Evidence from Mouthpart Structure on Interordinal Relationships in Endopterygota?

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> Abstract

The mouthpart structures of Endopterygota exhibit an extremely high diversity of form and function, yet they are composed of the same set of homologous components which are derived from arthropod limbs. Mouthpart features are prevalent in all studies of the high-level phylogeny of insects. Areas in which the phylogeny of Endopterygota has remained unresolved over the past decades concern the position of the Strepsiptera, the interrelationships of the orders of the Neuropterida, and the question of the sistergroup to the Siphonaptera. Paying attention to these unresolved internodes, the present review discusses current knowledge of mouthpart features and their value in deciphering the phylogeny of Endopterygota. Comprehensive comparative data for the mouthparts based on morphological studies have yet to be assembled and analysed in Endopterygota and their closest relatives. Providing such data would improve the hypotheses of the phylogeny of Endopterygota and could also contribute to a better understanding of mouthpart adaptation to various food sources.

> Key words

1.   Introduction

The diversity of insect mouthparts, especially in the Endopterygota (= Holometabola), is tremendous and at the same time puzzling. The diversity in this group is due in part to the different morphology between the mouthparts in larvae and adults, and it is intimately reflected in the manifold adaptations to various kinds of food sources. The ancestral mouthparts of the Endopterygota are functionally biting/chewing mouthparts adapted to feeding on different kinds of solid foods, while derived mouthparts include the various structures for fluid feeding (reviewed in Smith 1985; Krenn et al. 2005) and filter feeding on suspended particles in aquatic insect larvae. Because the mouthparts throughout the orders of Insecta are composed of a set of homologous components rich in variation they should, at least in principle, provide excellent data for phylogenetic studies. Indeed, mouthpart structure contributes to nearly all systems of insect classification and is central to the phylogenetic arguments on endopterygotan insects in classical, morphological studies (e.g., Kristensen 1975) as well as recent combined analyses (e.g., Wheeler et al. 2001).

The aim of this review is to survey the mouthparts and their traits which have been previously employed in phylogenetic discussions of the Endopterygota. In addition, I outline the phylogenetic conclusions which can be drawn from our current understanding of the endopterygotan ground pattern of mouthparts. This review is based mainly on the comparative morphological and anatomical studies of Crampton (1923), Das (1937), Hinton (1958), Matsuda (1965), Achtelig (1967), Kinzelbach (1971) and Michelsen (1997) as well, the summaries by Weber (1933), Snodgrass (1935), Kristensen (1975, 1981, 1997, 1999), Aspöck (2002), Willmann (2003a,b) and Grimaldi & Engel (2005).

2.   Insect mouthparts

The mouthparts of insects display a wondrous diversity of form and function, yet they are composed of the same set of homologous components which are ultimately derived from arthropod limbs. In the ground pattern of the Insecta the mouthparts of immatures and adults both belong to the biting/chewing functional type; they are composed of a pair of mandibles, a pair of maxillae and the unpaired labium, the latter

resulting from the median fusion of a pair of limbs. Further principal components are the unpaired labrum, which borders the preoral cavity anteriorly, and the hypopharynx, which forms a tongue-like organ in the posterior region of the preoral cavity that normally is associated with the opening of the labial salivary glands.

The unpaired labrum is a lobe suspending from the clypeus in front of the mouth opening and functionally forms the upper lip. It can be moved by extrinsic muscles to the head; internal labral muscles occur in various taxa. The labrum may correspond to reduced appendages (Rempel 1975; Rogers & Kaufman 1996; Scholtz & Edgecombe 2006; evidence from developmental studies have been discussed in Scholtz 1998), however in classical textbooks (e.g., Snodgrass 1935) it is considered to be part of the head like the epipharynx and hypopharynx. These structures are involved in feeding as well; they will be only briefly mentioned.

The paired mandibles are hard and sclerotized, their plesiomorphic function in Ectognatha is biting and chewing. In Pterygota and Zygentoma the mandibles articulate with the head at two points. A dicondylic mandible provided with a basal molar area and distal teeth seems to be plesiomorphic for Endopterygota. However it has to be mentioned that in a recent study in Lycidae (Coleoptera) the larval mandibular morphology was used for a not convincing argumentation for the parallel evolution of dicondyly (Kazantsev 2006). Most groups of Pterygota have antagonistic mandibular adductor and abductor muscles arising from the head capsule. Additional adductor muscles attached to the tentorium exist in some insects, e.g., Blattodea, Mantodea, Megaloptera and larvae of basal Lepidoptera (Matsuda 1965). Probably these muscles are remnants of a more complicated plesiomorphic musculature such as found in Zygentoma and Ephemeroptera (Staniczek 2000).

The maxilla is the most leg-like component of the mouthparts. It consists of the proximal cardo and stipes, the former being articulated to the head capsule. On the inner corner of the distal end of the stipes, the lacinia arises as a sclerotized and pointed structure. The lateral stipital side bears the galea which is soft and lobe-like in most taxa and provides the lateral closure of the preoral cavity. In addition, the stipes bears the leg-like palpus, which consists of a varying number of "segments" or palpomeres. Five may be the plesiomorphic number of palpomeres for the Endopterygota since this number can be found in representatives of Plecoptera, Embioptera (Matsuda 1965), Dermaptera, Orthoptera (Gullan & Cranston 1994), Blattodea (Weber 1933), Zoraptera (Matsuda 1965; Beutel & Weide 2005), Raphidioptera (Achtelig 1967), Neuroptera (New 1989) and many other taxa in various endopterygotan orders (Matsuda 1965).

Matsuda (1965) enumerated more than 10 muscles in the ground pattern of the ectognathan maxillae, which form three groups. Extrinsic muscles are those which insert on the cardo and stipes and have their origins on the head capsule or tentorium. They move the whole maxilla in relation to the head. Intrinsic muscles originate on the stipes, insert on the bases of the palpus, lacinia and galea, and effect movements of the maxillary endites and the maxillary palpus as a whole. The third group of muscles comprises those of the palpus, which extend between at least some of the palpomeres.

The labium is formed of the medially fused basal sclerites of the appendages of the last head segment and functions as a lower lip. The proximal part, called the postmentum, is subdivided in some insects into the submentum and mentum (Matsuda 1965). The distal part, the prementum, bears two pairs of endites, the mesal glossa and the lateral paraglossa, as well as the labial palpi. The plesiomorphic number of palpomeres in Endopterygota appears to be three as found in many "Lower Neoptera", such as representatives of Blattodea (Weber 1933), Dermaptera and Orthoptera (Gullan & Cranston 1994), Zoraptera (Matsuda 1965; Beutel & Weide 2005) and in many Endopterygota, such as Raphidioptera (Achtelig 1967), Neuroptera (New 1989), adult Coleoptera (Matsuda 1965) and adult Trichoptera (Matsuda 1965).

The muscles of the labium correspond in principle with those of the maxillae, there being several groups of extrinsic, intrinsic and palpal muscles. The extrinsic muscles run from the tentorium and/or the head capsule to the front and the back of the prementum. The intrinsic muscles extend between the postmentum and prementum and from these basal sclerites to the glossae and paraglossae as well to the bases of the labial palps. The intrinsic palpal musculature comprises flexors and extensors.

In addition, a complex musculature of the hypopharynx is closely associated with the labium in many taxa.

In some insects, for example Embioptera (Günther 2003), Zoraptera (Beutel & Weide 2005) and Raphidioptera (Achtelig 1967), a sclerite termed the gula exists between the postmentum and the cervix.

3.   Phylogenetic implications from mouthpart characters

A considerable number of mouthpart features have been used in hypotheses on the high level relationships of the Endopterygota. Commonly used mouthpart features are mapped onto a cladogram (Fig. 1) adopted and modified from Ax (1999) and Kristensen (1999).
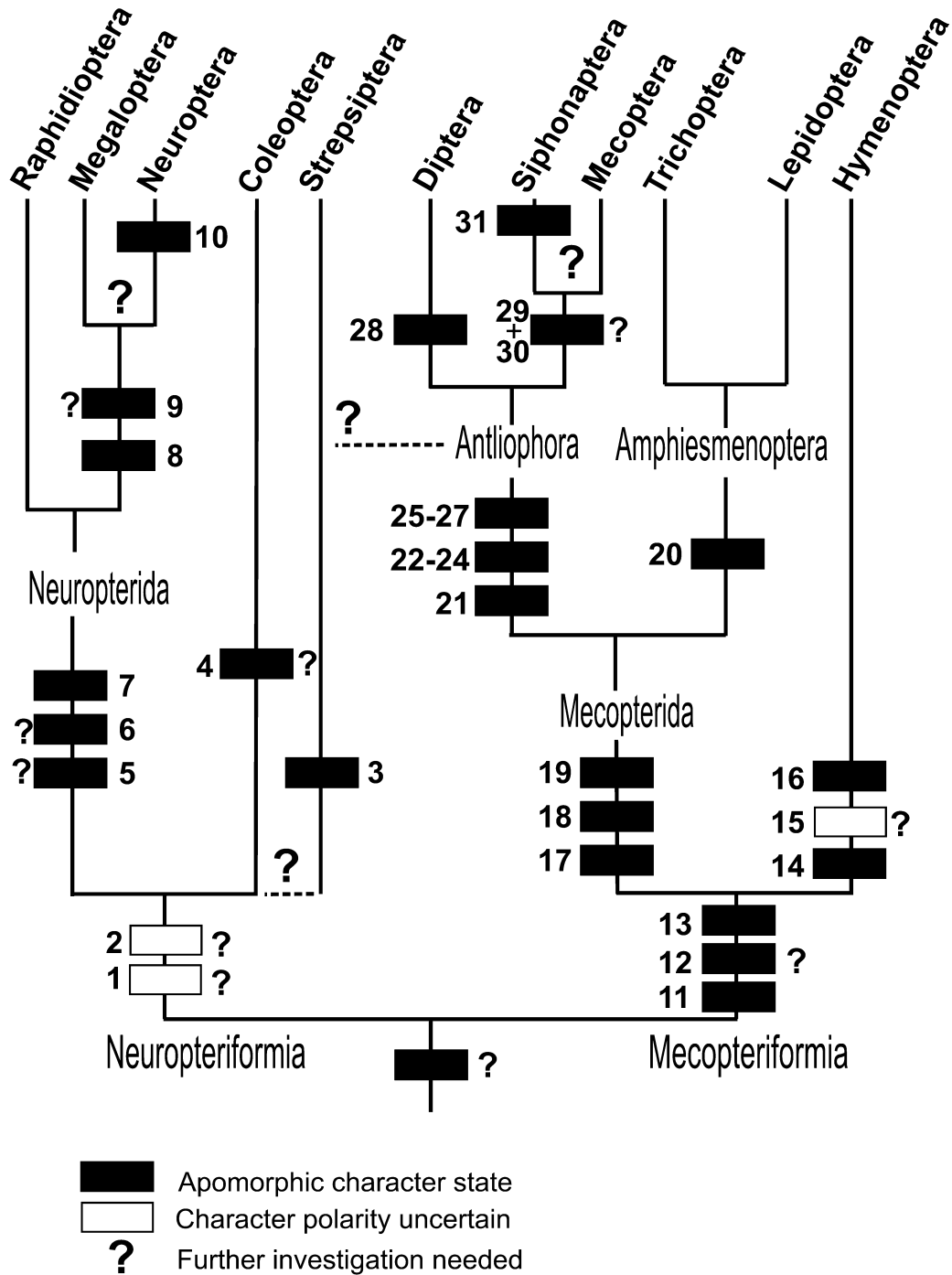
Fig. 1. Interordinal relationships of Endopterygota (Holometabola) based on Ax (1999) and Kristensen (1999). Selection of 31 mouthparts features are mapped onto the cladogram. The ground pattern of mouthparts has yet to be fully determined. Numbers refer to the following apomorphic conditions (if not mentioned otherwise, the adult condition is meant): (1) Presence of a gula plus prognathous position of mouthparts (Das 1937), uncertain character polarity; (2) Modified endites of labium, needs further investigation; (3) Reduced labium fused with hypopharynx and simplified maxillae (Kinzelbach 1971; Pohl & Beutel 2005); (4) Glossae and paraglossae fused and/or reduced (Matsuda 1965; Hörnschemeyer et al. 2002); (5) Paraglossae reduced (Matsuda 1965); (6) Premental muscles originate at tentorium in larvae (Das 1937); (7) Mola of mandible lost in larvae (Das 1937); (8) Larval cardo in oblique position and integrated into head capsule (Aspöck et al. 2001); (9) Stipes elongated (Boudreaux 1979); (10) Larval sucking tube formed by mandible and maxillae (Aspöck 2002); (11) Larval labial glands act as silk glands (Kristensen 1999); (12) Larval submental muscles lost (Das 1937); (13) Sitophore (Vilhelmsen 1996); (14) Labio-maxillary complex: functional unit of basal components of maxilla and labium; (15) Fused glossae, uncertain character polarity (Vilhelmsen 1996); (16) 4-segmented labial palpus (Vilhelmsen 1996); (17) Larval stipes obliquely divided (Hinton 1958); (18) Larval cardo without cranial promotor (Hinton 1958); (19) Larval labial palpus with 2 segments and without intrinsic muscles (Hinton 1958); (20) Larval labium-hypopharynx complex with spinneret (Hinton 1958); (21) Slender mandible, anterior articulation reduced (Willmann 2003b); (22) Postlabium reduced (Willmann 2003b); (23) Only 3 labial muscles present: retractor of prementum, basal and distal palpomere abductor (Willmann 2003b); (24) Labial palpus 2-segmented (Willmann 2003b); (25) Larvae lack lateral extrinsic labrum muscles (Hinton 1958); (26) Lack of tentorial cardo adductor (Hinton 1958); (27) No hypopharynx retractor (Hinton 1958); (28) Labial palps medially fused and modified into labellum; (29) No extrinsic labral muscle (Michelsen 1997); (30) Absence of labial endites (Michelsen 1997); (31) Piercing mouthparts, stylets formed by labrum and lacinia (Michelsen 1997).

The topology is in general agreement with most current views (e.g., Willmann 2003b; Grimaldi & Engel 2005) on the interrelationships of the Endopterygota. Figure 1 summarizes the mouthpart characters relevant to the discussion of the phylogeny for the orders of Endopterygota with particular emphasis on relationships which have remained unresolved, e.g., Strepsiptera, orders of the Neuropterida and Siphonaptera.

3.1.   Strepsiptera

The Strepsiptera have been suggested to be related either to the Antliophora (the "Halteria hypothesis"; Whiting et al. 1997; Wheeler et al. 2001) or, in the more traditional view, to the Coleoptera (Boudreaux 1979; Willmann 2003b). The discussion was recently reviewed in light of fossil discoveries (Pohl et al. 2004; Pohl & Beutel 2005; Grimaldi & Engel 2005).

Despite the fact that adult Strepsiptera do not take up food and that their mouthparts are vestigial especially in the females, the mouthparts may provide evidence for the phylogenetic relationship of this enigmatic taxon. The males possess moveable mandibles; their maxillae consist of two parts, a proximal part which is probably homologous to cardo plus stipes and a distal part which corresponds to the maxillary palpus (probably composed of fused palpomeres); the labium is strongly reduced and fused with the hypopharynx (Kinzelbach 1971).

Since the mandible of males is usually slender, stylet-like and its anterior articulation is reduced, it appears to resemble the condition in the Antliophora. It has been further argued that a close relationship to Diptera is indicated by the presence of at most one maxillary endite and by the labial morphology, these characters being putative synapomorphies for the taxon called Halteria (Whiting & Wheeler 1994). However fossil male Strepsiptera from Cretaceous Burmese amber and Eocene Baltic amber indicate that the ground pattern was more generalized since their mandibles are robust and curved, having a broad dicondylic base, and look similar to a biting mandible (Pohl et al. 2004; Grimaldi & Engel 2005). They do not resemble the mandibles of Antliophora.

The maxilla is simplified and basally fused with the head; the palpus appears three-segmented but is not actually subdivided into palpomeres; maxillary muscles are absent (Beutel & Pohl 2005). Neither a maxillary endite nor a labial palpus are present, but in the Antliophora at least a one-segmented palpus exists. The first larval stage is prognathous, i.e., mandibles point in a frontal direction whereas the maxillae are directed posteriorly (Pohl & Beutel 2005). The first larvae of some taxa possess a structure on the ventral head that is called a gula; however it is uncertain whether it is homologous to the gula of other insects. This structure was recently regarded as an apomorphic feature of Strepsiptera (Pohl & Beutel 2005).

At the moment there is no unambiguous support from the mouthparts for either phylogenetic position of the Strepsiptera. However, the putative presence of a robust mandible with dicondylic articulation in the ground pattern of male Strepsiptera is a strong argument against the Halteria hypothesis.

3.2.   Neuropteriformia

The Neuropteriformia comprise the Coleoptera and the superorder Neuropterida (with or without the Strepsiptera). They clearly share a number of morphological traits, for example in the ovipositor and wing articulation (Mickoleit 1973; Hörnschemeyer 2002). Molecular studies repeatedly recover a Coleoptera-Neuropterida clade (e.g., Wheeler et al. 2001; Kjer 2004), which has been named the Neuropteriformia (Ax 1999).

One of the most frequently cited possible synapomorphic features is the presence of a gula, which is directly associated with the mouthparts and their prognathous position. A gula is present in most Coleoptera, in Raphidioptera, Megaloptera (Beutel & Haas 2000) and the basal most group of the Neuroptera, the Nevrorthidae (Aspöck et al. 2001). This trait has been regarded as an autapomorphy of Coleoptera (Willmann 2003b) although it is highly variable and absent in some beetles (Snodgrass 1935). It can be argued that due to the frontally directed position of the mouthparts the gula could have evolved convergently in the Neuropteriformia. In the absence of recent comparative studies it cannot be convincingly argued that the gula is autapomorphic for the Neuropteriformia (Fig. 1, character 1).

The glossae and paraglossae of adult Coleoptera have a tendency to become reduced. They are represented by an unpaired median lobe or by paired lateral lobes. The former, called ligula, is probably the fused glossae (Fig. 1, character 4); the paired lobes might be the fused paraglossa and glossa (Matsuda 1965) or a division of the ligula. Various shapes of a ligula also occur in the Archostemata (Hörnschemeyer et al. 2002). In the Neuropterida the paraglossae are reduced (Matsuda 1965) (Fig. 1, character 5). Both features could be regarded as autapomorphies but further studies are needed. Two further probable apomorphic characters (Fig. 1, characters 6, 7) occurring in larvae of Neuropterida are the premental muscles that originate on the tentorium and the loss of the mola of the mandible (Das 1937; Ax 1999). Matsuda (1965) pointed out that in the ground pattern of larval

Coleoptera and Neuropterida the endites of the labium have the tendency to become reduced. If this general statement holds true then modified labial endites are either a synapomorphy uniting both taxa (Fig. 1, character 2) or a plesiomorphy belonging to the ground pattern of the Endopterygota (see below).

The monophyly of Neuropterida is not doubted, however the relationships among the three orders are currently under discussion (Aspöck 2002). The most recent and comprehensive studies on the relationships within the Neuropterida argue for a sistergroup relationship of the Megaloptera and Neuroptera. This is in contrast to the traditional view (reviewed in Willmann 2003a), but is well supported by morphological and molecular data (Aspöck et al. 2001; Aspöck 2002; Haring & Aspöck 2004). The monophyly of the Neuroptera is clearly supported by the unique construction of the larval mouthparts in which the mandibles and maxillae are interlocked to form a sucking tube for catching and feeding on prey. The larval mouthpart composition represents the most important apomorphy of the order although it is not entirely clear which part of the maxillae actually forms the sucking jaws (Fig. 1, character 10).

The sistergroup relationship of the Megaloptera and Neuroptera is supported by the integration of the larval cardo into the head capsule, where it assumes an oblique position (Fig. 1, character 8), as well as other features (Aspöck et al. 2001). This is a possible prerequisite for the evolution of the larval sucking jaws of the Neuroptera (Aspöck 2002). Another prerequisite may be the elongation of the stipes (Fig. 1, character 9) (Boudreaux 1979). A comparative morphological investigation of larval and adult mouthparts in Neuropterida would contribute to a better understanding of the phylogenetic value of these traits and help resolve the interrelationships of the Neuroptera, Megaloptera and Raphidioptera. Several aspects of the larval cardo strongly suggest a Megaloptera-Neuroptera sistergroup relationship; less certain however is the stipes morphology. Key features of the mouthpart musculature (Das 1937) need more detailed research before they can be properly phylogenetically evaluated (Fig. 1, characters 6).

3.3. Mecopteriformia

The second major branch of the Endopterygota comprises the Mecopterida (or Panorpoidea) and the Hymenoptera (Fig. 1). This assemblage was termed Mecopteriformia by Ax (1999). Several molecular studies support the monophyly of this group (Wheeler et al. 2001; Whiting 2001; Kjer 2004). The morphological autapomorphies related to feeding include the presence of silk secretion by larval labial glands (Willmann 2003a), modified larval submentum musculature (Das 1937) and the presence of the sitophore on the sucking pump in the head (Vilhelmsen 1996) (Fig. 1, characters 11–13). The latter is a sclerotized plate which forms the ventral side of the cibarium and may be a prerequisite for the evolution of suctorial mouthparts of adult insects (Kristensen 1999). It may be no coincidence that all major groups of nectar feeding insects (Krenn et al. 2005) and blood sucking Endopterygota (Lehane 2005) belong to this clade. Kristensen (1999) concluded that spore feeding and/or pollen feeding was ancestral in adults of Hymenoptera and Mecopterida. This contrasts with the predatory feeding behaviour of Neuropteriformia. If Kristensen's conclusion is correct, then adult mouthpart specialization to spore or pollen feeding and more pronounced differences to larval mouthparts might be a feature common to both, the Hymenoptera and Mecopterida.

The Hymenoptera are characterized by several morphological autapomorphies of the mouthparts (Fig. 1, characters 14–16). The most striking is the labio-maxillary complex, which is a functional unit formed by the maxillae and labium which are bound together by folds and sheets of membranous cuticle (Matsuda 1965). Additional mouthpart traits are interpreted as autapomorphic for Hymenoptera such as the 4-segmented labial palpus and the ventral margins of the clypeus being inflected and overlapping the proximal part of the labrum (Vilhelmsen 1996).

The Mecopterida are characterized by a number of derived morphological features. Some of these concern larval mouthparts, which were studied in detail by Hinton (1958), such as the divided stipes, the absence of extrinsic cardinal promotor muscle and the 2-segmented labial palpus lacking intrinsic muscles (Fig. 1, characters 17–19). Apart from the "Strepsiptera problem" the monophyly of the Mecopterida is widely accepted. Likewise, the monophyly of each of the high-ranking subgroups, Antliophora and Amphiesmenoptera, is not disputed. The latter is one of the best supported supraordinal groupings of insects.

The adult mouthparts of ancestral Amphiesmenoptera probably retained a number of primitive traits including a retractable labrum with extrinsic muscles, mandibles with tentorial adductors and a labium with paraglossal lobes. These ancestral conditions are still present in the most basal Lepidoptera and occur nowhere else in the Mecopterida (Kristensen 1981, 1999). Derived features have also been identified in the ground pattern of the mouthparts in Amphiesmenoptera, the most important is the fusion of the prelabium with the hypopharynx in the larvae (Hinton 1958) to form the so-called spinneret at the opening of the labial silk glands (Fig. 1, character 20).

3.4. Antliophora

The monophyly of the Antliophora, which comprises the Mecoptera, Siphonaptera and Diptera, is well supported by anatomical and molecular data, leaving aside the problematic Strepsiptera (WHEELER et al. 2001; KJER 2004).

Mouthpart synapomorphies of adult Mecoptera, Siphonaptera and Diptera were listed by WILLMANN (2003b). In summary, the mandible is slender and the anterior articulation is reduced or absent. Posterior parts of the labium are reduced and, probably in context with this, some labial muscles are absent which however are retained in the amphiesmenopteran ground pattern. Furthermore only two labial palp segments are present in the ground pattern of adult Antliophora (Fig. 1, characters 21–24). Synapomorphies of the larval mouthparts (Fig. 1, characters 25–27) include the absence the labral retractor muscle, the absence of the tentorial adductors of the cardo and the modified hypopharyngeal musculature (HINTON 1958, listed in WILLMANN 2003b).

Adult Diptera are characterized by the shortened labial palps which form the labellum of the sucking mouthparts (Fig. 1, character 28). Adult Mecoptera have retained biting mouthparts and show the most complete set of mouthpart structures in the Antliophora. In many but not all Mecoptera, the head is elongated and forms a beak-like rostrum which is composed of clypeus plus gena and the elongated postmentum of the labium on the posterior side. In Mecoptera the clypeus and labrum are fused and probably associated with this is the absence of extrinsic labral muscles. The piercing mouthparts of adult Siphonaptera are highly derived. The traditional interpretation of the homology of their components fails to provide evidence for a sister group relationship to either Diptera or Mecoptera. According to the study of MICHELSEN (1997), the piercing stylets consist of the elongated labrum and laciniae, both are enclosed by the secondarily subdivided labial palps. The maxillary palpus is conspicuous and the first palpomere is greatly enlarged. MICHELSEN's new interpretation of the mouthpart homologies of Siphonaptera is based on the musculature and led to a set of possible synapomorphies with the remaining taxa of Antliophora. For example, the Mecoptera + Diptera share the absence of the stipito-lacinial muscle and the lingua-mandibula muscle; the Siphonaptera + Mecoptera share the absence of extrinsic labral muscles and absence of labial endites (Fig. 1, characters 29, 30); the Siphonaptera + Nannochoristidae share a labrum lacking intrinsic muscles; and the Siphonaptera + Nannochoristidae + Diptera share the absence of the galea (MICHELSEN 1997).

Evidence for a close the relationship between fleas and Mecoptera first came from molecular data.

On the basis of DNA sequences the family Boreidae ("snow-fleas") was regarded as the sister group to fleas (WHITING 2001). KRISTENSEN (1999) deemed it a revolution in mecopteran phylogeny when evidence arose that the Siphonaptera were actually subordinal in the Mecoptera. Within the Mecoptera the Boreidae seem to be the closest relatives of the fleas, and the Nannochoristidae are probably the sister group to fleas plus Boreidae. This relationship is supported by similarities in the ovary structure and molecular characters (GRIMALDI & ENGEL 2005). Boreidae and Siphonaptera share the reduction of wings, the presence of a pupal silk-cocoon and the jumping ability, however the structural modifications for jumping have yet to be studied in detail in Boreidae (GRIMALDI & ENGEL 2005). A mouthpart feature mentioned by MICHELSEN (1997) which would unite Siphonaptera and Nannochoristidae is the absence of the intrinsic labral muscle, yet the condition in Boreidae remained unstudied. Furthermore, synapomorphies potentially uniting Siphonaptera and Mecoptera include the absence of extrinsic labral muscles and the absence of a ligula (Michelsen, personal communication). Unfortunately, mouthpart synapomorphies for fleas and Boreidae are not known. The new interpretation of the mouthparts of fleas and their membership in the Mecoptera may be correct, at least it makes sense in the various aspects discussed by KRISTENSEN (1999), however mouthpart features neither clearly support the sistergroup relationship of fleas to the Boreidae nor these together as the sister group to the Nannochoristidae.

4. Ground pattern of mouthparts in Endopterygota

Although mouthpart features have been extensively used for phylogenetic interpretation of the Endopterygota, the uncertain relationships, such as the Strepsiptera, the relationships among the neuropteridan orders and the sistergroup to the Siphonaptera cannot be unequivocally resolved based on current information of mouthpart characters. Part of the problem stems from the fact that many of the comparative anatomical works date back to the early decades of the last century. These studies did not explicitly assign plesiomorphic and apomorphic character states; furthermore reexaminations of these studies are often confusing due to older terminology. A dataset based on original studies is lacking that has been assembled with the aim of providing a matrix for phylogenetic analyses. One conclusion of this review of the present literature is that at least some features of the ground pattern of Endopterygota can be established.

(1) The mouthparts are identical in the larvae and adults.

(2) The mouthparts are biting/chewing.

(3) The mandibles are dicondylic and bear teeth.

(4) The maxillary palpus is 5-segmented.

(5) The labial palpus is 3-segmented.

The following questions could perhaps be easily answered if comparative morphological studies were conducted using outgroup taxa from "Lower Neoptera" and Paraneoptera.

(1) Is the plesiomorphic position of the mouthparts prognathous? An affirmative answer to this question is substantiated by the fact that prognathous mouthparts are also found in some amphiesmenopteran larvae (KRISTENSEN 1997).

(2) Is the gula part of the ground pattern? The important point here is to determine whether all structures which have been called "gula" are potentially homologous.

(3) Is the labrum moveable and exactly which labral muscles belong to the ground pattern?

(4) What is the plesiomorphic musculature of the mandibles?

(5) Which palpomeres of the maxillary palpus contain muscles?

(6) Is the fusion and/or reduction of the labial endites plesiomorphic for Endopterygota? It can be argued that modified labial endites might be a ground pattern feature of the Endopterygota since the Hymenoptera also have fused labial endites (Fig. 1, character 15).

Research on the mouthpart morphology of larval and adult insects with the aim of accumulating data for phylogenetic analysis might provide much needed input for the clarification of the phylogeny of Endopterygota. In addition it would contribute to a better understanding of organ evolution including the adaptation of mouthparts to various food sources.

5. Acknowledgements

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