

Atypical mating in a scorpionfly without a notal organ

Wen Zhong¹, Zi-Yi Qi¹, Bao-Zhen Hua^{1,2}

¹ State Key Laboratory of Crop Stress Biology for Arid Areas, Key Laboratory of Plant Protection Resources and Pest Management, Ministry of Education, Entomological Museum, Northwest A & F University, Yangling, Shaanxi 712100, China

² E-mail: huabzh@nwsuaf.edu.cn

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Abstract

Firm coupling of genitalia is critical for copulation in most groups of insects. To counter female resistance that usually breaks off genital connection, male scorpionflies (Mecoptera: Panorpidae) usually provide nuptial gifts for the female and seize their mates with grasping devices. The notal organ, a modified clamp on tergum III of male scorpionflies, plays a significant role in seizing the female wings and helping maintain mating position during copulation. The mating behaviour remains unknown for the scorpionfly *Furcatopanorpa longihypovalva* (Hua and Cai, 2009) whose male lacks a notal organ. In this paper, we first attempt to study the mating behaviour of *F. longihypovalva*. The results show that the male provides liquid salivary secretion through a mouth-to-mouth mode for the female, and maintains copulation mainly by continuous provision of salivary secretion rather than by seizing the female with grasping devices. Thus the male copulates with the female in an atypical O-shaped position, with only their mouthparts and genitalia connected to each other. The salivary glands exhibit remarkable sexual dimorphism: short and bifurcated in the female, but well-developed and multi-furcated in the male. The extremely developed salivary glands of the male lay a structural foundation for the male to continuously provide liquid salivary secretion, and to help the male to mediate female resistance, being likely to serve as a compensation to his absence of the notal organ. We also investigated the functional morphology and copulatory mechanism of the male and female genitalia. The evolution of the atypical mating pattern of *F. longihypovalva* is putatively discussed as an adaptation in the context of sexual conflict.

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Introduction

The firm coupling of genitalia is critical for successful copulation of internally inseminating insects (Matthews and Matthews, 2010; Chapman, 2013). This process, however, is frequently interrupted or terminated by the female during copulation due to sexual conflict (Parker, 2006). To counter female resistance, males usually seize their mates with modified grasping devices, including claspers and other non-genital structures (Eberhard, 2010). In some species of insects, including scorpionflies (Mecoptera: Panorpidae), males provide edible gifts for the female to help obtain copulation and mediate female resistance (Gwynne, 2008).

Scorpionflies are intriguing insects for their males having a genital bulb that is enlarged and recurved antero-dorsally, superficially resembling the tail of a scorpion (Byers, 2002). The male of scorpionflies usually employs elaborate nuptial feeding behaviour to obtain copulation with the female. Males of some Panorpidae species bear well-developed salivary glands (Grell, 1938; Ma *et al.*, 2011), thus they can secrete gelatinous salivary masses from their salivary glands as nuptial gifts to lure a female into copulation (Byers and Thornhill, 1983; Engqvist, 2007). If a male



Fig. 1. Copulation of *F. longihypovalva* (close-up photograph).

fails to offer salivary secretions, he alternatively provides a dead arthropod as a nuptial gift (Sauer *et al.*, 1998; Engqvist and Sauer, 2003). In some cases, the male can obtain copulation by seizing the female with his claspers and other grasping devices, rather than by provisioning nuptial gifts, the so-called ‘forced mating’ or ‘coercive copulation’ (Thornhill, 1981; Engqvist and Sauer, 2003).

In both the gift- and non-gift-providing copulations, the notal organ (a modified abdominal clamp on tergum III) of male scorpionflies is utilized to seize the female to maintain mating position (Thornhill, 1981; Thornhill and Sauer, 1991). In many *Panorpa* species, males clamp the anterior margin of wings of the female with the notal organ (Mickoleit, 1971), which is regarded as helpful to prolong copulation, especially against female interests (Thornhill and Sauer, 1991). Kock *et al.* (2009) contend this view because the notal organ of male *Panorpa vulgaris* Imhoff and Labram, 1836 does not prolong copulation after the last nuptial gift has been delivered. In *Neopanorpa longiprocessa* Hua and Chou, 1997, the extremely developed notal organ is utilized to steadily seize the female’s wings of one side, enabling the male to obtain copulation exclusively by seizing (Zhong and Hua, 2013b).

The notal organ not only plays a significant role in copulation (Thornhill and Sauer, 1991; Zhong *et al.*, 2015), but also exhibits a great diversity among vari-

ous species of Panorpidae (Issiki, 1933; Cheng, 1957). This important organ, however, is absent in the males of the scorpionfly *Furcatopanorpa longihypovalva* (Hua and Cai, 2009; Ma and Hua, 2011a). Here a question arises: how does such a male scorpionfly without a notal organ mate with the female? In this study, we investigate the mating behaviour and copulatory mechanism of *F. longihypovalva* to unravel the mating pattern of the scorpionfly without a notal organ.

Material and methods

Adult collecting

Adults of *F. longihypovalva* were collected along the Jialing River source (34°13’N, 106°59’E, elev. 1500–1800 m) in the Qinling Mountains, Shaanxi Province, China from the middle of May to the late June in 2013. All adults were caught at least a few days after eclosion because their bodies and wings were deeply pigmented.

Observation of the mating behaviour

The mating behaviour of *F. longihypovalva* was observed in the field, including the courtship, provisioning of nuptial gift, nuptial feeding, and copulation.

Photographs of mating behaviour were taken with a Nikon D200 digital camera (Nikon, Tokyo, Japan).

Light and scanning electron microscopy

For light microscopy, live adults were fixed in Carnoy's solution for 12 h before being preserved in 75% ethanol. Specimens were dissected under a Nikon SMZ1500 stereoscopic zoom microscope (Nikon, Tokyo, Japan). Male and female genitalia dissected were macerated in cold 5% sodium hydroxide solution for several hours and rinsed in distilled water. Micrographs were taken with a QImaging Retiga-2000R Fast 1394 Scientific CCD Camera (QImaging, Surrey, Canada) attached to a Nikon SMZ1500 microscope and were stacked with Syncroscope Auto-Montage software (Syncroscope, Cambridge, UK).

For scanning electron microscopy (SEM), ethanol-preserved specimens were dissected in 75% ethanol under a Nikon SMZ1500 microscope. The dissected genitalia and other genital components were dehydrated in a graded ethanol series after ultrasonic cleaning for 60 s. Then the samples were dried with liquid carbon dioxide in a critical-point dryer, sputter-coated with gold, and examined in a Hitachi S-3400N scanning electron microscope (Hitachi, Tokyo, Japan).

Morphology of the salivary glands

A total of 33 individuals of *F. longihypovalva* (18♂♂, 15♀♀) were dissected to study the morphology of the salivary glands. The salivary glands were rapidly dissected in Ringer's solution, and then fixed in Carnoy's solution for 12 h before being preserved in 75% ethanol. In addition, to avoid low nutritional status that may impede the development of salivary glands of males (Engqvist and Sauer, 2001; Engels and Sauer, 2008), we supplied the field-caught *F. longihypovalva* adults with sufficient dead arthropods before dissection and morphological investigation.

Results

Mating behaviour

Seven pairs of *F. longihypovalva* were observed to mate in the daytime: six in the afternoon and one in the morning. All of these matings were accompanied with nuptial feeding behaviour. The male exclusively provided liquid salivary secretion for the female. The

process of mating can be divided into two phases: courtship and copulation.

During courtship, the male vibrates his wings and swings his abdomen up-and-down rhythmically. Meanwhile, he releases sex pheromones from a pouch-like gland in the genital bulb to attract potential mates nearby (see Kock *et al.*, 2007). Once the male lured a female, he terminates the olfactory releasing, and secretes a drop of liquid salivary secretion, which adheres to his mouthparts. Then he moves to the lateral side of the female, seizing her abdominal segment IX with his gonostyli when she attempts to feed on the salivary secretion. Thus the male and female form an O-shaped mating position: the male and female only contact to each other with their mouthparts and genitalia (Fig. 1).

During copulation, the male continuously transfers liquid salivary secretion to the female by a mouth-to-mouth mode. The female usually cooperates with the male to maintain stable mating position when feeding on salivary secretion. After the male stopped providing salivary secretion, the female terminates copulation by lashing her abdomen to break off the genital coupling and then leaves the male.

Gross morphology of the salivary glands

The salivary glands are tubular labial glands, opening at the bottom of the salivarium between the labium and hypopharynx. They are similar to those of *Panorpa* species (see Grell, 1938). The salivary glands exhibit spectacular sexual dimorphism between the sexes: simply bifurcated and short in the female, but well-developed and multiple-furcated in the male (Fig. 2).

The salivary glands are undeveloped and short in the females, extending only to the prothorax, and consist of a salivary pump, a common salivary duct, and a pair of short secretory tubes. The salivary pump is swollen, and connects ventrally with the labium. The common salivary duct extends from the posterior end of the salivary pump, and runs along the rostrum, finally bifurcating to form a pair of secretory tubes (Fig. 2a).

The salivary glands are extremely well-developed in the males (Fig. 2b), usually extending to abdominal segment VI. The male salivary pump is very similar to that of the female. The common salivary duct extends posteriorly from the salivary pump along the rostrum of head and divides into two branches (salivary ducts) above the suboesophageal ganglion. Each of the branches expands into a sac and is subdivided

into three secretory tubes subsequently, resulting in six secretory tubes in the thorax. The subsequent parts of the salivary glands twine around the gut and branch twice in a dichotomous way, eventually form-

ing 24 distal secretory tubules that are convoluted in abdominal segments V and VI (Fig. 2b). In the male salivary glands, no prominent reservoirs were observed.

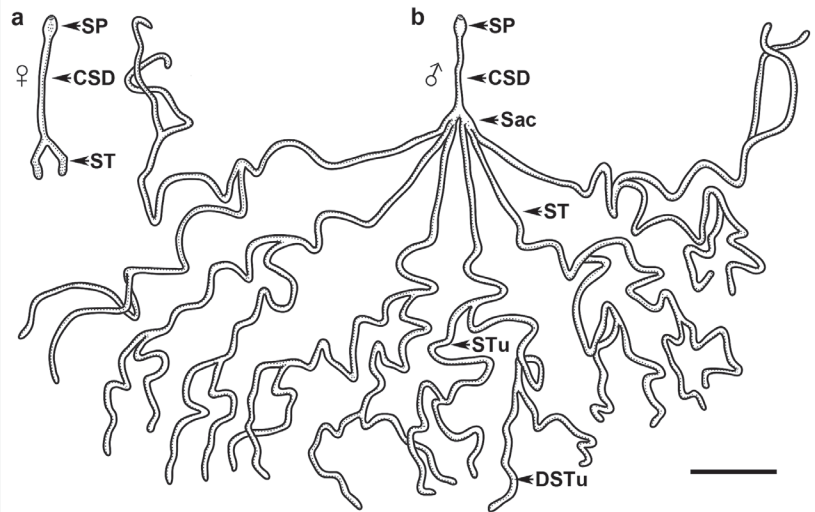


Fig. 2. Sexual dimorphism on salivary glands of *F. longihypovalva* (drawings). a, simple and undeveloped female salivary glands; b, well-developed male salivary glands. CSD, common salivary duct; DSTu, distal secretory tubule; SP, salivary pump; ST, secretory tube; STu, secretory tubule. Scale bar = 2.0 mm.

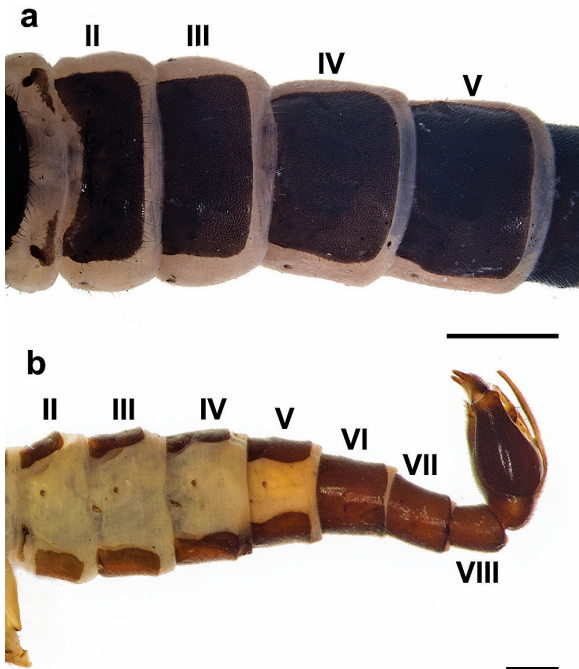


Fig. 3. Abdominal segments of male *F. longihypovalva* (microphotographs). a, dorsal view, scale bar = 0.5 mm; b, lateral view, scale bar = 1.0 mm.

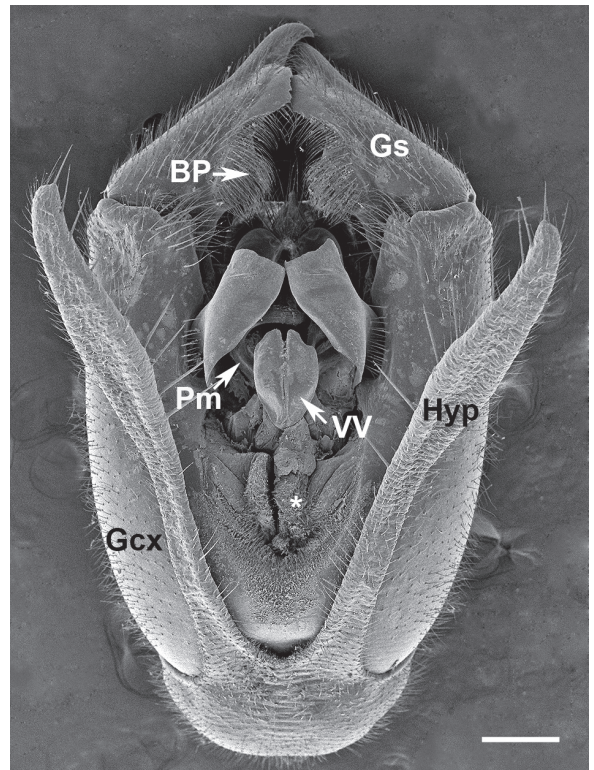


Fig. 4. Male genital bulb of *F. longihypovalva*, ventral view (SEMs). BP, basal process; Gcx, gonocoxite; Gs, gonostylus; Hyp, hypovalve; Pm, paramere; VV, ventral valve of aedeagus; *, pheromone gland. Scale bar = 300 μ m.

Male abdominal segments

The abdominal segments of males are simple in structure for terga II-V. It can be clearly seen that tergum III is devoid of a notal organ both from dorsal and lateral views (Fig. 3). Abdominal segments VI-VIII are greatly sclerotized into a ring. Tergum VI lacks any anal horn, and segments VII and VIII are thick and shortened, not constricted at the basal part (Fig. 3b).

Male genitalia

The male genitalia consist of the dorsal epandrium (tergum IX), the ventral hypandrium (sternum IX), the paired lateral gonopods, and the central aedeagal complex (Fig. 4).

The epandrium and hypandrium are fused at base, cupping the median aedeagal complex and the lateral gonopods. The epandrium is broad at the base and narrower toward the apex. The hypandrium is composed of a very short stalk and a pair of elongated hypovalves, each of which bears 8-10 thick bristles along the inner margin (Fig. 4).

The gonopod is composed of the basal gonocoxite and the distal gonostylus. The paired gonocoxites are fused together at the base, forming a deep U-shaped cavity, in which the aedeagal complex is inserted centrally (Fig. 4). The distal gonostyli serve as claspers during copulation. Each gonostylus has a broad basal process, which bears numerous setae and is serrate in distal margin. The median tooth is also broad and serrate in apical margin.

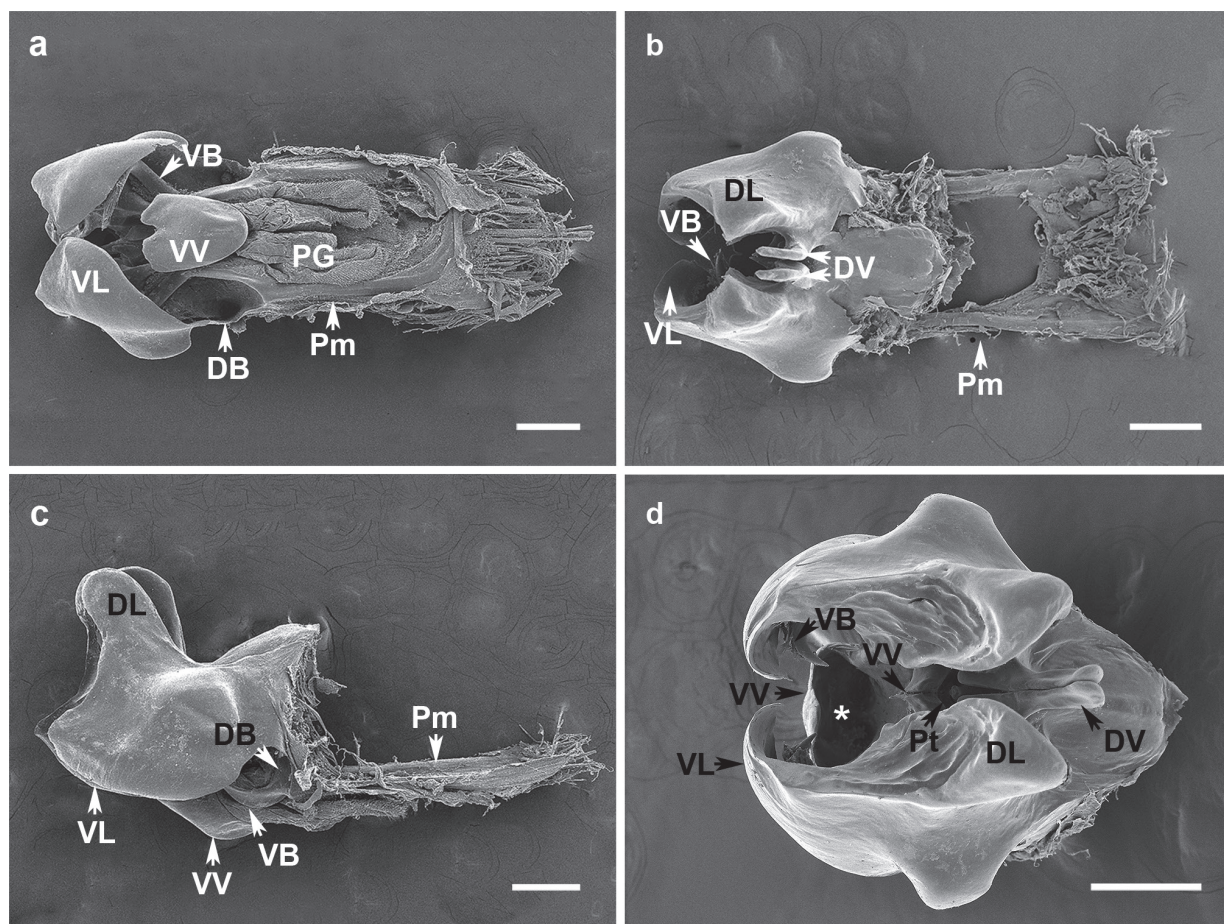


Fig. 5. Aedeagus and parameres of *F. longihypovalva* (SEMs). a, ventral view; b, dorsal view; c, lateral view; d, caudal view. DB, dorsal branch of paramere; DL, dorsal lobe of dorsal branch; DV, dorsal valve of aedeagus; PG, pheromone gland; Pm, paramere; Pt, phallosome; VB, ventral branch of paramere; VL, ventral lobe of dorsal branch; VV, ventral valve of aedeagus; *, ventral pouch of aedeagus. Scale bars = 200 μ m.

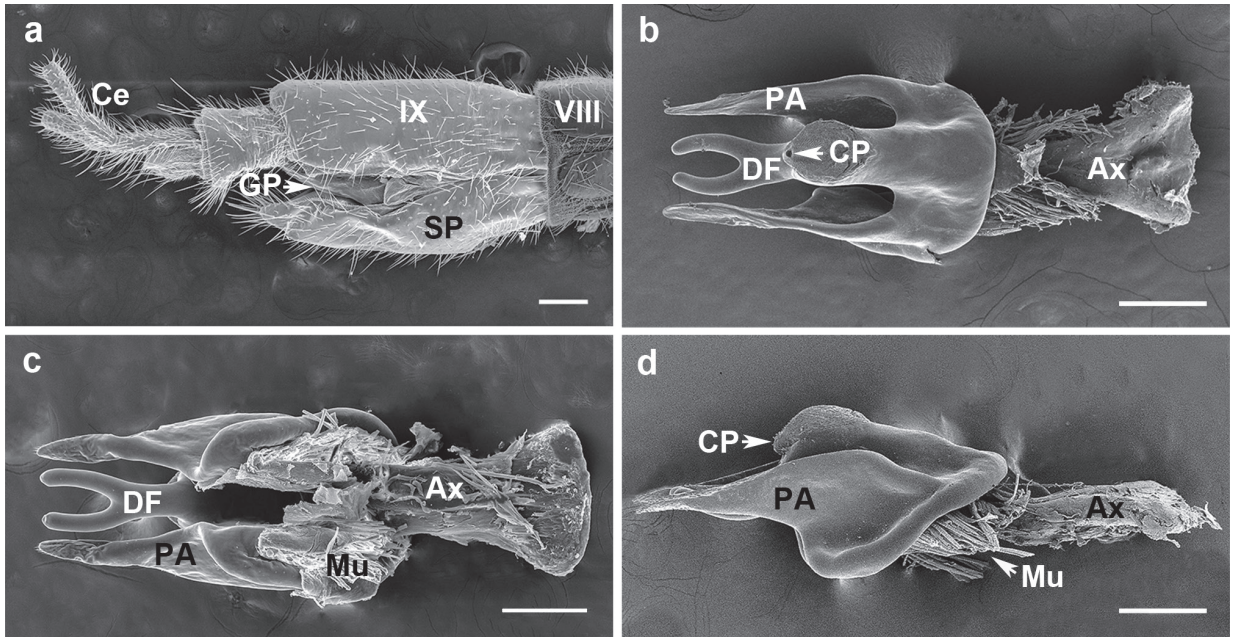


Fig. 6. Female genitalia of *F. longihypovalva* (SEMs). a, abdominal segments VIII-XI, lateral view; b-d, genital plate in ventral, dorsal, and lateral views. Ax, axis; Ce, cercus; CP, copulatory pore; DF, distal fork; GP, genital plate; Mu, muscles; PA, posterior arm; SP, subgenital plate; VIII and IX, tergum VIII and IX. Scale bars = 200 μ m.

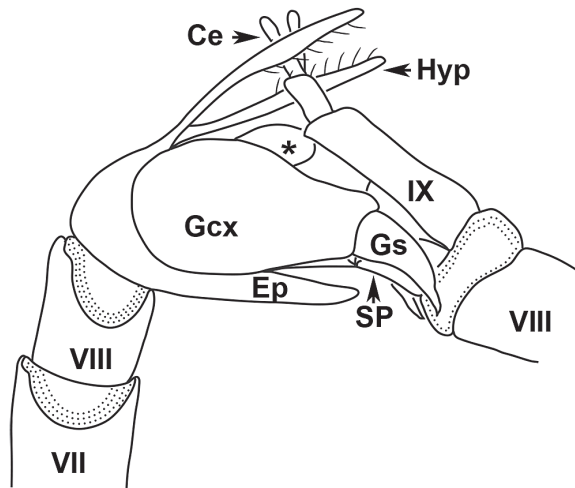


Fig. 7. Schematic drawing of the male grasping the abdomen of female with claspers and other grasping devices in copulation. Ce, cercus; Ep, epandrium; Gcx, gonocoxite; Gs, gonostylus; Hyp, hypovalve; SP, subgenital plate; VII, VIII, and IX, abdominal segment VII, VIII, and IX; *, everted swollen pheromone gland.

The aedeagal complex consists of an aedeagus and associated parameres. The aedeagus is composed of paired bilobed ventral and dorsal valves, basally fused with a pair of parameres (Figs 5a-c). The basal part of

ventral valves produces caudally from the base of aedeagus, being mesally fused to form a deep cuculiform pouch (Figs 5a, c, d). The weakly-developed distal parts of ventral valves are mesally fused with each other and are concealed behind the dorsal branch of parameres in ventral view, surrounding the phallotreme with dorsal valves to form a concavity (Figs 5a, d). The dorsal valves are slender and narrower toward the apex, and separated from each other (Figs 5b, d).

The paramere is Y-shaped in ventro-lateral view: a single basal stalk bifurcates into a slender ventral branch and a well-developed dorsal branch. The basal stalk is fused with the opposite one at the base (Figs 5a, b). The dorsal branch consists of a mesally curved ventral lobe and a broad dorsal lobe (Fig. 5c). The ventral branch is slender, twists in an S-shape at the distal half, which is densely set with long setae and is concealed behind the ventral lobe of dorsal branch in ventral view (Figs 5a, d).

Female genitalia

The female genitalia are located on the ventral side of abdominal segment IX, and consist of a subgenital plate and a genital plate (Fig. 6a). The subgenital plate curves dorsally on posterior and lateral sides to form a shallow

genital chamber above, in which the genital plate is situated. The genital plate consists of a main plate and a central axis. The broad main plate curves ventrally on lateral sides and extends caudally to form a pair of thick posterior arms. The axis passes through the main plate from dorsal to ventral side, and extends beyond the main plate slightly less than half its length. The posterior end of the axis protrudes beyond the main plate, with regular sculpturing on the ventral surface and a small copulatory pore (the orifice of the spermathecal duct) situated medially at the posterior apex. The main plate covers the posterior end of the axis from dorsal side, and bifurcates to form a pair of branches, the distal fork *sensu* Ma and Hua (2011a) (Figs 6b, c). In addition, bundles of longitudinal muscles attach to the anterior part of the axis as well as the dorsal surface of the main plate (Figs 6c, d). These muscles can stretch the genital plate out of the genital chamber, and allow the female copulatory pore to connect to the phallotreme of the male aedeagus.

Coupling of the genitalia

Stable coupling of the genitalia between the sexes ensures continuous sperm transfer, which is vital for a successful copulation. The structures of male genitalia can be divided into a central intromittent organ (the aedeagal complex in this context) and associated grasping devices. In scorpionflies the aedeagal complex is employed to connect to the orifice of the female spermathecal duct on the distal end of the genital plate to form a pathway for sperm transfer during copulation. The grasping devices include the gonostyli, epandrium, and hypovalves, and are used to grasp the particular part of the female body to ensure genital coupling. During copulation, the male seizes the basal abdominal segment IX of the female with his gonostyli, to open her genital chamber and to compel her to stretch out her genital plate. In addition, he uses his hypovalves to seize the abdominal segment IX or the cerci of the female, and keeps his pouch-like pheromone gland to swollen. This gland pushes up the abdominal segments X and XI of the female, thus opening the female genital chamber and enabling the phallotreme of the male aedeagus to contact to the copulatory pore of the female (Fig. 7).

Discussion

In the panorpid species whose mating behaviours have been studied to date, all the males use nuptial gifts and

grasping devices or both to obtain copulation with the female (Engqvist and Sauer, 2003; Ma and Hua, 2011b). For both tactics, the male seizes the female with his notal organ to sustain mating position (Thornhill and Sauer, 1991). In our present research of mating behaviour in *F. longihypovalva*, whose male is devoid of a notal organ, we found a novel, atypical mating pattern in the Panorpidae for the first time. The male and female copulate in an O-shaped manner with their mouthparts and genitalia connected to each other (Fig. 1), remarkably different from the V-shaped mating position in other scorpionflies studied (Ma and Hua, 2011b; Zhong and Hua, 2013b; Zhong *et al.*, 2015).

Owing to the absence of the notal organs in male *F. longihypovalva* (Ma and Hua, 2011a), it is reasonable for the male not to seize the female with that kind of clamping device. Instead, the male mediates the female resistance mainly by providing liquid salivary secretion as a nuptial gift through a mouth-to-mouth feeding during copulation, resembling the trophallaxis of social termites and ants to a great extent (Matthews and Matthews, 2010). This nuptial feeding behaviour is greatly different from that of other Panorpidae species whose male adheres solid or gelatinous salivary secretions on a leaf surface for the female (Thornhill and Alcock, 1983; Zhong *et al.*, 2015). Based on morphological studies by this investigation and others (Hua and Cai, 2009; Ma and Hua, 2011a), we assume that the formation of this atypical mating pattern is related to the well-developed salivary glands of the male and the genitalia of the male and female.

The greatly developed salivary glands of male *F. longihypovalva* provide a structural basis for this particular nuptial feeding behaviour, in which the male continuously provides liquid salivary secretion to the female. It is different from many other species of Panorpidae, whose males provide solid or gelatinous salivary secretion. This solid or gelatinous salivary secretion may be attributed to the male salivary glands of these species that include a dilated middle salivary reservoir to dehydrate liquid salivary secretion produced by the posterior secretory region (Ma *et al.*, 2011). We assume that the dehydrated solidified salivary secretions can lead the female to spend more time to consume the nuptial gifts, thus prolonging the copulation duration. In male *F. longihypovalva*, the middle salivary reservoir of the salivary glands is reduced or even absent. Furthermore, the secretory region is extremely elongated and each secretory tube bifurcates twice to form 24 distal secretory tubules totally. The combination of developed secretory region and undeveloped

middle dilated salivary reservoirs likely result in the failure of the male to dehydrate salivary secretion and to produce solidified salivary secretions. As a compensation, the developed secretory region of salivary glands is likely to greatly improve the male’s ability to produce salivary secretion, enabling the male to continuously provide liquid salivary secretion to sustain copulation. This is one of the possible explanations why the male continuously provides liquid salivary secretion through a mouth-to-mouth feeding.

In scorpionflies nuptial-gift-providing mating is much more effective to copulation than coercive mating (Sauer *et al.*, 1998; Kullmann and Sauer, 2009). On the other hand, seizing the female with his notal organ is likely not effective to mediate the female resistance or prolong copulation duration, as in *Panorpa vulgaris* (Kock *et al.*, 2009). The modified complex female genitalia of *F. longihypovalva* may reduce the ability of the male to copulate against female interests. The distal fork of the female genital plate increases the difficulty of coercive copulation by obstructing the coupling of genitalia. Based on morphological investigation, we assume that a male has to accurately locate the distal fork of the female genital plate into the ventral pouch of his aedeagus, thus he could correctly connect his phallotreme with the female copulatory pore to ensure sperm transfer. The female, however, can still easily break off the coupling of genitalia to terminate the copulation through retreating her genital plate. In this case, seizing the female only with his notal organ or

other clasping devices can have little help in obtaining copulation, which needs cooperation between the male and female. Thus we assume that in male *F. longihypovalva*, continuous provisioning of salivary secretion as nuptial gifts is likely used to ‘buy’ the female’s cooperation to obtain and sustain copulation. The salivary glands, notal organ, and genitalia of male and female likely play essential roles in the formation of the mating behaviour of *F. longihypovalva*. We summarized the morphological differences of these structures between *F. longihypovalva* and the ‘typical’ panorpid as exemplified by *Panorpa dubia* Chou in Table 1.

Sexual conflict is caused by divergent reproductive, evolutionary, and genetic interests between the sexes (Chapman *et al.*, 2003; Parker, 2006), and may also contribute to the formation of this atypical mating behaviour in *F. longihypovalva*. In the mating of scorpionflies, sexual conflict is mainly expressed as the fierce contest on control over nuptial gifts (Engqvist, 2011). Because providing salivary masses requires a huge nutrient investment for the male (Sauer *et al.*, 1998; Engels and Sauer, 2006), it is the male’s interest to avoid wasting his salivary secretion so as to maximize the number of his mates and guarantee his mating success rate (Zhong *et al.*, 2015). On the other hand, the female struggles to consume maximum salivary masses, probably impeding subsequent matings of the male (Engqvist, 2009). The males of *F. longihypovalva* have successfully solved this problem by con-

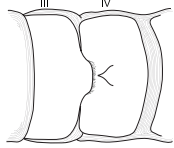
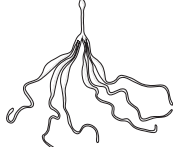
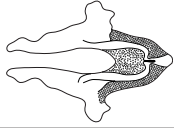

	<i>F. longihypovalva</i>		‘Typical’ panorpid <i>Panorpa dubia</i> Chou
Male notal organ	lacking (Fig. 3a)		moderately- or well-developed
Male salivary glands	secretory tubes bifurcated twice; , reservoirs undeveloped not expanded (Fig. 2b)		secretory tubes bifurcated once or not; reservoirs developed, usually expanded
Male aedeagus	with a ventral pouch (Figs 5a, d)		without a ventral pouch
Female genital plate	with a distal fork (Fig. 6b)		without a distal fork

Table 1. Morphological differences between *F. longihypovalva* and ‘typical’ panorpids.

tinuously providing liquid salivary secretion to the female through mouth-to-mouth feeding during copulation. It enables the male to terminate provisioning nuptial gift immediately if the female terminates copulation, thus avoiding wasting salivary secretion in fruitless courtship and failed matings that are too short to transfer enough sperm. Furthermore, continuous provisioning of liquid salivary secretion invalidates snatching of nuptial gifts by the female or conspecific males.

Based on the developmental degrees of the male notal organ and salivary glands, the nuptial feeding behaviour of scorpionflies can be broadly divided into four types: solid-salivary-mass-dominant mating, prey-gift-only mating, coercive copulation, and liquid-salivary-only mating. In the first type of mating, males of many *Panorpa* species mainly provide salivary secretions to obtain copulation, sporadically employing coercive copulation. These species bear a moderately developed notal organ (Zhong and Hua, 2013a: Fig. 1F), and have developed salivary glands (Ma *et al.* 2011: Fig. 1), which are able to produce enough salivary secretions as nuptial gifts (Grell, 1938; Engqvist, 2007; Kock *et al.*, 2009; Zhong *et al.*, 2015). In the second type, males of some *Panorpa* species, as exemplified in *P. liui* Hua and Chou, 1997, *P. nuptialis* Gerstaecker, 1863, and *P. japonica* Thunberg, 1784, have a moderately developed notal organ and reduced or weakly-developed salivary glands (Ma and Hua, 2011b: Figs 1, 2). They can only provide dead arthropods as nuptial gifts to the female or employ a coercive copulation since they are unable to produce enough salivary masses (Byers, 1963; Thornhill, 1992; Ma and Hua, 2011b). In the third type, males of *Neopanorpa longiprocessa* exclusively employ coercive copulation and provide no nuptial gifts. They bear a greatly developed notal organ (Zhong and Hua, 2013b: Figs 1, 3) and moderately developed salivary glands (Ma *et al.* 2011: Figs 2F, G), which are also unable to produce enough salivary secretions (Zhong and Hua, 2013b). In *F. longihypovalva*, owing to the absence of a notal organ, the male exclusively relies on a unique liquid-salivary-only nuptial feeding through a mouth-to-mouth transfer. Concomitantly, the male has extremely developed salivary glands to provide sufficient liquid salivary secretion to the female during copulation. This atypical mating behaviour of *F. longihypovalva* provides additional new evidence to support our recently proposed hypothesis that the developmental degree of salivary glands is negatively correlated with the notal organ in male scorpionflies (Zhong and Hua,

2013b). This hypothesis may help understand the formation and diversity of mating patterns of Panorpidae species in morphological aspect.

From a phylogenetic point of view, *F. longihypovalva* may evolve early in Panorpidae based on morphological characters (Ma and Hua, 2011a; Ma *et al.*, 2012). The morphological phylogenetic analysis indicates that the genus *Furcatopanorpa* forms a sister taxon to all the other genera in Panorpidae (Ma *et al.*, 2012). This probably explains why the mating behaviour of *F. longihypovalva* differs markedly from that of other panorpid in phylogenetic aspect. The recent molecular phylogenetic study, however, shows that *F. longihypovalva* forms a sister-group relationship with *Panorpa liui* based on mitochondrial and nuclear gene sequences (Hu *et al.*, 2015). From a behavioural point of view, this conclusion seems strange because the mating behaviours of *F. longihypovalva* and *P. liui* differ remarkably from each other as mentioned above. Further research is needed to solve this contradiction problem.

A similar mating pattern is also present in the mecopteran family Choristidae (Tillyard, 1926; Riek, 1970). According to R. Thornhill (personal communication), the males of *Chorista australis* Klug, 1836 in New South Wales, Australia, also lack a notal organ. The male and female *C. australis* form the O-shaped mating position and contact each other with mouthparts during copulation. This behaviour is regarded as a transfer of liquid salivary secretion from the male to the female through a mouth-to-mouth mode. In addition, Thornhill's observation shows that male *C. australis* does not provide salivary masses or putting salivary secretions on the substrate as nuptial gifts as in most other panorpid (R. Thornhill, personal communication). Since Choristidae is the sister group of Panorpoidea (Panorpidae + Panorpodidae) (Willmann, 1987), the absence of a notal organ and the O-shaped mating behaviour are very likely plesiomorphic characters in scorpionflies, suggesting that mating behaviour is closely related with morphology and may play a significant role in evolutionary and phylogenetic analyses in Mecoptera.

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