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**Title:** New Aleyrodidae (Hemiptera:Sternorrhyncha: Aleyrodomorpha) from Eocene baltic amber

**Author:** Jowita Drohojowska, Jacek Szwedo

New Aleyrodidae (Hemiptera: Sternorrhyncha: Aleyrodomorpha) from Eocene Baltic amber

JOWITA DROHOJOWSKA1, JACEK SZWEDO2,*

1Department of Zoology, University of Silesia, Bankowa 9, 40-007 Katowice, Poland, e-mail: jowita.drohojowska@us.edu.pl;
2Department of Palaeozoology, Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland, e-mail: szwedo@miiz.waw.pl (*corresponding author)

ABSTRACT. A new genus and species of whitefly from Eocene Baltic amber is described. Paernis gregorius gen. et sp. n. is placed in the subfamily Aleurodicinae. Other findings of Aleyrodidae including ‘Aleyrodes’ aculeatus MENGE, 1856 from Baltic amber are discussed.

KEY WORDS: Paernis gen n., P. gregorius, sp. n., ‘Aleyrodes’ aculeatus MENGE, Aleyrodidae, whiteflies, Baltic amber, new genus, new species, fossil, taxonomy.

INTRODUCTION


The Aleyrodidae are small sap-sucking insects whose adults bear a remarkable superficial resemblance to tiny moths. Indeed, the European cabbage whitefly (Aleyrodes proletella) was initially described as a moth by LINNAEUS (1758), and only subsequently recognized as hemipterous by LATREILLE (1795). The common name, ‘whitefly’, is derived from the presence of secreted powdery wax which is preened over the body and wings by the adults of almost all species. Adult whiteflies measure 1-3 mm in body length; they possess seven-segmented antennae and a fore wing venation that is reduced to a simple or once-branched major vein (R + Rs), with R1 variably developed. A structure unique to aleyrodids is the ‘vasiform orifice’: this comprises the anus, a ‘lingula’ which ejects excreta, and an ‘operculum’, which partially or wholly covers the orifice itself (GILL 1990). Whiteflies are often pests that have become a major agricultural problem. Although a mainly tropical group, noxious species are to be found in all the warmer parts of the world, and several are serious pests in glasshouses in temperate areas. The Aleyrodidae is the least speciose amongst the four Recent groups of the Sternorrhyncha, with 1556 available species names (MARTIN 2007), in comparison with about 2500 psylloids (OUVRARD 2011), over 4500 aphidoids (REMAUDIÈRE & REMAUDIÈRE 1997, BLACKMAN & EASTOP 2006) and about 7500 coccoids (MILLER & BEN DOV 2010). This apparent paucity of species is unlikely to reflect reality: recent tropical field collecting of whiteflies indicates that only a very small proportion of species has been described (MARTIN 2007). The systematics of whiteflies is currently based almost solely on the puparial stage, and adults can be identified only rarely. The structure of the adults is the largest area of ignorance concerning whitefly taxonomy. A taxonomic approach that is focused on puparial stages, with many characters untested for their importance and significance, has not encouraged systematists to become involved with the group. Whitefly systematics suffers from a serious problems in its history, which has undoubtedly diverted the attentions of systematists elsewhere (MARTIN 2003).

Though fossil adult Aleyrodidae are well represented in collections, knowledge about them is scarce. The earliest taxa ascribed to this family are placed in the extinct subfamily Bernaeinae, reported from the Upper Jurassic to the Cretaceous/Palaeogene of Asia (SHCHERBAKOV 2000). The oldest fossil representatives of the Aleyrodinae have been recorded from the Lower Cretaceous (SCHLEE 1970, SHCHERBAKOV 2000, DROHOJOWSKA & SZWEDO 2011). Aleurochiton petri RIETSCHEL, 1983 (puparium) is reported from the Pliocene deposits of Germany (RIETSCHEL 1983). Another fossil species, ‘Aleurodicus’ burmiticus COCKERELL, 1919 from Lower Cretaceous, Aptian Burmese amber (COCKERELL 1919), seems to be a member of Aleurodicinae, as suggested by SHCHERBAKOV (2000), but SCHLEE (1970) placed it in Aleyrodinae. Undescribed Udamoselinae are mentioned from Lebanese amber (SHCHERBAKOV 2000). Aleyrodidae are also mentioned and illustrated from Lower Cretaceous Jordanian amber (KADDUMI 2005, DROHOJOWSKA & SZWEDO 2011), the Upper Cretaceous amber of Ethiopia (SCHMIDT et al. 2010), Lowermost Eocene
Oise amber, Eocene Baltic amber (SHCHERBAKOV 2000), Miocene Dominican and Mexican ambers (POINAR 1992), and the Miocene amber of Peru (ANTOINE et al. 2006). The taxonomic position of ‘Aleyrodes’ aculeatus MENGE, 1856 from Eocene Baltic amber remains unclear (see Discussion).

Acknowledgements
We wish to kindly thank Mr Jonas Damzen from Vilnius, Lithuania, who kindly donated the specimen to the Museum of Amber Inclusions of the Gdańsk University. We also wish to thank Mrs Marzena Zmarzły for the pencil drawings of the specimen.

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This paper is a contribution in celebration of the 75th birthdays of two eminent palaeontomologists, Dr. Yuri A. Popov and Professor Alexandr P. Rasnitsyn, who inspired and encouraged us to work with fossil insects.

MATERIAL AND METHODS

A Nikon MZ1500 stereoscopic microscope and a Nikon Microphot-FX (objective lenses from 4× to 40×) equipped with a camera lucida and changeable direct and transmitted light were used for the microscopic examination. Measurements are approximate because of shrivelling and possible optical deformations. The photographs were taken using the Nikon Microphot-FX with a Nikon Eclipse E 600 digital camera and Lucia® software, and adjusted using Adobe® Photoshop Elements 6.0.

The general lack of descriptions of extant adult whiteflies makes the description of fossil taxa challenging, as no descriptive ‘template’ is available. In selecting the features, we have followed suggestions from available publications, mainly SCHLEE (1970) and MARTIN (2007). The terminology of the thoracic sclerites is according to DROHOJOWSKA & SZWEDO (2011), the venation nomenclature follows the suggestions of SHCHERBAKOV (2000), and the measurements are in accordance with the model proposed by MARTIN (2007).

SYSTEMATICS

Order Hemiptera LINNAEUS, 1758
Suborder Sternorrhyncha AMYOT et SERVILLE, 1843
Infraorder Aleyrodomorpha CHOU, 1963
Family Aleyrodidae WESTWOOD, 1840
Subfamily Aleurodicinae QUAIN TANCE et BAKER, 1913
**Paernis gen. n.**

**Type species**
*Paernis gregorius* sp. n.; by present designation.

**Etymology**
The generic name is derived from the Inari Sámi (native inhabitants of the northern areas of the Scandinavian Peninsula) word ‘pärni’ – meaning ‘boy’. Gender: masculine.

**Diagnosis**
Antennomeres 1-5 separated, remaining segments fused, in the form of a narrow flagellum, longer than half the combined length of the preceding segments (in *Aleurodicus* and *Aleyrodes* antenna distinctly 7-segmented, apical portion not elongated in the form of a process, narrower than preceding segments); 2nd segment not bulbous, about ¾ of 3rd segment length (2nd segment bulbous, about twice as long as wide in *Aleurodicus* and *Aleyrodes*); 3rd segment the longest (as in *Aleurodicus* and *Aleyrodes*); 2nd and 3rd segments of similar thickness; 4th and 5th segments less thick, terminal portion of antenna distinctly narrower.

**Description**
Head with compound eyes narrower than pronotum. In dorsal view vertex in major part covered with bubble of gas. Coronal suture not visible. Anterior margin of vertex arched, posterior margin of vertex anguately concave. Frons smooth, without setae or hairs. Compound eyes subdivided in middle, upper portion seems to be slightly bigger and produced aneriad. Lateral ocellus close to the upper margin of compound eye. Base of antennae placed slightly below and in front of anterior margin of compound eye. Antennae with basal 5 segments separated and apical segments fused, distinctly narrower, without filament terminalis; 3rd, 4th and 5th segments with short setae; rhinaria (primary sensoria) and sensorial cones not visible. Thorax relatively large and convex, elevated above the disc of vertex.

Forewing translucent, 2.1 times as long as wide, with apical portion widened and all margins with tubercles; Stem Sc+R long, straight, parallel to forewing axis, forked apicad at half of forewing length, slightly apicad of claval apex, branch R1 shallowly curved, directed aneriad, not reaching costal margin; branch Rs straight, directed towards posteroapical angle of forewing, not reaching margin.

Hind wing slightly shorter than fore wing, twice as long as wide; stem Sc+R long, forked at 2/3 of hind wing length, forked at an angle of about 50°, not reaching margin.

**Remark**
We decided to compare this new fossil with the genera *Aleyrodes* LATREILLE, 1796: 93; type species: *Phalaena* (Tinea) *proletella* LINNAEUS, 1758: 537, by subsequent designation and monotypy, and *Aleurodicus* DOUGLAS, 1892; type species *Aleurodicus anonae*

MORGAN, 1892: 32, by subsequent designation by QUAIN TANCE 1908: 8. [Synonymized with A. cocois CURTIS (1846: 284-285) by MOUND & HALSEY 1978: 228] for several reasons. Firstly, knowledge of adult Aleyrodidae is still very far from complete and imaginal characters are available for only a few genera. Secondly, the only known fossil from Baltic amber is highly enigmatic, but was originally placed in the genus Aleyrodes (but see discussion below). Thirdly, in our opinion it is more reasonable to draw a comparison with the type genus of the family, when the knowledge and rank of the available characters of the fossil are limited.

Paernis gregorius sp. n.
(Figs 1-20)

Type material

Etymology
The specific epithet is dedicated to the firstborn son of JD – Grzegorz (in Latin Gregorius).

Diagnosis
Claspers about 0.2 of total length of abdomen with genital block; basal portion of claspers with process directed dorsally; apical portions of claspers dorsally, acutely pointed; ventral margin with subapical tooth at about middle of clasper length, two basal setae and four subapical setae. Aedeagus acutely pointed, tapered posteriad, with tip at about 2/3 of clasper length. Operculum wider than long, with apical margin shallowly excavated.

Description
Measurements: for the basic measurements of main body parameters, see Table 1.
Coloration (in amber). Body brown, thorax slightly darker, hind wings uniformly yellowish; legs and abdomen with pygofer and forceps brown.
Head. Head with relatively small compound eyes, with distinct ommatidia. In dorsal view the vertex is broader than long, slightly wider at base than at apex, trapezoid. Median suture not visible (masked under a gas bubble), in dorsal view anterior margin of vertex slightly arched. Lateral ocelli visible. The antenna with five basal segments visible, first segment thick, about twice as long as wide; second antennal segment about as wide as third, but slightly shorter. Third segment the longest, following segments (4th and 5th) of similar
length, thinner than earlier segments (2\textsuperscript{nd} and 3\textsuperscript{rd}). Ventral side of head not visible, concealed under a gas bubble.

Table 1. Basic measurements of the specimen.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length total (including claspers)</td>
<td>1.97</td>
</tr>
<tr>
<td>Head length in mid line</td>
<td>0.17</td>
</tr>
<tr>
<td>Head with compound eyes width</td>
<td>0.37</td>
</tr>
<tr>
<td>Vertex width</td>
<td>0.28</td>
</tr>
<tr>
<td>Forewing length</td>
<td>2.25</td>
</tr>
<tr>
<td>Forewing width</td>
<td>1.08</td>
</tr>
<tr>
<td>Hind wing length</td>
<td>1.72</td>
</tr>
<tr>
<td>Hind wing width</td>
<td>0.79 (left) 0.83 (right)</td>
</tr>
<tr>
<td>Fore femur + trochanter cumulative length</td>
<td>0.40</td>
</tr>
<tr>
<td>Fore tibia length</td>
<td>0.40</td>
</tr>
<tr>
<td>Fore basitarsomere length</td>
<td>0.31 (left) 0.25 (right)</td>
</tr>
<tr>
<td>Fore apical tarsomere length</td>
<td>0.16</td>
</tr>
<tr>
<td>Fore claw length</td>
<td>0.05</td>
</tr>
<tr>
<td>Mid femur + trochanter cumulative length</td>
<td>0.40 (left) 0.37 (right)</td>
</tr>
<tr>
<td>Mid tibia length</td>
<td>0.53 (left)</td>
</tr>
<tr>
<td>Mid basitarsomere length</td>
<td>0.21 (left) 0.20 (right)</td>
</tr>
<tr>
<td>Mid apical tarsomere length</td>
<td>0.13 (left) 0.10 (right)</td>
</tr>
<tr>
<td>Mid claw</td>
<td>0.039 (left) 0.41 (right)</td>
</tr>
<tr>
<td>Hind femur + trochanter cumulative length</td>
<td>0.34 (left) 0.35 (right)</td>
</tr>
<tr>
<td>Hind tibia length</td>
<td>0.77 (left) 0.70 (right)</td>
</tr>
<tr>
<td>Hind basitarsomere length</td>
<td>0.25</td>
</tr>
<tr>
<td>Hind apical tarsomere length</td>
<td>0.13 (left) 0.10 (right)</td>
</tr>
<tr>
<td>Hind claw</td>
<td>0.031(left) 0.056 (right)</td>
</tr>
<tr>
<td>Abdomen length including claspers</td>
<td>0.91</td>
</tr>
<tr>
<td>Claspers length</td>
<td>0.39</td>
</tr>
</tbody>
</table>

Thorax. Thoracic sclerites separated. Pronotum collar-like, narrow, smooth, about as long in mid line as in lateral portions, curved anteriad. Mesopraescutum relatively big, as long as wide, in mid line about three times as long as pronotum in mid line, arched at anterior margin, acutely curved at posterior margin. Mesoscutum narrower in middle, with
distinct concavities at anterior and posterior margins in median portion. Lateral part of mesoscutum huge, protruding anteriad, forming distinctly acute margins. Parapteron oval, convex. Mesoscutellum narrow. Mesopostnotum triangular, as wide as long in mid line, twice as long in mid line as mesoscutellum. Metascutum like mesoscutum with distinct concavities at anterior and posterior margins, narrower in middle. Posterior margin in lateral part arched. Metascutellum is narrower and shorter in mid line than metascutum, slightly curved anterior. Metapostnotum is a very short and thin strip, half as long as metascutellum in mid line.

Legs. Fore- and midlegs of similar length, coxae conical, huge, trochanters distinct, femora shorter than tibiae, tarsi two-segmented. Forelegs with basitarsomere about 1.5-1.9 times as long as apical tarsomere, tarsal claws distinct; Midlegs with tibia 2.6 times as long as basitarsomere and basitarsomere about 2 times as long as apical tarsomere; basitarsomere and apical tarsomere with distinct setae.

Hind leg longer than fore- and midleg, hind femur about as long as mid femur, hind tibia elongate about twice as long as hind femur, with four rows of setae, external rows anterodorsal and anteroventral with setae scarcely evenly spaced, rows posterodorsal and posteroventral close each other, along posterior margin, with setae scarcely but evenly dispersed. A few apical setae present; hind tibia almost 3 times as long as basitarsomere. Hind tarsus long, about half of length of hind tibia; basitarsomere about 2 times as long as apical tarsomere; tarsal claws distinct, paronychium not visible (spine-like, shortened?).

Abdomen in ventral view major portion covered with a gas bubble; in dorsal view sunken, covered with a gas bubble. Wax plates not visible. Pygofer (segment IX) subquadrangular with distinct median eminence in basal portion. Operculum slightly wider than long. Aedeagus relatively long and straight, gradually narrowing towards apex. Long claspers placed laterally, curved medially, basal portion triangularly produced dorsally; internal margin with small teeth, two basal long setae and four subapical setae; in lateral view apical portions of claspers acute, curved dorsally.

Type horizon and age

Baltic amber, Middle Eocene. This fossil resin is aged within the 38-47 Ma range (RITZKOWSKI 1997, PERKOVSKY et al. 2007). Absolute dating analyses of glauconites from the Sambian Peninsula showed that the “blue earth” formation (amber-bearing Prussian Formation) is allocated to the Middle Eocene (Lutetian: 44.1 ± 1.1 Ma) and is thus significantly older than previously assumed (WAPPLER 2003, 2005, WEITSCHAT & WICHARD 2010). Limnic sediments of Eckfeld Maar, aged 44.3 ± 0.4 Ma, correlate with K-Ar radiometric data from the Sambian Peninsula and contain insect genera known only from Baltic amber (WAPPLER 2005). However, assumptions for the Middle Eocene age of Baltic amber was argued by PERKOVSKY et al. (2007), and the Upper Eocene (Bartonian/Priabonian: 37.7 ± 3 Ma) age of the Prussian Formation is preferred by these authors.
Figs 1-3. Paernis gregorius gen. sp. n.: 1 – body, dorsal view, 2 – right antenna, ventral view, 3 – right fore- and mid-legs.
Figs 4-8. *Paernis gregorius* gen. sp. n.: 4 – head and pronotum, dorsal view, 5 – meso- and metathorax, dorsal view, 6 – metathorax and base of abdomen, dorsal view, 7 – abdomen, ventral view, 8 – right hind leg, ventral view.
Figs 9-10. *Paernis gregorius* gen. sp. n.: 9 – right fore and hind wing, dorsal view, 10 – left fore and hind wing, ventral view.
DISCUSSION

*Aleyrodes* aculeatus MENGE, 1856 was the only formally described taxon of Aleyrodidae from Eocene Baltic amber. The original description of MENGE (1856) is very enigmatic: that author compared the fossil with *Aleyrodes chelidonii* LATREILLE, 1807; [the species synonymized under *Aleyrodes proletella* (LINNAEUS, 1758)], stating that the fossil species differed in the sharper abdominal tip and the two small apical processes at the apex (claspers?). The species was never illustrated and the type specimen seems to have been lost, as no data about the site of its preservation is given in the original paper. Fossil
whiteflies were not covered by Martin & Mound (2007) in their world catalogue of Aleyrodidae. Evans (2008) listed this species in the genus Aleurodicus (Aleurodicinae) but gave no data in support of doing so. In our opinion it is not possible to resolve this problem and we propose placing ‘Aleyrodes’ aculeatus Menge, 1856 in Aleyrodidae but without subfamilial ordination and only formal placement in the genus Aleyrodes Latreille, 1796.

Figs 13-17. Paernis gregorius gen. sp. n.: 13 – fore leg, 14 – mid leg, 15 – hind leg, 16 – apical tarsomere of hind tarsus, 17 – apical tarsomere of hind tarsus.
Fig. 18. Paernis gregorius gen. sp. n.: body, dorsal view.
The genus and species described above is placed in the subfamily Aleurodicinae, based on its more developed venation of the fore and hind wings and other morphological features. Traditionally, whitefly taxonomy has been almost exclusively based on characters of the last (fourth) larval stage – termed the ‘puparium’ or ‘pupal case’. It is a sessile form, and the fully mobile adult emerges from this larval stage. In the Aleurodicinae the adults of most species retain a slightly more extensive wing venation. However, we agree with the opinion of Bink-Moennen & Mound (1990), following Schlee (1970), that the larger number of veins is not a plesiomorphic condition in Aleyrodidae, and is thus of little value in defining the phylogenetic group. The more developed venation is definitely a result of body size: there has been an evolutionary trend towards the extremely simplified wing venation seen in over 90 percent of extant whitefly species, and this trend may have been reversed for larger species (Martin 2007). The fore wing with R forked to form R1 and Rs
is present in most members of the Aleurodicinae, and this feature is present in Paernis gen. n., despite its minute size. In most Aleurodicinae the vein M is recognizable (sometimes very weakly), which is not the case with Paernis gen. n. Unfortunately the wax-secreting plates on the abdomen are not available for observation in this fossil. Also, the details of the apical tarsomere cannot be interpreted unequivocally, the paronychium is not visible (it may be shortened or reduced); the tarsal claws are well developed, however. Therefore in our opinion the paronychium is rather spine- or seta-like (i.e. regarded as a diagnostic aleurodicine feature), and not thickened and clothed with spinules (microsetae) on the plantar surface (i.e. regarded as a diagnostic feature of Aleyrodinae). In most cases the paronychium is well developed in Aleyrodinae, while in Aleurodicinae it could be very small, so this would suggest the aleurodicine affinity of Paernis gen. n. The vertex in Paernis gen. n. is about as long in the mid line as it is wide at the base, which is a feature rather of Aleurodicinae (in Aleyrodinae the vertex is usually distinctly wider than long). The compound eyes are usually plainly visible in Aleurodicinae; in Paernis gen. n. they are also visible from above. The structure of the male genitalia, relatively short and without additional structures, appears to represent the model found in Aleyrodinae. The recurved aedeagus, shorter than the claspers, is a feature of Aleyrodicus, but in the majority of aleurodicines the claspers are distinctly elongated. Unfortunately, none of these features constitute a clear apomorphy that could be used to define the subfamilies. In our opinion the genus Paernis gen. n. should be placed in the subfamily Aleurodicinae, albeit with certain reservations.

The newly described genus Paernis gen. n. has a unique antennal structure, with the terminal 6th and 7th segments fused in the form of a filiform process. In the vast majority of whiteflies the antennae are seven-segmented. Occasionally, one or more apical segments may be fused in some specimens, but this is regarded as an exception or as a malformation (Gill 1990). In the genus Paraleyrodes Quaintance, 1909 (Aleurodicinae) the male antenna has four terminal segments fused into one, long, thickened structure. In the males of the genus Aleurocybotus Quaintance et Baker, 1914 (Aleyrodinae), the subterminal and terminal segments are strongly elongated and filiform, resembling slightly but artificially the situation in Paernis gen. n. Unfortunately the state of preservation of the fossil is too poor to compare the placement of the primary sensoria (rhinaria) and sensorial cones with the Recent whiteflies. However, the setose appearance of the antennal segments seems to be related to the presence of sensorial structures. Another feature of the newly described genus is the structure of the tibia, which have no distinct combs composed of hairs. In Paernis gen. n. the mesotibia is covered with ordinary rows of spines, but the brushes of the setae are not visible. The metatibial combs of the posterodorsal and posteroventral rows are composed of evenly dispersed spines, but both rows are placed close to each other, along the margin. Such a distribution of spines differentiates the new
genus from the Recent ones, along with the lack of brushes composed of setae. Among the Recent Aleyrodidae, the combs and brushes are used for wax grooming (GILL 1990).

The finding of Aleurodicinae in Baltic amber is also interesting from the biogeographical point of view. Recent members of this subfamily are (natively) distributed in the tropical and subtropical zones of the Neotropical, Oriental and Australo-Oriental Regions (MARTIN 2008). So far, the only representative of Aleurodicinae has been ‘Aleurodicus’ burmiticus COCKERELL, 1919 from Lower Cretaceous Burmese amber, as suggested by SHCHERBAKOV (2000). The finding of a representative(s) of this subfamily in European Palaeogene deposits could be another argument for the wider distribution of this group in the past and could shed new light on the taxonomic relationships within the subfamily as well as on the biogeographical scenario of Aleurodicinae. The other aspect of finding Paernis gen. n. in the Eocene Baltic amber is its importance for palaeoclimatic interpretations. The presence of this subtropical-tropical group could be related to more equable climatic conditions, the Eocene Thermal Maximum (ETM2) and the subsequent Early Eocene Climatic Optimum (ZACHOS et al. 2008). Whiteflies are considered the tropical equivalent of aphids owing to their ordinal characteristics and their scarcity in temperate climates (BYRNE & BELLOWS 1991). The ‘hothouse’ conditions during the Eocene very probably affected the distributional pattern of whiteflies, like that of many other insects. The time of divergence of the aleyrodine and aleurodicine lineages, calculated on the basis of molecular evidence (CAMPBELL et al. 1994), is estimated at 92 Ma, clearly falling into Middle Cretaceous. It is also close to the estimated time for the effective separation of Africa from South America (PLETSCH et al. 2001, SOMOZA & ZAFFARANA 2008). The present-day distribution of Aleyrodidae lineages shows that Aleurodicinae are distributed mainly in the Neotropical and Australasian regions, while Aleyrodinae have a worldwide distribution (MOUND & HALSEY 1978, MARTIN & MOUND 2007, EVANS 2008). This distributional pattern as well as the availability of fossil data suggests the Palaeotropical origin of the whiteflies (MOUND 1984, BINK-MOENEN & MOUND 1990, MANZARI & QUICKE 2006), which is also supported by fossil data (DROHOJOWSKA & SZWEDO 2011).

New data and new material of Aleyrodidae from fossil resins provide an excellent opportunity for acquiring a better understanding of the morphological disparity of whiteflies, and also for getting to know the evolutionary pattern and process of these insects.

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