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**MORPHOLOGY OF PSOCOMORPHA
(PSOCODEA: 'PSOCOPTERA')**

By KAZUNORI YOSHIZAWA

Abstract

YOSHIZAWA, K. 2005. Morphology of Psocomorpha (Psocodea: 'Psocoptera'). *Ins. matsum. n. s.* 62: 1–44, 24 figs.

Adult integumental morphology of the suborder Psocomorpha (Psocodea: 'Psocoptera') was examined, and homologies and transformation series of characters throughout the suborder and Psocoptera were discussed. These examinations formed the basis of the recent morphology-based cladistic analysis of the Psocomorpha (Yoshizawa, 2002, *Zool. J. Linn. Soc.* 136: 371–400).

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INTRODUCTION

Psocoptera (psocids, booklice or barklice) are a paraphyletic assemblage of non-parasitic members of the order Psocodea (Lyal, 1985; Yoshizawa & Johnson, 2003, 2005; Johnson et al., 2004), containing about 5500 described species (Lienhard, 2003). They are about 1 to 10 mm in length and characterized by well-developed postclypeus, long antennae, pick-like lacinia, reduced prothorax, well-developed pterothorax, etc.

Phylogenetically, Psocoptera compose a monophyletic group (the order Psocodea) with parasitic lice ('Phtiraptera': biting lice and sucking lice) (Lyal, 1985; Yoshizawa & Johnson, 2003, in press; Johnson et al., 2004). The order is related to Thysanoptera (thrips) and Hemiptera (bugs, cicadas, etc.) (Yoshizawa & Saigusa, 2001, 2003, but see also Yoshizawa & Johnson, 2005). The above-mentioned three orders compose the monophyletic group Paraneoptera, and Psocoptera retain the most plesiomorphic states of characters in the group. Therefore, a morphological study of Psocoptera is important in interpreting morphology and evolution of paraneopteran insects, as well as in estimating phylogeny and evolution of Psocoptera (Yoshizawa, 2002; Yoshizawa et al., in press). The morphology of Psocoptera was extensively studied by Badonnel (1934), and it remains the most comprehensive morphological study on Psocoptera. However, he examined only one species, *Stenopsocus stigmaticus* (Imhof & Labram, 1846), and a detailed comparative analysis was lacking.

In the present study, the integumental morphology of Psocomorpha is investigated, and homologies and transformation series of characters throughout Psocoptera are discussed. These analyses form the basis of the recent morphology-based phylogenetic analysis of Psocomorpha (Yoshizawa, 2002). Methods and terminology followed Yoshizawa (2002) and Yoshizawa & Saigusa (2003). For deciding homology of external structure, musculature and other internal structures were also studied in some cases. Discussion of character polarities in this paper was based mainly on the results of the recent morphology-based cladistic analysis (Yoshizawa, 2002).

RESULTS AND DISCUSSION

Head (Figs. 1–3)

The vertex of Psocomorpha is usually rounded, but sharply angled in some taxa such as Calopsocidae. The latter character state is widely observed in Trogiomorpha and Troctomorpha, but angled vertex in Psocomorpha is regarded as a secondarily derived condition. The exuvial cleavage line is very clear on the vertex, but faint along the frons.

The occipital suture is hardly recognized. A faint line is observed along the posterolateral edge of the head capsule which possibly represents the occipital suture. The postoccipital suture is distinct. The subgenal suture is observed along the ventral margin of the gena. It terminates anteriorly at the anterior tentorial pit, and continues to the epistomal suture.

The postclypeus is usually large and strongly bulged. This structure is once considered to be homologous with the frons (DuPorte, 1962; Matsuda, 1965; Hamilton, 1981) but, as shown by Yoshizawa & Saigusa (2003), the bulged structure of Psocomorpha should be regarded as the postclypeus (Badonnel, 1934). In Trogiomorpha, the post- and anteclypeus are less differentiated (Fig. 2A).

The anteclypeus of the Psocomorpha is represented by a transverse sclerite observed

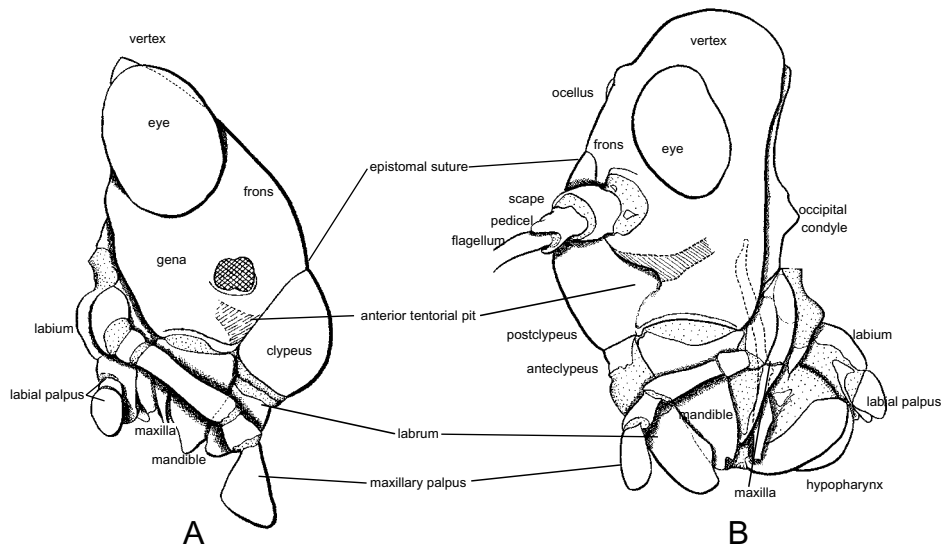


Fig. 1. Head, lateral aspect. (A) *Echmepteryx lunulata* (Trogiomorpha: Lepidopsocidae); (B) *Longivalvus nubilus* (Psocidae).

between the postclypeus and labrum. It is clearly divided from the postclypeus by a deep internal ridge, and from the labrum by a narrow membranous region (Fig. 3A). The anteclypeus is completely membranous in some taxa such as Hemipsocidae.

The epistomal suture usually possesses an internal ridge. In Troctomorpha and Trogiomorpha, the internal ridge of the epistomal suture is well developed (Fig. 2A). In contrast, it is less developed (Fig. 2C, D) in most psocomorphan taxa except Archipsocidae, Caeciliusoidea, Elipsocidae and Mesopsocidae (Fig. 2BD). Phylogenetic analysis indicated that a well-developed epistomal ridge observed in the latter three taxa has been secondarily derived from a less developed epistomal ridge. In Hemipsocidae, Epipsocidae, and Cladiopsocidae, the epistomal suture is reduced and only distinguishable around the anterior tentorial pits (Fig. 2D).

The postocciput has a well developed triangular occipital condyle that articulates with the lateral cervical sclerite (Fig. 3B). Anterior, posterior, and dorsal tentorial arms are present. The posterior tentorial arm is invaginated from just ventral to the base of occipital condyle. The anterior tentorial arm originates at the middle of the posterior tentorial bridge, and is strongly twisted near its base. In most cases, the anterior tentorial arms are basally separated from each other but, in Epipsocetidae, they are united basally, forming a trapezoid plate. The anterior tentorial pit is usually invaginated from the ventral end of the epistomal suture, but in some taxa, such as Psocidae and Epipsocidae, it is separated from the ventral margin of the cranium. The dorsal tentorial arm arises from near the middle of the anterior tentorial arm. Basally, the arm forms a wide triangular plate, but is filiform distally. The dorsal tentorial arm is attached to the internal ridge of the epistomal suture near the antennal socket.

The antennal socket is almost circular in shape, and surrounded by a well-developed antennal sulcus. The antennifer is weakly projected from the ventral margin of the socket, and articulated with the scape.

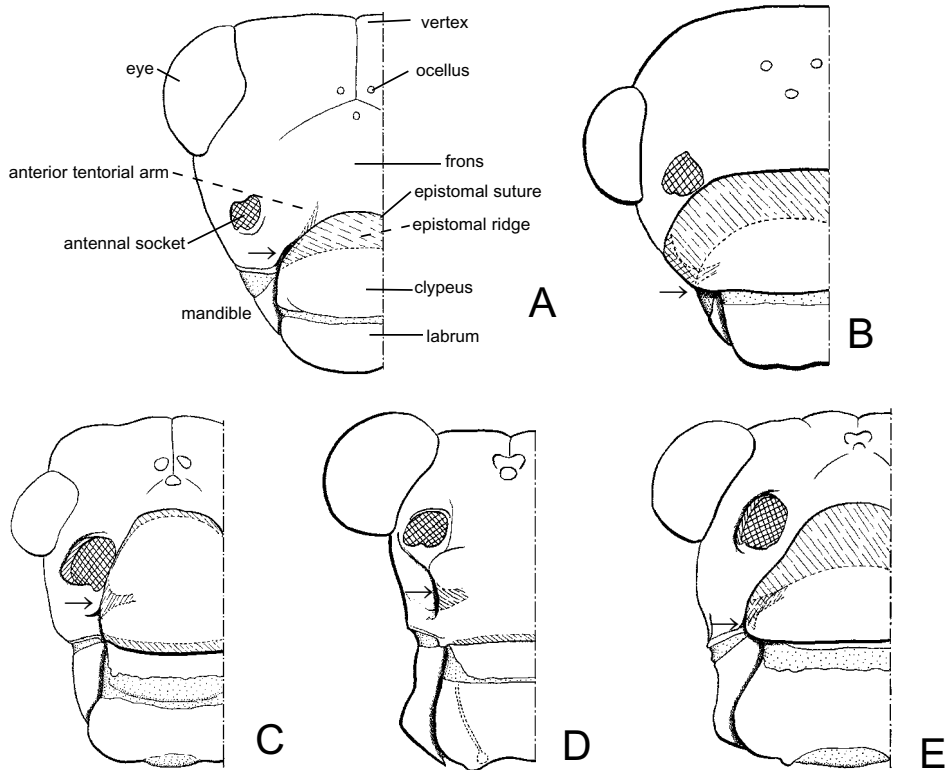


Fig. 2. Head, anterior aspect. (A) *Echmepteryx lunulata* (Lepidopsocidae); (B) *Archipsocus* sp. (Archipsocidae); (C) *Longivalvus nubilus* (Psocidae); (D) *Epipsocopsis* sp. (Epipsocidae); (E) *Stenopsocus* sp. (Stenopsocidae). Arrow indicates the position of the anterior tentorial pit.

Eyes and Ocelli (Figs. 1–2)

Three ocelli are usually present, normally in a triangular arrangement, two laterally on the vertex and one medially at the dorsal end of the frons. In wingless forms, ocelli are often absent. Ocelli are sometimes grouped on a small tubercle.

The compound eye is large and hemispheric. The male compound eye is usually much larger than the female. Internally, a well-developed ocular ridge is observed around the compound eye.

Antennae

The antenna of Psocomorpha comprises a short scape, short pedicel, and eleven long flagellomeres. Lengths of flagellomeres are progressively shorter distally. Flagellomeres are clothed densely with long setae, usually denser in males than in females. The number of flagellomeres is reduced in some wingless forms. In some taxa, three tiny sclerites surround the base of the scape. The distal margin of the scape has a pair of distal projections at the dorsal and ventral edges. Flagellomeres are usually thicker in males than in females.

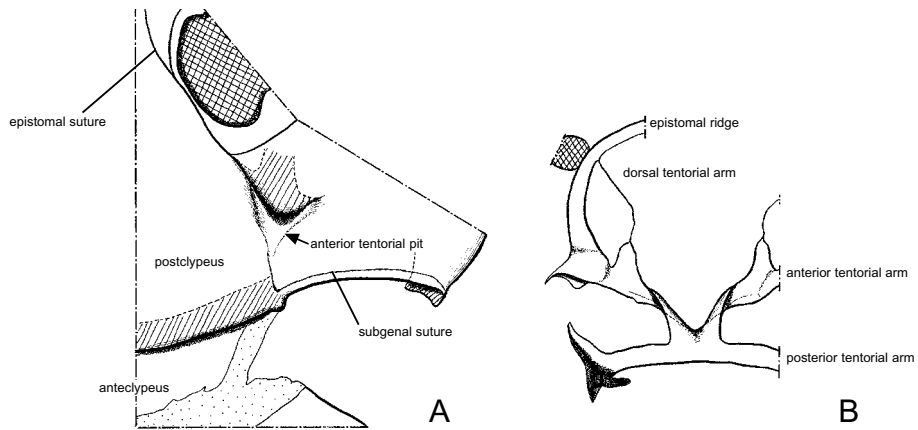


Fig. 3. *Longivalvus nubilus* (Psocidae) (A) head capsule, around anterior tentorial pit, magnified; (B) tentorium, posterior aspect.

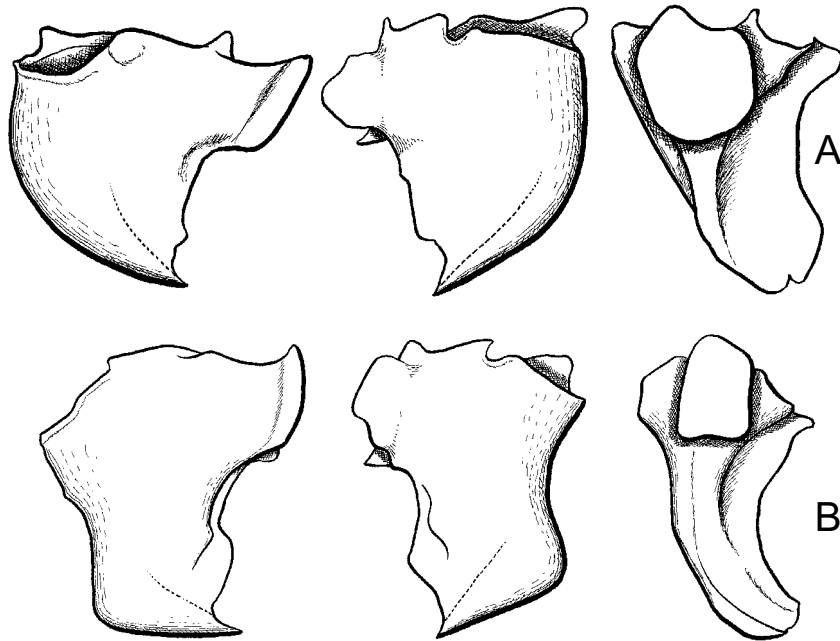


Fig. 4. Mandible, right from anterior aspect (right), left from anterior aspect (left), and left from internal aspect (middle). (A) *Longivalvus nubilus* (Psocidae); (B) *Matsumuraiella radiopicta* (Amphipsocidae).

Mouthparts

Labrum (Fig. 2)

The labrum of Psocomorpha is basically orthopteroid type. Its distal margin has rows of sensilla, and their number and arrangement are often used as diagnostic characters. In Epipsocetae, each lateral half of the labrum has a slender sclerites extending nearly or for its entire length, and with a small lobe at the ventral end of the

slender sclerite.

Mandible (Fig. 4)

The mandible of Psocomorpha is of ordinary, orthopteroid biting type. Two types of mandibles are observed within the Psocomorpha. In all psocomorphan families except that of Calopsocidae, Caeciliusetae and Epipsocetae, the shape of the mandible is almost uniformly triangular, with its outer margin smoothly rounded and its posterior margin not deeply concaved (Fig. 4A). This condition is also observed in all Trogiomorpha and Troctomorpha. In Caeciliusetae, Epipsocetae, and Calopsocidae, the mandible is elongate, with its outer margin angled, and its posterior margin deeply concaved (Fig. 4B). The mandible of Calopsocidae is somewhat intermediate between the triangular and elongate types. Its outer margin is almost smoothly rounded or slightly angled, with its posterior margin deeply concaved.

Maxilla (Fig. 5)

Homology of the maxillary structures has discussed in detail previously (Yoshizawa & Saigusa, 2003).

The maxilla of Psocoptera is highly characteristic. The lacinia is a slender pick-like structure. The stipito-lacinial muscle (6) act as protractors of the lacinia, and is split into three bundles, one of which inserts onto the basal margin of the galea. The apex of the lacinial pick is usually broadened, bearing minute denticles. In Amphientomidae, it is very broad with many minute denticles, which was thought as the plesiomorphic condition of Psocomorpha by Mockford (1967). However, the Archipsocetae, which is regarded to have splited off from the most basal node of the Psocomorpha (Yoshizawa, 2002; Johnson & Mockford, 2003) have a narrow lacinial tip.

The cardo and stipes are completely fused and almost indistinguishable. The stipes usually has an ovoidal swelling where one of three stipito-lacinial muscles is inserted. The narrow region anterodorsal to the ovoidal swelling possibly represents the cardo. The palpifer is apparently separated from the stipes by a clear internal ridge, but is largely membranous in some taxa such as Caeciliusidae.

The galea forms a distinct lobe, and articulates basally with the stipes. Masumoto & Nagashima (1993) regarded the distal lobe of the maxilla as stipes rather than galea. However, external morphology and musculature of the maxilla clearly show that the distal lobe of the maxilla is the galea. The galea is largely membranous and a strap-like sclerite surrounds its external and ventral surfaces.

The maxillary palpus of Psocomorpha is always four-segmented. The fourth segment of Psocomorpha is simply cylindrical whereas it is distally broadened and the distal surface flattened in Trogiomorpha (Fig. 1).

Labium (Figs. 6–7)

The submentum is weakly sclerotized, or completely membranous in Psocomorpha. In Amphientomidae, the submentum is narrowly sclerotized. The mentum is almost membranous, sometimes represented by narrow lateral sclerites. The prementum is well sclerotized, with a pair of swellings latero-distally.

Three different interpretations have been proposed concerning the homology of labial structures in psocids as summarized in Fig. 6A. Among them, the interpretation proposed by Cope (1940) is considerably different from those of the others. Cope

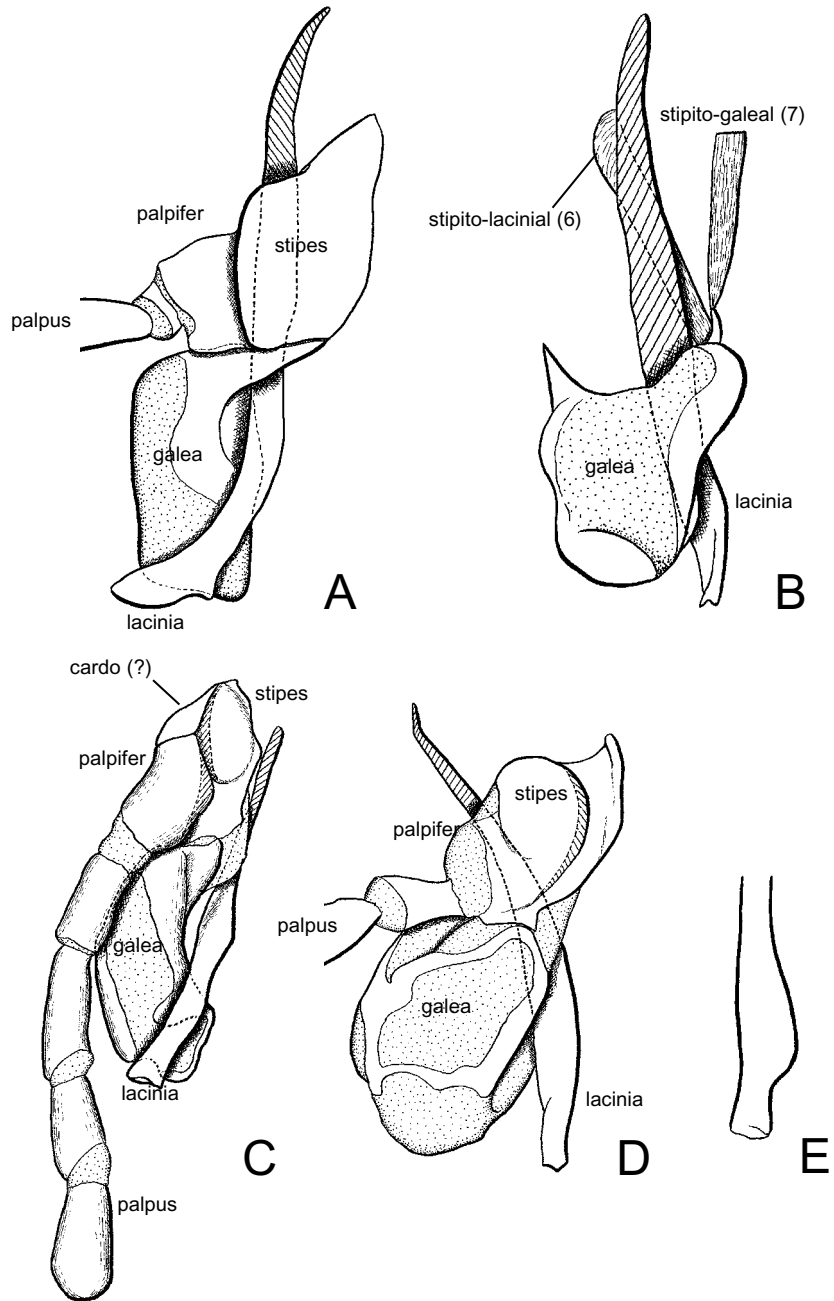


Fig. 5. Maxilla. (A) *Paramphientomum* sp. (Amphientomidae), lateral aspect; (B) ditto, showing muscles attached to galea, anterior aspect; (C) *Longivalvus nubilus* (Psocidae), lateral aspect; (D) *Matsumuraiella radiopicta* (Amphipsocidae), lateral aspect; (E) lacinial tip of *Notiopsocus aldretei* (Asiopsocidae), anterior aspect.

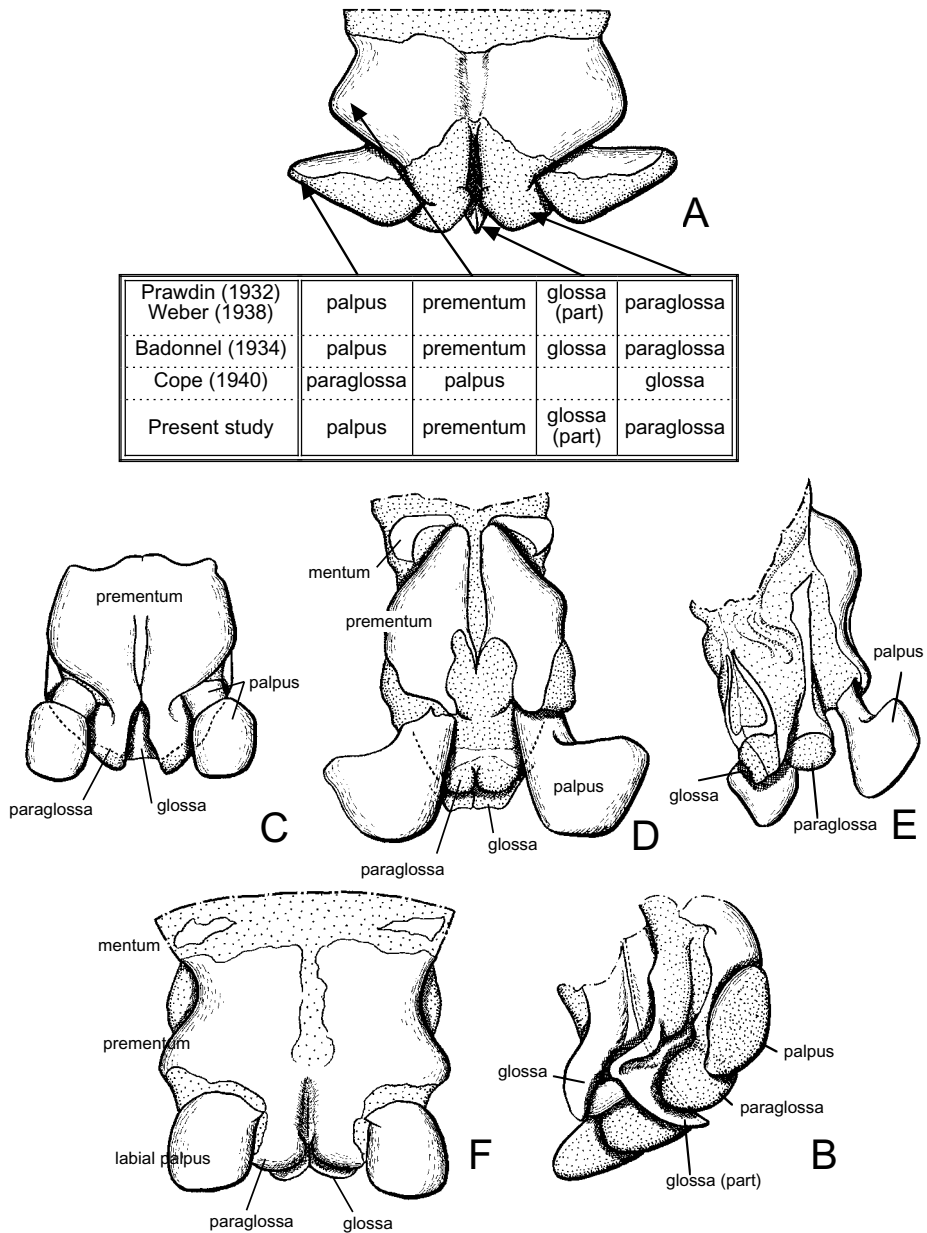


Fig. 6. Labium of (A) *Stenopsocus* sp., posterior aspect, with different interpretations of labial structures in Psocoptera; (B) ditto, anterolateral aspect; (C) *Echmepteryx madagascariensis* (Trogiomorpha: Lepidopsocidae), posterior aspect; (D) *Paramphientomus* sp. (Troctomorpha: Amphientomidae), posterior aspect; (E) ditto, anterolateral aspect; (F) *Longivalvus nubilus* (Psocidae), posterior aspect.

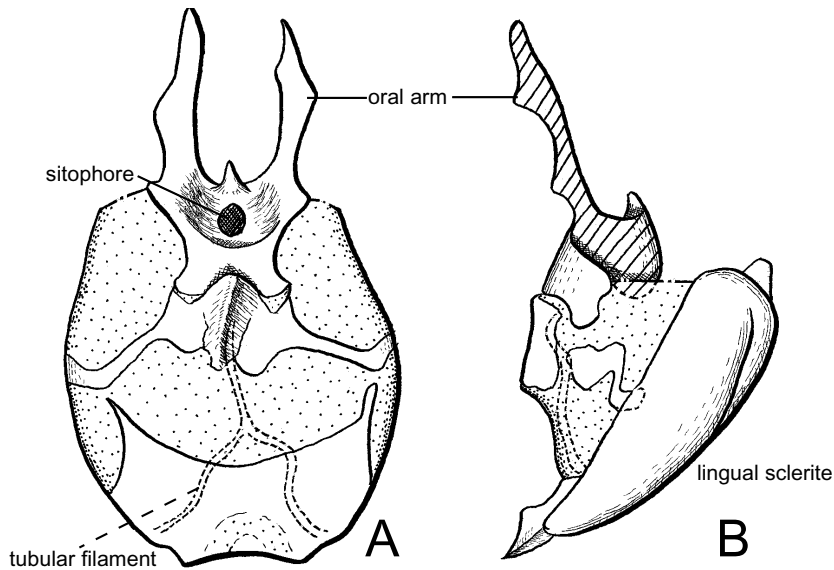


Fig. 7. (A) hypopharynx of *Longivalvus nubilis* (Psoicæ), anterior aspect; (B) lateral aspect.

(1940) considered the lateral lobe of the prementum of other authors as the labial palpus (Fig. 6A), and the palpus and paraglossa of other authors as the paraglossa and glossa, respectively (Fig. 6).

Interpretations of the labial palpus and paraglossa are identical among Prawdin (1932), Weber (1938), and Badonnel (1934). Another ambiguity in the interpretation of homology concerns the glossa. Weber (1938) identified the plate-like structure located anterior to the paraglossa as the glossa (Fig. 6A). The figure of the labium given by Prawdin (1932: fig. 23) is too unclear to identify his interpretation but he appears to consider the structure placed anterior to the paraglossa of a species of *Lepinotus* as the glossa. This interpretation is identical with that of Weber (1938). In contrast, Badonnel (1934), followed by Matsuda (1965), regarded a conical lobe extending along the glossal groove (salivary duct) and located between the paraglossae in *Stenopsocus stigmaticus* as the glossa (Fig. 6A). This interpretation is different from that of Prawdin (1932) and Weber (1938) in regarding the conical lobe as the glossa itself, and not as a part of the glossa.

The structure called to be the mentum by Badonnel (1934) is labeled to be prementum by Matsuda (1965). However, Badonnel used the term mentum as being equivalent with palpiger (=prementum: Snodgrass 1935) and thus, there is no disagreement about the interpretation of this structure.

Results of our observation show that Cope's interpretations are not acceptable for the following reason. The paraglossa of Cope (1940) is two-segmented in some psocids such as in lepidopsocids (Trogimorpha) (Fig. 8A). The paraglossa is never segmented in any insect and thus the two-segmented structure must be the labial palpus. Homology of this structure throughout Psocoptera is doubtless judging from external and internal structure. Consequently, the interpretation proposed by Cope (1940) must be rejected. Musclature of labium shown by Badonnel (1934) also contradict with the Cope's interpretation.

Our investigation shows that the conical lobe located between the paraglossae is not always present (Fig. 6C–F). The structure is extended along the salivary duct (Fig. 6B), and is well developed in Psocomorpha (Fig. 8D), but never observed in Trogiomorpha and Troctomorpha (Fig. 6C–E). We consider that the conical lobe itself does not represent the glossa, but is an extension from the median part of the glossa. By comparison with orthopteroid labia, we conclude that the glossa of psocids is placed anterior to the paraglossa, and is thin and plate-like (Fig. 6B,E). Its anterior surface is continuous proximally with a pair of concavities on the anterior surface of the labium that fit into ovoidal sclerites of the hypopharynx. This interpretation of the glossa is identical with that of Weber (1938) and (probably) Prawdin (1932).

Hypopharynx (Fig. 7)

The hypopharynx of Psocoptera is highly modified. On the posterior surface, a pair of ovoidal sclerites are present, each of which has a longitudinal median ridge. A tubular filament is attached to the ventral end of this ridge, and the other end of the filament is attached to the bottom of the sitophore. The ridge and filament act for a water vapor uptaking system (Rudolph, 1982). The ovoidal sclerite have been homologized with the lingual sclerite (Snodgrass, 1944).

The sitophore sclerite forms the floor of the cibarium. The oral and posterior arms of the hypopharynx are present but the loral arm is completely absent. The sitophore is deeply concave and cup-shaped.

Thorax

Neck region (Fig. 8)

The neck region of Psocomorpha is rather long, with a pair of lateral cervical sclerites only. The lateral cervical sclerite is simple, long and narrow, with a median longitudinal ridge from anterior to posterior end. Its anterior end articulates with the occipital condyle and the posterior end with the anteroventral margin of the preepisternum of the prothorax.

Prothorax (Fig. 8)

The pronotum of Psocomorpha is usually reduced both in length and height. It is weakly bulged dorsally in almost all Psocomorpha but well bulged in Archipsocidae, Hemipsocidae, and outgroup suborders Trogiomorpha and Troctomorpha. The pronotum is fused laterally with the propleuron.

The propleuron is also reduced in length. The pleural suture is always present but sometimes unclear. Its ventral end articulates with the coxal margin. Neither the paracoxal nor anapleural sutures are distinguishable. The episternum is well retained and the pleural arm pit is invaginated from its ventral end. The preepisternum is reduced to a small plate, and sometimes detached from the episternum. Crampton (1926) and Cope (1940) regarded it as a part of lateral cervical plate. However, judging from its position, this plate should be regarded as the preepisternum. The preepisternum is usually rounded, squared or triangular in shape but, in Caeciliusetae, Ectopsocidae, Lachesillidae, and Peripsocidae, it is elongate. The epimeron is well developed and rather broad, but sometimes very thinly sclerotized. The trochantin is well developed, and usually directly articulated with the coxal margin. It is often detached from the pleural sclerite basally.

The prosternum (Fig. 13) is roughly X-shaped. Its anterior arm articulates with the

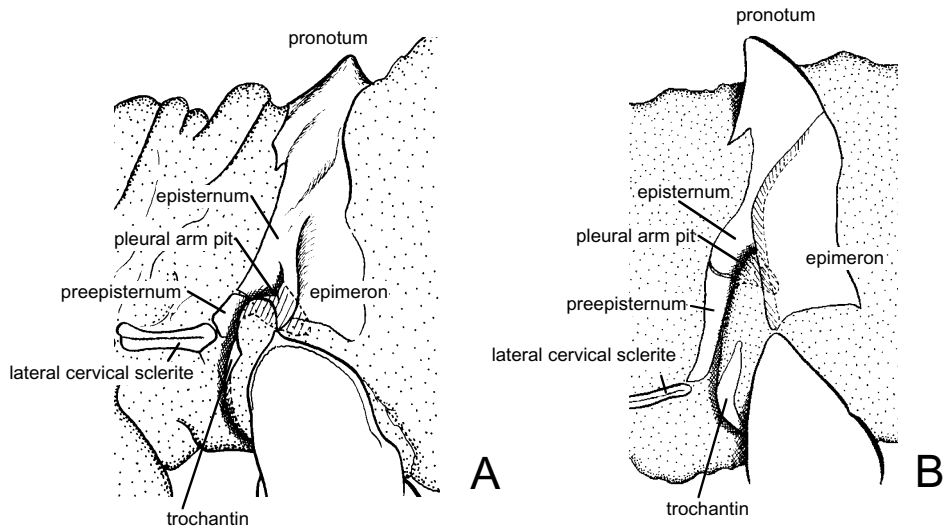


Fig. 8. Prothorax, lateral aspect. (A) *Longivalvus nubilus* (Psocidae); (B) *Ectopsocus* sp. (Ectopsocidae).

antero-internal margin of procoxa. Its posterior arm bears an invagination to the furca. The furca is broadened apically. The prothoracic spina is apparently represented by a membranous pit posterior to the furcal invagination.

Mesothorax (Figs. 9, 10)

The mesonotum is greatly bulged antero-dorsally in most psocomorphan families except Archipsocidae and brachipterous or apterous forms. The scutum is divided into a anterior scutal lobe and pair of lateral scutal lobes by the lateral parapsidal sutures. The anterolateral scutal suture is observed on the anterior margin of the lateral scutal lobe. Weakly developed first phragma is formed beneath the antecosta although Matsuda (1970) mentioned it is absent in Psocoptera. On the anterior surface of the mesothorax, a large rectangular sclerite occurs lateral to the anterior scutal lobe. The sclerite is the prealar arm which is divided from the scutum by the prescutoscutal suture. The suture sometimes becomes faint and indistinguishable.

Three notal wing processes, anterior, median, and posterior notal wing processes, are distinguishable. Posterolateral scutal suture is observed along the lateral margin of the median notal wing process. The posterior notal wing process is invaginated antero-distally.

The prealar sclerite is a small sclerite located on the membranous region surrounded by the basalare, prealar arm and lateral scutal lobe. The prealar sclerite with internal ridge forms a rather large plate.

The scutoscuteellar suture is faint medially. Central part of the scutellum forms a triangular or pentagonal structure.

The mesopleuron is divided into the anterior episternum and the posterior epimeron by the almost straight pleural suture. Its dorsal end forms the pleural wing process, and ventral end articulates with the coxal margin. The pleural arm is not invaginated from the pleural suture, but a triangular internal apophyses is observed near the base of the

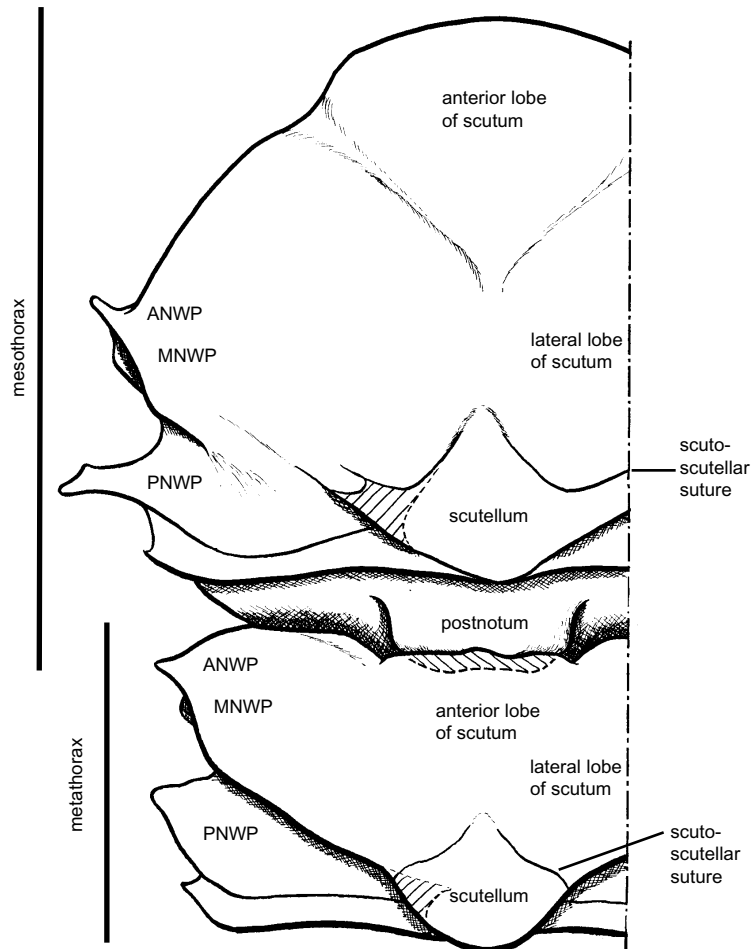


Fig. 9. Meso- and metathorax of *Longivalvus nubilus* (Psocidae), dorsal aspect.

pleural wing process. The episternum is usually clearly divided into dorsal anepisternum and ventral preepisternum + katepisternum by the anapleural suture. The anapleural suture of some psocids is faint or completely indistinguishable. The anapleural suture is absent within several families and thus, absence of the anapleural suture is regarded as homoplastic, independently derived several times. This suture, when present, is formed by a shallow internal ridge, and its posterior end fused with the pleural suture.

The basalare is not externally membranously divided from the anepisternum, but internally, it can be recognized by an internal apophysis. The epimeron is a large triangular sclerite. The subalare is a rather large, oval sclerite placed just dorsal to the epimeron.

The postnotum forms a large second phragma. Its posterior surface is swollen medially, and fused with the apical lobe of the metascutum.

There are two large sclerites on the antero-ventral surface (ventral to the anapleural suture) of the mesothorax, called precoxal bridge and trochantin (Fig. 11). The precoxal

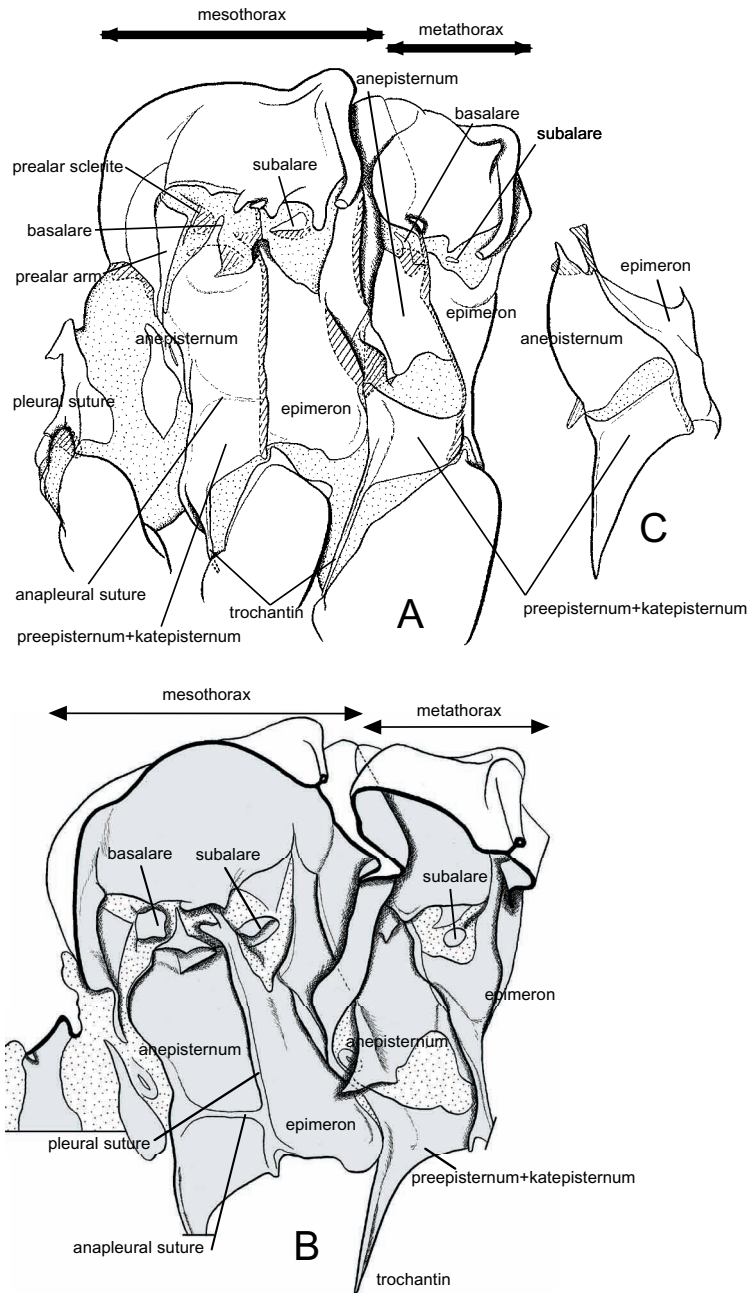


Fig. 10. Thorax. (A) *Longivalvus nubilus* (Psocidae), lateral aspect; (B) internal aspect; (C) metapleuron of *Hemipsocus chloroticus* (Hemipsocidae), lateral aspect.

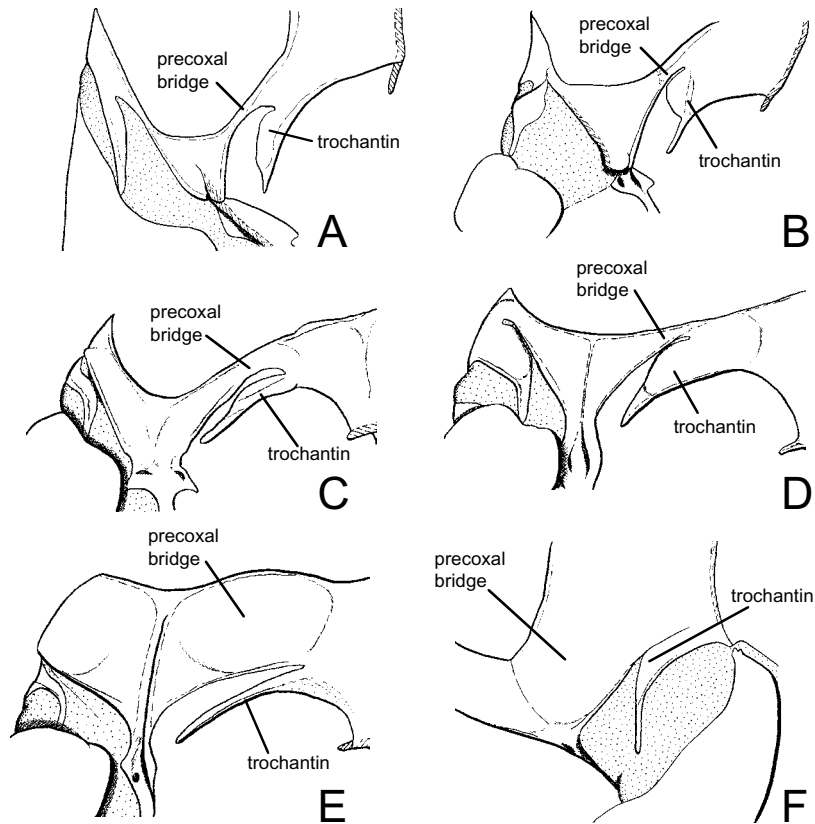


Fig. 11. Precoxal bridge and trochantin of mesothorax. (A) *Tineomorpha* sp. (Troctomorpha: Amphientomidae); (B) *Hemipsocus chloroticus* (Hemipsocidae); (C) *Myopsocus* sp. (Myopsocidae); (D) *Longivalvus nubilis* (Psocidae); (E) *Stenopsocus* sp. (Stenopsocidae); (F) *Pararchipsocus pacificus* (Archipsocidae).

bridge is probably composed of the preepisternum + katepisternum and involving the basisternum. In Trogiomorpha and Troctomorpha, both precoxal bridge and trochantin are narrow and the less developed dorso-ventral flight muscle (probably corresponding to t-p 5, 6 and t-ti2) is inserted to the base of the trochantin (Fig. 12A, B). This character state is regarded as the most plesiomorphic state of the Psocodea. Reduction of the flight muscle is probably correlated with lower flight activities. Brodsky (1994) mentioned that feeding specializations (feeding on vegetative tissues or mycophagy) led to the decreased importance of flight for Paraneoptera. Within the Psocomorpha, Hemipsocidae, Psocidae, and Myopsocidae have a plesiomorphic narrow precoxal bridge and the dorsoventral flight muscle is attached to the trochantin. The trochantin of Hemipsocidae and Psocidae are broadened, reflecting the thickening of their flight muscle.

In contrast, the dorso-ventral flight muscles of other psocomorphan families are split into two, one is attached to the trochantin and the other to the precoxal bridge (Fig. 12C–E). Among those families, musculature of Archipsocidae is completely different from the other families in that have a divided dorsoventral flight muscle. In Archipsocidae,

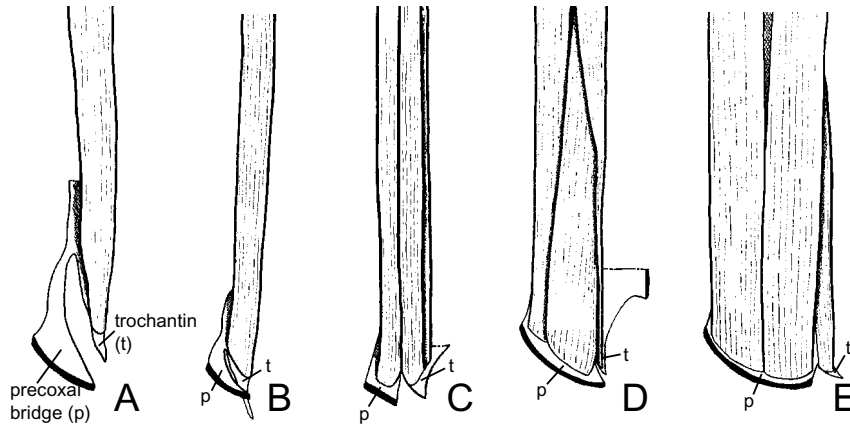


Fig. 12. Dorso-ventral flight muscle of mesothorax. (A) *Paramphientomum* sp. (Troctomorpha: Amphientomidae); (B) *Longivalvus nubilus* (Psocidae); (C) *Epipsocopsis* sp. (Epipsocidae); (D) *Stenopsocus* sp. (Stenopsocidae); (E) *Pararchpsocus pacificus* (Archipsocidae).

the larger inner muscle is inserted onto the precoxal bridge and the smaller outer muscle is inserted onto the trochantin (Fig. 12E), whereas in the other families, the smaller inner muscle is inserted onto the trochantin and the larger outer muscle is inserted onto the precoxal bridge (Fig. 12C, D). This indicates that splitting of the dorsoventral flight muscles have evolved independently at least twice. The precoxal bridge of Epipsocetae is relatively narrow but that of Homilopsocidea and Caeciliusetae are broadened reflecting the thickening of the muscle attached to the precoxal bridge. Condition of the flight muscles in Epipsocetae are somewhat intermediate between the undivided dorso-ventral flight muscle (such as Psocetae) and musculature observed in Homilopsocidea and Caeciliusetae.

In some species of Homilopsocidea and Caeciliusetae, a clear suture-like structure is observed at the base of the precoxal bridge. This structure does not correspond to any primary sutures and is regarded as secondarily derived to reinforce the precoxal bridge.

Matsuda (1970) discussed the morphology of the precoxal bridge and trochantin of Psocoptera. He considered that, the broad trochantin in Psocidae is composed of preepisternum + katepisternum + trochantin and the narrow precoxal bridge as corresponding to the basisternum. Alternatively, in Stenopsocidae, the broad precoxal bridge was regarded to be composed of preepisternum + katepisternum + basisternum. I consider that the membranous cleft observed between the precoxal bridge and trochantin is homologous throughout Psocoptera and there is no difference between a broad and narrow precoxal bridge except in their size. Thus, differences in musculatures should be regarded as due to a shift from the trochantin to the precoxal bridge that enables increased flight activity.

The mesosternum is narrow (Fig. 13), hollowed along a median line, and laterally with a pair of projections near the furcal pit that articulate with the internal margin of the mesocoxa. The furca is usually composed of a narrow basal straight bar and a broad apical plate. The mesothoracic spina is absent.

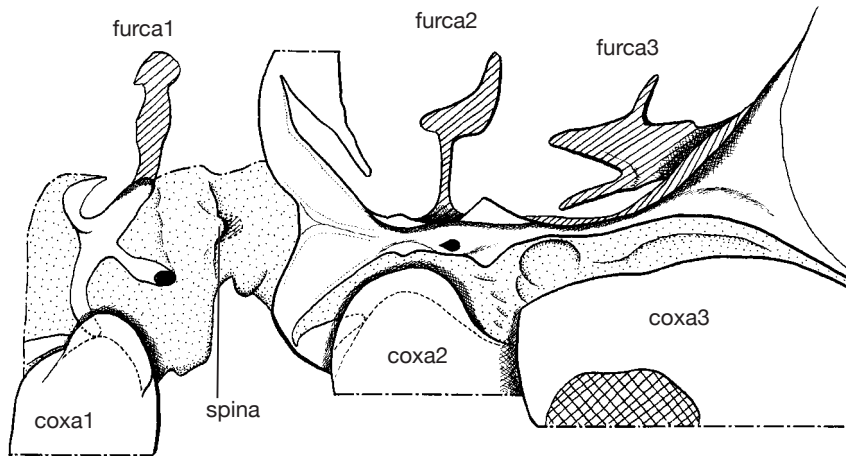


Fig. 13. Thorax of *Longivalvus nubilus* (Psocidae), ventrolateral aspect.

Metathorax (Figs. 9, 10)

The scutum is divided into three lobes as in the mesothorax, but the lateral parapsidal suture is rather indistinct. The anterior lobe is fused with the mesothoracic postnotum without infolding between them, and forms a large internal ridge. The anterior part of the lateral scutal lobe is strongly bent ventrally, and a deep concavity is formed between the mesothoracic postnotum and the lateral scutal lobe of the metanotum. The prealar arm is absent or indistinguishable. The scutoscutellar suture is complete. Central part of the scutellum forms a triangular or pentagonal structure. The postnotum forms the third phragma, and is almost flat or slightly swollen posteriorly.

Three notal wing processes, anterior, median, and posterior notal wing process are distinguishable. The posterolateral scutal suture is observed along the lateral margin of the median notal wing process. The posterior notal wing process is weakly sclerotized, without any invagination as in the mesothorax.

The metapleuron is divided into the anterior episternum and the posterior epimeron by the pleural suture. The pleural arm is not invaginated from the pleural suture. The anepisternum and the preepisternum + katepisternum are usually broadly separated by a membranous region and anapleural suture is indistinct. The anepisternum possesses a triangular internal plate antero-ventrally. The prealare sclerite is present ventral to the anterior margin of the lateral scutal lobe. The basalare is externally undivided from the anepisternum. Internally, the basalare can be recognized by the internal apophysis. The preepisternum, katepisternum, and trochantin are completely fused with each other. The sclerite composed of the pre- and katepisternum plus trochantin is tapered ventrally, its anterior margin strongly sclerotized, and its ventral tip articulates with the antero-internal margin of the metacoxa. The epimeron is very narrow in ventral half, and continuing to the metasternum ventrally.

The metasternum (Fig. 13) consists of a Y-shaped or roughly triangular sclerite. It is deeply hollowed medially and the broad furcal plate is invaginated at the bottom of this hollow. The metasternal sclerite is continuous from the mesosternum. The mesothoracic spina is absent and thus, the segmental border between mesosternum and metasternum is

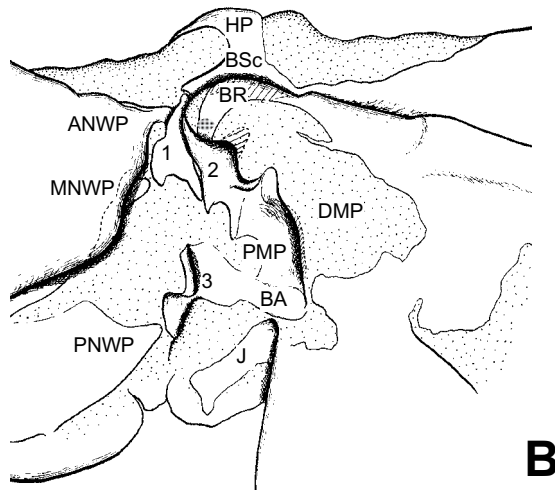
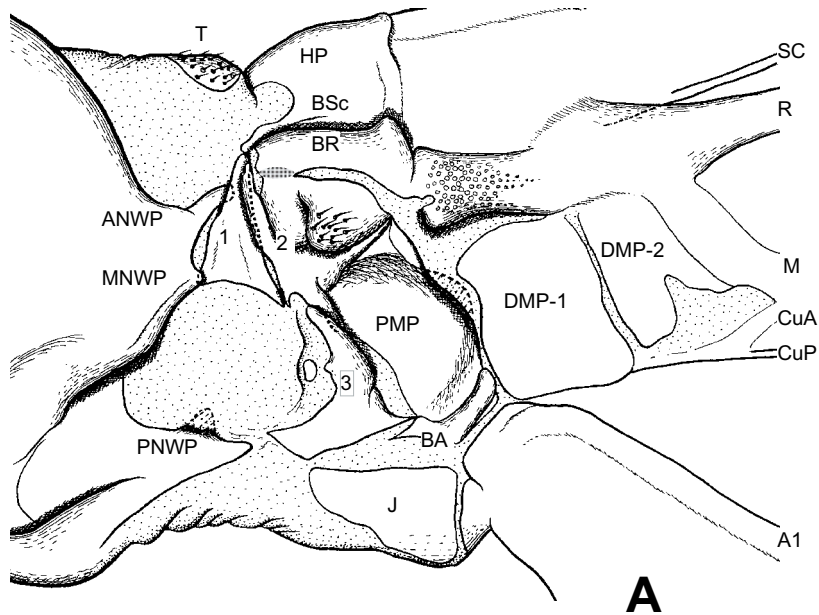


Fig. 14. Wing base of *Longivalvus nubilus* (Psocidae). (A) forewing; (B) hindwing. For explanation of abbreviations, refer to text.

unclear.

Wing base structures

Forewing base (Fig. 14A)

The forewing articulation in the Psocomorpha consists of the fundamental elements of the neopteran wing base.

The tegula [Tg] is present although Cope (1940) and Matsuda (1970) mentioned that

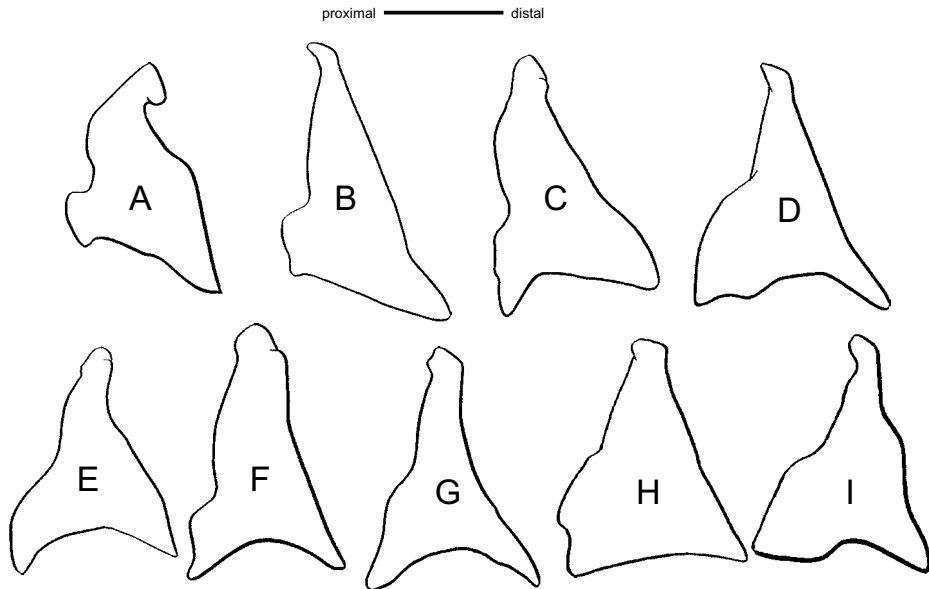


Fig. 15. First axillary sclerite, dorsal aspect. (A) *Paramphientomum* sp. (Troctomorpha: Amphientomidae); (B) *Pararchipsocus pacificus* (Archipsocidae); (C) *Hemipsocus* sp. (Hemipsocidae); (D) *Longivalvus nubilus* (Psocidae); (E) *Trichopsocus dali* (Trichopsocidae); (F) *Pseudocaecilius kagoshimensis* (Pseudocaeciliidae); (G) *Idatenopsocus orientalis* (Mesopsocidae); (H) *Triplocania spinosa* (Ptiloneuridae); (I) *Stenopsocus* sp. (Stenopsocidae).

it was absent in the Psocoptera. In Psocomorpha, Tg is usually a thin sclerotized structure bearing some minute setae, but well developed and strongly sclerotized in Trogiomorpha and Troctomorpha.

The humeral plate [Hp] is a large plate located on the anterior margin just distal to Tg. Distal margin of Hp is slightly trenched.

The basisubcostale [BSc] is anteriorly fused with Hp and posteriorly with basiradiale. A longitudinal median ridge is always observed on BSc. The apex of BSc articulates with the anterior tip of the first axillary sclerite.

The basiradiale [BR] is a broad, well-sclerotized, strongly bulged sclerite placed just posterior to BSc. It is fused with the second axillary sclerite posteriorly. The anterior axillary fold-line (*sensu* Wootton, 1979) runs between them and the fused region becomes bending cuticle. Anterior margin of BR projects anteriorly and then bent posteriorly at its distal end. The basal region of R bears numerous campaniform sensilla.

The first axillary sclerite [1Ax] (Fig. 15) of Psocomorpha is roughly triangular in shape. It articulates proximally with the anterior and median notal wing processes respectively, and distally with the second axillary sclerite by two articulations. The neck of the anterior arm is reduced (Fig. 15). Its anterior tip usually has a small process anteroproximally (Fig. 15B, D, G–I) but sometimes indistinguishable in such families as Hemipsocidae, Pseudocaeciliidae, Calopsocidae, and Trichopsocidae (Fig. 15C, E, F). In these families, the anterior part of 1Ax is broadened and this character states is regarded as the more derived condition than the condition observed in other psocomorphan

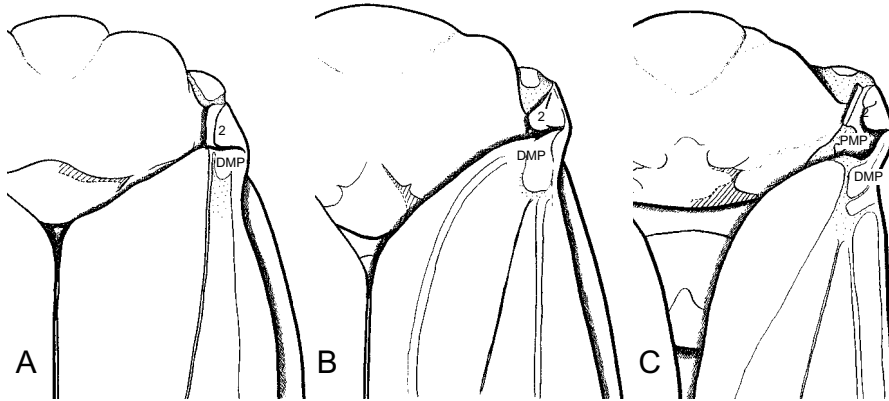


Fig. 16. Mesothorax and forewing showing wing base and wing margin while wings are closed. (A) *Paramphientomum* sp. (Troctomorpha: Amphientomidae); (B) *Hemipsocus chloroticus* (Hemipsocidae); (C) *Longivalvus nubilus* (Psocidae).

families. The postero-proximal margin of 1Ax is usually strongly protruded proximally articulating with the median notal wing process. Shape and size of this region are variable among families. The distal margin of 1Ax is almost straight or slightly arched. The posterior margin of 1Ax is usually hollowed to variable depths.

Anterior half of the second axillary sclerite [2Ax] is swollen and the invagination toward the ventral 2Ax occurs at the middle of this swelling. The 2Ax is fused with BR antero-proximally and the fused region forms an area of bending cuticle. The swollen region of 2Ax usually bear some setae. Posterior to this swelling, a triangular sclerite is observed and represents the posterior part of 2Ax. The 2Ax is articulated with 1Ax by the proximal margin of this triangular sclerite, and its distal margin is usually fused with the proximal median plate. A narrow process extends from the postero-distal margin of the triangular sclerite, and articulates with the anterior part of the third axillary sclerite.

The third axillary sclerite [3Ax] has three arms. The distal arm is very short, usually fused with the basanale, with the fused region forming an area of bending cuticle. The anterior arm is long, narrowed apically, and usually strongly arched. This arm firmly articulates with the posterior process of 2Ax. Near the middle of the anterior arm, a large triangular dorsal process is observed. The process usually articulates with a tiny sclerite appearing near the proximal margin of the anterior arm of 3Ax. The proximal arm is well developed, almost straight and usually broadened proximally. The 3Ax is articulated with the posterior notal wing process by the proximal arm.

The proximal median plate [PMP] is deeply concaved. Its antero-proximal margin is usually completely fused with 2Ax, and becomes immobilized except in Archipsocidae and Hemipsocidae within the Psocomorpha. In Trogiomorpha and Troctomorpha, PMP is not fused with 2Ax and articulates with each other along a convex hinge. The outer margin of PMP is strongly sclerotized, much stronger than other regions of PMP. PMP is fused with the basanale posteriorly.

The distal median plate [DMP] is broad and thin, located just distal to PMP, and articulated with it along a convex hinge (Convex Axillary Fold-line *sensu* Wootton, 1979). DMP is sometimes divided into two sclerites [proximal DMP-1 and distal DMP-2].

The basanale [BA] is located between the distal arm of 3Ax and the base of the

anal vein. It is sometimes regarded as part of 3Ax (eg. Brodsky, 1994), but the sclerite is apparently articulated with 3Ax and should be regarded as an independent sclerite. The terminology of this sclerite follows to Matsuda (1970: figs. 55A & 82D).

The jugum [J] is represented by a weakly sclerotized triangular region.

Hindwing base (Fig. 14B)

The hindwing base structures are similar to those of the forewing base. Tg is absent. Hp is fused with BSc posteriorly, with its proximal region largely membranous.

The 1Ax is triangular, with shape of its apical region usually showing similar trends with that of the forewing.

Anterior half of 2Ax is swollen, and invagination toward ventral 2Ax occurs at the posterior margin of the swelling. This swollen region is widely membranous. The posterior region of 2Ax is similar to that in the forewing.

The 3Ax has three arms. The distal arm is fused with BA, and the fused region becomes bending cuticle. The anterior arm is reduced, shortened, and lacks firm articulation with the posterior process of 2Ax. The proximal arm is strongly sclerotized, a deep concavity is observed at the base of the proximal arm.

PMP is deeply concaved. Its anteroproximal margin is usually fused with 2Ax and immobilized. Distal margin of PMP is well sclerotized. PMP is fused with basanale posteriorly.

DMP is absent with this region broadly membranous.

Wings

Forewing (Figs. 18, 19)

The forewing of Psocomorpha is characterized by the thickened pterostigma, presence of the nodus, and structure of the nodulus. The nodulus, a wing coupling structure, in Psocomorpha is a hook composed of truncated spines fused basally. Whereas, in Trogiomorpha, the nodulus are truncated spines set close together or a set of pointed, separated spines in Troctomorpha. The nodus, a ventral swelling at the proximal end of pterostigma, fits with the anterior margin of the hindwing when the wings are closed, is present in Psocomorpha whereas it is indistinctive in Trogiomorpha and Troctomorpha.

The anterior margin of the forewing is almost straight or slightly arched. Its posterior margin is almost straight in basal half and usually strongly arched distal to the nodulus. In most Psocomorpha, the forewing is widest around the distal 1/3. Alternatively, in most Trogiomorpha and Troctomorpha, the anterior and posterior margins are almost parallel, and gradually tapered apically, such that the widest point in the forewing is not distinctive. The postero-proximal margin of the forewing is usually rounded, but strongly angled in Archipsocidae and Hemipsocidae (Fig. 18B, C). The latter character state is widely observed in Trogiomorpha and Troctomorpha (Fig. 18A).

The subcosta is reduced to a fine vein, often only basally distinctive and faded within the costal cell or connected with R₁ vein. Distally, Sc arises from R₁ and borders the proximal end of the pterostigma. R is branched into R₁ and Rs around the middle of the wing length. R₁ borders the posterior and distal margin of the pterostigma, and is often strongly sinuated. Rs usually branches into R₂₊₃ and R₄₊₅. M arises from the base of R, and is strongly arched basally. M vein approaches to Rs around the center of the forewing, and is either connected by a cross vein, meet at a point, or fused for various

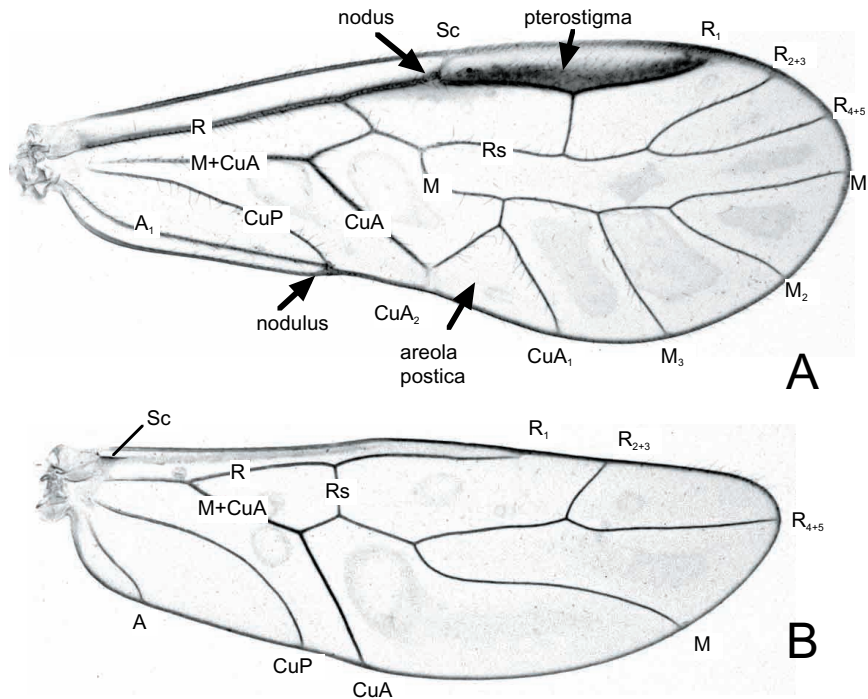


Fig. 17. Fore- (A) and hindwing (B) of *Stenopsocus* sp. (Stenopsocidae).

lengths. M is usually 3-branched. Cu is forked into CuA and CuP basally, with CuA approaching M basally and fused together for a long distance before separating around the center of the wing. CuA is usually forked distally into CuA₁ and CuA₂, and they surround the cell called areola postica. The top of the areola postica, anteriorly arched portion of CuA₁, and M are sometimes fused or connected by a cross vein. CuP is finer than other veins, paralleled by the claval fold, terminating at the nodulus. Usually only one anal vein is recognized in Psocomorpha. A₁ terminates at nodulus with CuP. A₂ is observed in some species of Archipsocidae and almost all species of Dolabellapsocidae, Ptiloneuridae and Cladiopsocidae. A₂ of Archipsocidae is very faint whereas that of the latter three families is very clear, terminating either at the wing margin, on A₁, or within the anal cell. In outgroups, A₂ is usually recognized.

The wing margin and veins are often setose, sometimes with more than one row of setae. Absence of setae on the wing margin and veins is regarded as a derived condition in the Psocomorpha. Membranous regions always bear dense microtrichia. Macrotrichia rarely occur on the membrane.

Hindwing (Fig. 18)

The hindwing of Psocomorpha is always smaller than the forewing. Its venation is basically similar with that of the forewing but further reduced. It differs in the following points: R₁ is not sinuated; M usually does not fork; CuA does not fork so that areola postica is not formed; A terminates far proximal to the end of CuP; R and M+Cu are

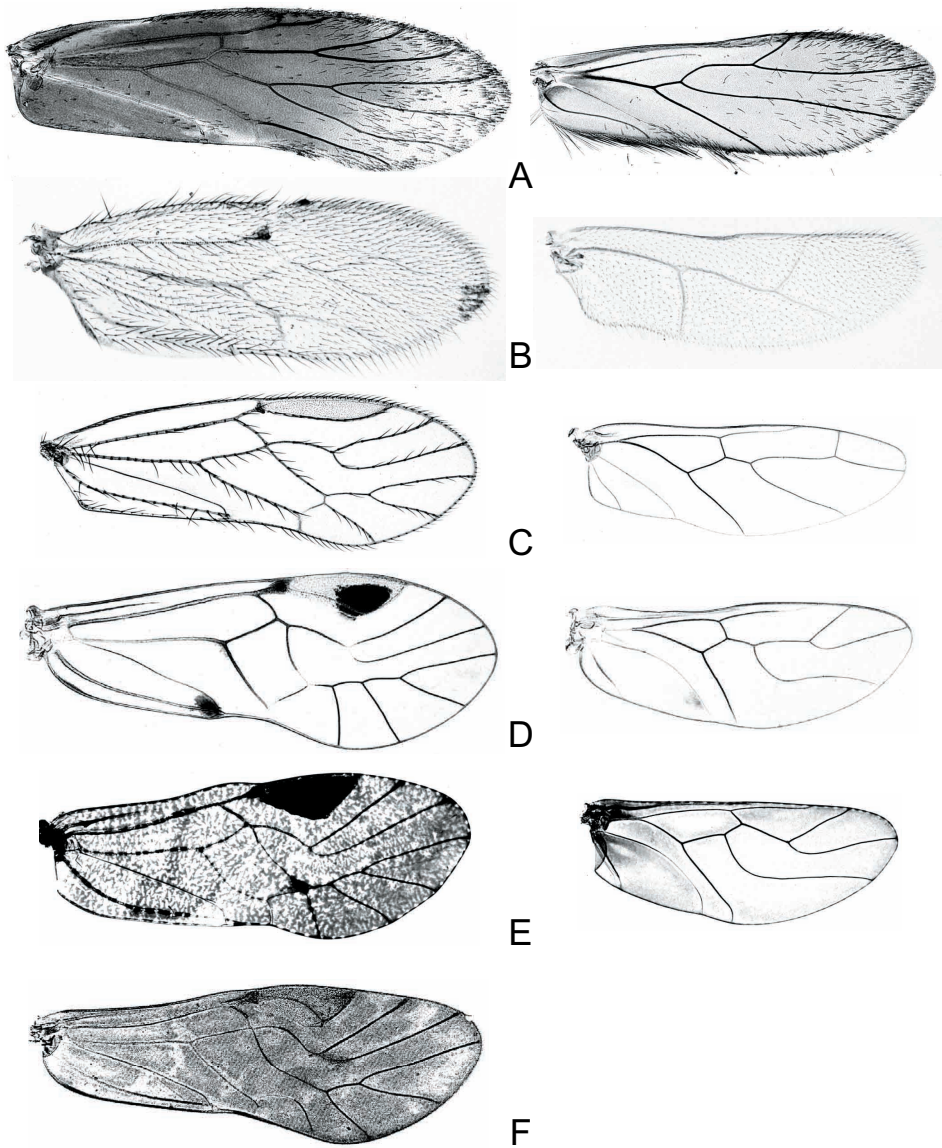


Fig. 18. Fore- (left) and hindwing (right). (A) *Paramphientmum* sp. (Troctomorpha: Amphientomidae); (B) *Pararchipsocus pacificus* (Archipsocidae); (C) *Hemipsocus chloroticus* (Hemipsocidae); (D) *Psocus* sp. (Psocidae); (E) *Lichenomima muscosa* (Myopsocidae); (F) *Psilopsocus nebulosus* (Psilopsocidae) [from Mockford, 1961]

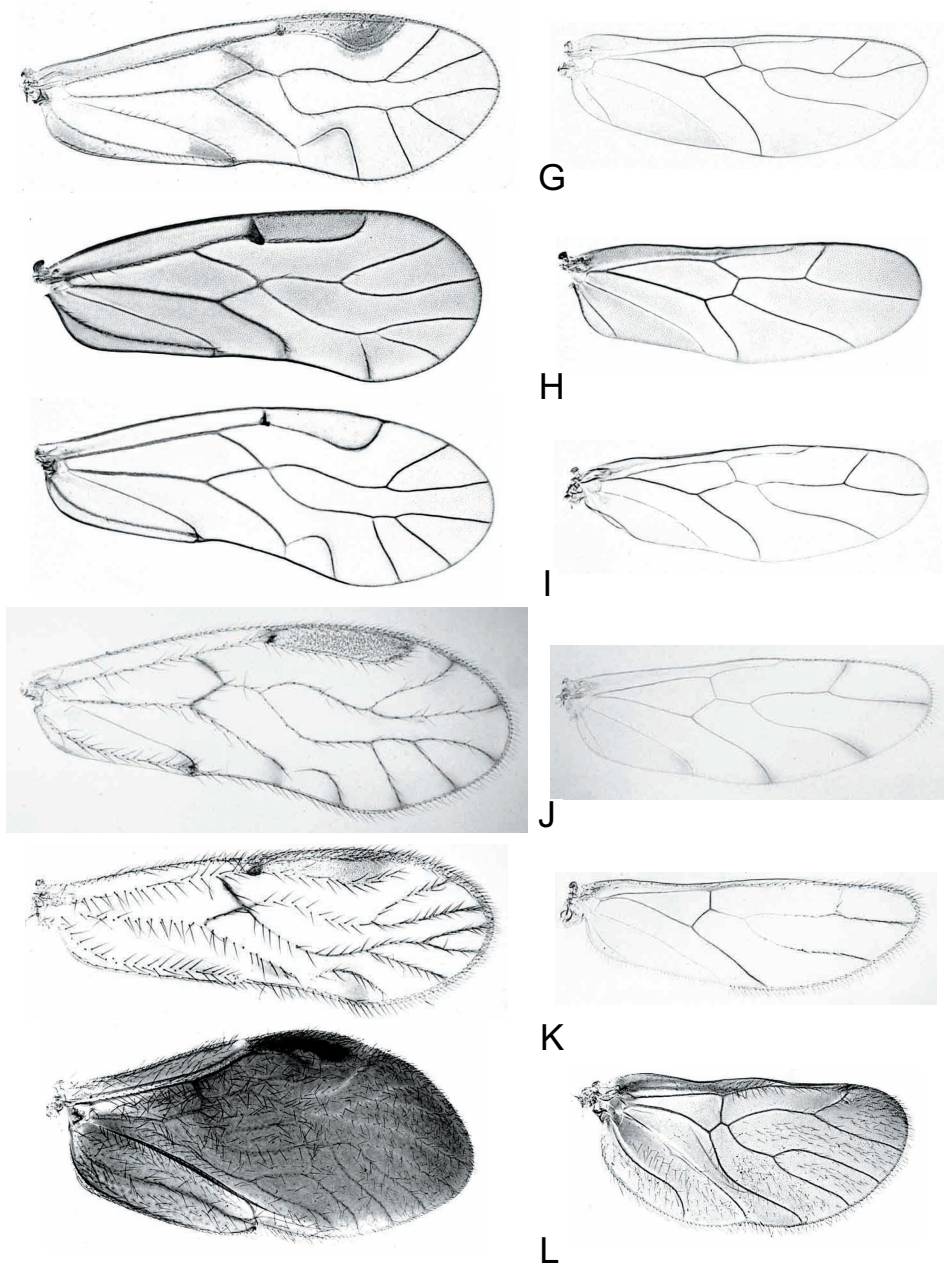


Fig. 18 (continued). (G) *Elipsocus abdominalis* (Elipsocidae); (H) *Ectopsocus* sp. (Ectopsocidae); (I) *Lachesilla pedicularia* (Lachesillidae); (J) *Trichopsocus dali* (Trichopsocidae); (K) *Pseudocaecilius citricola* (Pseudocaeciliidae); (L) *Calopsocus infelix* (Calopsocidae)

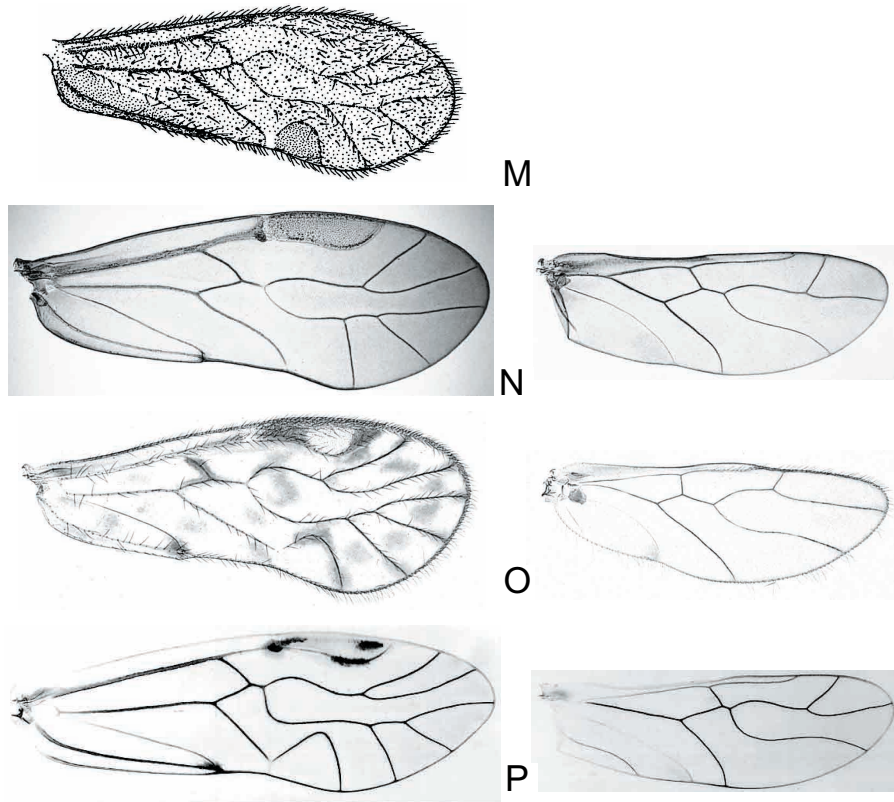


Fig. 18 (continued). (M) *Bryopsocus townsendi* (Bryopsocidae) [from Thornton et al., 1977]; (N) *Peripsocus quercicola* (Peripsocidae); (O) *Philotarsus picicornis* (Philotarsidae); (P) *Mesopsocus dislobes* (Mesopsocidae)

usually fused for a short distance basally; Rs and M are usually fused for a short length but connected by a crossvein in Ectopsocidae and some genera of Myopsocidae.

The hindwing margin is usually setose. Veins are sometimes setose in one or two rows, and, if setose, setae are restricted in the distal half only. Membranous regions are covered with microtrichia and macrotrichia are observed in Archipsocidae only.

The anterior margin possesses a trench. The nodulus of forewing is hooked to this trench when the wings are open, effectively coupling both wings.

Legs (Fig. 20A–E)

All legs are usually slender and similar. The hind coxa of most families possesses the Pearman's organ (supposed stridulatory organ) on its inner surface. The organ consists of a small rugose dome and an adjacent membranous area of integument. The trochantin lacks movable articulation with the femur. The tibia is long, cylindrical, apically spurred, bearing a row of ctenidiobothria. The tarsus is 2- or 3-segmented and always bears a row of ctenidiobothria. The apical segment has two variable pulvillus and two pretarsal claws, each toothed or not.

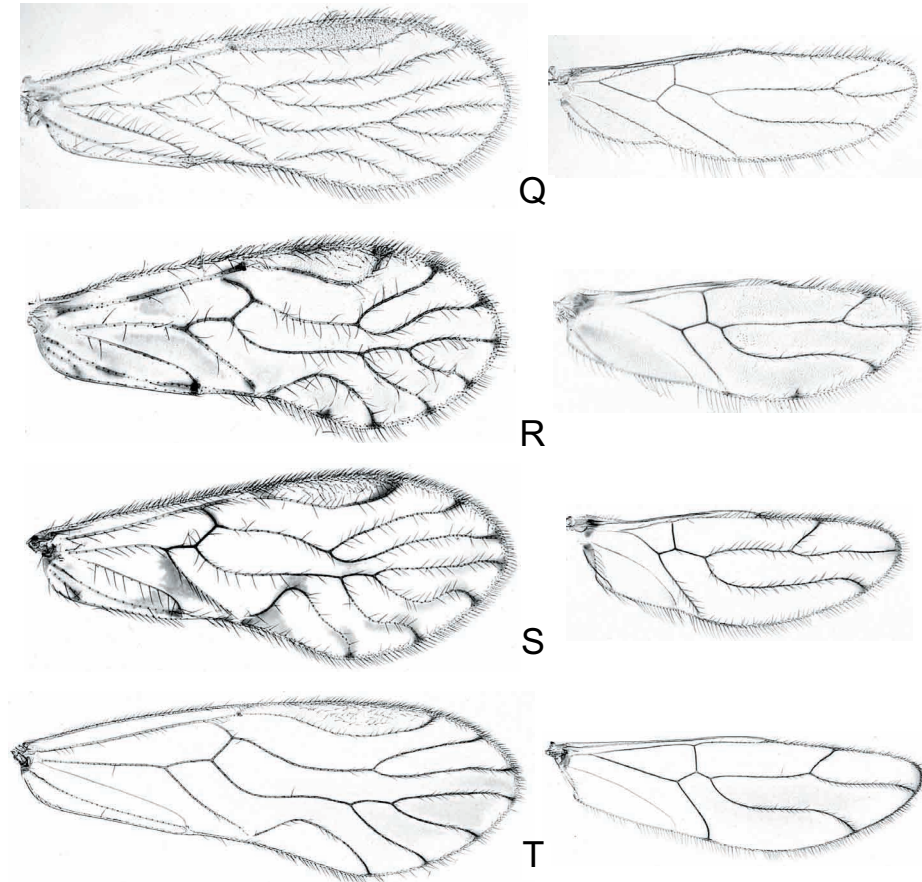


Fig. 18 (continued). (Q) *Cladiopsocus garciai* (Cladiopsocidae); (R) *Dolabellopsocus roseus* (Dolabellopsocidae); (S) *Triplocania spinosa* (Ptiloneuridae); (T) *Epipsocopsis* sp. (Epipsocidae)

Pregenital abdominal segments (Fig. 20F)

The pregenital abdominal segments of Psocomorpha are wholly membranous except the basal two segments having well sclerotized plates. Only in Arechipsocidae and Hemipsocidae, weakly sclerotized tergum and sternum are observed throughout all pregenital abdominal segments. Badonnel (1934) regarded the basal two segments as the divided first segment. Matsuda (1976) mentioned that they are the true first and second segments but did not give a reason for this interpretation. Judging from external structure, musculature, and total number of abdominal segments, they should be regarded as true first and second abdominal segments. The first segment has a transverse sclerite dorsally. The second segment has a dorsal transverse sclerite, ventral ringlike sclerite, and lateral C-shaped sclerites. All abdominal segments have a dorsal row of setae on the distal margin. Usually eight pairs of spiracles are observed, spiracles of the 2nd abdominal segment are not distinctive.

A few abdominal eversible vesicles are observed on the ventral surface in

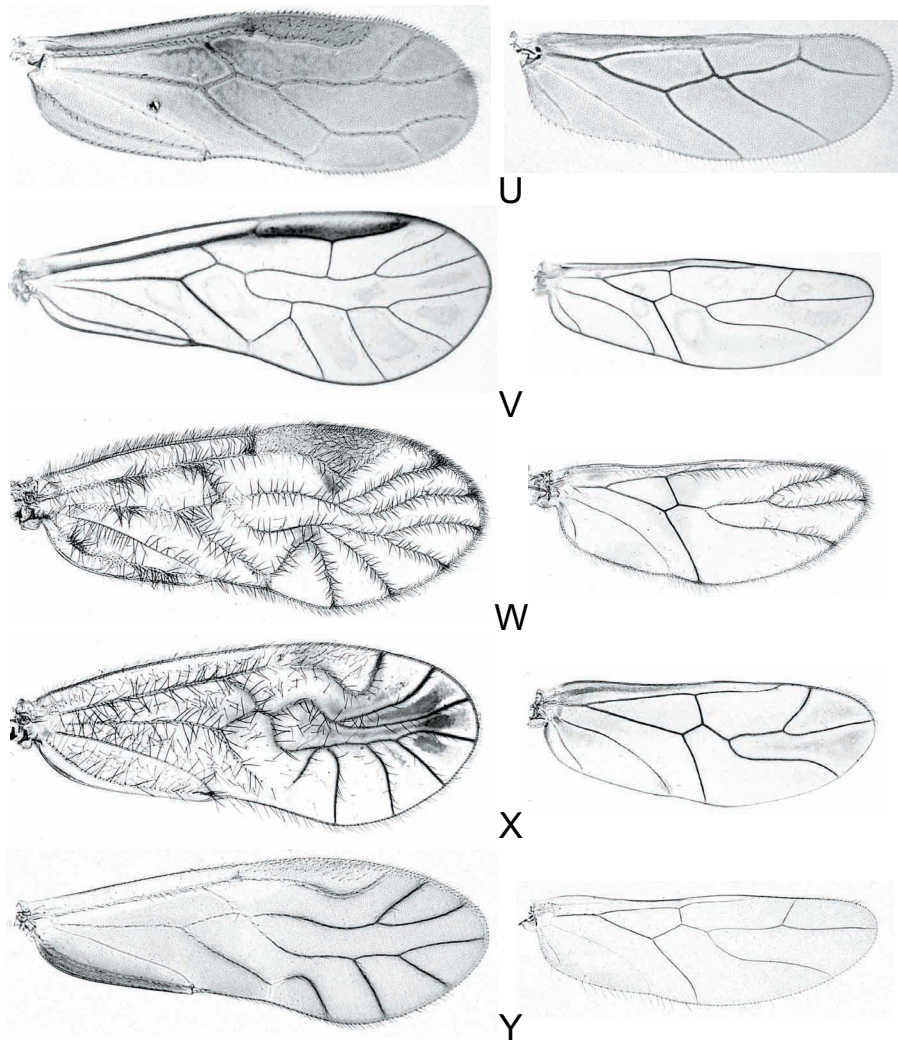


Fig. 18 (continued). (U) *Notiopsocus aldretei* (Asiopsocidae); (V) *Stenopsocus* sp. (Stenopsocidae); (W) *Amphipsocus japonicus* (Amphipsocidae); (X) *Matsumuraiella radiopicta* (Amphipsocidae); (Y) *Valenzuela flavidus* (Caeciliusidae).

Caeciliusoidea and Pseudocaecilioidea. This structure seems strongly correlated with living-foliage dwelling as mentioned by New (1987) and Yoshizawa (1999).

Male terminalia

Clunium (Fig. 21)

The male clunium usually comprises the 10th tergum. In some taxa, the 9th paratergum or whole 9th tergum is involved in this structure. Its ventrodistal region usually projects postero-internally, and is articulated with the ventral margin of the paraproct. The dorsodistal margin of the clunium often has serrations, flap-like

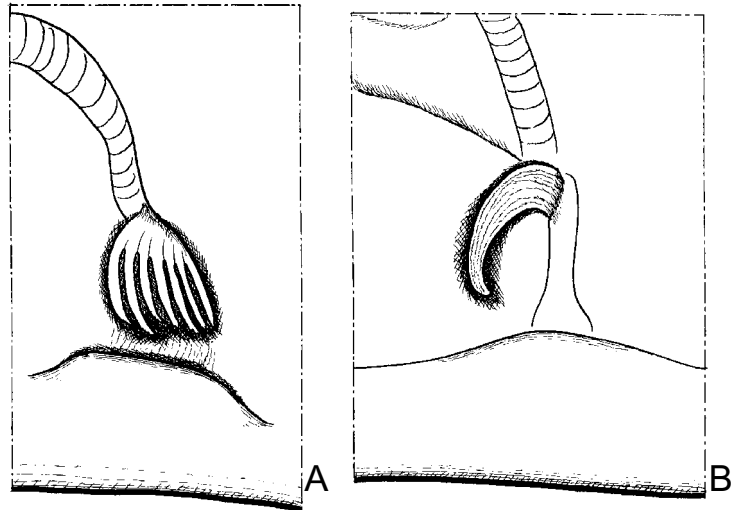


Fig. 19. Nodulus. (A) *Paramphientomum* sp. (Troctomorpha: Amphientomidae); (B) *Longivalvus nubilus* (Psocidae).

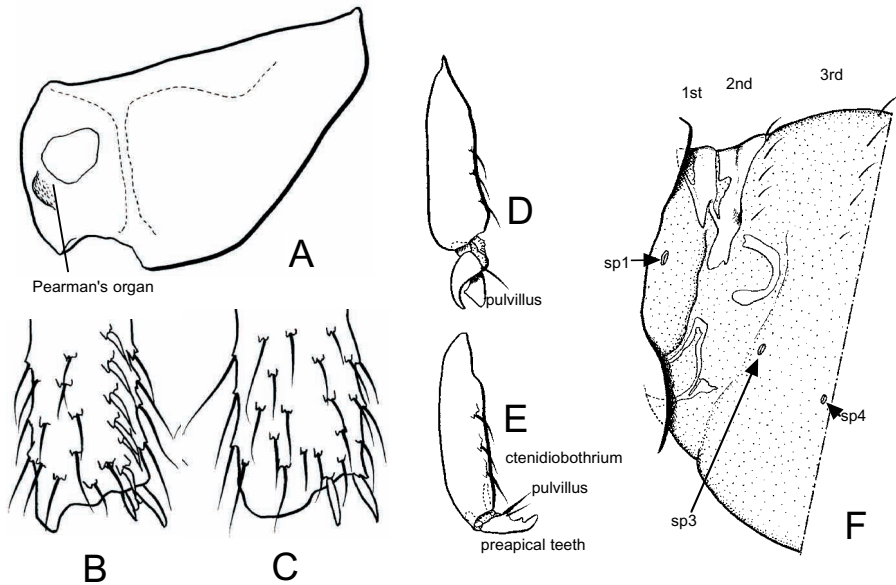


Fig. 20. (A) Coxa of *Hemipsocus chloroticus* (Hemipsocidae); (B) apex of hind tibia of *Psocus* sp. (Psocidae); (C) ditto, *Stenopsocus* sp. (Stenopsocidae); (D) distal tarsomere and claws of *Stenopsocus* sp. (Stenopsocidae); (E) ditto, *Psocus* sp. (Psocidae); (F) first three abdominal segments of *Longivalvus nubilus* (Psocidae).

extensions, or unique processes.

Epiproct and Paraproct (Fig. 21)

The epiproct and paraproct are lobe-like structures surrounding the anus. They were considered to represent 11th (Snodgrass, 1935) or 12th (Matsuda, 1976) segment. The paraproct represents, at least in part, the 11th abdominal segment because it involves the reduced cercus (trichobothrial field). The trichobothrial field is observed on the external surface of the paraproct except in some wingless forms. This structure was regarded as the cercus by Matsuda (1976), whereas Smithers (1972) regarded it not homologous with the cercus. Judging from its position, the trichobothrial field should be regarded as a reduced cercus. The male epiproct and paraproct sometimes have processes or additional lobe-like structures, such as the epiproct lobe (Fig. 21B) (Psocidae: Ptyctini) or distal process of the paraproct (Fig. 21B) (Hemipsocidae, Lachesilliidae, Psocidae).

Hyandrium

The hyandrium is composed of the 9th sternum and rarely the 8th sternum. In the plesiomorphic condition, the hyandrium is simply rounded posteriorly without processes or lobes (Fig. 21A). The hyandrium is usually fused with the 9th tergum anterodorsally (Fig. 21A), but separated and articulated with each other in Psocidae, Pseudocaediliidae, Philotarsus, etc (Fig. 21B, C). In these taxa, the hyandrium is highly modified, bearing distal processes or lobes. The shape of the hyandrium is highly variable among different taxa at any taxonomic level.

Phallosome (Fig. 22)

The phallosome of Psocomorpha usually consists of the parameres (external paramere), the aedeagus (mesomere, internal paramere), the phallobase (basal plate), and the endophallus. Badonnel (1934) mentioned that the external paramere (= paramere) and internal paramere (= aedeagus) of Psocoptera correspond to the paramere and aedeagus of Homoptera and Matsuda (1976) basically agreed with this scheme. I think homologies of the coupling organ between Psocoptera and Homoptera (or other insects) are still uncertain. In contrast, homology of these structures is relatively well established by Lyal (1986) and Yoshizawa & Johnson (in press).

The endophallus with or without a sclerotized portion. Usually, a pair of weakly sclerotized plates are observed on the permanently-everted part of the endophallus next to the opening of the un-everted endophallus (*sensu* Lyal, 1986), but absence of the sclerites is also frequent. In Hemipsocidae, Caeciliusetae, Elipsocidae, and Mesopsocidae, groups of minute sclerotized papillae are often observed on the endophallus. Sometimes these areas look like a plate-like structure when the endophallus is closed. In many taxa of Homilopsocidea, rod-like sclerites are observed on the endophallus. The number of the sclerites are basically three, but in some Peripsocus, those sclerites are united with each other, forming a unique structure. The rod-like sclerites on the endophallus are secondarily lost in Lachesilla, some genera of Philotarsidae, and Mesopsocidae.

The parameres are usually a pair of stick-like sclerites arising from the internal margin of the distal end of the phallobase, supporting the ventrolateral surface of the endophallus. The aedeagus is a narrow to broad sclerotized strip supporting the dorsodistal margin of the endophallus. The ejaculatory duct is always ventral to the aedeagus and dorsal to the paramere. Therefore, the ejaculatory duct can be used for a

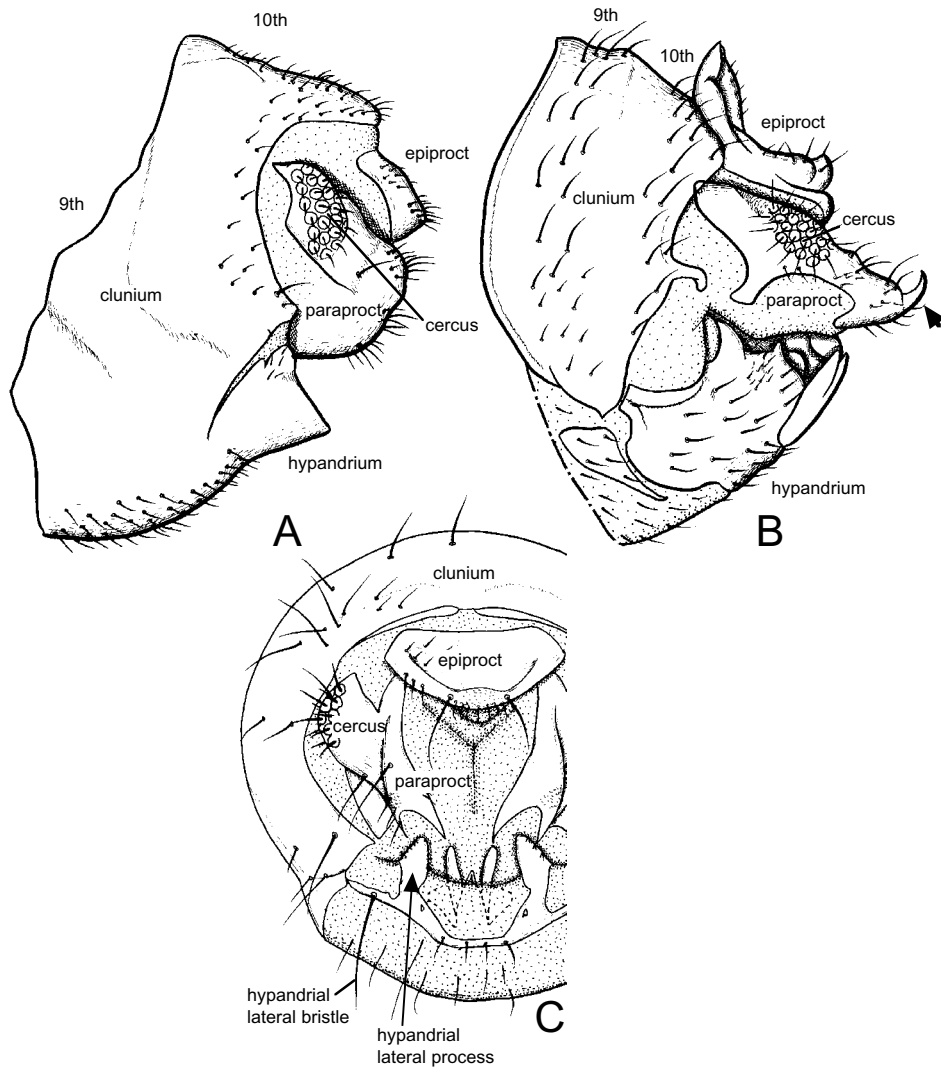
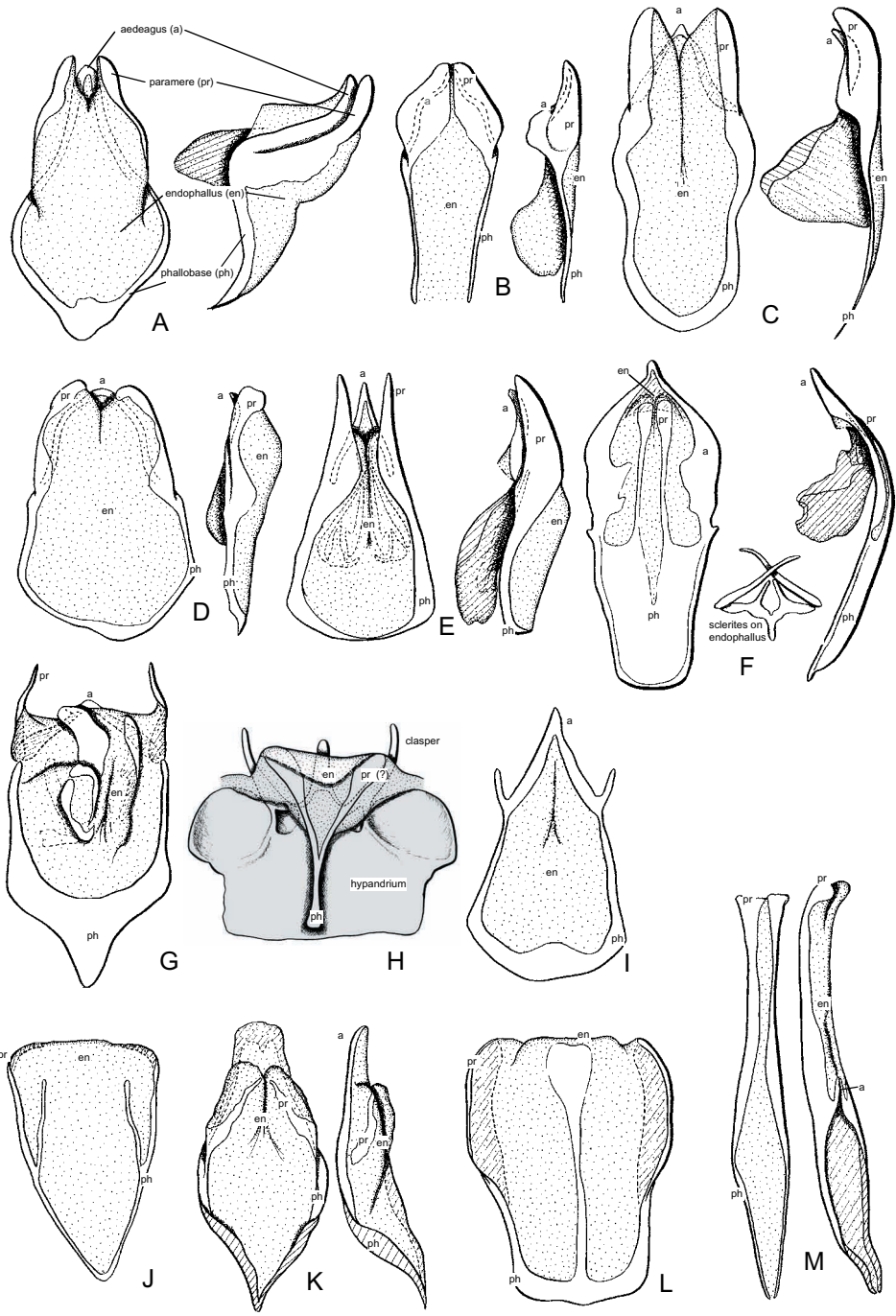


Fig. 21. Male genitalia. (A) *Idatenopsocus orientalis* (Mesopsocidae), lateral aspect; (B) *Trichadenotecnum sexpunctatum* (Psocidae), lateral aspect, arrow indicates paraproctal distal process; (C) *Heterocaecilius fuscus* (Pseudocaeciliidae), posterior aspect.

reliable landmark to decide the homology of structures in the phallosome. The phallobase is a ringlike, narrow sclerite supporting the anteroventral margin of the endophallus. In some taxa, the anterior margin of the phallobase is membranous.

The structure of the phallosome shows great diversity among families and it is very difficult to determine transformation series corresponding to the phylogeny of psocids. Thus, in the following lines, I will discuss the morphology of the male phallosome in each psocomorphan taxon.

The most basic psocomorphan phallosomal characters (not most plesiomorphic



character states of the suborder) may be represented by those in the Caeciliusetae (Fig. 22A). The aedeagus and phallobase are fused, comprising a ring-like structure. The apex of the aedeagus is pointed, and anterior margin of the phallobase is closed and rounded, with no significant apodeme. The paramere arises from the internal margin of the ring, supporting the ejaculatory bulb ventrally. The phallosome of Caeciliusetae is characterized by upright and strongly arched parameres and aedeagus (Fig. 22A). Phallosome of families of Caeciliusetae are all very similar.

Phallosome of Epipsocetae is very similar to that of Caeciliusetae in the plesiomorphic state (Fig. 22B), but shows great diversity within the taxon. I have examined only a few male specimens of Epipsocetae, and cannot discuss the homology and transformation series of the phallosome in this family group at the present time.

Basic phallosomal structures of most families of Homilopsocidea (*sensu* Yoshizawa, 2002), such as Elipsocidae, Trichopsocidae, Pseudocaediliidae, Calopsocidae, most genera of Philotarsidae and Mesopsocidae, are almost identical with those of Caeciliusetae in basic structures (Fig. 22C–E) but the parameres and aedeagus are not held upright nor arched. In some taxa, the aedeagus is detached from the phallobase and rounded apically. The anterior margin of the phallobase is sometimes opened.

In Ectopsocidae (Fig. 22G), basic structures of phallosome are almost identical with those of Elipsocidae, etc. In contrast, the paramere is articulated basally with the phallobase.

Genitalia of *Lachesilla* are very characteristic in having a Y- or T-shaped phallosome, with a long apodeme apically (Fig. 22H) with lateral claspers on the hypandrium. According to Klier (1956), the phallosome of this genus underlies the ejaculatory duct. Mockford (1985) studied the genus *Nadleria*, considered to retain the plesiomorphic condition of the subfamily Lachesillinae, and some genera of the subfamily Graphocaeciliinae, considered to retain the most primitive condition of this family, and proposed a hypothesis about the evolution of the male genitalia in Lachesillidae. He mentioned that the Y-shaped phallosome and the clasper on the hypandrium can be derived from the closed phallosome and the simple hypandrium seen in the other homilopsocid psocids, such as Elipsocidae. The claspers on the hypandrium were presumably derived from the parameres and the aedeagus is completely membranous. However, I doubt this hypothesis. As discussed above, the paramere always arises from the internal margin of the phallobase and is associated with the endophallus basally. However, in a species of *Lachesilla* I examined (Fig. 22H; member of the *L. pedicularia* group collected from Vietnam), the claspers on the hypandrium arise lateral to the external margin of the phallosome without connecting with the endophallus. This

← Fig. 22. Phallosome, ventral (left) and lateral (right) aspect. (A) *Dypsocus coleopteratus* (Caeciliusidae); (B) *Isthmopsocus* sp. (Dolabellopsocidae); (C) *Elipsocus abdominalis* (Elipsocidae); (D) *Haplophallus* sp. (Philotarsidae); (E) *Heterocaecilius anomalis* (Pseudocaeciliidae); (F) *Peripsocus quercicola* (Peripsocidae); (G) *Ectopsocopsis cryptomeriae* (Ectopsocidae), ventral aspect; (H) *Lachesilla* sp. (Lachesillidae), dorsal aspect including hypandrium; (I) *Pararchpsocus pacificus* (Archipsocidae), ventral aspect; (J) *Hemipsocus chloroticus* (Hemipsocidae), ventral aspect. (K) *Sigmatoneura kolbei* (Psocidae), ventral (left) and ventro-lateral (right) aspect; (L) *Myopsocus* sp. (Myopsocidae), ventral aspect; (M) *Lichenomima muscosa* (Myopsocidae), ventral (left) and dorsolateral (right) aspect.

character condition suggests that the clasper on the hypandrium is not homologous with the paramere. Thus, it is reasonable to regard that the hypandrial clasper is derived from the hypandrium and the Y-shaped phallosome is formed by reduction of the parameres and aedeagus. Matsuda (1976) mentioned that the genitalic character condition of *Lachesilla* is neotenous, and the hypandrium is represented by paired coxopodites bearing a style. I think Matsuda's hypothesis is more probable.

As mentioned by Mockford (1993), the phallosome of Peripsocidae is unique (Fig. 22F), and homology of the peripsocids phallosome is often misinterpreted. For example, Smithers (1972) noted that the “external parameres (= parameres) are united posteriorly in a point”. However, the structure he mentioned as the paramere is actually the aedeagus, and the paramere are represented by a pair of median longitudinal strap-like sclerites. This modification is autapomorphic for Peripsocidae.

In Psocidae (Fig. 22K), the parameres are usually reduced or completely absent. Weakly sclerotized parameres are observed in *Sigmatoneura* and a well-developed paramere is observed in *Psocidus* s. str.. It is presently uncertain whether or not the well-developed paramere observed in these taxa represent the most plesiomorphic condition of the family. A pair of posterior projections somewhat similar to the parameres are observed in some species of *Trichadenotecnum*, but the structures are considered not to be homologous with the parameres (Yoshizawa, 2003) and thus are termed as pseudoparamere (Yoshizawa, 2004).

The phallosome of Myopsocidae is greatly variable within the family. In *Mesopsocus* (Fig. 22L), the aedeagus is completely membranous, the anterior margin of the phallobase is closed and rounded, and on the endophallus, a sclerotized strap is observed. Alternatively, the phallosome in *Lichenomima* is greatly elongate, the parameres are strongly protruded posteriorly, the aedeagus is observed dorsal to the base of the paramere, and the phallobase is separated apically (Fig. 22M). Transformation series of the phallosome within the family are completely unknown presently.

In Hemipsocidae (Fig. 22J), the aedeagus is completely membranous and the phallosome is composed of a narrow phallobase and parameres. In some species, such as *Hemipsocus chloroticus*, a pair of narrow sclerites arise from the internal margin of the phallobase. They are somewhat similar to the paramere, but judging from their position, they should be regarded as secondary structures and not homologous with any primary component of the phallosome.

In Archipsocidae (Fig. 22I), the paramere is usually absent and the phallosome becomes a ring composed of the phallobase and aedeagus. Anterior margin of the phallobase is often detached. Although not examined, some species of *Archipsocus* have weakly developed parameres (New, 1973: figs. 36, 42, 43). In the subfamily Pararchipsocinae, a pair of lateral processes arise from the external margin of the phallic ring which is the extended attachment of the retractor muscle of the phallosome.

Female terminalia

Clunium (Fig. 23A)

Female clunium of Psocomorpha consists of the 10th tergum and the 9th paratergum.

The posterior margin of the 8th paratergum is sometimes also incorporated. Its posteroventral region usually extends postero-internally and articulates with the ventral margin of the paraproct.

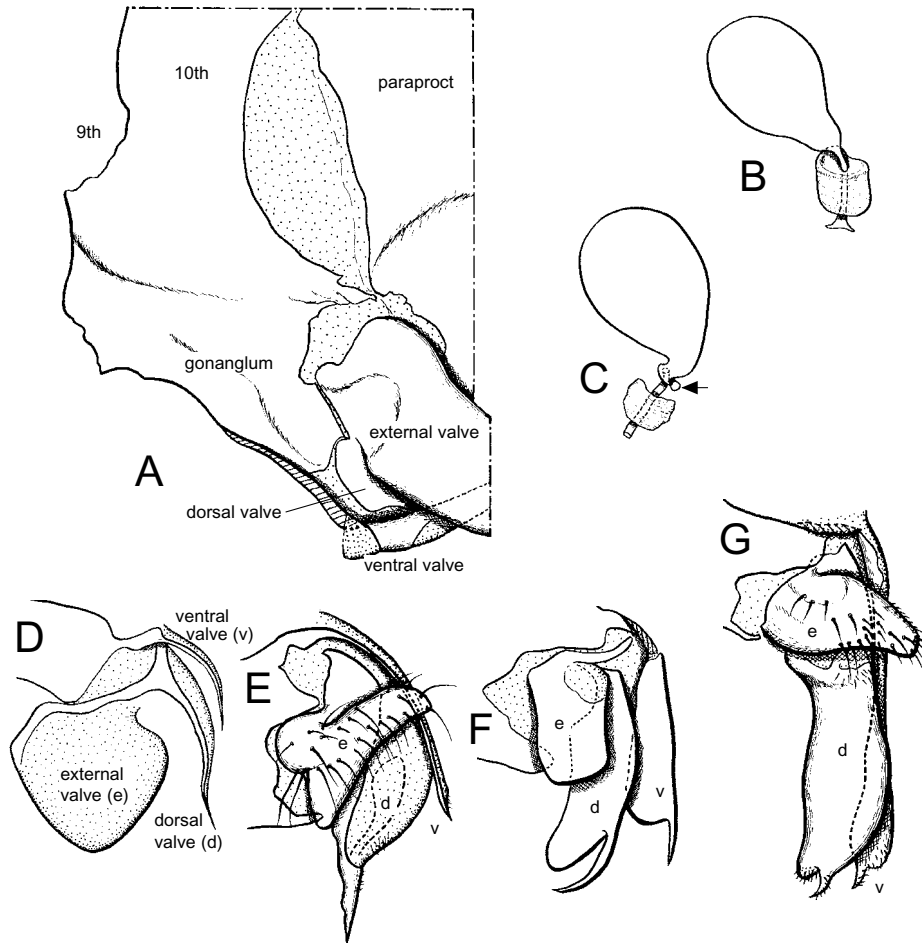


Fig. 23. Female genitalia. (A) *Mesopsocus hongkongensis* (Mesopsocidae); (B) spermatheca of *Matsumuraiella radiopicta* (Amphipsocidae); (C) ditto, *Stenopsocus* sp. (Stenopsocidae), arrow indicates the lateral pouch; (D) gonapophyses of *Hemipsocus chloroticus* (Hemipsocidae); (E) ditto, *Trichadenotecnum sexpunctatum* (Psocidae); (F) ditto, *Heterocaecilius anomalus* (Pseudocaeciliidae); (G) ditto, *Mesopsocus dislobes* (Mesopsocidae).

The gonangulum is usually completely fused with the 9th paratergum, and often indistinguishable with each other. The gonangulum is fused or articulates with the base of the ventral valve anteriorly and articulates with the dorsal valve of the gonapophysis posteriorly.

Epiproct and Paraproct (Fig. 24)

Female epiproct and paraproct are almost the same in basic structure as those of the male, but processes never occur on these structures in females. The paraproct of Hemipsocidae and Psocetae extends distally as a conical projection, which is possibly related to the egg lying behavior. In Mesopsocidae, a well-developed ventral lobe of

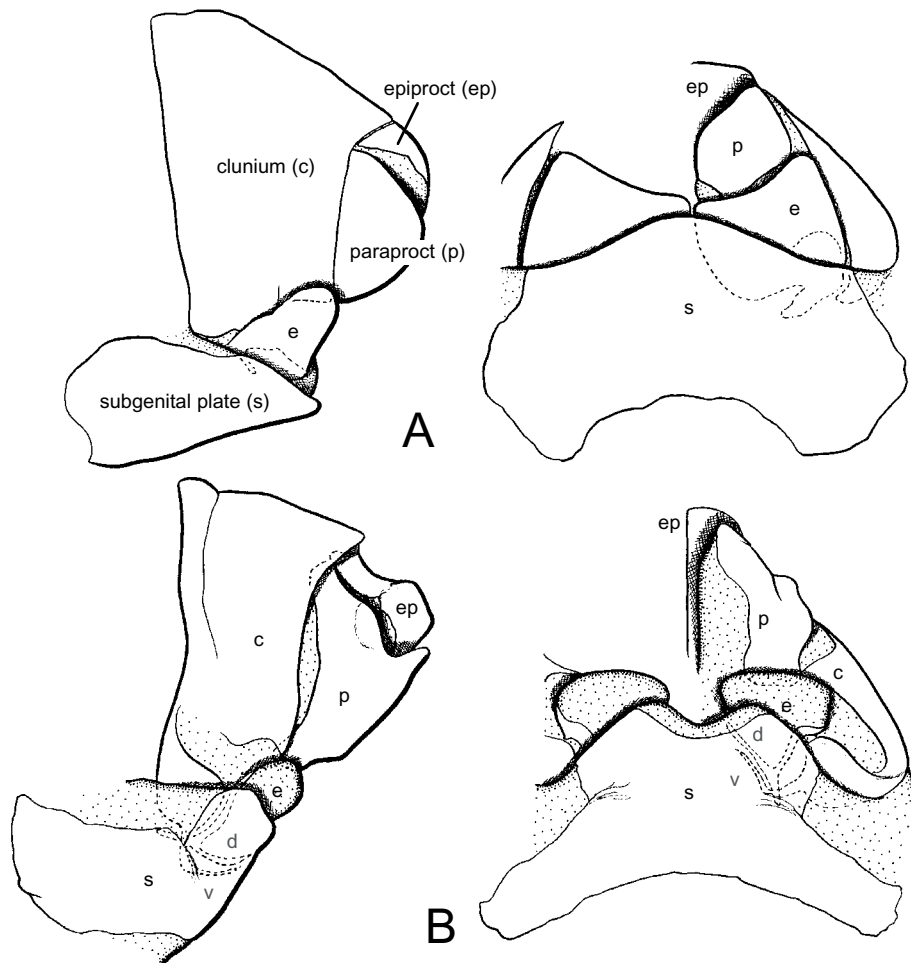


Fig. 24. Female genitalia, lateral (left) and ventral (right) aspects. (A) *Archipsocus* sp. (Archipsocidae); (B) *Hemipsocus chloroticus* (Hemipsocidae)

the paraproct is observed, which supports the ovipositor laterally. The paraproct of *Dasydemellidae* has some very strong spines on its distal margin. Similar spines are also observed in nymphs of many psocids. Mockford (1978) regarded the presence of these spines in *Dasydemellidae* as neotenic character states. *Dasydemellidae* also has similar spines on the epiproct that are regarded as another example of neoteny in the family by Mockford (1978).

Subgenital plate (Fig. 24)

The subgenital plate of Psocomorpha is formed by the 8th sternum and its posterior extension. Between the 8th sternum and its extension, dense and/or strong wrinkles are often observed and are regarded as the border between the 8th sternum and its extension.

In the primitive condition, the posterior margin of the subgenital plate is smoothly rounded or slightly hollowed medially (Fig. 24A, B, J–M). Alternatively, in Psocetæ and

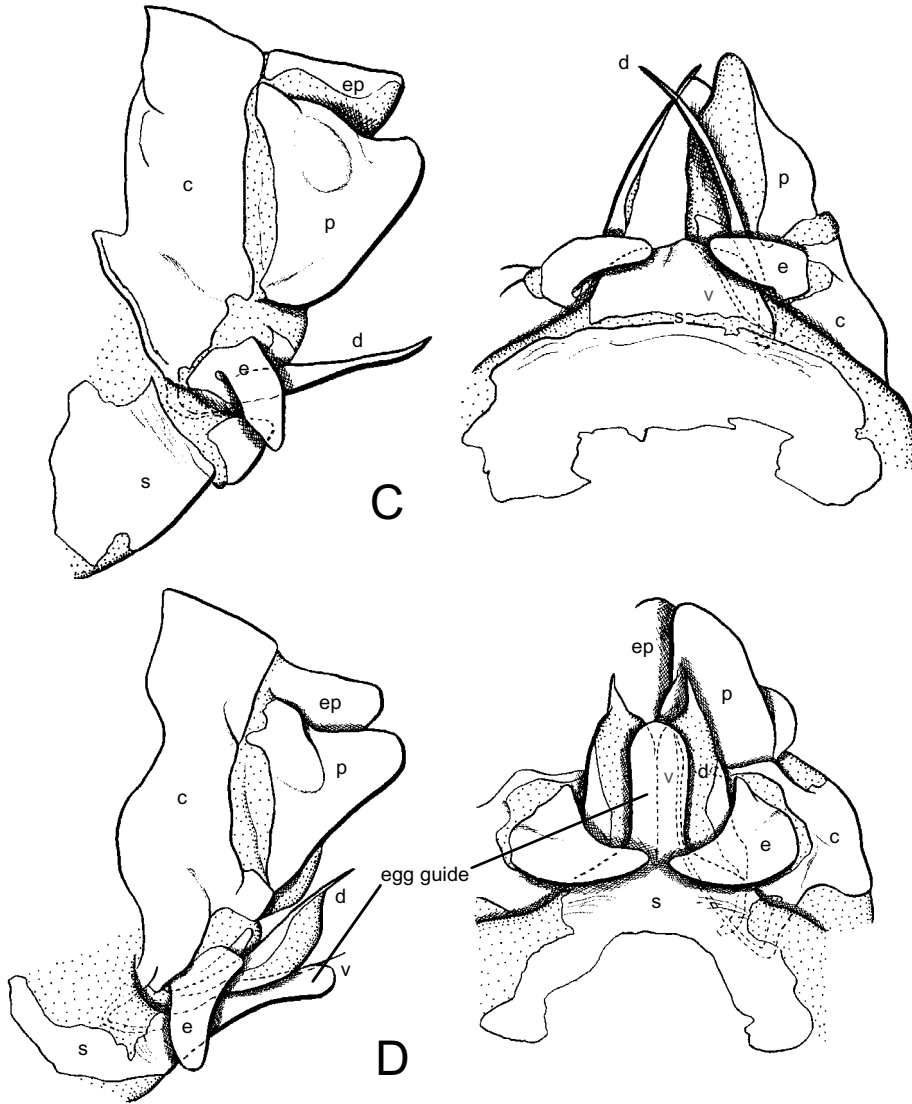


Fig. 24 (continued). (C) *Lichenomima muscosa* (Myopsocidae); (B) *Psocidus* sp. (Psocidae)

Homilopsocidea, the posterior margin of the subgenital plate is often extended, forming an egg guide (Fig. 24D–G). In Psocetae, the egg guide is regarded as an extension of the ventrodistal margin of the subgenital plate and the ventral margin of the subgenital plate (including the egg guide) is straight or smoothly arched in lateral aspect (Fig. 24D). In contrast, the egg guide of Homilopsocidea is regarded as an extension of the dorsodistal margin of the subgenital plate and the ventral margin of the subgenital plate is strongly dorsally bent at the base of the egg guide in lateral aspect (Fig. 24E). Consequently, the egg guide of these two taxa are different in their origin and non-homologous.

The egg guide of Elipsocidae (Fig. 24E) is composed of a pair of small tubercles

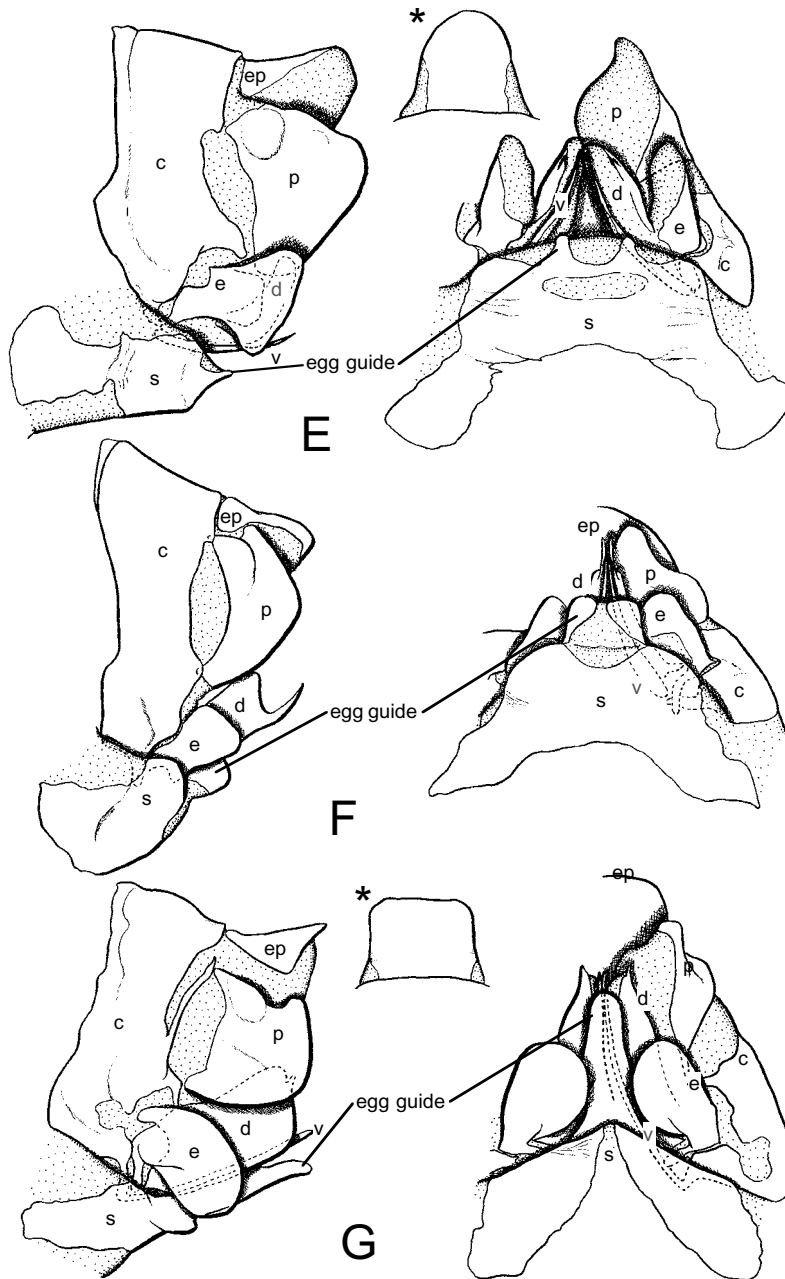


Fig. 24 (continued; * epiproct, dorsal aspect). (E) *Elipsocus abdominalis* (Elipsocidae); (F) *Heterocaecilius anomalis* (Pseudocaeciliidae); (G) *Haplophallus* sp. (Philotarsidae).

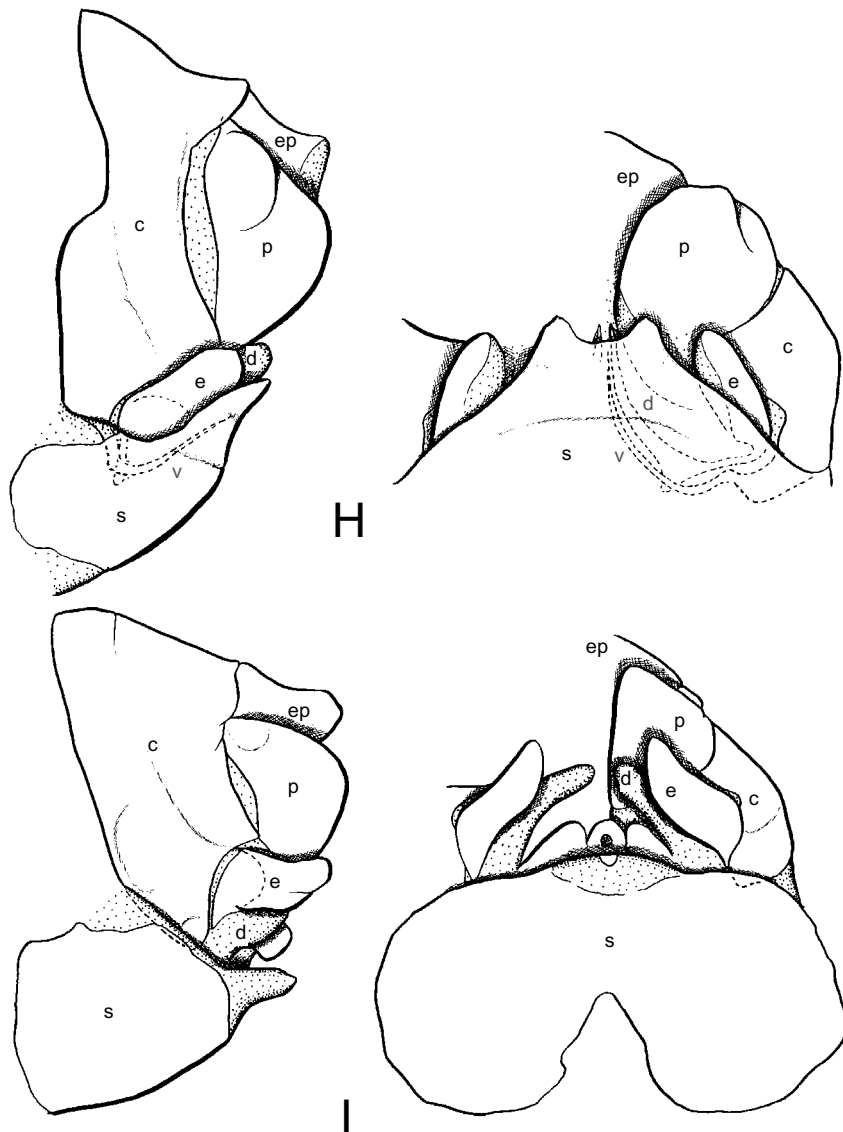


Fig. 24 (continued). (H) *Ectopsocus* sp. (Ectopsocidae); (I) *Lachesilla* sp. (Lachesiliidae)

bearing some apical setae (stage 1) whereas that of Ectopsocidae, Pseudocaeciliidae, and Calopsocidae is well projected posteriorly, bilobed apically, each lobe bearing apical setae (stage 2) (Fig. 24F). The structure of the apex of the egg guide in stage 2 is basically identical with the egg guide in stage 1. Therefore, the egg guide in stage 2 was probably derived from stage 1. The egg guide of Peripsocidae, Philotarsidae, and Mesopsocidae are well projected posteriorly, one-lobed, and usually lacks apical setae (stage 3) (Fig. 24G). The egg guide of some peripsocids is one-lobed but slightly hollowed apically, and somewhat intermediate between stages 2 and 3. Therefore, one-lobed egg guide is



Fig. 24 (continued). (J) *Notiopsocus aldretei* (Asiopsocidae); (K) *Triplocania spinosa* (Ptiloneuridae).

probably derived from stage 2. To summarize, a transformation series of the egg guide from stage 0 (no egg guide, outgroup) to stage 3 in Homilopsocidea can be hypothesized.

Gonopore plate (Internal plate)

The gonopore plate or internal plate is a sclerite surrounding the opening of the spermathecal duct. It is regarded as the 9th sternum, and located above the subgenital plate. Shape and size of the plate are variable among taxa and usually with some pockets



Fig. 24 (continued). (L) *Matsumuraiella radiopicta* (Amphipsocidae); (M) *Stenopsocus* sp. (Stenopsocidae)

on the plate. Betz (1983) found that the hypandrial distal processes of *Trichadenotecnum alexandrae* fit in the pockets on the gonopore plate when coupled (Betz, 1983: fig. 4).

Gonapophyses (Fig. 23D–G)

Three pairs of valves (ventral, dorsal, and external), are usually observed. Size, shape, and structure of the gonapophysis are variable among taxa at any taxonomic level.

The ventral valve arises from the membranous region of the 8th segment. It is usually a simple needle-like process, and articulated or fused basally with the gonangulum. In some taxa such as Mesopsocidae, the ventral valve is broadened apically,

and with an apical process.

The dorsal valve arises from the 9th sternum, and articulates basally with the gonangulum. This valve is usually narrow and needle-like, but broadened in Psocidae and Homilopsocidea. In both cases, the dorsal valve composes a well-developed ovipositor together with the ventral valve and the egg guide. However, morphology of the dorsal valve is quite different between those two taxa. In Psocidae, the ventro-internal region of the dorsal valve is swollen and the apical process arises from its dorso-external region. Alternatively, in Homilopsocidea, the dorsal region of the dorsal valve is swollen and the apical process arises from its ventral region. These morphological differences suggest their independent origin.

The external valve arises laterally from the base of the dorsal valve, and is fused with it basally. Shape and size of this valve is variable.

In most families, three pairs of valves are observed and, in such cases, homology of each valve is easily recognized. However, in some taxa one or two valves are reduced or fused with each other, and sometimes causes confusion for interpretation of their homology.

In Archipsocidae (Fig. 24A), the ventral valve is completely absent. The dorsal valve is also reduced or absent, except Pararchipsocus has a narrow dorsal valve. The external valve is very large, subtriangular. In Archipsocopsis, a viviparous taxon, all three valves are completely absent. Smithers (1990) called the dorsal valve of Pararchipsocus as the 'ventral valve' in his key, but the valve apparently arises from the 9th segment and should be considered as the dorsal valve. Badonnel et al. (1984) also referred to this as the dorsal valve.

In Epipsocetidae (Fig. 24K), the external and dorsal valves are fused, and often look like a single valve. The ventral valve is often absent.

In Ectopsocidae, three valves are usually observed (Fig. 24H). However, the dorsal and ventral valves are reduced in some taxa. Especially in Ectopsocopsis, these valves are greatly reduced, fused with the gonopore plate, and compose a unique structure.

In Lachesillidae, *Eolachesilla* was regarded as the most plesiomorphic taxon of the family (Mockford & Sullivan, 1984), and possesses three pairs of valves in the gonapophyses. However, in the other lachesillid genera, the gonapophyses are greatly reduced and often only one large setose valve is observed. Roesler (1940) regarded the large setose valve as the dorsal valve. Mockford (1972) and García Aldrete (1974) regarded the large setose valve as the external valve and the smaller pair of membranous lobes observed in *Anomopsocus* and some species of *Lachesilla* as the dorsal valve. In contrast, Mockford & Sullivan (1984) discussed the morphology of the gonapophyses of Lachesillidae, and concluded that the large setose valve contains elements of the dorsal and external valves and the small membranous lobe is the ventral valve. I have examined one species of *Lachesilla* sp. (Fig. 24I) that has a small membranous lobe on the gonapophyses. The lobe apparently arises from the 9th segment, and should be regarded as the dorsal valve. Judging from the illustration in Mockford (1972: fig. 16), the valve which was regarded as the dorsal valve and later regarded as the ventral valve by Mockford & Sullivan (1984) also arises from the 9th segment, and should be regarded as the dorsal valve. Consequently, the large setose valve should be regarded as composed of the external valve only.

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REFERENCES

- Badonnel, A. 1934. Recherches sur l'anatomie des Psoques. Bulletin Biologique de France et de Belgique. Paris. Suppl. 18: 1–241.
- Badonnel, A., Mockford, E. L. & García Aldrete A. N. 1984. Pararchipsocinae, nouvelle subdivision des Archipsocidae (Insecta: Psocoptera), avec description de *Pararchipsoocus* n.g. et de onze espèces inédites de cette sous-famille. Bulletin du Muséum national d'Histoire naturelle (2) 42: 741–768.
- Betz, B. W. 1983. The biology of *Trichadenotecnum alexandrae* Sommerman (Psocoptera: Psocidae). IV. Mechanism of genitalic coupling. Journal of the Kansas entomological Society 56: 427–433.
- Brodsky, A. K. 1994. The evolution of insect flight. Oxford University Press, NY.
- Cope, O. B. 1940. The morphology of *Psocus confraternus* Banks (Psocoptera: Psocidae). Microentomology 5: 91–115.
- Crampton, G. C. (1926) A comparison of the neck and prothoracic sclerites throughout the orders of insects from the standpoint of phylogeny. Transactions of the American Entomological Society 52: 199–248.
- DuPorte, E. M. 1962. The anterior tentorial arms in insects and their significance in interpreting the morphology of the cranium of the cicadas. Canadian Journal of Zoology 40: 137–144.
- García Aldrete, A. N. 1974. A classification above species level of the genus *Lachesilla* Westwood (Psocoptera: Lachesillidae) Folia Entomologica Mexicana 27: 1–88.
- Hamilton, K. G. A. 1981. Morphology and evolution of the rynchotan head (Insecta: Hemiptera, Homoptera). The Canadian Entomologist 113: 953–974.
- Johnson, K. P. & Mockford, E. L. 2003. Molecular systematics of Psocomorpha (Psocoptera). Systematic Entomology 28: 409–416.
- Johnson, K. P., Yoshizawa, K. & Smith, V. S. 2004. Multiple origins of parasitism in lice. Proceedings of the Royal Society of London (B) 271: 1771–1776.
- Klier, E. 1956. Zur Konstruktionsmorphologie des männlichen Geschlechtsapparates der Psocopteren. Zoologische Jahrbücher (Abteilung Anatomie) 75: 207–286.
- Lienhard, C. 2003. Nomenclatural amendments concerning Chinese Psocoptera (Insecta), with remarks on species richness. Revue suisse de Zoologie 110: 695–721
- Lyal, C.H.C. 1985. Phylogeny and classification of the Psocodea, with particular reference to the lice (Psocodea: Phthiraptera). Systematic Entomology 10: 145–165.

- Lyal, C.H.C. 1986. External genitalia of Psocodea, with particular reference to lice (Phthiraptera). *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 114: 277–292.
- Masumoto, M. & Nagashima, T. 1993. Head structure of the psocid *Longivalvus nubilus* (Enderlein) (Psocoptera, Psocidae). *Japanese Journal of Entomology* 61: 671–678.
- Matsuda, R. 1965. Morphology and evolution of the insect head. *Memoirs of the American Entomological Institute* 4: 1–334.
- Matsuda, R. 1970. Morphology and evolution of the insect thorax. *Memoirs of the Canadian Entomological Society* 76: 1–483.
- Matsuda, R. 1976. Morphology and evolution of the insect abdomen. Pergamon Press, Oxford. 534 pp.
- Mockford, E. L. 1967. The electrentomoid psocids (Psocoptera). *Psyche* 74: 118–165.
- Mockford, E. L. 1972. *Anomopsocus* and *Antipsocus*: synonymy, species, and taxonomic position (Psocoptera: Lachesillidae). *Annals of the Entomological Society of America* 65: 1359–1364.
- Mockford, E. L. 1978. A generic classification of family Amphipsocidae (Psocoptera: Caecilietae). *Transactions of the American Entomological Society* 104: 139–190.
- Mockford, E. L. 1985. Systematics of the genus *Nadleria* (Psocoptera: Lachesillidae) with description of a new species and hypotheses on evolution of male external genitalia in the family Lachesillidae. *Annals of the Entomological Society of America* 78: 94–100.
- Mockford, E. L. 1993. North American Psocoptera. *Fauna and Flora Handbook*. Vol. 10. Sandhill Crane Press Inc., Netherland, xviii+455pp.
- Mockford, E. L. & Sullivan D. M. 1986. Systematic of the graphocaeciliine psocids with a proposed higher classification of the family Lachesillidae (Psocoptera). *Transactions of the American Entomological Society* 112: 1–80.
- New, T. R. 1973. The Archipsocidae of South America (Psocoptera). *Transactions of the Royal Entomological Society of London* 125: 57–105.
- New, T. R. 1987. Biology of the Psocoptera. *Oriental Insects* 21: 1–109.
- Prawdin T. 1932. Beiträge zur Kenntnis des Baues des Kopfes der Insekten. Zum Bau des Kopfes der Copeognathen. *Zoologicheskii Zhurnai* 11: 159–172. (In Russian with German summary)
- Roesler, R. 1940. Neue Copeognathen. *Arbeiten über morphologische und taxonomische Entomologie* 7: 236–244.
- Rudolph, D. 1982. Site, process and mechanism of active uptake of water vapour from the atmosphere in the Psocoptera. *Journal of Insect Physiology* 28: 205–212.
- Smithers, C. N. 1972. The classification and phylogeny of the Psocoptera. *Memoirs of the Australian Museum* 14: 1–349.
- Smithers, C. N. 1990. Keys to families and genera of Psocoptera (Arthropoda: Insecta). *Technical Reports of the Australian Museum* 2: 1–82.
- Snodgrass, R. E. 1935. *Principles of Insect Morphology*. McGraw-Hill, NY.
- Snodgrass, R. E. 1944. The feeding apparatus of biting and sucking insects affecting man and animals. *Smithsonian Miscellaneous Collections* 104(7): 1–113.
- Weber H. 1938. Beiträge zur Kenntnis der Überordnung Psocoidea. 1. Die Labialdrüsen der Copeognathen. *Zoologische Jahrbücher Abteilung Anatomie* 64: 243–286.
- Wootton, R. J. 1979. Function, homology and terminology in insect wings. *Systematic Entomology* 4: 81–93.
- Yoshizawa, K. 1999. Morphology, Phylogeny, and Higher Classification of the Suborder Psocomorpha (Insecta: Psocoptera). Unpublished PhD thesis, Kyushu University.
- Yoshizawa, K. 2002. Phylogeny and higher classification of suborder Psocomorpha (Insecta: Psocodea: 'Psocoptera'). *Zoological Journal of the Linnean Society* 136:

371–400.

- Yoshizawa, K. 2003. Two new species that are likely to represent the most basal clade of the genus *Trichadenotecnum* (Psocoptera: Psocidae). *Entomological Science* 6: 301–308.
- Yoshizawa, K. 2004. Molecular phylogeny of major lineages of *Trichadenotecnum* and a review of diagnostic morphological characters (Psocoptera: Psocidae). *Systematic Entomology* 29: 383–394.
- Yoshizawa, K. & Johnson, K. P. 2003. Phylogenetic position of Phthiraptera (Insecta: Paraneoptera) and elevated rate of evolution in mitochondrial 12S and 16S rDNA. *Molecular Phylogenetics and Evolution* 29: 102–114.
- Yoshizawa, K. & Johnson, K. P. 2005. Aligned 18S for Zoraptera (Insecta): Phylogenetic position and molecular evolution. *Molecular Phylogenetics and Evolution* 37: 572–580.
- Yoshizawa, K. & Johnson, K. P. In press. Morphology of male genitalia in lice and their relatives and phylogenetic implications. *Systematic Entomology*.
- Yoshizawa, K., Lienhard, C. & Johnson, K. P. In press. Molecular systematics of the suborder Trogiomorpha (Insecta: Psocodea: 'Psocoptera'). *Zoological Journal of the Linnean Society*.
- Yoshizawa, K. & Saigusa, T. 2001. Phylogenetic analysis of paraneopteran orders (Insecta: Neoptera) based on forewing base structure, with comments on monophyly of Auchenorrhyncha (Hemiptera). *Systematic Entomology* 26: 1–13.
- Yoshizawa, K. & Saigusa, T. 2003. Reinterpretations of clypeus and maxilla in Psocoptera, and their significance in phylogeny of Paraneoptera (Insecta: Neoptera). *Acta Zoologica (Stockholm)* 84: 33–40.

APPENDIX. TAXA EXAMINED. FAMILY ORDER FOLLOWS YOSHIZAWA (2002).

LEPIDOPSOCIDAE

Echmepteryx lunulata Thornton, Lee & Chui, 1972

PACHYTROCTIDAE

Tapinella sp. [from Taiwan]

TROCTOPSOCIDAE

Gen. sp. [from Malaysia]

AMPHIENTOMIDAE

Paramphientomum yumyum Enderlein, 1907; *Paramphientomum* sp. [from Taiwan]; *Cymatopsocus* sp. [from Malaysia]

ARCHIPSOCIDAE

Archipsocus sp. [from Mexico]; *Archipsocopsis fernandi* (Pearman, 1934); *Archipsocopsis* sp. [from Mexico]; *Pseudarchipsocus veracruzanus* Badonnel, Mockford & García Aldrete, 1984; *Pararchipsocus pacificus* Badonnel, Mockford & García Aldrete, 1984.

HEMIPSOCIDAE

Hemipsocus chloroticus (Hagen, 1858); *Hemipsocus* sp. [from Ryukyus, Japan]

MYOPSOCIDAE

Lichenomima muscosa (Enderlein, 1906); *Myopsocus* sp. [from Honshu, Japan]

PSOCIDAE

Ampnigerontia jozanensis Okamoto, 1907; *Sigmatoneura kolbei* (Enderlein, 1906); *Longivalvus nubilus* (Enderlein, 1906); *Psocidus* sp. [from Ryukyus, Japan]; *Trichadenotecnum sepxunctatum* (Linnaeus, 1761); *Psocus* sp. [from Hokkaido, Japan]

ELIPSOCIDAE

Reuterella helvimacula (Enderlein, 1901); *Elipsocus abdominalis* Reuter, 1904; *Elipsocus* sp. [from

Kyushu, Japan]; *Hemineura dispar* Tetens, 1891

LACHESILLIDAE
Lachesilla pedicularia (Linnaeus, 1758); *Lachesilla* sp. [*pedicularia* group, from Vietnam]

ECTOPSOCIDAE
Ectopsocopsis cryptomeriae (Enderlein, 1907); *Ectopsocus pumilis* (Banks, 1920); *Ectopsocus* sp.
[from Ryukyus, Japan]

TRICHOPSOCIDAE
Trichopsocus dali (McLachlan, 1867)

CALOPSOCIDAE
Calopsocus infelix (Hagen, 1858)

PSEUDOCAECILIIDAE
Pseudocaecilius citricola (Ashmead, 1879); *P. kagoshimensis* (Okamoto, 1910); *Heterocaecilius anomalis* (Thornton, 1961); *H. fuscus* Yoshizawa, 1996; *Allocaecilius sinensis* Lee & Thornton, 1967; *Ophiodopelma glyptocephalum* Lienhard, 1985

PERIPSOCIDAE
Peripsocus ignis Okamoto, 1910; *P. quercicola* Enderlein, 1906; *Peripsocus* sp. [from Ryukyus, Japan]

PHILOTARSIDAE
Philotarsus picicornis (Fabricius, 1793); *Haplophallus* sp. [from Ryukyus, Japan]; *Aaroniella* sp. [from Hokkaido, Japan]

MESOPSOCIDAE
Idatenopsocus orientalis (Vishniakova, 1986); *Mesopsocus unipunctatus* (Müller, 1764); *M. hongkongensis* Thornton, 1959

DOLABELLAPSOCIDAE
Dolabellopsocus roseus Eertmoed, 1973; *Isthmopsocus* sp. [from Mexico]

CLADIOPSOCIDAE
Cladiopsocus garciai Eertmoed, 1973; *Spurostigma epirotica* Eertmoed, 1973

PTILONEURIDAE
Euplocania badonneli New & Thornton, 1988; *Triplocania spinosa* Mockford, 1957

EIPSOCIDAE
Epipsocus sp. [from Malaysia], *Epipsocopsis* sp. [from Taiwan]

ASIOPSOCIDAE
Notiopsocus aldretei Badonnel, 1986

STENOPSOCIDAE
Stenopsocus aphidiformis Enderlein, 1906; *S. niger* Enderlein, 1906; *Graphopsocus cruciatus* (Linnaeus, 1768)

AMPHIPSOCIDAE
Amphipsocus japonicus (Enderlein, 1906); *Kolbea fusconervosa* Enderlein, 1906; *Taeniosigma* sp. [From Taiwan], *Matsumuraiella radiopicta* Enderlein, 1906; *Kodamaius* sp [from Taiwan]

CAECILIUSIDAE
Valenzuela flavidus (Stephens, 1836); *V. oyamai* (Enderlein, 1906); *Isophanes* sp. [from Ryukyus, Japan]; *Dypsocus coleopteratus* (Hagen, 1858)