Article

Are contemporary whiteflies "living fossils"? Morphology and systematic status of the oldest representatives of the Middle-Late Jurassic Aleyrodomorpha (Sternorrhyncha, Hemiptera) from Daohugou

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Abstract

A new genus *Sinicoselis* **gen. nov.**, with new species *Sinicoselis weberi* **gen.** and **sp. nov.** is described from Middle-Upper Jurassic, Daohugou Bed, Inner Mongolia, China. It is the oldest representative of whiteflies placed in the subfamily Bernaeinae. Its morphological features and taxonomic position with respect to other aleyrodids from the subfamilies Bernaeinae and Udamoselinae are briefly discussed.

Keywords: *Sinicoselis* **gen. nov.**, *Sinicoselis weberi* **gen.** and **sp. nov.**, whiteflies, Bernaeinae, Middle-Late Jurassic, Daohugou, taxonomy

Introduction

The whiteflies Aleyrodidae Westwood, 1840, although rather small in size (usually ca. 2 mm) and taxonomically not very diverse, with about 1,500 species in 161 genera (Martin & Mound, 2007; Ouvrard & Martin, 2019), are among the most economically important pests of plants throughout the world due to their high reproductive potential, resistance to pesticides and ability to vector viruses. These issues are the focus of interest of most specialists studying this group of animals. Much less attention has been devoted to the history and phylogeny of these plant sucking insects. Presently, the whiteflies (Aleyrodomorpha Chou, 1963) are often classified as one of four contemporary infraorders of the suborder Sternorrhyncha Amyot & Audinet-Serville, 1843 (Hemiptera Linnaeus, 1758) along with the Aphidomorpha Becker-Migdisova & Aizenberg, 1962 (aphids), Coccidomorpha Heslop-Harrison, 1952 (scale

insects), and the Psyllodea Flor, 1861 (jumping plant-lice) (Wegierek, 2002; Szwedo, 2018).

The subfamilies of Aleyrodidae currently recognized are the extinct Bernaeinae Shcherbakov, 2000, and the recent ones Aleurodicinae Quaintance & Baker, 1913, Aleyrodinae Westwood, 1840 and Udamoselinae Enderlein, 1909 (Drohojowska & Szwedo 2011a, 2011b, 2013a, 2013b, 2015); the taxonomic status of the last mentioned is disputed (Shcherbakov 2000, Martin 2007). The classification of the contemporary whitefly taxa has been based on features found in the last larval stage, the so-called puparium (Gill, 1990; Evans, 2008). Characteristics of the adult stages for most whitefly species have not been studied in detail and compared in order to understand the relationship between genera, except for the separation of the two main subfamilies, Aleurodicinae and Aleyrodinae. Evidence supporting these two distinct lineages is found in characteristics of both the adults and puparia. Due to their sedentary nature and obligatory association with plants, the immature stages are usually easily accessible and their host plant association certain, however considerable morphological diversification occurs in this developmental stage and determining the phylogenetic relationships between taxa may be problematic (Mound, 1965, 1966; Bink-Moenen, 1983; Martin, 2003). Due to taphonomic reasons, whiteflies known from fossil material are represented in the overwhelming majority of cases by adult alate morphs (Szwedo & Drohojowska, 2016). Therefore, understanding the evolution and phylogeny of this group requires that the morphology of the imago must be studied. For a long time, difficulties of this kind have prevented the study of the evolution of whiteflies although specimens are not rare in fossil material, especially in various resins (Poinar, 1992; Shcherbakov,

2000; Schmidt, *et al.*, 2010). During recent years, a number of studies devoted to this group of insects have been published (Shcherbakov, 2000; Drohojowska & Szwedo, 2011a, 2015; Drohojowska *et al.*, 2015; Szwedo & Drohojowska, 2016). Especially valuable have been the studies focusing on the Mesozoic representatives of the group (Drohojowska & Szwedo, 2011b; Drohojowska & Szwedo, 2013a, b). Schlee (1970) described two species – *Heidea cretacica* Schlee, 1970, *Bernaea neocomica* Schlee, 1970, from Lower Cretaceous Lebanese amber (130 Ma), which made it possible for researchers to become acquainted with the morphology of the oldest whiteflies. Another step towards expanding the knowledge about evolutionary history of whiteflies on the basis of actual fossil material was the study by Shcherbakov (2000). Taxa described in that study originated from the late Jurassic period, i.e. 158–152 Ma, from Karatau (Kazakhstan) and Late Jurassic–Lower Cretaceous locations Hutel-Hara and Hotont in Mongolia.

In the present study, numerous impressions of whiteflies collected from Daohugou beds at Inner Mongolia, China (late Middle–early Late Jurassic, approximately 165−161 Ma; Huang, 2019) were examined and considerably extended our knowledge regarding the history of the group, providing an opportunity to become acquainted with morphological features of the oldest representatives of the Aleyrodomorpha.

Material and methods

A total 30 specimens of new species were examined and 8 well-preserved specimens (NIGP170200–170207) are illustrated here. All these fossils were collected from various layers of the middle-upper Daohugou Bed, near the Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, northeastern China (for a detailed locality map, see Huang, 2015: Fig. 1). The specimens were exquisitely preserved as a brownish organic film in the gray-whitish tuffaceous shale. Whiteflies are supposedly relatively large but most of them from the Daohugou were ignored by previous collectors due to their small size and always crinkled wings.

Photographs were taken using a digital camera attached to a Zeiss Discovery V20 microscope, and some were moistened with 70% ethanol for seeing fine details (Figs 1C, E, 2A, C, E; 3E, G). The material studied here including all type specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

The general morphological terminology follows Weber (1935); the thoracic sclerites terminology is according to Drohojowska & Szwedo (2011a); the venation nomenclature follows the suggestions of Shcherbakov (2000) modified by Drohojowska & Szwedo (2013a).

Systematic palaeontology

Order Hemiptera Linnaeus, 1758
Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843
Infraorder Aleyrodomorpha Chou, 1963
Family Aleyrodidae Westwood, 1840
Subfamily Bernaeinae Shcherbakov, 2000

Genus *Sinicoselis* gen. nov.

Type species. *Sinicoselis weberi* **gen.** and **sp. nov.**; here designated.

Etymology. The genus name refers to China (Latin *sinicus* = Chinese), where it was found; and the recent whitefly genus *Udamoselis* Enderlein, 1909.

Diagnosis. Imago. Compound eyes undivided, antennae 9- or 10-segmented. Rostrum reaches beyond the posterior coxae. Differs from *Juleyrodes* Shcherbakov, 2000 by the median ocellus present, the fold in front of vein Sc+R present, a single A_1 vein present that arches towards the posterior margin of the wing. Lack of vein M (in *Juleyrodes* vein M is well developed). Abdomen with two gland plates (lack of gland plates in *Juleyrodes*). Claspers and the ovipositor are parallel to the axis of the body and the ovipositor is wide, with a blunt tip.

Sinicoselis weberi **gen.** and **sp. nov.**

Diagnosis. As for genus.

Description. Body short (2.01−3.2 mm, females larger than males, female body length 2.8−3.2 mm, males body length 2.01−2.7 mm), thorax clearly wider than the slim abdomen. The wings reach far beyond the abdomen. The head, in the lateral view, has an ellipsoidal shape and from the dorsal side it is slightly narrower than the pronotum (Fig. 1). Epicranium has the shape of a uniform, trapezoidal plate. Sutures separating particular elements of the head capsule are not visible. At the sides of the epicranium there are large compound eyes, composed of homogeneous ommatidia. The compound eyes extend to the ventral part of the head (Fig. 2A−D). Antennal scapus situated on ventrally on the head, next to the internal margins of compound eyes, at the level of 2/3 of the length of the eyes. Median ocellus present, located between the antennal scapi, in front of the fore margin of the compound eyes (Fig. 2A−D). The antennae are thread-like, with 9 or 10 segments (Fig. 2E, F). The third segment is the longest;
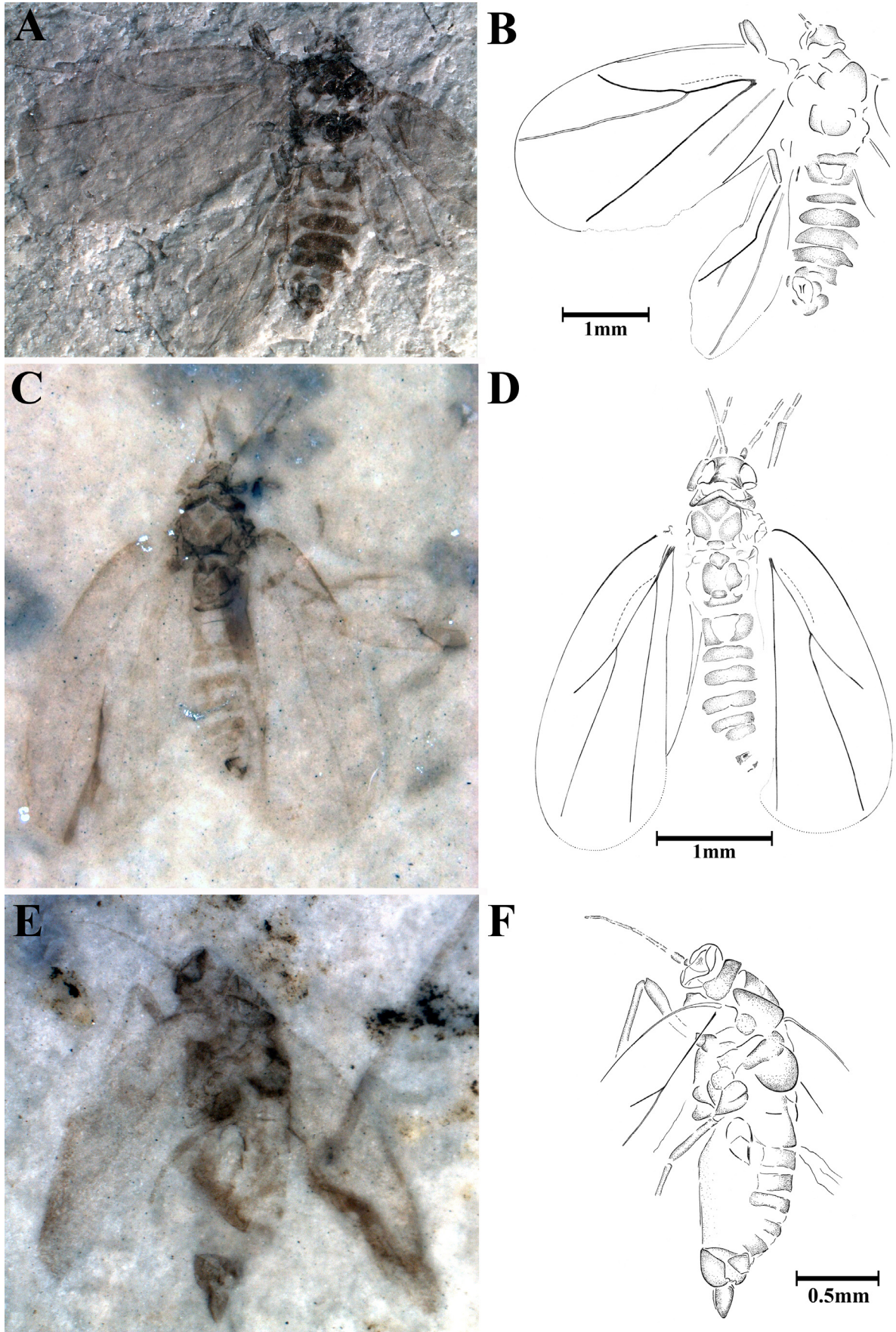
DROHOJOWSKA *ET AL.*

FIGURE 1. *Sinicoselis weberi* **gen.** and **sp. nov.** from the Daohugou Bed, general habitus. **A**, Holotype (NIGP170200), a female. **B**, Line drawing of **A**. **C**, A complete specimen (NIGP170201) in dorsal view. **D**, Line drawing of **C**. **E**, A lateral view specimen (NIGP170202), male. **F**, Line drawing of **E**.
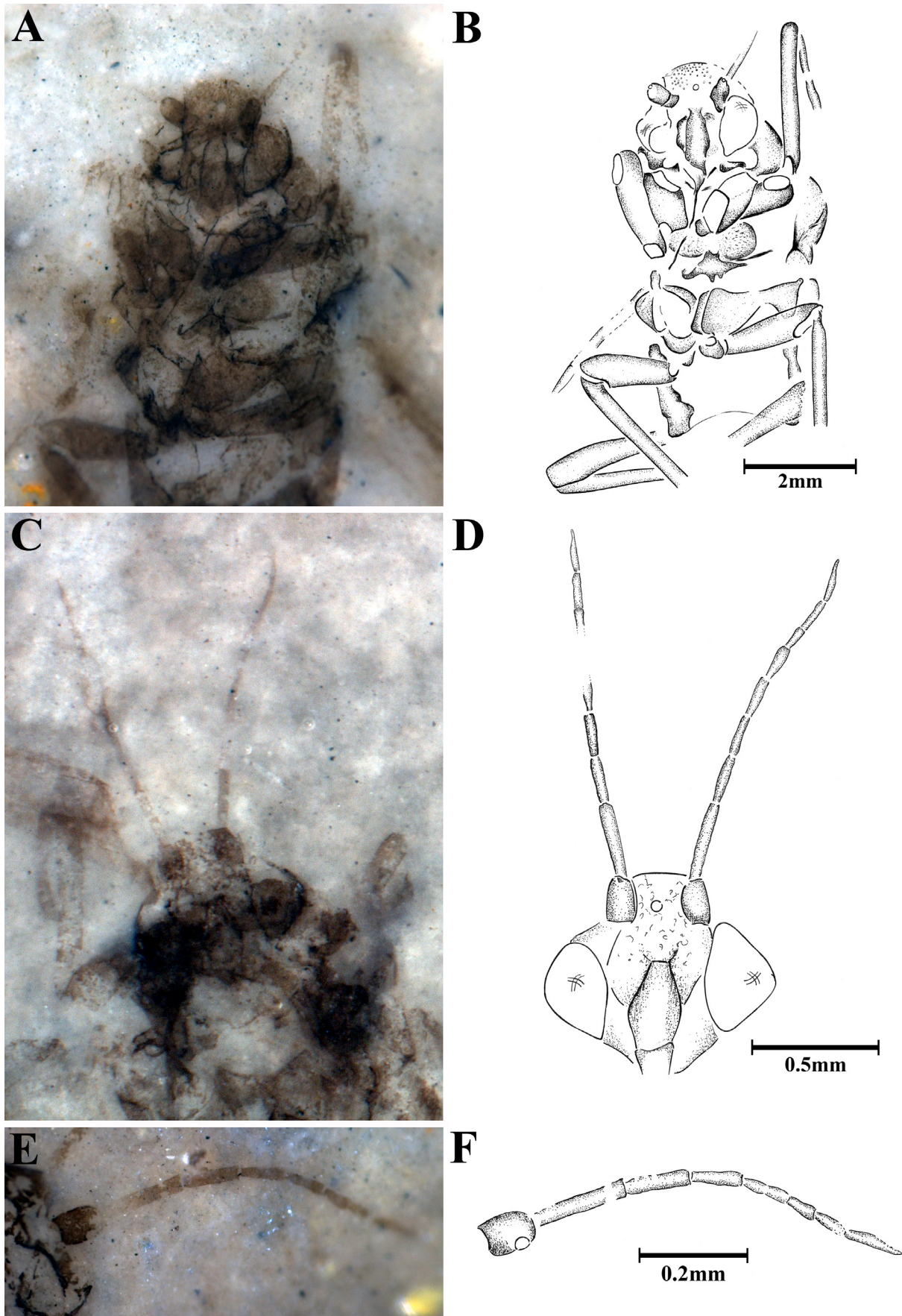
FIGURE 2. *Sinicoselis weberi* **gen.** and **sp. nov.** from the Daohugou Bed, morphological details. **A**, Ventral view of the specimen (NIGP170203). **B**, Line drawing of **A**. **C**, A specimen (NIGP170204) in ventral view showing the head. **D**, Line drawing of **C**. **E**, A specimen (NIGP170205) showing the antenna. **F**, Line drawing of **E**, antenna.
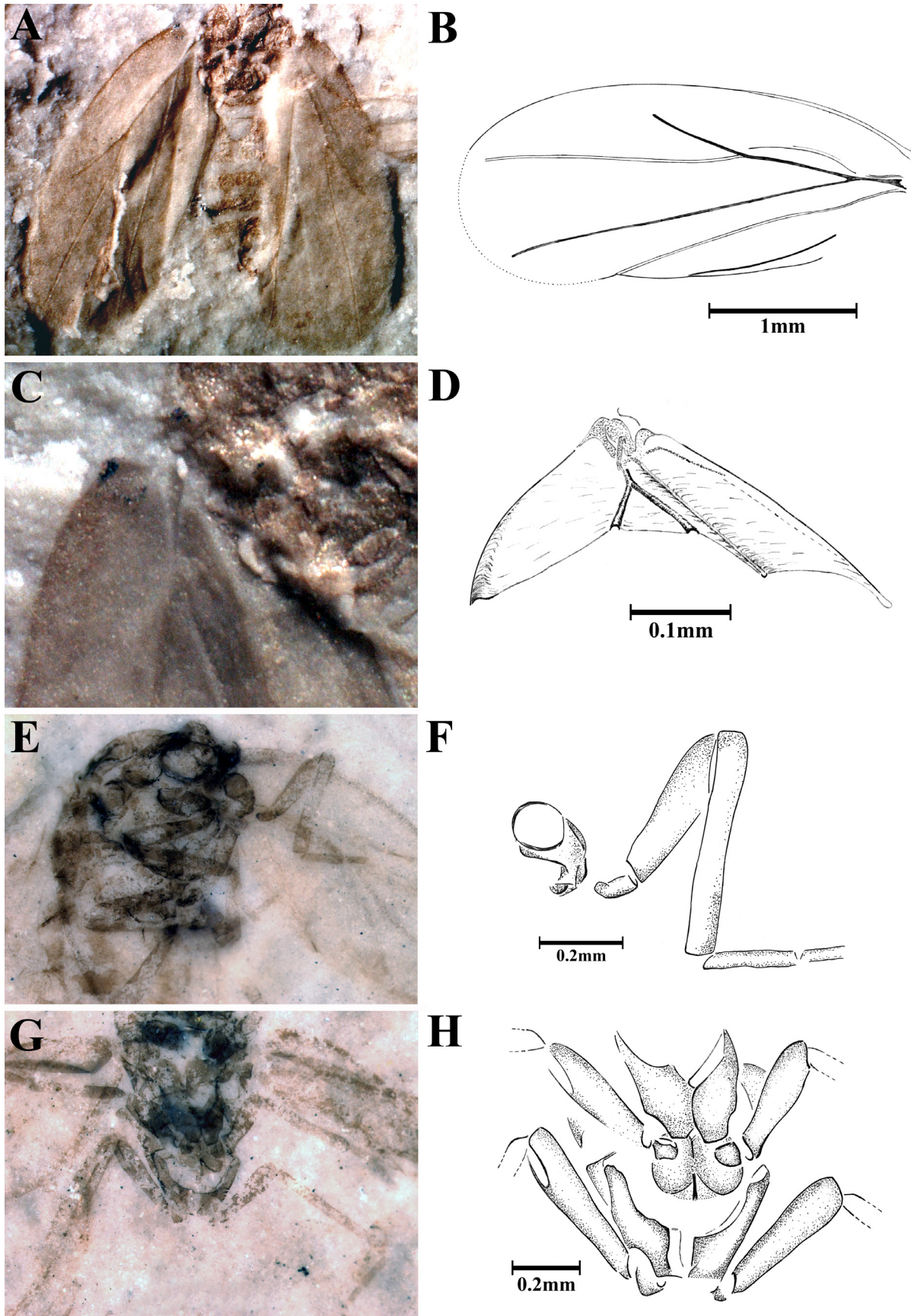
FIGURE 3. *Sinicoselis weberi* **gen.** and **sp. nov.** from the Daohugou Bed, morphological details. **A**, NIGP170201 showing a pair of complete forewings. **B**, Line drawing of **A**, showing the forewing. **C**, Enlargement of **A**, showing the base of forewing. **D**, Line drawing of base of forewing. **E**, NIGP170206, showing the fore leg. **F**, Line drawing of **E**, fore leg. **G**, NIGP170207, showing the middle and hind legs. **H**, Line drawing of **G**.

the remaining segments of the flagellum are similar in length, each one only half as long as the third segment. The last antennal segment gradually narrows starting at the midpoint along its length and its apical part forms a "sharp" pointed tip. The pedicellus contains a Johnston's organ (Fig. 2E, F). The clypeus is distinct, lenticular in shape and is twice as long as wide. Its front margin is at the level of half of the length of compound eyes. The labrum is short and only slightly distinct (Fig. 2A, B). The labium is long and reaches beyond the posterior coxae (Fig. 2A, B). The last segment of the rostrum is short.

The pronotum has the shape of a band encompassing the prothorax from the dorsal side and reaches far over the sides of the body. Viewed from the dorsal side, the pronotum has the shape of a narrow slat bent forwards; the length of the pronotum is half or less of the length of the head. The lateral parts of the pronotum are less sclerotized and slightly wider. The tergal region of the mesothorax (Fig. 1A−D) is well developed. Three typical subunits can be differentiated in the mesonotum: mesopraescutum, mesoscutum and mesoscutellum. The mesopraescutum is diamond-shaped. The mesoscutum is the largest part of the mesonotum. A straight edge separates the mesoscutum from the mesoscutellum, which is a small sclerite. At the sides of the body, below the mesoscutum there are round parapteron and tegula; they are elements of the joint connecting the forewings with the thorax. The sternites of the mesothorax (Figs. 2A, B, 3G, H) are small, consisting of plates of a complex shape. The lateral arms of that sternite are triangular and their central parts are rectangular-shaped; notches are clearly visible in the shorter sides of the rectangle. The size of the metathorax, and especially its height, is similar to that of the mesothorax (Fig. 1E, F). The metascutum is only slightly smaller than the mesoscutum. The anterior margin of the metascutum is indented. The lateral parts of the metascutum are domed and slightly protrude forward over the mesopostnotum. The metascutellum is similar to the mesoscutellum (Fig. 1C, D). The metapostnotum tightly adheres to the metascutellum. The metapostnotum has the shape of a slightly bent horseshoe with arms spreading laterally and gradually narrowing. The metasternite has the shape of an oval plate; a metasternal suture runs across its center (Fig. 3G, H).

Forelegs with coxae cylindrical, large and robust, situated on the sides of the body (Fig. 3E, F). Their width is comparable to the width of the femora and their length reaches up to half of the length of the femur. The tibiae are short, only slightly longer than the femora. The tarsi are long and two-segmented with the first segment of the tarsus longer than the second one. The coxae of the middle legs are large, wider than the femora and are situated close to each other, in the middle of the prothorax. The lengths of these two leg segments are comparable. The trochanter

is small. The tibiae are 1.5 times longer than the femora. The tarsi are two-segmented and the first segment is longer than the second (Fig. 3G, H). The coxae of the hind legs also adhere closely and their sizes are similar to the coxae of the middle legs, although they are slimmer. At the base they are funnel-shaped, widely open in the direction of the segment. The trochanter is small and the hind femora are longer than the middle ones. The tibiae are long, almost twice as long as the femora. The tarsi are two-segmented and the first segment is clearly longer than the second.

The wings are longer than the body (Figs 1A−E, 3A). Their lengths range from 2.2 mm to 3.3 mm, widths range from 1.3 mm to 1.8 mm. Comparatively narrow at the base, the wing becomes wider distally, reaching its maximum width halfway its length, then narrows slightly (Fig. 3A, B). The apical part is wide and oval. The costal margin is slightly bent and thickened at the basal part. From the base of the wing, the Sc runs diagonally towards the R+CuA common stem. At the place where Sc+R and CuA forks towards the branch of R_1 and R_S, there runs a suture arched towards the anterior margin of the wing. Between that suture and the Sc+R vein the surface of the wing displays a characteristic fold (Fig. 3A−D). R_1 and Rs branch off the Sc+R vein at the height of 1/3 of the wing length. The length of R_1 vein is comparable to the length of Sc+R vein; assuming an arched shape, R_1 is arched, bending towards the anterior margin of the wing, reaching it beyond half of the wing length. Rs is twice as long as Sc+R. It assumes the shape of a strongly stretched letter "S". CuA branches off the common Sc+R+CuA stem, nearly the whole length of the vein is straight, curving slightly only in the apical part. It reaches the wing margin definitely below the apex. CuP vein runs from the base of the wing similarly to Sc+R+CuA. CuP is straight and separates the claval part of the wing, reaching the posterior margin of the wing at the height of 2/3 of its length. The clavus has the shape of an elongate triangle and is five times shorter in height than its longest side. The A_1 vein is very long, arched at the base, it reaches the posterior margin of the clavus at 3/4 of its length.

The lengths of the hind wings resemble those of the forewings, but the hind wings are slimmer and narrower (Fig. 1A, B). Two veins run from the narrow base. In the apical part of the wing, Sc+R vein forks into R_1 and Rs veins. The lengths of the two are comparable. CuA runs very close to Sc+R vein until the middle part of the wing and then arches towards the posterior margin of the wing.

In lateral view, the abdomen is egg-shaped; it is widest at 1/3 of its length from the base and then its height gradually decreases towards the base of the genitalia. From the dorsal side it is elongate, finger-shaped. The sides of the abdomen are nearly parallel to each other;
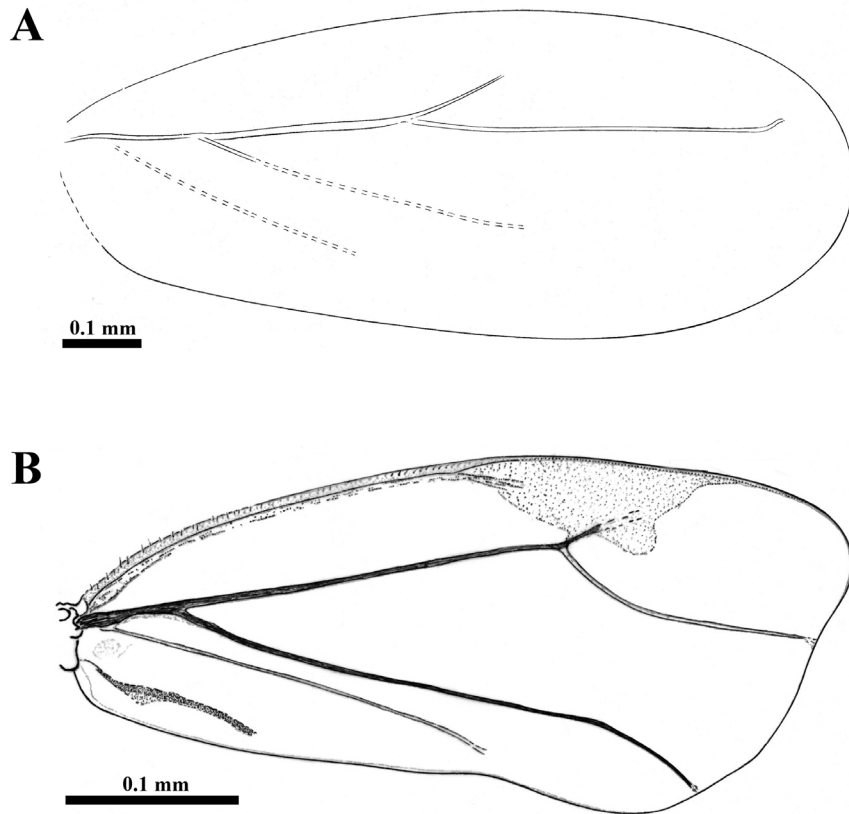
FIGURE 4. Forewing of other fossil whiteflies. **A**, Forewing of *Bernaea neocomica* Schlee, 1970. **B**, Forewing of *Udamoselis estrellamarinae* Martin, 2000.

only in the apical part there can be observed a definite narrowing. On the dorsal side of first and second visible abdominal segments, there are truncheon-shaped plates located symmetrically on both sides; they constitute elements of tergites and are joined by their wider tips at the border of the segments (Fig. 1A−D). On the second segment, apart from the slat, there is a U-shaped sclerite. The remaining tergites form transverse, rectangular plates reaching over the sides of the abdomen. Sometimes, due to individual variability, the central part of the tergite is less sclerotized. In the second abdominal sternite the central part is reduced and only the lateral parts of the sternite have been preserved. They are stretched into finger-like structures that run along the sides of the abdomen and reach up to the base of the coxae (Fig. 3G, H). On the side of the abdomen, on the third and fourth segments, at mid-height of the abdomen there are two sclerotized slats. The front one is arched towards the ventral margin of the abdomen and the other one is straight. Most probably they constitute a frame for slightly distinct gland plates located on the third and fourth segments. At the posterior apex of the abdomen, on the ventral side there is a plate on which the anal tube is situated (Fig. 1A, B).

At the end of the abdomen of the male (Fig. 1E, F) there is a capsule surrounding the apical segments that is formed from the posterior tergites and well developed sternites. Claspers (elements of the male copulatory organ) are situated parallel to the axis of the body. They are triangular in shape, widest at the base, twice as long as wide with rounded apices. Similar to the male, the last segments of the female abdomen are sclerotized. The ovipositor is triangular, situated parallel to the axis of the body and only slightly protrudes beyond the abdomen. The ovipositor valves are sharply pointed.

Etymology. This species name honors Hermann Weber, a German zoologist whose works devoted to the morphology and anatomy of jumping plant-lice, aphids and whiteflies are unparalleled.

Material. Holotype female NIGP170200, preserved in tuffaceous shale of Daohugou Bed. Eight paratypes illustrated here, numbers NIGP170201−170208, and total of 30 specimens examined.

Type locality, formation and age. The localities near the Daohugou Village, Wuhua Township, Ningcheng County, Inner Mongolia, China; Middle-Upper Jurassic Haifanggou Formation (these fossil layers would be the earliest Late Jurassic).
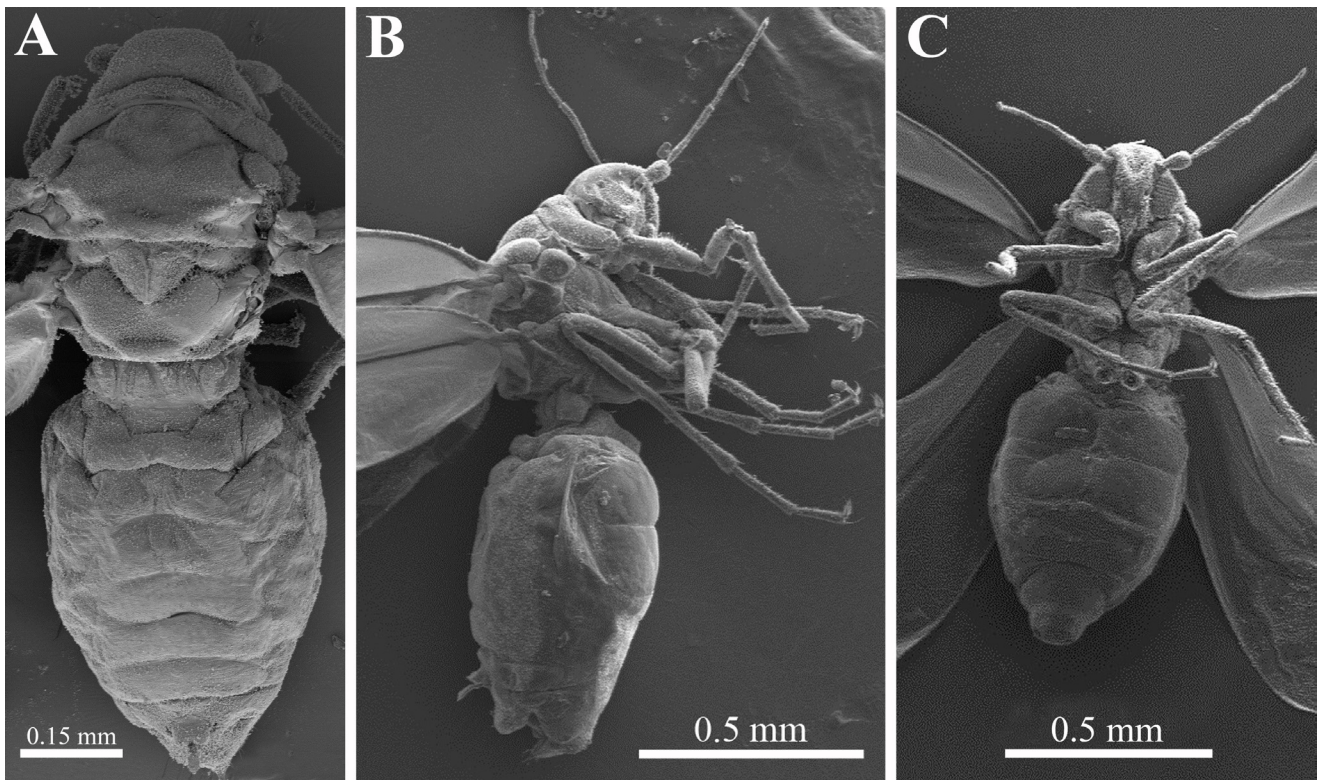
FIGURE 5. SEM photos of *Aleyrodes proletella* Linnaeus, 1758. **A**, Dorsal view. **B**, Lateral view. **C**, Ventral view.

Discussion

Sinicoselis weberi **gen.** and **sp. nov.** from the Middle-Upper Daohugou beds (fossiliferous layers would be 163.5−161.0 Ma) of Haifanggou Formation (168–161 Ma), Inner Mongolia, China is the oldest known representative of whiteflies. However, the venation of the forewings in *Juleyrodes* Shcherbakov, 2000 and *Burmoselis* Shcherbakov, 2000, where the M vein has been preserved, indicates that their forms are more basal phylogenetically and perhaps they should form a separate taxon.

In the newly described species, the venation of the forewings is close to that found in the *Bernaea* Schlee, 1970, a typical genus of the Mesozoic family Bernaeinae (Fig. 4A). Interestingly, a similar wing pattern can be seen in the contemporary genus *Udamoselis* (Fig. 4B). Contrary to the *Bernaea*, the hind wing venation in representatives of *Udamoselis* is similar to that found in *Sinicoselis weberi* **gen.** and **sp. nov.** (Fig. 1A, B). Thus, it can be assumed that the discussed model of wing venation was already established at the Jurassic evolutionary stage and has been preserved both in the Mesozoic and the contemporary whiteflies (only the vestigial Sc vein is reduced and the fold in front of Sc+R). The fold is a unique structure, observed only in *Sinicoselis weberi* **gen.** and **sp. nov.** Therefore, the described venation

model is not an adaptation to gigantism (body length of 6.3–10.5 mm) as was believed by Martin (2007) who analyzed the morphology of the representatives of the genus *Udamoselis* and other forms similar to it. Despite similarities in wing pattern, the remaining morphological characters in *Sinicoselis* **gen. nov.**, such as the presence of the median ocellus, undivided compound eyes, clearly distinct clypeus, and the form of the abdomen (Figs. 1, 2A–D) do not allow for uniting the subfamilies Bernaeinae and Udamoselinae Enderlein, 1909 into one taxon.

The state of preservation of the Jurassic whitefly representatives described by Shcherbakov (2000) did not allow for analyses in this study of the morphological evolution of the insects in question. However, the description of *Sinicoselis weberi* **gen.** and **sp. nov.** enables us to draw a number of conclusions about early evolutionary stages of the group.

Already at the Jurassic stage of their evolution, whiteflies underwent miniaturization and the lengths of their bodies did not exceed 3.2 mm. Since the Jurassic period the majority of whiteflies have had a similar range of variability with respect to body lengths. More than two times larger body sizes achieved by some representatives of the contemporary groups (Udamoselinae) should be treated as a secondary environmental adaptation (Martin, 2007).

No major changes have taken place since the Jurassic

period regarding the head design in whiteflies. Although most contemporary species have not retained the median ocellus, a characteristic indentation is still visible where it used to be situated (Wegierek, 2002). Furthermore, in several Jurassic and contemporary taxa the median ocellus is still present (Gill, 1990; Shcherbakov, 2000; Drohojowska & Szwedo, 2015). In Jurassic and Cretaceous representatives of whiteflies, the division of compound eyes into a ventral and dorsal part has not been described as yet, in spite of the fact that the compound eyes reach to the ventral side (Schlee, 1970; Shcherbakov, 2000; Drohojowska & Szwedo, 2011b, 2013b, 2015). Such a division of compound eyes can often be encountered in contemporary groups, but even in the present time the process of eye diversification is varied and some species have uniform eyes (Shcherbakov, 2000).

It should be noted that even at the early evolutionary stages, the antennae already assumed their characteristic thread-like shape and the number of segments (9−10) was similar to that encountered in Cretaceous specimens from Lebanese amber representing the genera *Baetylus* (Drohojowska & Szwedo 2011), *Gapenus* (Drohojowska & Szwedo 2013b), *Shapashe* and *Milqartis* (Drohojowska & Szwedo, 2015), which have 10−segmented antennae or *Yamis* and *Aretsaya* (Drohojowska & Szwedo, 2015) which have 11−segmented antennae. In the Paleogene amber from Oise all described species belonging to five genera have 8-segmented antennae (Drohojowska & Szwedo, 2013a). Recent species have fewer segments in the antennae, most frequently 7 (Gill, 1990), as *Paernis gregorius* (Drohojowska & Szwedo, 2011) and *Snotra christelae* (Szwedo & Drohojowska, 2016) described from the Baltic amber, or 6, as the species belonging to the genera *Heidea, Bernaea* and *Rovnodicus* (Schlee, 1970, Drohojowska *et al.*, 2015). The proportions in the design of the prothorax in *Sinicoselis weberi* **gen.** and **sp. nov.** do not show that this segment of the body is much smaller than the remaining components of the thorax (Fig. 1), as can be observed in the imagines of modern forms (e.g., *Aleyrodes proletella* Linnaeus, 1758; Fig. 5A, B). Nevertheless, the exoskeleton displays a tendency for the merging of the sclerites of the prothorax and their reduction (Fig. 5A, B). In *Sinicoselis,* we see the merging of the notum with the pleura, which leads to a reduction of the lateral surfaces. This feature distinguishes the Aleyrodomorpha from other groups that used to be included earlier into the 'Homoptera' (Weber, 1935). According to Weber (1935), a characteristic design of the prothorax in whiteflies, i.e. the formulation of marginal cushions is connected with the metamorphosis specific to this group and facilitates the process of moulting.

Contrary to other groups of the Sternorrhyncha, in contemporary whiteflies the fore- and hindwings are not joined during flight. As a result, they have a well-developed metathorax, as there are situated the muscles that move the wings and the muscles connected with saltatorial legs (Weber, 1935). In all possibility, Jurassic whiteflies also moved both pairs of wings independently. The proportions between the tergal regions of the mesothorax and metathorax (Fig. 5A) indicate that the musculature of the hindwings was comparable with the musculature of the forewings. It is difficult to establish whether *Sinicoselis weberi* **gen.** and **sp. nov.** was able to jump. The lengths of the posterior and middle coxae are similar. However, their design is identical to the design of posterior coxae of contemporary whiteflies (cf., Fig. 5B, C), characterized by the funnel-shaped form widely open towards the segment bore, enabling the connection between the coxae and the muscles of the thorax responsible for jumping (Weber, 1935). Therefore, in the case of whiteflies, these are not the exceptionally large coxae and associated musculature that determine the ability for jumping, as it is in the Psylloidea, but the manner in which the posterior coxae are joined with the thorax, and their shape.

The basal part of the abdomen of contemporary whiteflies has a specific design, a characteristic solely for this group of insects and has been analyzed in detail by Weber (1935). The first abdominal segment forms a petiole and is narrower and much lower than the remaining segments (Fig. 5A, B). Ventrally, on the sides of the petiole there are sclerotized rods that form the elements of the notum of that segment. The second abdominal segment constitutes a passage between the narrow petiole and the wider part of the abdomen. A pair of strong, elongated slats, or bars, is visible in the tergal region from the dorsal side, on the lateral margins of the segment. Away from those slats, situated closer to the center, there are vaguely visible halves of a divided tergite. On the basis of the analyzed fossil material, it cannot be concluded whether or not the first abdominal segment is narrowed in the Jurassic whiteflies. Atrophy of typical tergites on the first two abdominal segments and preservation of just the lateral slats and the U-shaped tergite elements on the second abdominal segment indicate that the process of transformation of the first segment into the petiole had at least begun in Jurassic whiteflies. An additional point confirming the changes leading to the formation of the petiole is the design of the sternites of the second abdominal segment in *Sinicoselis*; the lateral arms of the sternite are stretched out finger-like and directed toward the upper margin of the abdomen (Fig. 2B, H). In Early Cretaceous Bernaeinae (*Bernaea*) we can start to see the connection between the abdomen and the thorax that is typical for whiteflies (Schlee, 1970).

One of the characteristic features of the abdominal design of contemporary whitefly imagines is the presence of wax-secreting areas. Shcherbakov (2000) assumed

that the wax-secreting areas on the abdomen (although initially they might not be clearly separated) together with the complex process of waxing had already been acquired by the first (Jurassic) Aleyrodidae. This assumption is corroborated by features seen in *Sinicoselis* (Fig. 1E, F). Further evolution led to increasing the number of wax-secreting areas to up to four pairs in male Aleyrodinae and female Aleurodicinae. The anal tube is homologized with 8−10 merged tergites (according to Weber, 1935). However, in the *Bernaea*, at least the 8th tergite is still free (Shcherbakov, 2000). An analysis of the structure of the abdomen of *Sinicoselis* (Fig. 1A, B, E, F) indicates that the process of tergite merging had already been completed. Both the ovipositor and the parameres were situated horizontally in the Jurassic whiteflies, similar to many contemporary taxa. However, in the representatives of the Bernaeinae from the Lower Cretaceous, the claspers might be situated vertically with respect to the axis of the body and the ovipositor was capable of moving upwards (Shcherbakov, 2000).

On the basis of the morphological and comparative analysis above, it can be concluded that major stages of morphological evolution of whiteflies were completed towards the end of the Jurassic period, prior to 150 million years at the latest. The applied strategy led to the development of a small body characterized by a uniform morphological structure. The homogeneous character of the developed model is most convincingly confirmed by the fact that only one family is differentiated among whiteflies, namely that of Aleyrodidae. The progress of further processes of morphological evolution had a mosaic character and referred mainly to the modification of particular structures (e.g., lack of the fold before Sc+R, division of compound eyes, atrophy of the median ocellus, increased number of abdominal glands) or atrophy of appendages (reduced number of antennal segments, reduced venation). Some features of whitefly morphology indicate that one of their developmental stages was that of the puparium, characteristic only for whiteflies.

Thus, it can be assumed that while the environment was changing and new groups of host plants appeared, i.e., angiosperms in the Cretaceous (Krassilov, 2003), whiteflies have been undergoing biological evolution for 150 million years, at the same time retaining their basic morphological characters. As the final result of this process, almost all whiteflies host-shifted to angiosperms (Mound & Halsey, 1978). Only one family among gymnosperms, i.e., the Zamiaceae (Cycadophyta), has been colonized, or most probably recolonized, by the extensively polyphagous *Trialeurodes vaporariorum* (Westwood, 1856). Whiteflies have been reported from ten families of host plants belonging to the Pteridophyta (Mound *et al.*, 1994; Martin *et al.*, 2000). All of these are species in the

subfamily Aleyrodinae, considered to be the youngest of the three extant subfamilies, which also confirms that this group of host plants has been recolonized (Dubey & Ko, 2006).

Whiteflies, similar to scale insects and contrary to aphids, in the course of their history have not changed their predilection for warmer climates (Heie, 1994, 1996). In fossil material, they have been encountered in the largest numbers in such locations where warm climate has been reconstructed (Mound, 1984; Bink-Moenen & Mound, 1990; Manzari & Quicke, 2006). Furthermore, contemporary taxa of whiteflies are also associated with warm climatic zones (Mound & Halsey, 1978; Gill, 1990; Martin & Mound, 2007; Evans, 2008).

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