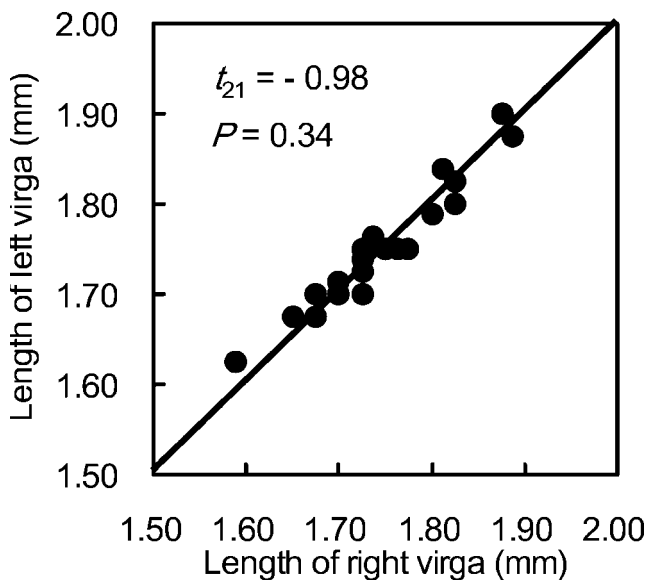


Fig. 5. Relationships between the lengths of right and left virgae of *Labidura riparia*. Each dot represents the value for a newly emerged male in which both the right and left virgae point posteriorly. A diagonal line illustrates right and left virgae of equal length.

TABLE 2. Laterality in penis use and abdominal twisting behavior during mating in male *Labidura riparia*

Population	Penis used	Abdominal twist		Total	P (binomial test)
		CW	CCW		
KG	Right (R)	7	7	14	R vs. L: 0.002 CW vs. CCW: NS
	Left (L)	1	0	1	
	Total	8	7	15	
IM	R	7	5	12	R vs. L: 0.037 CW vs. CCW: NS
	L	1	2	3	
	Total	8	7	15	

CW, clockwise; CCW, counter-clockwise.

The freeze-fixation experiment confirmed that a virga is directly inserted into the spermatheca during copulation, as shown in Figure 1A. As in the resting state, the use pattern of penises was also significantly biased toward the right side (Table 2). The direction of the abdominal twisting was biased toward neither CW nor CCW (Table 2). Irrespective of the highly right-biased use pattern of penis, 75% of the males whose right penis had been ablated could mate and successfully inseminate females, as did the left-penis ablated specimens (81%; Table 3). Although the resting state could not be determined for the males prior to surgery, the results of this experiment indicate that penises flexed in a forward-pointing direction are not impotent organs.

In all 36 samples of five single-penis species, the males possessed a nonfunctional, closed ejaculatory duct on the left side of their body (stained with blue dye) and a functional ejaculatory duct on their right side (stained with red dye; Fig. 3C; Table 4).

DISCUSSION
Origin of Asymmetries

Male *Labidura riparia* predominantly use the right penis for insemination, although both penises are functional without any detectable morphological differentiations between them. Such behavioral bias in virga use was also manifested in the directionally biased asymmetry in the penile resting state toward R-ready. This laterality was established without any

TABLE 3. Reproductive performances of male *Labidura riparia* from which one penis had been experimentally ablated

Population	Ablated penis	No. of successful surgery	No. of successful matings	No. of successful inseminations
KG	Right	8	8	5
	Left	8	7	7
IM	Right	8	8	7
	Left	8	8	6

TABLE 4. Laterality in ejaculatory ducts in five single-penis species of earwigs

Species (Family)	Locality in Japan (n) [collection date]	Rudimentary ejaculatory duct	
		Right	Left
<i>Paralabellula curvicauda</i> (Spongiphoridae)	Komae, Tokyo (11) [Sept. 2004] ^a	0	11
<i>Proreus simulans</i> (Chelisochidae)	Ishigaki Is., Okinawa (8) [Aug. 2004]	0	8
<i>Forficula scudderi</i> (Forficulidae)	Nagaoka, Niigata (2) [Sept. 2004]	0	8
	Sapporo, Hokkaido (6) [Jun.–Sept. 2005]		
<i>Forficula mikado</i> (Forficulidae)	Kushiro, Hokkaido (4) [Aug. 2004]	0	4
<i>Anechura harmandi</i> (Forficulidae)	Yamato, Yamanashi (5) [Oct. 2004]	0	5

^aAll male samples were derived from one field-caught female; thus the independence these samples is not satisfied.

mating experience, suggesting underlying genetic controls. Popham (1965a, 1969) claimed that the flexed penises of the Labiduridae (and other families with bidirectional penises) were nonfunctional. As in the case of the Anisolabididae (Kamimura and Matsuo, 2001; Kamimura, 2003a), this study revealed that this notion lacks foundation. Further, I was able to confidently reject or support several anecdotal descriptions of prior studies. Without reporting the sample size, Bhatnagar (1964) described male genitalia of *L. riparia* as R-ready. However, I detected L-ready males accounting for about 10% of the male populations. Concerning the direction of abdominal twisting during mating, Singh et al. (1982) noted that “the male then twists the posterior end of the abdomen from the left side through an angle of 180°.” Similarly, Joshi (1960) noted that “the abdomen was twisted laterally, with left side turned upward.” Although their descriptions are in accord, twisting in both the CW and CCW directions was observed in the *L. riparia* examined in this study. Similar phenomena have been reported for the anisolabidid *E. plebeja* (Kamimura, 2003b). These discordances between the present and previous studies emphasize the importance of sampling of numerous individuals and of reporting the sample sizes used in laterality research.

The data presented here raise two fundamental questions: Why are male *Labidura riparia* predominantly right-handed? Why are a few males left-handed? No credible answer is presently available for the first question. As Huber (2004) pointed out, no general explanation has been proposed to date for the evolution of asymmetric genitalia. According to Ludwig (1970), asymmetric copulatory positions and asymmetry in female genitalia are possible causes for the evolution of asymmetric male genitalia. The first scenario is not likely to be applicable to *L. riparia* because the copulatory positions (i.e., males twist their abdomen in the CW or CCW direction) were not correlated with the penis use pattern. The structure and position of the spermatheca in female *L. riparia*, which directly receive sperm from the male virgae, may explain the extreme right-handedness in males. Although a spermatheca lies at the dorsal side of the common oviduct running

along the median line of a female body, Hudson (1973) described a peculiarly coiling structure in the basal part of the spermatheca having an opening pointing to the lateral side of the body. Such asymmetrical structures in females may generate differential insemination success between right- and left-handed males; however, the success difference may be slight, as I detected no significant deference in 1-day-pairing insemination success between the two types of males (Table 3). In future studies, female-male genital contacts should be studied in further detail.

There are two possible origins of the left-handed males. Because one-third of L-ready males had an abnormally pigmented or broken right penis (Table 1), it is likely that these genital troubles led to switching of penis use from right to left. In anisolabidid earwigs characterized by highly elongated virgae, similar genital damage is sporadically observed and is considered to have been incurred accidentally during copulation (Kamimura and Matsuo, 2001; Kamimura, 2003a). If genital problems in *Labidura riparia* also mainly occur during mating, it can explain the occurrence of genital abnormalities being biased toward the frequently used right-side penises.

Not all L-ready males showed genital abnormalities of their right penis (Table 1), and an L-ready individual had no mating experience (Fig. 4). In many animal species with DA, individuals showing complete situs inversus or complete reversal of laterality are sporadically observed. A famous example is the rare sinistral mutant among common dextrals in *Lymnaea* snails (Sturtevant, 1923). Are the left-handed *Labidura riparia* without genital damage also such mutant individuals? Although *L. riparia* is almost entirely bilaterally symmetric other than in its genitalia, the left tegmen (forewing) overlaps the right one, as in the all earwig species (Haas, 1995). All male *L. riparia* samples examined in this study consistently showed this lateral tegmina state (the left over the right; data not shown). This finding suggests that laterality in the genitalia is controlled independently of that in the tegmina, at least to some degree. Similar side-switch phenomena that are restricted to male genitalia have been reported for several Mantodea and Blattaria species (Klass and Meier, 2006).

Relationship Between Structural and Behavioral Asymmetries

Dichotomous classification of animal asymmetries either into structural or behavioral categories is problematic when we consider the underlying mechanisms of "behavioral" asymmetries. For example, right-handedness in humans is considered to relate to the laterality in brain structures (structural asymmetries), even if there is no morphological difference between the right and left hands themselves (e.g., Bryden et al., 1997). Similarly, the resting state of *Labidura riparia* (R- or L-ready) may have presently unknown structural bases such as muscular and/or neural differentiations between the right and left penis lobes. Nevertheless, the following two characteristics illustrate that *L. riparia* represents a rare example of behavioral asymmetry preceding the evolution of structural asymmetry of the focal organ: 1) It is likely that most males of *L. riparia* die without having used their left penis, and nevertheless, 2) the left penis is potent without being apparently differentiated from the right penis.

These transitional characteristics are especially interesting when considering the evolutionary loss of a penis in the earwig phylogeny. This study demonstrated that all five species belonging to the Eudermaptera (the single-penis families) have a vestige of the left ejaculatory duct. This finding provides further support for the monophyly of this taxon, i.e., it is plausible that the left ejaculatory duct and penis were lost in the common ancestor of the Eudermaptera as a single evolutionary event. Given the possible sister relationship between the Labiduridae and the Eudermaptera, it is possible that such behavioral bias in penis use observed in *Labidura riparia* caused the eventual loss of the infrequently used left penis. To confirm that the behavioral laterality of *L. riparia* is not a species-specific phenomenon, future studies should test its generality among other members of the Labiduridae.

Recently, Will et al. (2005) compiled examples and explanations of "absence asymmetry," i.e., the "asymmetrical loss of a plesiomorphically paired organ," among animals. Examples in hexapods are astonishingly rare, even after adding the examples of earwig genitalia not included in their literature. They concluded that making room for expensive accessory reproductive glands is the most likely element associated with the loss of one testis (monorchy) in several carabid ground beetles. Females of scarab beetles and some aphid species have only one functional ovary (Halffter and Matthews, 1966; Woodward et al., 1970; Halffter and Edmonds, 1982), and monorchy has also been reported for ptiliid beetles (de Marzo, 1992). In these cases, the production of large gametes, coupled with space limitations, is a plausible cause for the absence of asymmetry (see Will et al., 2005 for details). Among these examples, the case of earwig genitalia is an exception, characterized by the redun-

dant nature of the presumed ancestral state; only one penis seems sufficient, unless accidental genital damage occurs (Kamimura, 2004a). In most earwig species, tiny penises seem almost free from competition for space in visceral packing. Why, then, did a spare penis degenerate in some ancestral earwigs? Irrespective of the presently unknown reason why the ancestor of earwigs had obtained two functional penises, it is easy to assume that mutant individuals devoid of the spare left penis had few disadvantages in reproductive success when the probability of genital accidents is fairly low. Clearly, comparative studies are needed to confirm the reduced risk of genital damage in earwigs possessing only a single penis.

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