

The first holistic SEM study of Coniopterygidae (Neuroptera) – structural evidence and phylogenetic implications

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Abstract. Adults of two coniopterygid species, *Aleuropteryx juniperi* Ohm, 1968 (Aleuropteryginae) and *Semidalis aleyrodiformis* (Stephens, 1836) (Coniopteryginae), were studied using scanning electron microscopy. Interspecific differences in the ultrastructure of the integument of all the major parts of the body were identified and described, and the functional and phylogenetic implications of the differences discussed. Additionally, the enlarged terminal segment of the labial palps of the Coniopterygidae and the Sisyridae, which up to now has been used as an argument for a sister-group relationship between these two families, was subjected to a thorough comparison. The very different morphology makes independent enlargement of the terminal palpal segment in both families plausible. This finding is congruent with the earlier hypothesis of a sister-group relationship between Coniopterygidae and the dilarid clade, which was proposed on the basis of molecular data, larval morphology and male genital sclerites. Finally, a new classification of the coniopterygid subfamilies is presented based on characters of the larval head (prominence of the ocular region, relative length of sucking stylets). The following relationship is hypothesized: (Brucheiserinae + Coniopteryginae) + Aleuropteryginae, and the implications of this hypothesis for the phylogenetic interpretation of the ultrastructural differences that we found are discussed: (1) The wax glands, as well as plicatures, are interpreted as belonging to the ground pattern of the family Coniopterygidae, and (2) the wax glands are considered to have been reduced in Brucheiserinae and the plicatures in Coniopteryginae. A distinct (though reduced) spiraculum 8 was detected in *Semidalis aleyrodiformis*; as a consequence the hypothesis that the loss of spiraculum 8 is an autapomorphy of Coniopteryginae is refuted.

“Phylogenetic hypotheses must largely remain matters of individual opinion, and while the writer considers himself to have selected significant facts, time alone can prove their worth.”
(Withycombe, 1925)

INTRODUCTION

Coniopterygidae are the midgets of the order Neuroptera. It is remarkable that both the first mention and illustration of dustywings in the literature date back to the 18th century (Block, 1799; Aspöck & Aspöck, 2009). Another milestone in neuropterology was the introduction of genital sclerites for identification of Coniopterygidae by Enderlein (1906).

Since Withycombe (1925) the family was believed to be an early offshoot of neuropterous stock, mainly because of the reductions associated with their small body size. Aspöck et al. (2001b) were the first to question Withycombe's hypothesis based on a holomorphological cladistic analysis of the Neuroptera (with Nevrothiformia, Hemerobiiformia and Myrmeleontiformia as suborders). Their analysis indicates that the Coniopterygidae is a sister-group of Sisyridae, which entailed a shift from an isolated position to the suborder Hemerobiiformia.

In a subsequent molecular phylogenetic analysis (Haring & Aspöck, 2004) Coniopterygidae emerged as a sister-group of Dilaridae. A long-branch attraction of the

two families was suggested since a sister-group relationship of Coniopterygidae with the whole dilarid clade (Dilaridae, Mantispidae, Rhachiberothidae, Berothidae) seemed more plausible, as the dilarid clade is well supported by larval and adult characters. This hypothesis is supported by an analysis of the genital sclerites (Aspöck & Aspöck, 2008).

The present study is embedded in the contradictory context of recent phylogenetic studies. It is the first holistic analysis of the ultrastructure of the surface of Coniopterygidae. Two species, *Aleuropteryx juniperi* Ohm, 1968 (Aleuropteryginae) and *Semidalis aleyrodiformis* (Stephens, 1836) (Coniopteryginae), were examined under a scanning electron microscope. The objectives were to determine ultrastructural similarities and differences in regard to their function and their phylogenetic relevance. Furthermore, the structure of the enlarged terminal segment of the labial palps of Sisyridae [*Sisyra nigra* (Retzius, 1783) and *Sisyra terminalis* Curtis, 1954] and the two coniopterygid species were compared to test whether this character, the main argument for the sister-group relationship (Aspöck et al., 2001b), is a synapomorphy of the two families. Addition-

ally, the recently discovered larva of the subfamily Brucheiserinae (Sziráki & Flint, 2007) allows to introduce a first hypothesis on the relationship of the subfamilies.

Coniopterygidae Burmeister, 1839

Classification: About 500 species of Coniopterygidae are known (Aspöck & Aspöck, 2007). The family includes three subfamilies:

1. Aleuropteryginae Enderlein, 1905: with a worldwide distribution and about 160 described species (Aspöck et al., 2001a).

2. Brucheiserinae Navás, 1927: distributed in the dry mountainous regions of Chile and Argentina and consisting of four species (Riek, 1975; Sziráki, 2007; Sziráki & Flint, 2007).

3. Coniopteryginae Burmeister, 1839: with a worldwide distribution and about 290 described species (Aspöck et al., 2001a).

Their common name, dustywings, refers to the white waxy coating secreted by wax glands, which are modified hypodermal cells (Meinander, 1972). Wax glands occur all over the body, but particularly on the abdomen. They are present in Aleuropteryginae and Coniopteryginae, but missing in Brucheiserinae (Sziráki, 2007). Another characteristic of Coniopterygidae is their small body size, with the forewing not exceeding 5 mm in length and in several species it is less than 2 mm. Maxillary and labial palps are well developed and both are equipped with special sensory hairs on a distinct sensory area ventro-anteriorly on the terminal segment.

On the abdomen, the plicatures are a spectacular feature of Coniopterygidae. They are arranged in two lateral rows in Aleuropteryginae, in two lateral plus one ventral median row in Brucheiserinae (Sziráki, 2007) and missing in Coniopteryginae.

The strongest autapomorphy of Neuroptera are the sucking tubes of their larvae, which were recognized as a unique feature by Brauer (1857). They consist of modified maxillae and mandibles. In the plesiomorphic state they are curved, which enables them to catch mobile prey. In Coniopterygidae the sucking tubes are stileto-shaped. This character state is apparently an adaptation to feeding on immobile prey and evolved independently several times within the Neuroptera. In Aleuropteryginae, the elongated stylets of the sucking tube extend beyond the anterior margin of the head, whereas in Brucheiserinae and Coniopteryginae only the tips of the sucking tubes extend beyond the anterior margin of the head (MacLeod, 1964; Sziráki, 2007; Fig. 3). The presence of a large anterior process on the larval prelabium is unique among Neuroptera, although a superficially similar but much smaller process occurs in berothid larvae (MacLeod, 1964). The ocular area of coniopterygid larvae contains four to five equally sized corneae. In Brucheiserinae and Coniopteryginae it is raised on a low, rounded mound, which extends the head laterally (MacLeod, 1964; Sziráki, 2007; Fig. 3). Coniopterygidae have three larval instars (Meinander, 1972), which is typical for most Neuroptera.

The classic work of Killington (1936) is still valuable both as a source of information and for its profound introduction to the study of Coniopterygidae.

MATERIAL AND METHODS

Species studied

Aleuropteryx juniperi Ohm, 1968

A. juniperi belongs to the *Aleuropteryx loewi* group (Meinander, 1972), which includes 20 species and is characterized by features of the male genitalia. *A. juniperi* feeds mainly on scale insects (Coccoidea), in particular *Carulaspis juniperi* (Ward, 1970; Henry, 1976). The larva of *A. juniperi* was studied by MacLeod (1964) under the name “*Helicoconis lutea*”. *A. juniperi* was introduced into North America, and its native distribution is Central, Southern and Western Europe, Morocco and Tunisia (Aspöck et al., 2001a).

Semidalis aleyrodiformis (Stephens, 1836)

S. aleyrodiformis constitutes, together with 28 other species, the *Semidalis aleyrodiformis* group, which is characterized by distinctive features of the male genitalia (Sziráki, 2005). The adults scan the underside of leaves with their mouthparts in search of aphid secretions. They are predators of small insect eggs, immature aphids and mites (Gepp & Stürzer, 1986). The head of the larva has been studied in detail by Rousset (1966). *S. aleyrodiformis* is widely distributed in Europe, Morocco and Tunisia, as well as Central and Southeast Asia (Aspöck et al., 2001a).

Sisyridae: *Sisyra terminalis* Curtis, 1854 and *S. nigra* (Retzius, 1783)

The adults of European Sisyridae are polyphagous, feeding mainly on pollen in spring and aphids in summer (Weißmair, 1999, 2005). Pollen from various plant species (e.g., *Pinus* spp.), algae and fungi have been identified in the crop and gut contents of *S. terminalis* (Kokubu & Duelli, 1983). *S. nigra* feeds on the eggs of *Sialis lutaria* (Sialidae) (Tjeder, 1944). The larvae of Sisyridae have needle-shaped sucking stylets and feed on freshwater sponges and Bryozoa (Weißmair, 1999). *S. terminalis* occurs only in Europe. *S. nigra* is Holarctic, widely distributed in Europe and North America (Aspöck et al., 2001a).

Material examined

A. juniperi: Four adult specimens (coll. Aspöck & Rausch) in 75% alcohol; collecting data: Pella Agros, Macedonia, Greece, 29.vii.1978; H. & U. Aspöck, H. & R. Rausch leg.

S. aleyrodiformis: Four adult specimens (coll. Aspöck & Rausch) in 75% alcohol; collecting data: Heiligenkreuz, Lower Austria, Austria, 26.v.1963; H. & U. Aspöck leg.

14 live specimens; collecting data: Purgstall an der Erlauf, Lower Austria, Austria, 48°03'N, 15°09'E, 25.v.2004; H. Rausch leg.

Sisyra nigra: One adult specimen, Sardinia, reared by W. Weißmair, vii.1993.

Sisyra terminalis: One adult specimen in 75% alcohol; collecting data: Korneuburger Au, Lower Austria, Austria, 29.vii.2008; U. Aspöck, H. Aspöck, Anderle & Randolph leg.

Methods

For scanning electron microscopy, 15 specimens of *S. aleyrodiformis* and two of *A. juniperi* were dehydrated in increasing concentrations of ethanol, put into 100% acetone, dried using hexamethyldisilazane and mounted on stubs with adhesive pads. Two specimens each of *S. aleyrodiformis* and *A. juniperi* were macerated in KOH and fixed in osmium tetroxide in order to prevent thin-cuticled structures from shrinking (Klepál & Hör-

mann, unpubl.). The specimens were dehydrated in increasing concentrations of ethanol and critical-point dried before being mounted onto stubs with adhesive pads.

The specimens were coated with gold (Sputter Agar B7340) and studied using a Philips XL20 scanning electron microscope at 15 kV. Measurements were taken using the software "Microscope Control".

Nomenclature

The various kinds of sensilla and other structures studied are listed and defined. Their potential functions are based on information in Altner (1977).

Sensilla chaetica: Sturdy, pointed bristles with grooved surface and a flexible socket. Potential function: mechanoreceptive.

Sensilla trichodea: Hair-like sensilla with a smooth surface. Potential functions: mechanoreceptive, olfactory or gustatory.

Sensilla basiconica: Rather short more or less cone-shaped (smooth transition to trichoid shape) sensilla with a smooth surface but lack a flexible socket (e.g., Figs 1D on galea, 2C and 2F). They can have a terminal pore (uniporous sensilla). Potential functions: olfactory, gustatory, thermoreceptive, hygroreceptive.

Claviform sensilla: Like sensilla basiconica but club-shaped.

Sensilla campaniformia: Flattened oval discs with a protuberance in the middle (Fig. 1H). Potential function: mechanoreceptive.

Microtrichia: Non-innervated, thin, hair-like surface structures (e.g., Fig. 1H located all round campaniform sensilla or as in Fig. 2J around wax glands).

Protuberances: Non-innervated, small, blunt structures (Fig. 1H below sensilla campaniformia) (Klepal & Kastner, 1980).

Tooth rows: 1–6 non-innervated teeth, arranged in short rows with no common base (Fig. 2N).

Comment on sensilla: It was not the objective of this paper to provide a description of all the sensilla. Only those on the structures studied are described.

Pores on sensilla were mentioned whenever visible. If no pores were visible this is not mentioned expressis verbis in order to avoid false negative statements. This does not necessarily mean that pores are absent. It is most probable that small pores (e.g., wall pores) were overlooked due to low resolution.

RESULTS

Aleuropteryx juniperi Ohm, 1968 (Fig. 1A–O)

Head (Fig. 1A–G)

Frons covered with microtrichia and long sensilla chaetica. Frontal area below anterior tentorial pits elongate (Fig. 1A); distance between pits 110 μm . Head with faint suture on each side from dorsal margin of occipital foramen to dorsal margin of compound eye. Ventrally hypostomal bridge connecting postgenae between base of labium and postoccipital foramen (Fig. 1B); suture present between ventro-lateral margins of postgenae and hypostomal bridge. Coronal suture absent. Ocelli absent. Compound eyes with 182 ommatidia; distance between eyes measured across frons 235 μm . Antennae of 22 segments inserted into large oval antennal foramina; distance between insertions of antennae 140 μm . Scapes with wax glands and sensilla campaniformia. Spine ventrally on pedicels (Fig. 1A) distally shallowly furrowed and without microtrichia or sensilla. Antennal segments covered with short sensilla chaetica, long blunt trichoid sensilla, few campaniform sensilla and distad with few

claviform sensilla; intersegmental membrane lamellate, lamellae partly fused; degree of fusion different in various specimens. Unlike in *S. aleyrodiformis* (see below), there are no minute (0.5 μm) basiconic sensilla on apices of antennae. Proximal margin of clypeus marked by broad transverse shallow furrow with about 10 long sensilla chaetica; clypeus short and smooth. Labrum 85 $\mu\text{m} \times 40 \mu\text{m}$, on dorsal surface four short uniporous blunt sensilla basiconica basally and four slightly longer pointed uniporous sensilla basiconica distally; on distal margin distinct chasm with about ten short thick projecting sensilla basiconica (Fig. 1E). Mandible with two distinct spines on ventral margin (Fig. 1C). Hypopharynx large and prominent, with spines directed proximad ventro-basally (Fig. 1C), with long blunt trichoid sensilla laterally, thicker shorter and thinner longer sensilla basiconica medio-ventrally and very short uniporous sensilla basiconica distally.

Maxilla: Cardines with microtrichia on basal edge. Stipites with a few sensilla chaetica and campaniform sensilla laterally, otherwise smooth, fused with laciniae. Laciniae long and slender, distally with four stout sensilla chaetica 15 μm long and 4.5 μm in diameter and three slenderer 15 μm long and 1.6 μm in diameter (Fig. 1D), a few short pegs on inner surface. Galeae with a distinct distal segment bearing on apex a field with short thick uniporous sensilla basiconica (Fig. 1D), basal segment with only a few sensilla basiconica. Terminal segment of maxillary palps covered with microtrichia, short sensilla chaetica, several long blunt trichoid sensilla and few sensilla campaniformia, on inner side with a sharply delimited sensory area with protuberances arranged in a network and uniformly distributed thin and thick blunt uniporous sensilla basiconica (Fig. 1F); sensory area about half of inner surface of terminal maxillary palp.

Labium consisting of submentum, mentum and praementum. Submentum smooth except for a few microtrichia medially; mentum with six long sensilla chaetica; praementum with 3-segmented labial palps inserted on palpigers; palpiger with one 60 μm long socketed sensillum trichodeum medio-distally and a few sensilla chaetica; first palpomere with one long socketed sensillum trichodeum in the same position as on palpiger, sensilla campaniformia, long blunt trichoid sensilla and a few microtrichia, second palpomere again with one long socketed sensillum trichodeum in the same position as on segment 1 and palpiger, with long blunt trichoid sensilla and more microtrichia; terminal segment of labial palps bulbously widened, with microtrichia, short socketed sensilla trichodea, long blunt trichoid sensilla and campaniform sensilla; dorsally more long blunt trichoid sensilla and less microtrichia. Distal half of inner (ventral) surface with a sharply delimited sensory area with protuberances and uniformly distributed thin and thick blunt uniporous sensilla basiconica as on maxillary palp (Fig. 1G). Praementum with a large distal ligula, consisting of completely fused glossae, ventrally with uniporous sensilla basiconica and a few microtrichia.

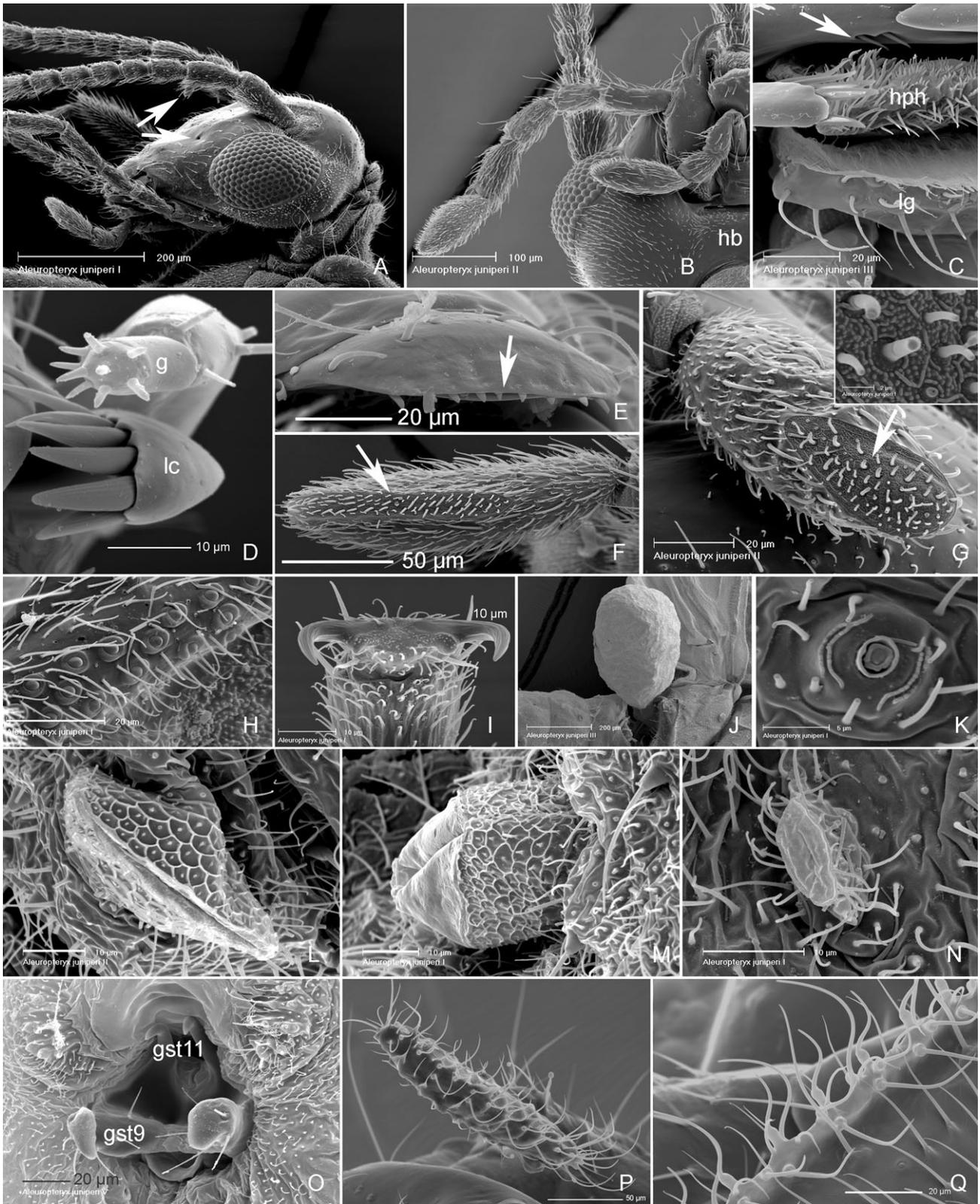


Fig. 1. A–O: *Aleuropteryx juniperi*, male. A – head, lateral view; spine on pedicel (upper arrow), anterior tentorial pit (lower arrow); B – head, ventral view, hypostomal bridge (hb); C – ventral margin of mandible with spines (arrow), hypopharynx (hph) and ligula (lg); D – galea (g), lacinia (lc); E – labrum, chasm with sensilla basiconica (arrow); F – terminal maxillary palpomere with sensory area (arrow); G – terminal labial palpomere with sensory area (arrow); inserted detailed view of sensory area; H – wing base, campaniform sensilla and protuberances; I – tarsus, claws; J – crop, diverticulum; K – wax gland; L – closed plicature; M – open plicature; N – rudimentary plicature; O – male genitalia, caudal view, styli of gonocoxites 9 (gst9) and gonocoxites 11 (gst11). P–Q: *Sisyra terminalis* (Sisyridae), female. P – terminal labial palpomere, ventral view; Q – apical margin of terminal labial palpomere, detailed lateral view.

Thorax (Fig. 1H–J)

Wax glands laterally on thorax and, together with campaniform sensilla, along wing venation (Fig. 1H). Proximally on forewings a field of sensilla campaniformia and a field of protuberances below (Fig. 1H). No bristles on anterior edge of hindwings.

Legs: Distally on fore tibiae a short section with long bristles. Long sensilla chaetica on tarsomere 5 extending over praetarsi. Arolium absent. Claws distally furrowed lengthwise; basally with protuberances; on plantae 15 short uniporous sensilla basiconica (Fig. 1I).

During preparation of two specimens a “balloon”, half the size of the abdomen, emerged at the junction of thorax and abdomen (Fig. 1J). It was identified as a crop diverticulum.

Abdomen (Fig. 1K–O)

On each tergite and sternite up to three wax glands; opening roundish, 5 μm in diameter, seamed by two elevated rings (Fig. 1K); wax glands encircling plicatures. Plicatures on sternites; fully developed on segments 3, 4 and 5 (Fig. 1L,M), rudimentary on segments 6 and 7 (Fig. 1N); plicatures proximally clam-shaped with reticulated surface, inside each mesh one sensillum-shaped structure of variable length, apparently with apical pore (Fig. 1L). When clam-shaped part open, an inner, soft-skinned part more or less extruded and distally invaginated (Fig. 1M). Spiracula on segments 1–8. Tooth rows on segments 5–7 between spiracula and plicatures and on segment 8 beneath spiracula.

Male genital sclerites (Fig. 1O): Ectoprocts with microtrichia. Between ectoprocts and sternum 9 two protruding sclerite pairs, dorsal ones representing gonostyli 11, ventral ones gonostyli 9 (Aspöck & Aspöck, 2008).

Semidalis aleyrodiformis (Stephens, 1836) (Fig. 2A–P)

Head (Fig. 2A–F)

Frons covered with microtrichia and long sensilla chaetica. Tentorial pits located just above clypeus, facial region short (Fig. 2A); distance between tentorial pits 140 μm . Head with suture on each side from dorsal margin of occipital foramen to dorsal margin of compound eye. Hypostomal bridge connecting postgenae between base of labium and postoccipital foramen; suture present between ventro-lateral margins of postgenae and hypostomal bridge. Posterior tentorial pits situated on postoccipital suture (Fig. 2B). Coronal suture absent. Ocelli absent. Compound eyes with 297 ommatidia; distance between eyes measured across frons 140 μm . Antennae of 30 segments inserted in large oval antennal foramina; distance between insertion points of antennae 30 μm . Scapes covered with wax glands and sensilla campaniformia; antennal segments covered mainly with short sensilla chaetica and long blunt and pointed trichoid sensilla, distad also with variously sized sensilla basiconica; intersegmental membranes lamellate, lamellae partly fused; degree of fusion similar in each specimen. On apices of antennae six minute (0.5 μm) basiconic sensilla (Fig. 2C). Transverse furrow marking proximal margin of clypeus; clypeus with nine long pointed trichoid sensilla; clypeus

of females 125 μm \times 40 μm ; clypeus of males very short, 100 μm \times 15 μm . Labrum of females 100 μm \times 75 μm ; labrum of males 85 μm \times 55 μm ; dorsally with three long pointed trichoid sensilla medially and one pointed trichoid sensilla latero-dorsally on each side, four uniporous sensilla basiconica in between; distal margin with distinct chasm from which six sensilla basiconica protrude. Mandible without spines on ventral margin. Hypopharynx ventrally with tooth rows directed distad.

Maxilla: Cardines with a few sensilla chaetica and with microtrichia on basal edge. Stipites with some sensilla chaetica, campaniform sensilla and a small area covered with microtrichia laterally and medially; fused with laciniae. Laciniae distally with 11 sensilla trichodea 15 μm long with diameter of 1.6 μm at base (Fig. 2D). Galeae one-segmented, broad and thick, basally covered with pointed trichoid sensilla, on the tip area with variously sized uniporous sensilla basiconica partly raised on small prominences (Fig. 2D). Terminal segment of maxillary palps with microtrichia and long pointed trichoid sensilla, entire inner side with a distinctly delimited sensory area with rather regularly distributed protuberances and thinner and thicker uniporous blunt trichoid sensilla (Fig. 2E).

Labium consisting of submentum, mentum and praementum. Submentum with three pointed trichoid sensilla and with microtrichia. Mentum with seven pointed trichoid sensilla with flexible sockets, otherwise smooth. Praementum with 3-segmented labial palps inserted on palpiger; palpiger with small area covered with microtrichia medio-distally, laterally furrowed and covered with protuberances. First and second labial palpal segments with sensilla chaetica, trichoid sensilla, sensilla campaniformia and microtrichia; terminal segment of labial palps bulbously widened, with microtrichia and pointed trichoid sensilla; inner side completely covered with a distinctly delimited sensory area with protuberances forming a network and with two types of uniporous blunt evenly distributed sensilla basiconica (Fig. 2F) and a few sensilla trichodea on outer margin of sensory area. Ligula with short blunt uniporous sensilla basiconica raised on prominences medio-distally, pointed trichoid sensilla laterally and ventrally and microtrichia dorsally.

Thorax (Fig. 2G–I)

Wax glands on thorax and, together with sensilla campaniformia, along wing venation. Seven long bristles on anterior edge of hindwings (Fig. 2G). Proximally on forewings a field with about 30 sensilla campaniformia.

Legs: Femora densely covered with sensilla campaniformia. Strong bristles ventrally along fore tibia, becoming stronger and broader distad (Fig. 2H). Arolium absent. Claws distally furrowed lengthwise; basally with protuberances; plantae with two long uniporous trichoid sensilla (Fig. 2I).

Abdomen (Fig. 2J–P)

Abdominal tergites and sternites with wax gland fields (Fig. 2J) consisting of up to 70 wax glands; wax glands with cruciform openings (Fig. 2L), 4 μm in diameter; in

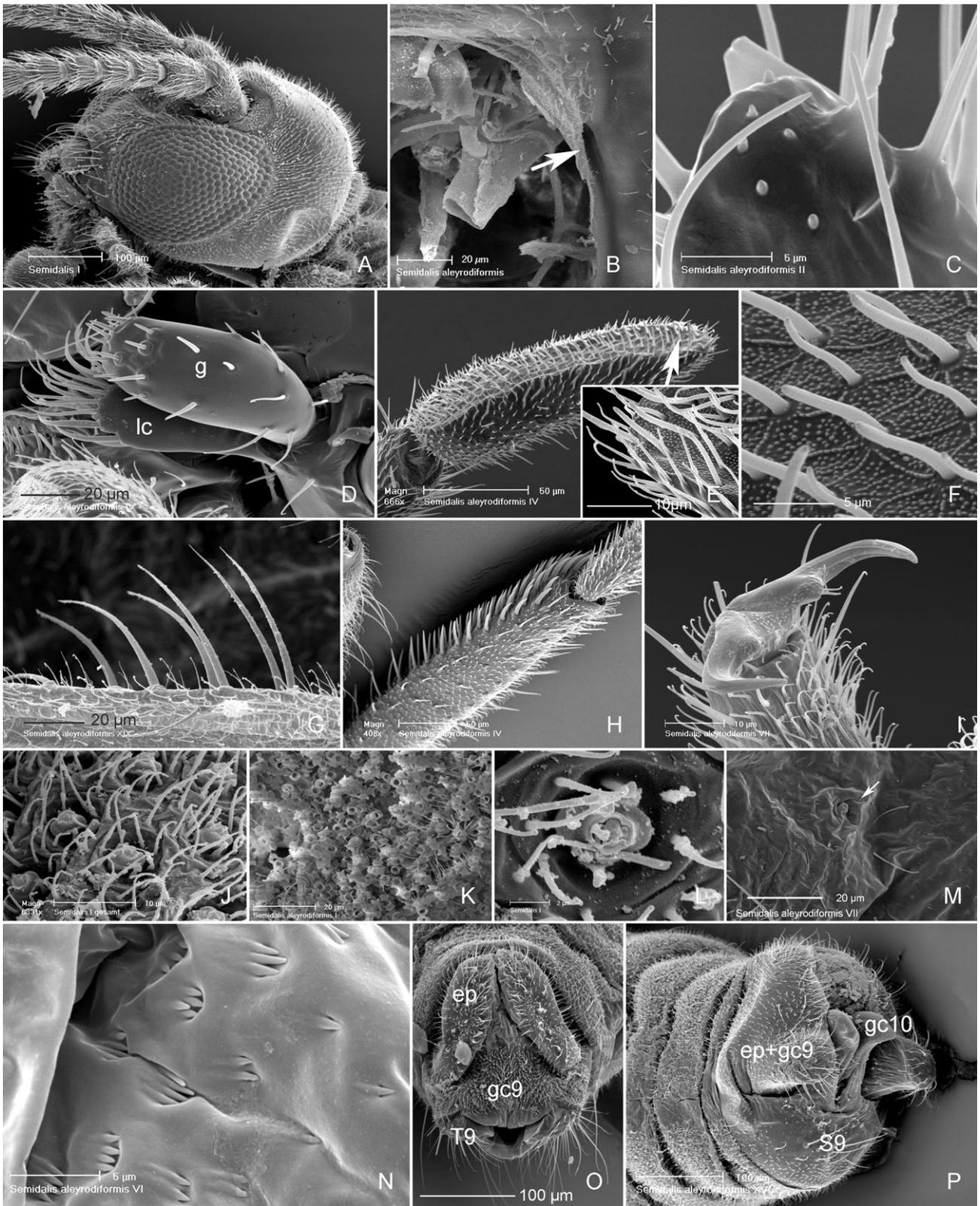


Fig. 2. A–P: *Semidalis aleyrodiformis*. A, B, G, J, K, L, N, P – male, C, D, E, F, H, I, M, O – female. A – head, lateral view; B – occipital foramen with posterior tentorial pit (arrow); C – apex of antenna, minute sensilla basiconica; D – galea (g), lacinia (lc); E – terminal maxillary palpomere with sensory area (arrow), inserted detailed view of sensory area; F – sensory area on terminal labial palpomere, detailed view; G – wing margin, bristles; H – fore tibia, bristles; I – tarsus of mid leg, claws; J – field of wax glands; K – wax covering; L – wax gland; M – spiraculum 8; N – tooth rows on abdomen; O – female genitalia, caudal view, ectoproct (ep), fused gonocoxites 9 (gc9) and tergite 9 (T9); P – male genitalia, caudo-lateral view, ectoproct (ep) + gonocoxites 9 (gc9), gonocoxites 10 (gc10), sternite 9 (S9).

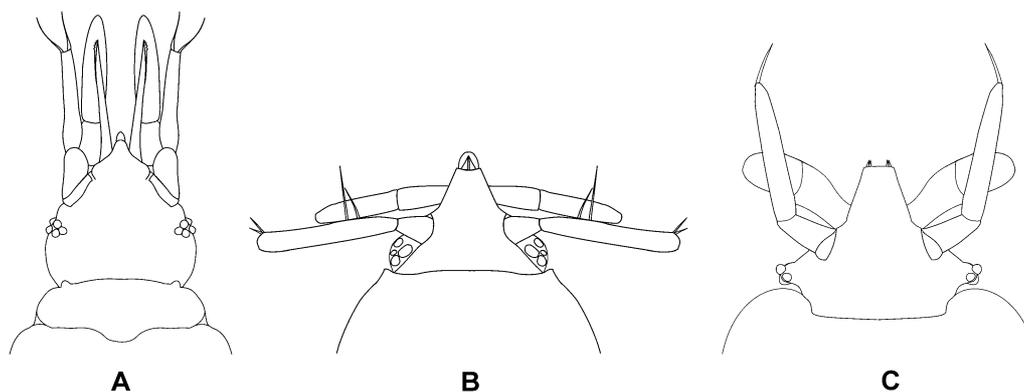


Fig. 3. Scheme of larval heads, dorsal view. A – Aleuropteryginae, modified after MacLeod (1964); B – Bruchaiserinae, modified after Sziráki & Flint (2007); C – Coniopteryginae, modified after MacLeod (1964).

females wax gland fields on tergites 2–7 and sternites 2–6, in males on sternites and tergites 2–7, respectively. Spiracula on segments 1–8, 8th reduced in size (Fig. 2M). Tooth rows (Fig. 2N) on segments 4–7 in both sexes ventral to spiracula, in females also on segments 8 and 9 and in males on segment 8 at level with spiracula.

Female genital sclerites (Fig. 2O): Paired ectoprocts with microtrichia and long sensilla chaetica. Plate with microtrichia below anal field. Ventro-laterally paired sclerites with long sensilla trichodea. Cuticle ventral to genital opening strongly wrinkled.

Male genital sclerites (Fig. 2P): Paired ectoprocts, which make up the amalgamated gonocoxites 9 (Aspöck & Aspöck, 2008), with microtrichia and aporous socketed sensilla chaetica. Inner sides of these sclerites smooth. Paired sclerites protruding between ectoproct + gonocoxite complex interpreted as gonocoxites 10. Sternum 9 with a few sensilla chaetica and sensilla trichodea.

Sisyridae: *Sisyra terminalis* Curtis, 1854 and *Sisyra nigra* (Retzius, 1783)

Only the terminal segments of the labial palps were studied in the two *Sisyra* species in order to test whether the enlargement of the labial palps in species of Sisyridae and Coniopterygidae should be considered homologous. No differences between the two species were observed: Terminal palpomere of the labial palp is flatly broadened (Fig. 1P), laterally densely covered with sensilla chaetica, at distal margin bearing pointed sensilla trichodea with a raised base (Fig. 1Q); no delimited sensory area is present.

DISCUSSION

1. The wax covering

Wax glands occur on thorax and abdomen of both species. In the two coniopterygid species investigated differences in the shape of the wax glands were observed (Figs 1K, 2L). The suggestion that the pattern in Aleuropteryginae and Coniopteryginae differs is premature, but it is worth mentioning that published data on the wax glands of three species of Coniopteryginae (Navone, 1987; Nelson et al., 2003) seem to correspond to the *S.*

aleyrodiformis type in the shape of the opening and the absence of seaming rings.

In general, the wax covering of Coniopterygidae (Fig. 2K) may be advantageous in terms of thermal isolation, respiration and camouflage (Hadley, 1984). As suggested by the name, “dustywings”, the wax secretions of Coniopterygidae create a powdery surface. This might prevent adhesion and protect them not only against parasites but also against predators that capture prey by means of adhesion (Betz & Kölsch, 2004). Altogether the wax covering seems to be a crucial innovation in the evolution of Coniopterygidae.

2. Structures studied

Head

An exceptional feature of the coniopterygid head is the presence of a hypostomal bridge (Fig. 1B). It is noteworthy that there is a distinct suture between the postgenae and the hypostomal bridge. In Neuroptera a hypostomal bridge is further present in *Plega* (Mantispidae) (Ferris, 1940) and at least some Nemopteridae (Acker, 1958: *Nemopterella* sp., Fig. 8C and *Stenorrhachus walkeri*, Fig. 9C; Krenn et al., 2008: *Nemoptera sinuata*, Fig. 7). Whether this character is of systematic relevance remains open at the moment.

Although we still lack an explanation, we want to point out that the eyes of *S. aleyrodiformis* consist of about one third more ommatidia than those of *A. juniperi*.

The spine on the pedicels of the males of *A. juniperi* (Fig. 1B) is a specific feature of the genus *Aleuropteryx*. Distinctive modifications of the basal antennal segments are secondary sexual characters and occur several times in both subfamilies (Meinander, 1990). Antennae are used by the male for holding the female during mating in several species (Meinander, 1972).

The antennae of *A. juniperi* clearly have a higher density of long blunt trichoid sensilla than those of *S. aleyrodiformis*. The sensilla lacking a terminal pore and a socket are likely to be olfactory sensilla (Altner, 1977). Olfaction might be more important for this specialized predator. It is surprising and interesting that there are minute basiconic sensilla only on the antennae of *S. aleyrodiformis*. The absence of a socket and a terminal porus,

their position at the apex of the antennae and their sparse-ness (only six sensilla of this type were found) indicate that they might be thermo- and hygroreceptors (Altner, 1977).

Differences between the sexes in size of clypeus and labrum were observed in *S. aleyrodiformis*.

The laciniae of *A. juniperi* are covered with about half as many bristles, which are twice as thick as those of *S. aleyrodiformis*. Here, we suggest an association between bristle characteristics and the respective feeding habits of the species. The bristles of the laciniae of *S. aleyrodiformis* may serve for feeding on soft-skinned prey or as a pollen harvesting structure whereas the firmness of the bristles of *A. juniperi* enables them to remove scale insects from a leaf.

The labial palps of Coniopterygidae are conspicuous within Neuroptera: They are large with a bulbous terminal segment bearing a sensory area on the inner side. The only other family in which the labial palps have an enlarged terminal segment is the Sisyridae. In contrast to Coniopterygidae, the terminal palpomere of the labial palps of Sisyridae is flatly broadened and not bulbous as in Coniopterygidae, and they do not possess a distinct sensory area (Fig. 1P, Q). The very different morphology makes independent enlargement of the terminal palpal segment in both families plausible. The sensory area on the terminal segment of the labial and maxillary palps of both coniopterygid species (Figs 1E, F; 2E, F) is worthy of closer examination. It is covered with two different types of blunt uniporous sensilla basiconica. According to Altner (1977) a terminal pore apparatus characterizes contact chemoreceptors. Between the sensilla the surface of the sensory area is covered with protuberances. It is questionable what function they fulfil on the sensory area. Protuberances are thought to be contact-minimizing structures, e.g., on the body of springtails (Eisenbeis & Wichard, 1985). In the case of those that occur in all insects at joints such as the insertion points of the head, antennae and mouthparts, they serve as intersegmental fixators (Gorb et al., 2002; Gorb, 2008). In *A. juniperi* the sensory area covers about half of the inner surface of the terminal palpomere (Fig. 1E), whereas in *S. aleyrodiformis* it covers nearly the whole inner surface. This difference is not a subfamily character since Meinander's (1972) drawings of *Heteroconis* (Aleuropteryginae) indicate that the sensory area in this species covers nearly the whole inner surface of the terminal labial palpomere, as is the case in *S. aleyrodiformis*.

In the neuropteran families Myrmeleontidae, Ascalaphidae, Nymphidae and Mantispidae sense organs on the terminal labial palpomeres consist of a deep pit, which is densely lined with sensilla basiconica (Eisner, 1953). These sense organs in Myrmeleontidae and Nymphidae were referred to as palpimaculae by Crampton (1921). Assuming that the "palpimaculae" are homologous in the rather distantly related Myrmeleontidae and Mantispidae as suggested by Eisner (1953), it is possible that this organ is part of the ground pattern of Neuroptera and has been reduced several times independently. It is question-

able whether the "palpimacula" is homologous with the sensory area in Coniopterygidae since not only does it strongly differ in structure but also in position, with the "palpimacula" located dorsally and the sensory area of Coniopterygidae located ventrally on the palpomere. However, both structures consist of a delimited area with sensilla basiconica on the terminal labial palpomere.

Thorax

Seven stout hamuli-like bristles on the costa of the hindwings of *S. aleyrodiformis* (Fig. 2G) are part of a wing-coupling device that New (1989) describes as characteristic of Coniopterygidae. They interlock with the anal margin of the forewings. In *A. juniperi* no corresponding structure is present, although it occurs in several Aleuropteryginae species (Meinander, 1972).

Sensilla campaniformia on the wings of both species probably serve to measure wing distortion during flight. Dorsally on the forewings of *A. juniperi* there is an area with protuberances near the wing base (Fig. 1G). As it is on the dorsal surface it does not correlate with the area of modified microtrichia that is interpreted by Riek (1967) as a stridulatory organ and by Henry (1980) as a structure associated with wing retention along the thorax.

The fore tibiae of *S. aleyrodiformis* are covered with a row of stiff bristles, mainly apically and on the inside (Fig. 2H). Navone (1987) observed the coniopterygid species *Conwentzia psociformis* (Curtis) and *Coniopteryx haematica* McLachlan (both Coniopteryginae) using the tibia for the distribution of the wax secretions over their bodies. Comparable structures in Cicadellidae and Aleyrodidae are a good example of convergent evolution (Navone, 1987). The function of the tibia as a clip organ in males (Sziráki & Greve, 1996) might have evolved secondarily in certain taxa. The drawings of Riek (1975) indicate similarly structured tibiae in *Brucheiser argentinus* Navás, 1927. In *A. juniperi* long, but not distinctly strengthened bristles occur only on the very distal part of the tibia.

The presence of an arolium varies among Neuroptera. It is missing in Coniopterygidae, Sisyridae, Myrmeleontiformia and Ithonidae and present in Chrysopidae and representatives of other groups (Beutel & Gorb, 2001).

The crop diverticulum, which appeared between the thorax and abdomen of *A. juniperi* (Fig. 1J), is described by Withycombe (1922) as a "median dorsal food reservoir" filled with air, possibly to increase the pressure within the pupal skin prior to emergence. It is supplied with air by ramifications of two large tracheae from the second abdominal spiracula (Withycombe, 1922).

Abdomen

Discrepancies are found in the literature on the Coniopteryginae regarding the presence of spiracula 8. While Tjeder (1957) indicates its presence in some of his drawings, Meinander (1972) held that the obliteration of spiracula 8 was an apomorphy of the Coniopteryginae. Here we confirm the presence of the spiracula 8, although reduced in size, in Coniopteryginae.

TABLE 1. Summary of the structural characters studied that might be valuable for further phylogenetic studies on Neuroptera: present (1) and absent (0) in *Aleuropteryx juniperi* (AJ) and *Semidalis aleyrodiformis* (SA).

	AJ	SA
Basiconic sensilla on apex of antenna	0	1
Chasm on distal margin of labrum	1	1
Mandible with spines on ventral margin	1	0
Hypopharynx with sensilla	1	0
Spines on inner surface of lacinia	1	0
Segmentation of galea	1	0
Area covered with microtrichia on cardo	1	1
Area covered with microtrichia on stipes	0	1
Sensory area on terminal segment of maxillary palp	1	1
Sensory area on terminal segment of labial palp	1	1
Labial palps with palpimaculae	0	0
Bristles on the anterior edge of hindwing	0	1
Tarsus with arolium	0	0

The most remarkable abdominal structures are the plicatures on the abdomen of Aleuropteryginae (Fig. 1K–M). Meinander (1972) describes plicatures on segments 3–6 and sometimes on the second segment of both sexes of *Aleuropteryx* species. In *A. juniperi* the plicatures are fully developed on segments 3–5 and rudimentary on segments 6 and 7. Neither the origin nor the function of the plicatures is yet understood. Withycombe (1925) suggests they may be repugnatorial glands and Tjeder (1957) that they are remains of organs without any special function. Morphologically they may have their origin in ancestral extremities. Protura, Collembola, Thysanura and Diplura have comparable eversible sacs (Matsuda, 1976). Another example is the eversible sacks protruding from a region interpreted as the gonocoxites 11 in adult males of certain Sialidae and Corydalidae (Aspöck & Aspöck, 2008).

Three possible functions of the plicatures are presented below:

1. Absorption of moisture. A transport epithelium is present in the coxal organs of Diplura, Zygentoma, Archaeognatha and Collembola (ventral tube). When water is required, these insects soak up water by applying the epithelium of the coxal organs to a humid substrate (Eisenbeis & Wichard, 1999). If plicatures fulfil an analogous function then Coniopterygidae should behave similarly.

2. Dispersal of pheromones. This could easily be achieved by evaginating the plicatures. The fact that the smooth inner surface can either be evaginated or hidden within the closed outer parts of the plicatures accords with this hypothesis.

3. Sensory reception. The evaginability of the plicatures provides little support for this hypothesis. The sensilla-like structures situated on the plicatures are not considered to be sensory organs as their openings are not large enough to serve as terminal pores.

The fact that the distal end of all the plicatures examined is turned inwards and some plicatures are firmly

closed indicates that the diverticulum of the ventral tube is retracted by muscles and extruded by hydrostatic pressure of the haemolymph, as is the case in Collembola (Schaller, 1970). Illustrations in Sziráki (2007) indicate that this is also true for the subfamily Brucheiserinae.

Genital sclerites: One characteristic of the ectoproct of Neuroptera is a rosette of trichobothria. In Coniopterygidae and other Neuropteran families it has been reduced several times, independently. No traces of trichobothria were observed using scanning electron microscopy. There are only long sensilla chaetica on the ectoproct and they are not interpreted as traces of trichobothria.

Gonocoxites 9 and 11 are connected in Neuroptera. In Coniopteryginae the gonocoxites 9 are fused with the ectoprocts (Fig. 2N), which is a derived condition (Aspöck & Aspöck, 2008).

The plate below the anal field of females of *S. aleyrodiformis* (Fig. 2M) is interpreted as the fused gonocoxites 9. The ventro-lateral sclerites are identified as derivatives of tergite 9 (Fig. 2M) according to similar structures in other families, e.g., the so-called “pseudohypocaudae” of *Austroberothella* and *Protobiella* (Berothidae) (Aspöck & Aspöck, 1985) and appendages of *Psectra diptera* (Hemerobiidae) (Tjeder, 1936).

As they are based on limited material the generality of our findings now needs to be tested by further studies. A summary of the structural characters that might be valuable for further phylogenetic studies on Neuroptera is provided in Tab. 1.

3. Phylogenetic implications

The following argument is based mainly on our results and is presented in the broad context of the relevant literature. The recent (Sziráki & Flint, 2007) discovery of a larva of the subfamily Brucheiserinae means that larvae of all three subfamilies are now available for study.

Internal relationships within Coniopterygidae

So far, there are no hypotheses concerning relationships of the three subfamilies of Coniopterygidae. Our hypothesis of (Brucheiserinae + Coniopteryginae) + Aleuropteryginae is based on the following:

(a) The larvae of both the Coniopteryginae (described in Brauer, 1857 and figured in Löw, 1885) and Brucheiserinae (Sziráki & Flint, 2007) have laterally extended heads as a result of the prominence of the ocular regions (Fig. 3B,C).

(b) The larvae of both subfamilies possess sucking stylets which barely project beyond the tip of the labral margin (Fig. 3B,C).

We consider these characters to be synapomorphies uniting Coniopteryginae and Brucheiserinae. In Aleuropteryginae the stylets extend far beyond the labral margin (Fig. 3A), which is a plesiomorphic condition.

Assuming a sister-group relationship of Coniopteryginae and Brucheiserinae, the plicatures should be interpreted as belonging to the ground pattern of the Coniopterygidae and their absence in Coniopteryginae as secondary. Furthermore, the presence of wax glands needs to be understood as an autapomorphy of the whole

family, despite its reduction in the Brucheiserinae. An indication of former wax glands in Brucheiserinae is the row of bristles on the tibia (Riek, 1975), which is also well-developed in Coniopteryginae and used to distribute wax particles over the body (Navone, 1987). The earliest evidence of dustywings is from the late Jurassic and apparently referable to Aleuropteryginae (Meinander, 1975; Grimaldi & Engel, 2005). This is in accord with the proposed sister-group relationship Coniopteryginae + Brucheiserinae.

The systematic position of Coniopterygidae within Neuroptera

Hitherto three alternative hypotheses on the sister-group relationship of Coniopterygidae within Neuroptera existed:

- (1) Ithonidae + (Coniopterygidae + (all other Neuroptera)),
- (2) Coniopterygidae + Sisyridae, and
- (3) Coniopterygidae + dilarid clade (= Dilaridae, Mantispidae, Rhachiberothidae, Berothidae).

To (1): Withycombe (1925) considered Coniopterygidae to be an early offshoot from all other Neuroptera but Ithonidae. This hypothesis is based mainly on plesiomorphic characters that Coniopterygidae share with Megaloptera, e.g., the presence of a projecting labrum and six Malpighian tubes in the larva. A projecting labrum occurs also in other neuropteran families, e.g. Berothidae (MacLeod, 1964), the absence of a projecting labrum, therefore, cannot be treated as a synapomorphy of all other Neuroptera. The presence of six Malpighian tubes is not necessarily a plesiomorphic character as most other Neuroptera and especially Nevrothidae, which are hypothesized to be the sister-group to all other Neuroptera (Aspöck et al., 2001; Haring & Aspöck, 2004; Beutel et al., 2009) have eight Malpighian tubes (e.g., Gaumont, 1976, who studied *Myrmeleon formicarius*, *Chrysoperla carnea*, *Drepanopteryx phalenoides*, *Sisyra nigra* and *Nevrothus fallax*). It seems plausible that six Malpighian tubes represent a reduction.

To (2): The holomorphological analysis of Aspöck et al. (2001a) resulted in a sister-group relationship between Sisyridae and Coniopterygidae. Two characters form the basis of this hypothesis: The enlarged terminal segments of the labial palps and the narrowing of the larval cardines into narrow sclerites. The homology of the enlarged terminal segments of the labial palps is put in doubt by the present results. It is questionable whether the shape of the larval cardines alone is sufficient to uphold this hypothesis.

To (3): In a molecular phylogenetic analysis (Haring & Aspöck, 2004), Coniopterygidae emerged as the sister-group of Dilaridae. A long-branch attraction of the two families was discussed – a sister-group relationship with the whole dilarid clade seemed more plausible as the dilarid clade is strongly supported by larval and adult characters. Subsequently the sister-group relationship Coniopterygidae + dilarid clade was hypothesized based on an analysis of the genital sclerites of Neuropterida (Aspöck & Aspöck, 2008). The complex arrangement of

gonocoxites 10 in the shape of a long and coiled “penisfilum” in derived representatives of Coniopterygidae, Berothidae, Rhachiberothidae and Mantispidae is an example of parallelism par excellence and can be interpreted as evidence of a common gene pool (Aspöck & Aspöck, 2008).

At present, the sister-group relationship of Coniopterygidae and the dilarid clade is the best supported hypothesis. Concomitant with this hypothesis, the straight sucking tubes of the dilarid clade + Coniopterygidae are considered to have evolved independently from those in Sisyridae. Further data on the structure of the sucking tubes is needed to clarify the relationships within Neuroptera.

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