Reinterpretations of clypeus and maxilla in Psocoptera, and their significance in phylogeny of Paraneoptera (Insecta: Neoptera)

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Abstract

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Morphology of the head and mouthparts in Psocoptera was investigated, and revised interpretations for clypeus and maxilla were proposed. The convex plate in the frontal region of the head capsule is the postclypeus, rather than the frons; the galea is clearly differentiated from the stipes and the origin of the stipito-lacinial muscle is partly shifted from the stipes to the base of the galea; the cardo is completely fused with the stipes without any suture or sulcus. Brief discussions on the evolution of piercing and sucking mouthparts and on the phylogeny of Paraneoptera were provided, based on these revised interpretations.

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Introduction

Psocopterans are the most basal group of Paraneoptera (Kristensen 1991, 1995; Yoshizawa and Saigusa 2001). They have biting-type mouthparts with some modifications showing an intermediate condition between initial biting-type mouthparts and the piercing and sucking-type mouthparts (Heming 1980; Hamilton 1981). Therefore, morphological studies of the head and mouthparts in psocopterans are important in interpreting the evolution of the piercing and sucking mouthparts in thysanopterans and hemipterans. Accordingly, the head and mouthparts in psocopterans have been studied extensively. However, there is some disagreement about the interpretation of some key structures.

First, there are two different interpretations of the homology of a convex plate at the front of the head capsule: is it the postclypeus or frons? Originating on the inner surface of the convex plate is the large dilator muscle of the cibarium. In hemipterans, this muscle is inserted on to the sucking pump and produces power for sucking up liquids (Chaudonneret 1990). Consequently, enlargement of this muscle directly correlates with the evolution of the piercing and sucking-type of feeding mechanism and different interpretations of the convex plate provide different hypotheses about the evolution of this feeding mechanism.

Second, there is no consensus about the homology of the maxillary structures. The maxilla in psocopterans, especially the pick-like lacinia, has been considered to represent an intermediate condition between biting- and piercing and sucking-type mouthparts (Hamilton 1981). Thus, morphological studies of the maxilla can also contribute to an understanding of the evolution of piercing and sucking-type mouthparts.

Here the morphology of head and mouthparts in psocopterans is revised to resolve these problems. This information is the background for a discussion of the evolution of piercing and sucking mouthparts and the phylogeny of Paraneoptera.

Materials and Methods

The species examined in this study are listed in the Appendix. Dried or alcohol preserved specimens were used. For examination of the external structures, the head was separated and placed in 5% KOH solution at about 45 °C for 1–3 h, depending its size. The material was then washed with distilled water and stored in 80% ethanol for subsequent dissection, observation and illustration. For the examination of internal structures, alcohol preserved specimens were used and stained with Methylene
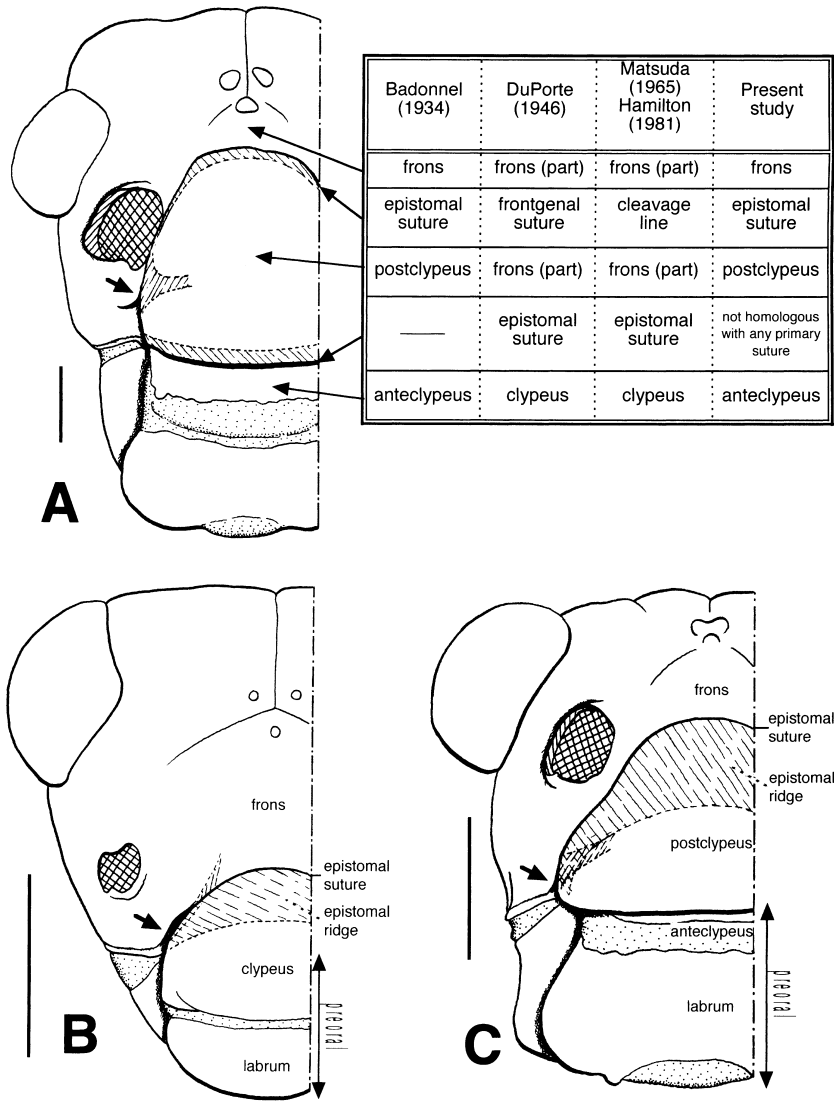
	Badonnel (1934)	DuPorte (1946)	Matsuda (1965) Hamilton (1981)	Present study
	frons	frons (part)	frons (part)	frons
	epistomal suture	frontgenal suture	cleavage line	epistomal suture
	postclypeus	frons (part)	frons (part)	postclypeus
	——	epistomal suture	epistomal suture	not homologous with any primary suture
	anteclypeus	clypeus	clypeus	anteclypeus

Fig. 1—Head of Psocoptera, anterior aspect —**A**. *Psococerastis nubila* (Psocomorpha: Psocidae), with different interpretations of head structures of Psocoptera. Each row shows different interpretation by authors (given at the top) of the structrue indicated by arrow —**B**. *Echmepteryx lunulata* (Trogiomorpha: Lepidopsocidae) —**C**. *Stenopsocus* sp. (Psocomorpha: Stenopsocidae). Arrow indicates the position of the anterior tentorial pit. Scale = 0.5 mm.

Blue. To examine the musculature and the nervous system of the head, specimens were bilaterally divided using a fine razor. A Leica MZ12 stereoscopic microscope was used to examine and illustrate the specimens. Terms for the muscles follow Matsuda (1965). Muscle numbers shown in parentheses after the name of the muscle follow Matsuda's system.

Frons or postclypeus

Previous interpretations (Fig. 1A). A large convex plate observed on the front of the head capsule in psocopterans has generally been thought to be the postclypeus (e.g. Badonnel 1934; Weidner 1972; Dennis and Bitsch 1973; Richards & Davies 1977; Fig. 1A). However, DuPorte (1946), Matsuda (1965) and Hamilton (1981) regarded this convex plate to be the frons. Matsuda's interpretation was based on three landmarks:

anterior tentorial pits, dilator muscle of the cibarium (82), and the frontal ganglion and on the position of the plate.

Badonnel (1934) observed that the anterior tentorial pits are situated at the ventral limit of the convex plate in a species of *Stenopsocus* Hagen, 1866. Based on this observation, Matsuda (1965) considered the suture bordering the ventral limit of the plate as the epistomal suture.

Matsuda (1965) also noted that the position of the frontal ganglion always indicated the boundary between the clypeal and frontal areas. Based on the Badonnel's (1934) observation, Matsuda (1965) pointed out that the frontal ganglion in psocopterans occurs far below the level of the dorsal limit of the convex plate (Fig. 3) and thus regarded the convex plate as the frons.

In psocopterans, the dilator muscle of the cibarium (82) originated on the inner surface of the convex plate (Badonnel 1934; Fig. 3). The muscle usually has its origin on the
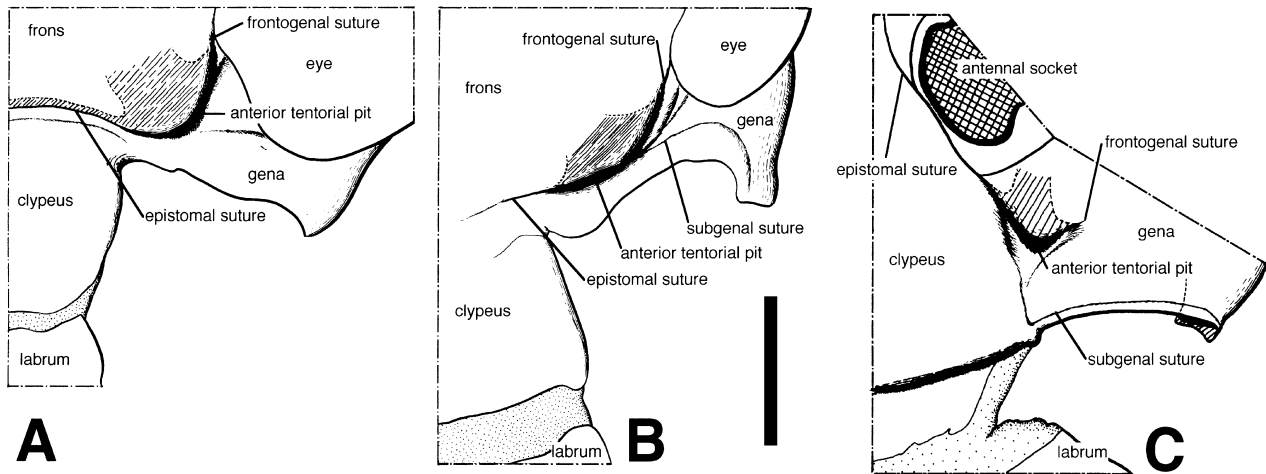
Fig. 2—Anterior tentorial pit and surrounding structures —**A**. *Acromantis japonica* (Mantodea) —**B**. *Pycnoscelus surinamensis* (Blattodea) —**C**. *Psococerastis nubila* (Psocoptera). Scale = 0.5 mm.

clypeus, at least in orthopteroids (e.g. Snodgrass 1935; Matsuda 1965). However, Matsuda (1965) stressed that the insertion point of this muscle varies between members of different insect orders. Then, he considered that the origin of the dilator muscle of the cibarium shifted from the clypeus to the frons in psocopterans. Matsuda (1965) also noted that the convex plate is not the clypeus, because the plate is not preoral.

Prior to Matsuda, DuPorte (1946, 1956, 1962) also considered the convex plate in psocopterans to be the frons. He criticized Snodgrass' criterion about the relationship between anterior tentorial pits and the epistomal suture and mentioned that the anterior tentorial pits are sometimes distant from the epistomal suture but on the frontogenal suture. He considered the suture surrounding the dorsolateral margins of the convex plate to be the frontogenal suture and concluded that the convex plate was the frons.

Hamilton (1981) also considered the convex plate in psocopterans as the frons. His scheme was based on that of DuPorte (1946) and Matsuda (1965).

Reinterpretation

Using Matsuda's three landmarks and the position of the convex plate in many psocopterans (Appendix), we reinterpreted the homology of the convex plate as follows.

Anterior tentorial pits. *Contrary to Matsuda (1965), the anterior tentorial pits are not always situated at the ventral limit of the convex plate but always on the lateral margin of the plate (Fig. 1: arrow) and the anterior tentorial arms attach vertically to the lateral margins of the plate (Fig. 2C). There are no continuous relationships between the anterior tentorial pits and the ventral limit of the convex plate, even if the pits are situated at the ventral*

end of the plate. As noted by Snodgrass (1935), the anterior tentorial arms usually arise from the epistomal ridge in the pterygotes. Thus, judging from the condition of the anterior tentorial pits in psocopterans and based on Snodgrass' criterion, the suture surrounding the convex plate dorsolaterally should be interpreted as the epistomal suture.

We also examined DuPorte's criterion about the relationships between the anterior tentorial pits and the frontogenal suture. As mentioned by DuPorte (1946, 1956), the frontogenal sutures continue to the anterior tentorial pits in orthopteroid insects (Fig. 2A,B). In psocopterans, a frontogenal suture is never observed but the anterior tentorial pits usually have a clear, external extension (Fig. 2C). By comparing this condition with the anterior tentorial pits in orthopteroids (Fig. 2A,B), we considered that the external extensions of the anterior tentorial pits in psocopterans correspond to the ventral end of the frontogenal suture (Fig. 2C). Thus, our interpretation of the convex plate does not conflict with either Snodgrass' or DuPorte's criteria concerning relationships between the anterior tentorial pits and sutures.

Frontal ganglion. We confirm that, as observed by Badonnel (1934) and noted by Matsuda (1965), the frontal ganglion occurs far below the level of the dorsal limit of the convex plate (Fig. 3). In contrast, in representatives of the basal groups of Psocoptera (Trogiomorpha and Troctomorpha) and of some specialized groups (e.g. Stenopsocidae), the suture surrounding the convex plate dorsolaterally possesses a broad ridge internally, the epistomal ridge (Fig. 1B,C), and we observed that the frontal ganglion always occurs slightly posterodorsal to this ridge (Fig. 3). This ridge is the internal border of this structure and thus the position of the frontal ganglion also indicates that the convex plate is the postclypeus.
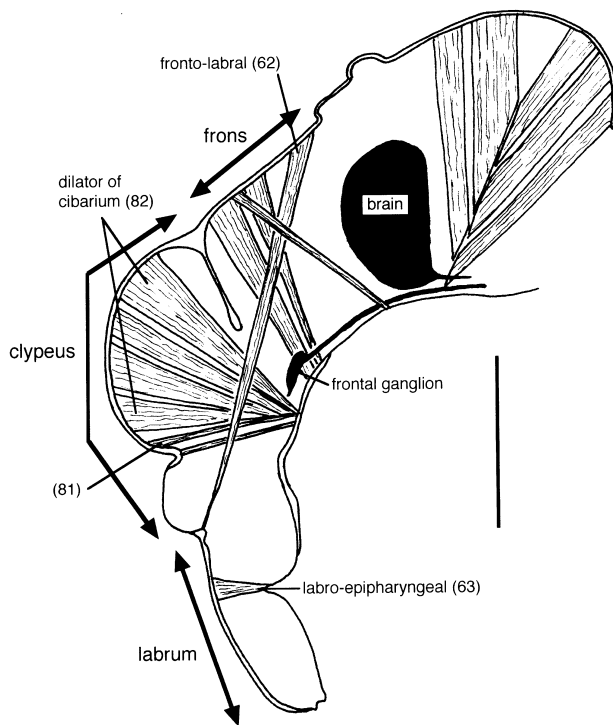
Fig. 3—Head of *Stenopsocus* sp., showing some muscles and the frontal ganglion. Scale = 0.5 mm.

Dilator muscle of the cibarium. The large dilator muscle of the cibarium (82) originates on the inner surface of the convex plate in psocopterans. As discussed earlier, two other landmarks proposed by Matsuda (1965) suggest that the convex plate is the clypeus. Shifting of the muscle in psocids, as noted by Matsuda (1965), should not be assumed without evidence. The position of the cibarial muscle in psocopterans provides additional support for our interpretation.

Position of convex plate. We agree with Matsuda (1965), that the convex plate is not topographically preoral in members of the higher lineages of Psocoptera (Fig. 1A,C). However, the convex plate partly occupies the preoral region in basal psocopterans, such as trogiomorphs (Fig. 1B). The convex plate is apparently homologous throughout the Psocoptera and thus the above-mentioned statement of Matsuda is incorrect. In a general manner, the part of the cranium from which the cibarial dilators originate can be said to be, by definition, morphologically preoral, irrespective of its topographical extent.

As discussed above, all three landmarks, plus the position of the convex plate, suggest that the plate is the clypeus, not the frons, and no external and internal structures conflict with this interpretation. Additionally, our interpretation is supported by the condition of the subgenal suture. In psocids,

the subgenal suture is anteriorly continuous with the suture that surrounds the convex plate dorsolaterally (Fig. 2C). As noted by Snodgrass (1935) and DuPorte (1946), the subgenal suture is continuous with the epistomal suture in many pterygote insects (Fig. 2B). Therefore, the convex plate should be interpreted as the postclypeus (Badonnel 1934), and the interpretations proposed by DuPorte (1946), Matsuda (1965) and Hamilton (1981) should be rejected.

Maxilla

Previous interpretations

(Fig. 4A). The most prominent confusion is seen in interpretations of the distal lobe of the maxilla (Fig. 4A). This structure has long been considered to be the galea (e.g. Badonnel 1934). However, Badonnel (1934) and Matsuda (1965) stated that the galea of psocopterans is continuous with the stipes, and there is no clear articulation between them.

Masumoto and Nagashima (1993) examined the musculature of the maxilla in *Psococerastis nubila* (Enderlein 1906) and interpreted the distal lobe of the maxilla to be the stipes rather than the galea, because one of three divided stipito-lacinial muscles (Lp_1 of Badonnel 1934) is arising from the base of the distal lobe. However, Badonnel (1934) noted that Lp_1 attaches to the stipital pad, close to the origin of the galea.

In addition, there is an ambiguity in the interpretation of the cardo. Badonnel (1934) noted that the cardo was completely absent. Cope (1940) mentioned that there was no well-defined suture to distinguish the cardo from the stipes. Matsuda (1965) noted that the cardo of psocopterans was either lost or indistinguishably fused with the stipes.

Reinterpretation

Although Badonnel (1934) did not observe any muscle arising from the distal lobe and inserted to the lacinia, we confirm the presence of a muscle arising from the base of the distal lobe and inserted to the lacinia in all psocopterans observed (Fig. 4D). As mentioned by Masumoto and Nagashima (1993), this muscle can be interpreted as a part of the stipito-lacinial muscle, because no muscle arising from the lacinia and inserted on the galea is known. Additionally, we can also confirm that the stipito-galeal muscle (7) is completely absent in psocomorphs, also in agreement with Masumoto and Nagashima's observations. In addition to the stipito-lacinial muscle, the stipito-galeal muscle (7) is also inserted on the dorsal margin of the distal lobe in a species of *Lepinotus* (Trogiomorpha: Prawdin 1932), *Echmepteryx lunulata* Thornton, Lee & Chui, 1972 (Trogiomorpha: pers. obs.), *Tapinella* sp. (Trogiomorpha: pers. obs.) and amphientomids (Troctomorpha: pers. obs.) (Fig. 4D). The presence of the latter muscle strongly suggests that the distal lobe in trogiomorphs and troctomorphs is the galea rather than the
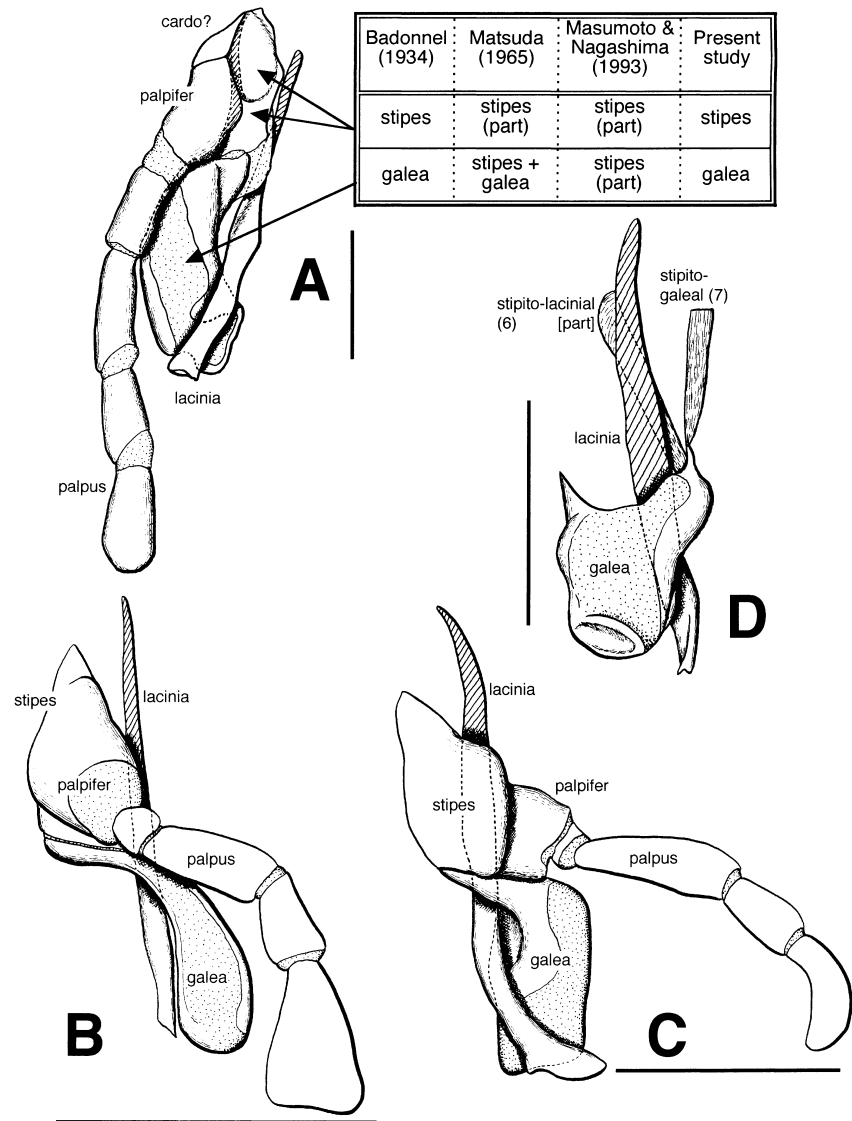
Badonnel (1934)	Matsuda (1965)	Masumoto & Nagashima (1993)	Present study
stipes	stipes (part)	stipes (part)	stipes
galea	stipes + galea	stipes (part)	galea

Fig. 4—Maxilla —**A**. *Psococerastis nubila* (Psocomorpha: Psocidae), lateral aspect, with different interpretations of the maxilla of Psocoptera —**B**. *Echmepteryx lunulata* (Trogiomorpha: Lepidopsocidae), lateral aspect —**C**. *Paramphientomum* sp. (Troctomorpha: Amphientomidae), lateral aspect —**D**. ditto, showing muscles attached to galea and lacinia, anterior aspect. Scale = 0.5 mm.

stipes, and its absence in psocomorphs can be considered as an autapomorphy of this suborder (Yoshizawa 2002).

Externally, the distal lobe is largely membranous and a strap-like sclerite surrounds its external and ventral surfaces and, contrary to Badonnel (1934), this sclerite apparently articulates dorsally with the stipes (Fig. 4A,B,C). Based on these external features, the distal lobes of psocomorphs and of members of other suborders can be determined as being homologous. Thus, although the stipito-galeal muscle is completely absent in psocomorphs, the distal lobe of the psocopteran maxilla can be regarded as the galea, rather than as part of the stipes.

As several authors have noted (e.g. Prawdin 1932; Badonnel 1934; Cope 1940; Masumoto and Nagashima 1993), the stipito-lacinial muscle of psocopterans is divided into three muscles: one arising from the ventral region of the stipes and inserted into the anterior surface of the lacinia (Lp_2 of Badonnel 1934); one from the dorsal region of the stipes to the posterior surface of the lacinia (Lp_3); and one from the dorsal margin of the distal lobe to the postero-internal surface of the lacinia (Lp_1). As discussed above, the distal lobe of the psocopteran maxilla is apparently the galea. As a consequence, shifting of part of the stipito-lacinial muscles (Lp_1) in relation to functional changes of the lacinia can be assumed.

By our observations, a small triangular region, clearly distinguished from the stipes and palpifer by sutures, is found in the articular region of the maxilla in *Psococerastis nubila* (Fig. 4A). Judging from its position and articulations with the head capsule, the triangular sclerite can be considered to represent the cardo. However, such a structure cannot be distinguished in representatives of trogiomorphs,

troctomorphs and most other psocomorphs (Fig. 4B,C). *P. nubila* is thought to be a more specialized psocids than trogiomorphs and troctomorphs (Yoshizawa 2002). Thus, it is unlikely that the maxilla of *P. nubila* represents the most plesiomorphic condition in Psocoptera. The most parsimonious interpretation is that the triangular sclerite in the maxilla of this species is secondarily derived, and a complete fusion of the cardo with the stipes is a 'ground plan' feature of the maxilla in psocopterans. No muscles, which are homologous with the tergo-cardinal or tentorio-cardinal muscles, are observed on the triangular sclerite of *P. nubila* nor the corresponding region of other psocopterans (Badonnel 1934; Cope 1940; Masumoto and Nagashima 1993; pers. obs.). The absence of these muscles supports our interpretation.

Discussion

The reinterpretations proposed in this study, together with previous interpretations are summarized in Figs 1A and 4A.

The reinterpretation of clypeus requires a modification to Hamilton's hypothesis about the evolution of the piercing and sucking-type mouthparts. Hamilton (1981) proposed that the modification of mouthparts for piercing and sucking was initiated by an enlargement and shifting of the points of insertion of the cibarial dilator muscle, and then an enlargement of the frons, supporting the enlargement of this muscle. However, our observations suggest that shifting of the cibarial dilator muscle did not occur at the basal lineage of Paraneoptera, and that enlargement of the muscle was associated with enlargement and dorsal extension of the clypeus, at least in psocopterans.

This hypothesis also provides an important insight about paraneopteran phylogeny. Interpretation of the homology of the convex plate in hemipterans still seems controversal. DuPorte (1946), Matsuda (1965) and Hamilton (1981) considered, as in the case of psocids, the convex plate in hemipterans as the frons and assumed a shifting of the cibarial dilator muscle from the clypeus to the frons (Hamilton 1981). If this is the case, independent origins of enlargement of the cibarial dilator muscle in psocopterans and hemipterans can be supposed. Alternatively, other authors (e.g. Evans 1968; Chaudonneret 1990) considered the convex plate of hemipterans to be the postclypeus. If this is the case, enlargement of the cibarial dilator muscle associated with enlargement of the clypeus can be considered as an autapomorphy of Paraneoptera. Even in this case, the dorsal extension of the clypeus in hemipterans needs to be examined. In flugoromorphs and some sternorrhynchs, the dorsal limit of the postclypeus is almost at the same level as the ventral limit of the head cupsle (Kramer 1950; Matsuda 1965; Evans 1968; pers. obs.). If this is the ground plan feature of hemipterans, as was assumed by Evans (1968), then independent origins of the dorsal extension of the clypeus in hemipterans and
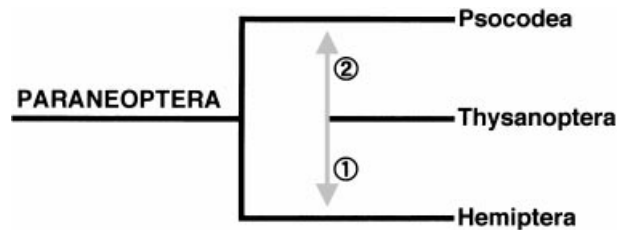

Fig. 5—Two alternative hypotheses about the phylogenetic position of Thysanoptera. Closer relationship between Thysanoptera and Hemiptera (1) is supported by mouthpart structures (Kristensen 1991, 1995) and forewing base structures (Yoshizawa and Saigusa 2001). Closer relationship between Thysanoptera and Psocodea (2) is supported by spermatological character (Jamieson 1987), 18S and 28S rDNA sequences (Wheeler *et al*. 2001), and possibly mitochondrial gene rearrangement (Shao *et al*. 2001).

psocopterans can be supposed. In thysanopterans, recent authors seem to be in agreement on the recognition that the postclypeus occupies a part of the head cupsule region, although the frons and the postclypeus of thysanopterans are indistinguished (Mickoleit 1963; Heming 1980, 1993; Moritz 1982, 1997). Therefore, the dorsal extension of the postclypeus is considered to be the ground plan feature of thysanopterans, as in psocopterans. Kristensen (1991, 1995) pointed out the similarity of configurations of the cibarial dilator muscle between psocopterans and thysanopterans. Understanding of homology and transformation series of the frons and clypeus in hemipterans and thysanopterans will provide important insight into the controversy about the phylogenetic position of Thysanoptera (Fig. 5) (Kristensen 1991, 1995; Shao *et al*. 2001; Wheeler *et al*. 2001; Yoshizawa and Saigusa 2001).

Reinterpretation of the maxilla also provides new insignt about the phylogeny of Paraneoptera. Heming (1980, 1993) suggested that the galea fused to the stipes is an apomorphic specialization of the stem species of Paraneoptera. However, our observations show that this character state should be excluded from the autapomorphies of Paraneoptera. Then, fusion of the galea with the stipes may be a synapomorphy of Thysanoptera and Hemiptera. The present observations also suggest the complete fusion of the cardo with the stipes to be the ground plan of psocopterans. As Mickoleit (1963), Matsuda (1965), and Moritz (1982) mentioned, a well-formed cardo can be observed in *Aeolothrips* species. Thus, fusion of the cardo with the stipes may be an autapomorphy of the Psocodea (= Psocoptera + Phthiraptera: the cardo is also indistinguishable in members of the latter group).

As discussed above, the psocopteran head and mouthparts show interesting modifications that appear to represent initial steps in the development of the piercing and sucking feeding mechanism in thysanopterans and hemipterans. In Table 1, presently detected modifications in the head and mouthparts of psoocopterans and their possible functional significance are summarized. Drastic modifications of the

Table 1 Modifications of head and mouthparts observed throughout Psocoptera and its functional significance. The one indicated by an asterisk is not observed in basal psocopterans but is present in psocomorphs

Modification	Function
Enlargement of clypeus	Supports larger dilator muscle of cibarium (82)
Enlargement of dilator muscle of cibarium (82)	Produces stronger sucking power (related to uptake of water vapour: Rudolph 1982)
Fusion of cardo + stipes	Unknown
Elongation of lacinia	Unknown for psocopterans (further modified to stylet in thysanopterans and hernipterans which provide a piercing and sucking type of feeding mechanism)
Splitting of stipito-lacinial muscle (6)	Enables complicated, 3D movement of lacinia
Elongation of stipito-lacinial muscle (6)	Provides stronger power to protract lacinia
Shifting position of part of stipito-lacinial muscle (6)	Enables further elongation of stipito-lacinial muscle
*Absence of stipito-galeal muscle (7)	Unknown

lacinia and associated muscles are especially important. Splitting of the stipito-lacinial muscle probably enabled the lacinia to perform complicated, three-dimensional movements. Additionally, by shifting the origin of one muscle from the stipes to the galea, the muscle became longer and made it possible for it to produce more power to protract the lacinia. Unfortunately, the use of the psocopteran lacinia is less understood. In thrips (Kirk 1997; Moritz 1997) and bugs (Cobben 1978), the laciniae are further modified into stylets, forming a tube for sucking up liquids, and the stipito-lacinial muscles are used to protract the stylets. We believe that modifications of the lacinia and the associated muscles in psocopterans were key innovations in the evolution of piercing and sucking mouthparts in Paraneoptera. Thus, functional morphological studies of these structures in psocids would be highly advocated.

Hemiptera constitute one of the most diverse and largest hemimetabolous insect orders, and this diversification was most probably accomplished by acquiring the piercing and sucking mouthpart structures and feeding behaviour. The present study provides a strong basis for additional morphological studies of the head and mouthparts in hemipteroid insects, based on comparative morphological studies between psocopterans and some orthopteroid insects. Further comparative morphological studies between Psocoptera, Thysanoptera and Hemiptera are strongly encouraged, in order to uncover the evolution of the piercing and sucking mouthparts and to reveal their phylogenetic affinities.

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Appendix – Species studied

PSOCOPTERA – Lepidopsocidae: *Echmepteryx lunulata* Thornton, Lee & Chui 1972; Pachytroctidae: *Tapinella* sp. [from Taiwan]; Troctopsocidae: Genus sp. [from Malaysia]; Amphientomidae: *Paramphientomum yumyum* Enderlein 1907; *Tineomorpha* sp. [from Malaysia]; Archipsocidae: *Archipsocopsis fernandi* (Pearman 1934); *Archipsocopsis* sp. [from Mexico]; *Pseudarchipsocus veracruzanus* Badonnel, Mockford & García Aldrete 1984; Hemipsocidae: *Hemipsocus chloroticus* (Hagen 1858); Myopsocidae: *Lichenomima muscosa* (Enderlein 1906); *Myopsocus* sp. [from Honshu, Japan]; Psocidae: *Ampnigerontia jozanensis* Okamoto 1907; *Sigmatoneura kolbei* (Enderlein 1906); *Psococerastis nubila* (Enderlein 1906); Elipsocidae: *Reuterella helvimacula* (Enderlein 1901); *Elipsocus abdominalis* Reuter 1904; Lachesillidae: *Lachesilla pedicularia* (Linnaeus 1758); *Lachesilla* sp. [*pedicularia* group, from Vietnam]; Ectopsocidae: *Ectopsocopsis cryptomeriae* (Enderlein 1907); *Ectopsocus pumilis* (Banks 1920); Trichopsocidae: *Trichopsocus dalii* (McLachlan 1867); Calopsocidae: *Calopsocus infelix* (Hagen 1858); *Cyclopsocus* sp. [from Malaysia]; Pseudocaeciliidae: *Pseudocaecilius citricola* (Ashmead 1879); *Heterocaecilius anomalis* (Thornton 1961); *Allocaecilius sinensis* Lee & Thornton 1967; *Ophiodopelma glyptocephalum* Lienhard 1985; Peripsocidae: *Peripsocus ignis* Okamoto 1910; *P. quercicola* Enderlein 1906; Philotarsidae: *Philotarsus picicornis* (Fabricius 1793); *Haplophallus* sp. [from Ryukyus, Japan]; *Aaroniella* sp. [from Hokkaido, Japan]; Mesopsociae: *Idatenopsocus orientalis* (Vishniakova 1986); *Mesopsocus unipunctatus* (Müller 1764); 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; Epipsocidae: *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 rubrostigma* Okamoto 1910; *Kolbia fusconervosa* Enderlein 1906; *Matsumuraiella radiopicta* Enderlein 1906; Caeciliusidae: *Caecilius flavidus* (Stephens 1836); *Isophanes* sp. [from Ryukyus, Japan]; *Dypsocus coleopteratus* (Hagen 1858). BLATTODEA. Blattidae: *Periplaneta americana* (Linnaeus 1758); Pycnoscelidae: *Pycnoscelus surinamensis* (Linnaeus 1758). MANTODEA – Acromantidae: *Acromantis japonica* Westwood 1889. ORTHOPTERA – Acridae: *Locusta migratoria* Linnaeus 1758.