

Functional morphology of the larval mouthparts of Panorpididae compared with Bittacidae and Panorpidae (Insecta: Mecoptera)

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Abstract In Mecoptera, the larvae of Bittacidae and Panorpidae are saprophagous, but the feeding habit of larval Panorpididae remains largely unknown. Here, we compare the ultramorphology of the mouthparts of the larvae among the hangingfly *Bittacus planus* Cheng, 1949, the scorpionfly *Panorpa liui* Hua, 1997, and the short-faced scorpionfly *Panorpodes kuandianensis* Zhong, Zhang & Hua, 2011 to infer the feeding habits of Panorpididae. The molar region of Panorpididae is glabrous, lacking the long spines for filtering (preventing larger particles from entering the pharynx) as found in Bittacidae or the tuberculate teeth for grinding as present in Panorpidae. The mandibles of Panorpididae are unsuitable for grinding, and most likely, larval Panorpididae have different feeding habits than larval Bittacidae and Panorpidae. The diversity of the larval feeding habits in Mecoptera and its evolutionary advantage are briefly discussed.

Keywords Panorpididae · Bittacidae · Panorpidae · Larva · Mouthparts · Feeding habits

Introduction

Mecoptera is a small order of holometabolous insects, composed of nine extant families, and exhibiting a high degree of

morphological and biological diversity (Byers and Thornhill 1983; Byers 1987, 1991; Grimaldi and Engel 2005; Ma et al. 2009, 2012). The feeding habits of adult Mecoptera vary among families (Palmer 2010): predacious in Bittacidae (Tan and Hua 2006; Ma et al. 2014b), phytophagous in Boreidae and Panorpididae (Carpenter 1953; Russell 1982; Beutel et al. 2008; Ma et al. 2013), and saprophagous in Panorpidae, Apteropanorpidae, Choristidae, Eomeropidae, and Meropidae (Palmer and Yeates 2005; Palmer 2010; Huang and Hua 2011). The knowledge of the feeding habits of larval Mecoptera, however, is still fragmentary.

The larvae of Mecoptera are morphologically diverse and inhabit a wide range of habitats (Byers 1987, 1991). The larvae of Nannochoristidae are campodeiform and live in the substrate of shallow streams (Pilgrim 1972; Beutel et al. 2009; Fraulob et al. 2012). The larvae of Boreidae are scarabaeiform and creep on or bore in live liverworts (Cooper 1974; Russell 1982). The larvae of Choristidae, Apteropanorpidae, Bittacidae, and Panorpidae are eruciform and have an edaphic lifestyle (Miyaké 1912; Setty 1940; Byers 1987, 1991; Tan and Hua 2008, 2009; Jiang and Hua 2013; Jiang et al. 2015). The larvae of Panorpidae are either epedaphic (living on soil surface as of *Panorpa obtusa*) or euedaphic (living underground as of *Neopanorpa lui*) (Jiang and Hua 2015). However, the feeding habits of larval Panorpididae remain largely unknown to date, although the morphology of the larvae is known (Carpenter 1953; Byers 1997; Pollmann et al. 2008; Jiang et al. 2014).

Mouthparts are closely associated with the feeding habits of insects (Stehr 1987; Labandeira 1997; Jervis 1998; Smith and Capinera 2005). The larval mouthparts of the scorpionfly *Panorpa communis* L. (Steiner 1930; Grell 1938; Potter 1938; Bierbrodt 1942), the snow scorpionfly *Boreus hyemalis* L. (Potter 1938), and the

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hangingflies *Apterobittacus apterus* (MacLachlan) and *Bittacus pilicornis* Westwood (Applegarth 1939; Setty 1940) were described using light microscopy. Recently, the larval mouthparts of Nannochoristidae (Beutel et al. 2009), Bittacidae (Jiang et al. 2015), and Panorpididae (Chen and Hua 2011; Ma et al. 2014a; Jiang and Hua 2015) are studied using scanning electron microscopy. However, morphological comparisons of mouthpart components in relation to their feeding habits have not been conducted.

The objective of this study was to unravel the feeding habits of Panorpididae through comparing the larval mouthparts of the short-faced scorpionfly *Panorpodes kuandianensis* Zhong, Zhang & Hua, 2011 with those of the hangingfly *Bittacus planus* Cheng, 1949 and of the scorpionfly *Panorpa liui* Hua, 1997, using scanning electron microscopy. In addition, the feeding behavior of the larvae was observed both in the field and in the laboratory.

Materials and methods

Insect collecting

Live adults of *B. planus* were captured using sweeping nets along the Jialing River source (34° 13' N, 106° 59' E, elev. 1500–1800 m) in the Qinling Mountains, Shaanxi Province of central China, from the middle of July to late August in 2013. Adults of *P. liui* and *P. kuandianensis* were collected from Huabo Mountain (41° 06' N, 125° 02' E, elev. 650–1100 m) in Liaoning Province, northeastern China, from late June to early August in 2010–2014.

Insect rearing

Adults of *B. planus* were reared in nylon gauze cages (40 cm × 40 cm × 60 cm) under semi-natural conditions (Tan and Hua 2009). Live potted plants were provided for suspending adults. Live houseflies were supplied three times a day. A piece of wet tissue was put on the bottom of cages for egg collection. Eggs were collected twice a day and transferred into plastic jars containing moist soil for overwintering. Larvae were collected from the soil surface in late March 2014.

Adults of *P. liui* and *P. kuandianensis* were reared in pairs in plastic jars covered with a piece of gauze under natural conditions (Jiang and Hua 2013; Jiang et al. 2014). The jars were filled with 4–5 cm of humid soil for the deposition of eggs. The adults and larvae of *P. liui* were provided daily with chopped mealworms. Adults of *P. kuandianensis* received drops of honey twice a day. First-instar larvae were collected from inside the soil.

Feeding experiments

For observing the feeding behavior, larvae were reared in plastic jars with humid soil at the bottom. The larvae of Bittacidae and Panorpididae were daily provided with chopped meal worms or housefly pupae on the soil surface. The larvae of Panorpididae were provided additionally with locally collected decayed leaves, stems, flowers, and roots. The feeding behavior was observed every 2 h during day time. Photographs were taken using a Nikon D90 digital camera (Nikon, Tokyo, Japan).

Scanning electron microscopy

For scanning electron microscopy (SEM), the larvae were fixed in Carnoy's solution for 12 h and preserved in 75 % ethanol. The fixed larval mouthparts were dissected and serially dehydrated in a graded ethanol series, replaced by tertiary butanol, freeze-dried for 3 h, sputter-coated with gold, and examined under a Hitachi S-3400N scanning electron microscope (Hitachi, Tokyo, Japan) at 5 kV.

Results

Larval feeding habits

The larvae of *B. planus* are saprophagous, feeding especially on the inner semi-fluid tissues of dead insects. Larvae crawl around appropriate dead insects, using their mandibles to pierce and cut the cuticle; insert their heads into the body cavity to chew the soft tissues; and at the end leave an empty exoskeleton on the ground (Fig. 1).

The larvae of *P. liui* are also saprophagous, consuming both the soft tissues and chitinous cuticle of dead insects. When the larvae find an appropriate dead insect, they burrow beneath it to feed on the carrion. The larvae usually pull small fragments into their burrow and feed on them underground.

The feeding habit of *P. kuandianensis* larvae remains unclear. During our rearing experiments, the larvae fed neither on dead arthropods nor on plant leaves, stems, seeds, and roots. Although a dark line was visible through the transparent



Fig. 1 A larva of *Bittacus planus* feeding on a housefly pupa

larval trunk (indicating the larvae had eaten some material), all the larvae died before molting within 19 days after hatching.

Gross morphology of the mouthparts

The larval mouthparts of Bittacidae, Panorpidae, and Panorpididae all are of the mandibulate (biting/chewing) type, consisting of a labrum-epipharynx, paired mandibles and maxillae, and a labium (Fig. 2).

The labrum is sub-rectangular, articulated proximally with the anterior region of the clypeus, and furnished apically with two pairs of setae (Fig. 2a–c: lm). The epipharynx is situated on the ventral surface of the labrum (Fig. 2d–f: ep) and is furnished with numerous microtrichia and various types of sensilla arranged symmetrically.

The paired mandibles are strongly sclerotized, curved inward, and cross each other apically (Fig. 2a–c: md). The mandible is typically dicondylic, bearing a notched ginglymus and a knob-like condyle on the dorsal and ventral corners, respectively (Fig. 2a–c: gg/cd). The mandible bears three sensilla trichodea on the lateral surface.

The paired maxillae each consist of a cardo-stipes, a galea, a lacinia, and a palp (Fig. 2d–f: mx). The basal cardo-stipes is

kidney-shaped, fused from the original cardo and stipes, and connected distally to the galea and lacinia medially and bears the palp laterally. The galea is weakly sclerotized at the basal half and membranous at the apical half, which bears numerous sensilla and microtrichia. The lacinia is quite small, broadly connected with the galea, and bears plenty of microtrichia on the mesal surface. The maxillary palp is three-segmented.

The labium is somewhat reduced and is composed of a postmentum, a prementum, and a pair of palpi (Fig. 2d–f: lb). The postmentum is merged with the cranium and bears two pairs of sensilla chaetica on the ventral surface. The prementum is mesally divided by the orifice of the salivary duct and connected distally with a pair of two-segmented palpi, which bear various numbers of sensilla on the apex (Fig. 2d–f).

Mouthparts of *B. planus*

The labrum is furnished apically with two pairs of labral setae and numerous microtrichia. The inner pair of setae is approximately two thirds the length of the outer pair (Fig. 3a: ls).

The epipharynx is grossly subdivided into a terminal rectangular plate and a proximal triangular plate, both furnished

Fig. 2 Mouthparts of the first-instar larvae. **a, d** *Bittacus planus*. **b, e** *Panorpa liui*. **c, f** *Panorpodes kuandianensis*. **a–c** Frontal views. **d–f** Ventral views. *ep* epipharynx, *cd* condyle, *gg* ginglymus, *lb* labium, *lm* labrum, *md* mandible, *mx* maxilla

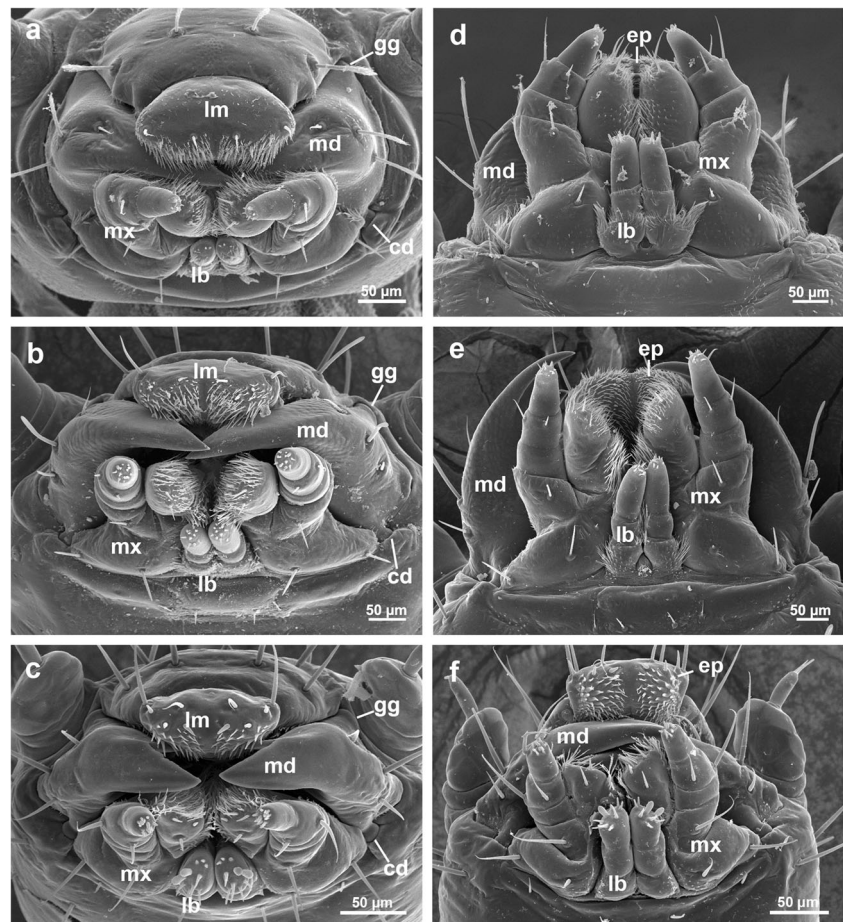
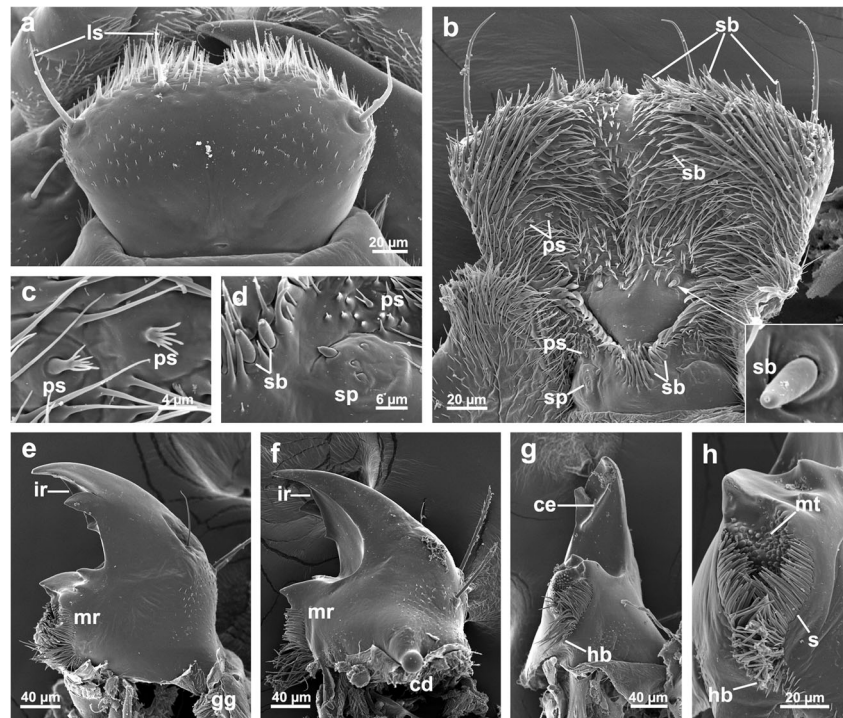


Fig. 3 Mouthparts of *Bittacus planus*. **a** Labrum. **b** Epipharynx. **c** Lateral palmate sensilla. **d** Sensory protuberance. **e–h** Mandibles, dorsal (**e**), ventral (**f**), and mesal views (**g**) and magnified aspect of the molar region (**h**). *cd* condyle, *ce* cutting edge, *gg* ginglymus, *hb* hair brush, *ir* incisor region, *ls* labral seta, *mr* molar region, *mt* molar teeth, *ps* palmate sensillum, *s* spine, *sb* sensillum basicicum, *sp* sensory protuberance



with numerous lateral microtrichia and various types of sensilla (Fig. 3b). Uniporous sensilla basiconica are arranged into two groups: three pairs on the apex of the epipharynx and four pairs on the inner surface (Fig. 3b: sb). The epipharynx is also furnished with two pairs of palmate sensilla on the lateromedial part (Fig. 3b, c: ps). The triangular plate is encompassed by two rows of spines and a basal tuft of microtrichia. This plate is equipped laterally with a pair of palmate sensilla (Fig. 3d: ps) and a pair of prominent sensory protuberances (Fig. 3d: sp), each bearing one larger and three smaller sensilla basiconica (Fig. 3d: sb).

The mandible is curved, tapers apically, and bears two distal cusps and a sharp cutting edge at the incisor region (Fig. 3e–g: ce/ir). The molar region is furnished with tuberculate molar teeth (Fig. 3h: mt), which are bordered laterally by long stiff spines (Fig. 3h: s). The mandible bears a tuft of hair brush (Fig. 3h: hb) sensu Lawrence (1991) on the baso-mesal corner and three long sensilla trichodea laterally. The middle one is shorter and setiform, and the basal two are longer and brush-shaped apically (Fig. 3f).

In total, the maxilla bears eight sensilla chaetica on the ventral surface: three on the cardo-stipes, one on the basal palpomere, two on the second palpomere, and two on the galea (Fig. 4a: sch). The galea bears dorsally numerous microtrichia and sensilla (Fig. 4b), including five sensilla basiconica on the apical half (Fig. 4c: sb) and two sensilla campaniformia on the basal half (Fig. 4d: sco). The lacinia is equipped with stiff spines directed mesally (Fig. 4b: s). The maxillary palp bears 14 sensilla basiconica apically (Fig. 4e).

The labium is remarkable for the hirsute prementum (Fig. 4a: prm), which is furnished with tufts of long microtrichia. The basal segment of the labial palp has mesally a short sensillum chaeticum subapically, and the apical segment has nine sensilla basiconica apically (Fig. 4f).

Mouthparts of *P. liui*

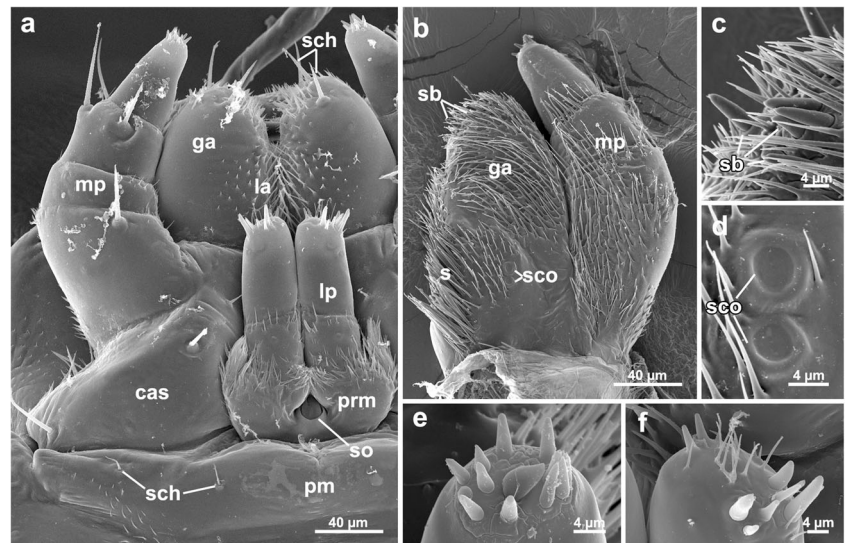
The labrum bears two pairs of setae at the apex, with the inner pair about half the length of the outer pair (Fig. 5a: ls).

The epipharynx is equipped with short microtrichia and various types of sensilla, including three pairs of sensilla basiconica at the apex, four pairs of uniporous sensilla basiconica along the mid-line (Fig. 5b: sb), and two pairs of palmate sensilla on the lateral part (Fig. 5c: ps). The triangular plate is equipped with numerous spines along the lateral edges, and is also furnished laterally with a pair of palmate sensilla and a pair of prominent sensory protuberances (Fig. 5b: ps/sp), which bear four minute sensilla basiconica (Fig. 5d).

The mandible bears apically two cusps and a cutting edge on the incisor region (Fig. 5e–g: ce/ir) and tuberculate teeth on the basal molar region (Fig. 5h: mt), which is bordered by two rows of short spines (Fig. 5h: s). Additionally, the mandible also bears three sensilla trichodea on the lateral surface and a hair brush tuft on the baso-mesal corner (Fig. 5h: hb).

The maxilla has eight sensilla chaetica on the ventral surface (Fig. 6a: sch), arranged in a pattern similar to that of

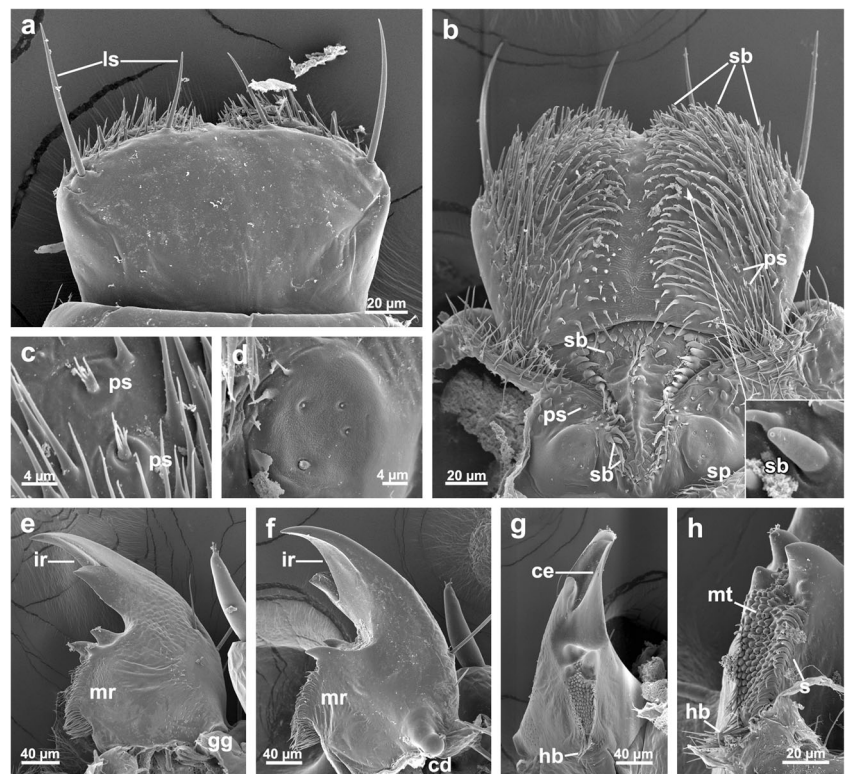
Fig. 4 Mouthparts of *Bittacus planus*. **a** Mouthparts, ventral view. **b** Maxilla, dorsal view. **c** Sensilla basiconica on maxilla. **d** Sensilla campaniformia on maxilla. **e** Apex of maxillary palp. **f** Apex of labial palp. *cas* cardostipes, *ga* galea, *la* lacinia, *lp* labial palp, *mp* maxillary palp, *pm* postmentum, *prm* prementum, *s* spine, *sb* sensillum basiconicum, *sco* sensillum campaniformium, *so* salivary orifice



B. planus. The galea bears one short sensillum basiconicum (Fig. 6b, c: sb), a palmate sensillum (Fig. 5b, d: ps) and a pair of sensilla campaniformia (Fig. 6b, e: sco) on the dorsal surface. The lacinia is furnished with numerous stiff cuticular protuberances on the mesal surface. The maxillary palp bears 14 sensilla basiconica on the apex (Fig. 6f).

The labium is less hirsute than of *B. planus* and is remarkable for the slender labial palp (Fig. 6a: lp). The distal palpomere is approximately three times as long as the basal palpomere and bears ten sensilla basiconica apically (Fig. 6g).

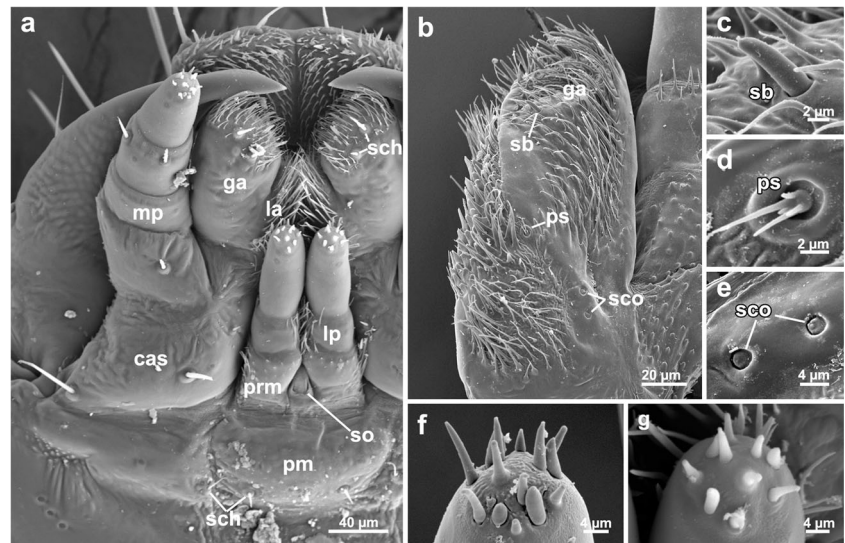
Fig. 5 Mouthparts of *Panorpa liui*. **a** Labrum. **b** Epipharynx. **c** Lateral palmate sensilla. **d** Basal protuberance. **e–h** Mandibles, dorsal, ventral, and mesal views and the magnified aspect of the molar region, respectively. *cd* condyle, *ce* cutting edge, *gg* ginglymus, *hb* hair brush, *ir* incisor region, *ls* labral seta, *mr* molar region, *mt* molar teeth, *ps* palmate sensillum, *s* spine, *sb* sensillum basiconicum, *sp* sensory protuberance



Mouthparts of *P. kuandianensis*

The labrum bears two pairs of prominent setae apically. The epipharynx is furnished with various types of sensilla arranged symmetrically (Fig. 7a–c), a pattern similar to those of *B. planus* and *P. liui*. The sensilla basiconica are remarkably prominent and exposed on the apical epipharynx, longer than most of the microtrichia. The microtrichia are relatively short and sparse, mostly present on the lateral part of the epipharynx, but absent on the central part and the basal triangular plate.

Fig. 6 Mouthparts of *Panorpa liui*. **a** Mouthparts, ventral view. **b** Maxilla, dorsal view. **c** Sensillum basiconicum on maxilla. **d** Palmate sensillum on maxilla. **e** Sensilla campaniformia on maxilla. **f** Apex of maxillary palp. **g** Apex of labial palp. *cas* cardostipes, *ga* galea, *la* lacinia, *lp* labial palp, *mp* maxillary palp, *pm* postmentum, *prm* prementum, *ps* palmate sensillum, *sb* sensillum basiconicum, *sch* sensillum chaeticum, *sco* sensillum campaniformium, *so* salivary orifice



The mandible has two distal cusps on the incisor region and is remarkably glabrous on the molar region, without molar teeth or spines (Fig. 7d–f). The mandible has three long sensilla trichodea laterally and a hair brush tuft on the baso-mesal corner.

The maxilla bears eight sensilla chaetica on the ventral surface (Fig. 8a), arranged in a similar pattern but more prominent (longer than apical segment of the maxillary palp) than those of *B. planus* and *P. liui*. The galea bears a sensillum basiconicum apically (Fig. 8b, c: sb), a palmate sensillum

centrally (Fig. 8b, d: ps), and a pair of sensilla campaniformia proximally on the dorsal surface (Fig. 8b, e: sco). The lacinia is glabrous on the mesal surface (Fig. 8b). The maxillary palp bears 13 sensilla basiconica apically (Fig. 8f).

The labium is stout and bears a pair of two-segmented labial palpi with the two palpomeres equal in length (Fig. 8a: lp). The labial palp has ten sensilla basiconica apically, eight normal and two papillary ones (Fig. 8g). The glabrous prementum is also mesally divided by the salivary orifice (Fig. 8h: so).

Fig. 7 Mouthparts of *Panorpodes kuandianensis*. **a** Epipharynx. **b** Lateral palmate sensilla. **c** Basal protuberance. **d–f** Mandibles, dorsal and ventral views and the magnification of molar region, respectively. *cd* condyle, *gg* ginglymus, *hb* hair brush, *ir* incisor region, *mr* molar region, *ps* palmate sensillum, *sb* sensillum basiconicum, *sp* sensory protuberance

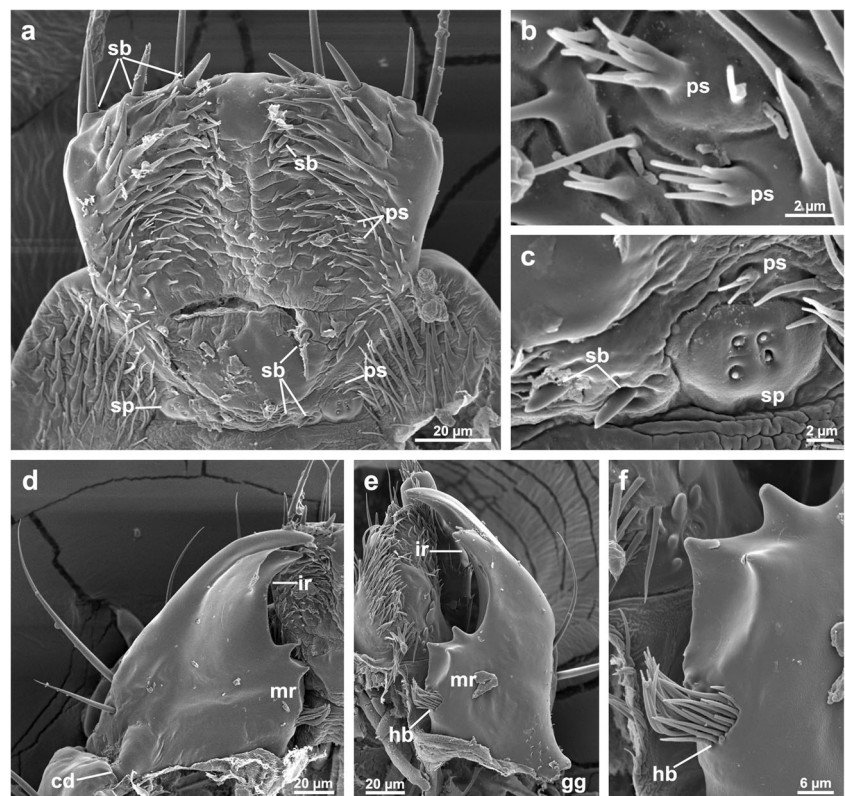
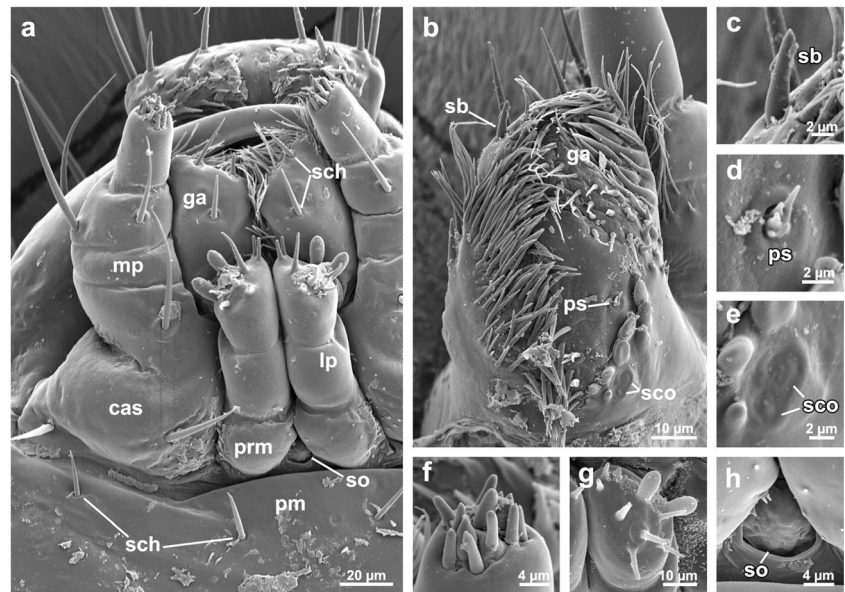


Fig. 8 Mouthparts of *Panorpodes kuandianensis*. **a** Mouthparts, ventral view. **b** Maxilla, dorsal view. **c** Sensillum basiconicum on maxilla. **d** Palmate sensillum on maxilla. **e** Sensilla campaniformia on maxilla. **f** Apex of maxillary palp. **g** Apex of labial palp. **h** Salivary orifice. *cas* cardo-stipes, *ga* galea, *lp* labial palp, *mp* maxillary palp, *pm* postmentum, *prm* prementum, *ps* palmate sensillum, *sb* sensillum basiconicum, *sch* sensillum chaeticum, *sco* sensillum campaniformium, *so* salivary orifice



Discussion

The feeding habits of the larvae of Panorpididae remain largely unknown (Pollmann et al. 2008; Jiang et al. 2014). In this study, we attempt to infer the feeding habit of the Panorpididae by comparing their mouthparts with those of Bittacidae and Panorpididae.

Mandibles and feeding habits

Mandibles of insects with biting mouthparts often have a dual function, cutting and grinding by the incisor and molar regions, respectively (Snodgrass 1935). Both of them are morphologically diverse among insect lineages that have different feeding habits (Chapman and de Boer 1995; Chapman 2013). In predacious insects, the apical cusps of incisor regions are usually more prominent adapted for penetrating the exocuticle of prey (Michat 2010; Lawrence et al. 2011; Cao and Liu 2013; Satar et al. 2014). In herbivorous insects, the molar regions are often furnished with flattened ridges for grinding strong leaf fibers (Chapman 1964; Smith and Capinera 2005). In Mecoptera, based on our investigations, the larval

mandibles exhibit distinct morphological differences, especially on the molar regions (Table 1). The mola of *B. planus* larvae bears prominent spines, which are just situated at the opening of the digestive tract, and may act as a filter to prevent the solid particles flowing into the alimentary canal during feeding on the tissue slurry. The mola of *P. liui* bears tuberculate molar teeth for grinding the exocuticle of dead arthropods. By contrast, the mola of *P. kuandianensis* is glabrous, devoid of molar teeth or spines, implying that these larvae are probably not feeding on solid food.

Sensilla and morphological adaptations

Sensilla on the larval mouthparts of *B. planus*, *P. liui*, and *P. kuandianensis* are arranged in a similar pattern, including sensilla basiconica on epipharynx, sensilla chaetica on maxillae and labium, palmate sensilla in cibarium, and grouped sensilla basiconica on the apex of palpi. This sensillum pattern is also shared by the larvae of other species in Bittacidae and Panorpididae (Chen and Hua 2011; Ma et al. 2014a; Jiang et al. 2015). However, these sensilla differ distinctly in their detailed morphology, especially the sensilla chaetica, which are

Table 1 Comparisons of larval feeding habits and mouthparts of three families in Mecoptera

	Bittacidae (<i>Bittacus planus</i>)	Panorpidae (<i>Panorpa liui</i>)	Panorpididae (<i>Panorpodes kuandianensis</i>)
Feeding habits	Saprophagous	Saprophagous	Unknown, likely phytophagous
Diets	Slurry only	Slurry and cuticle	Unknown
Molar region	With long spines	With protuberances	Glabrous
SC on MP	Normally sized	Normally sized	Prominent
SB on epipharynx	Less conspicuous	Less conspicuous	Prominent
SB on LP	Nine (normal)	Ten (normal)	Ten (eight normal+two papillary)

LP labial palp, MP maxillary palp, SB sensilla basiconica SC sensilla chaetica

normally sized in Bittacidae and Panorpidae (shorter than the distal segment of the maxillary palp), but prominent in Panorpididae (longer than the distal segment of the maxillary palp) (Table 1). Because the sensilla chaetica retain a function of mechanoreceptor (Zacharuk and Shields 1991; Shields 2008), these prominent sensilla chaetica may promote the mechanical sensation of the exclusively eyeless panorpidid larvae for sensing the shape and size of the food resource. In contrast, these sensilla chaetica are less developed in larval Bittacidae and Panorpidae and other Pistillifera, all of which bear well-developed larval compound eyes (Cooper 1974; Byers 1991).

Sensilla basiconica mainly perform gustatory, olfactory, and mechanical functions inferred from their external morphology (Zacharuk and Shields 1991; Chapman 2003; Shields 2008). Based on our present and previous investigations, the sensilla basiconica on the larval mouthparts differ morphologically among families. The sensilla basiconica on the larval epipharynx are smaller and situated among dense microtrichia in Bittacidae and Panorpidae, but are larger and protruding in Panorpididae. Moreover, the sensilla basiconica on the apex of labial palpi differ in number and morphology: ten normal in Panorpidae, nine normal in Bittacidae, but eight normal and two papillary in Panorpididae (Table 1). The special sensilla basiconica of Panorpididae may indicate a different feeding habit from others that feed on dead arthropods. The soil-dwelling larvae of Panorpididae may need a specialized olfactory system to compensate for the absence of visual organ (Jiang et al. 2014).

The larvae of *P. kuandianensis* did not feed on dead arthropods or on the plant tissue (Jiang et al. 2014), as found for *Brachypanorpa* (Carpenter 1953; Byers 1997). This may partly due to the rearing conditions that did not sufficiently simulate the local environment, or perhaps the plant tissue was not from the specific host plant. Because the larvae of Panorpididae are eyeless and sluggish living underground (Jiang et al. 2014), they are unlikely to prey on live animals. It is more likely that these edaphic larvae feed on tissue or juice of tender roots of some specific host plant. However, this needs verification of larvae in their natural environment.

Diverse larval feeding habits of Mecoptera

According to previous studies, the larvae are predacious in Nannochoristidae, feeding on small aquatic organisms (Beutel et al. 2009); phytophagous in Boreidae, feeding on/boring in moss tissues (Cooper 1974; Russell 1982); and saprophagous in most other families, consuming dead arthropods or decaying organic matters (Byers 1963, 1987, 1991; Tan and Hua 2008; Cai and Hua 2009; Jiang and Hua 2013). Based on our present investigation, the diets of saprophagous larvae in Mecoptera are more diverse than known before. Larvae of Bittacidae only feed on slurry, but the larvae of

Panorpidae consume both soft substrate and hard particles (Table 1). These differences in diet may help to avoid the food competition between closely related families.

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Conflict of interest The authors declare that they have no competing interests.

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