

***Talaya batraba* gen. et sp. nov. – the First Nymph of a Protopsyllidiid (Hemiptera: Sternorrhyncha: Psyllomorpha) from the Lower Cretaceous Amber of Lebanon**

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Abstract: A hemipteran nymph of the sternorrhynchan lineage, placed in the family Protopsyllidiidae is the first found in the fossil record, based on an inclusion in amber from the Lower Cretaceous of Hammana / Mdeyrij, Abeih Formation, Central Lebanon. Based on distinctive features such as a median dorsal elevation and the presence of a large, conical, exposed, setiferous anal tube, the fossil is placed in *Talaya batraba* gen. et sp. nov. and the newly erected taxon is compared to known nymphs of extinct Protopsyllidiidae. The evolutionary traits of the family and its relatives are considered.

Key words: Psyllomorpha, Hemiptera, taxonomy, evolution, Lebanese amber, Lower Cretaceous

1 Introduction

The Sternorrhyncha Amyot et Serville, 1843 (jumping plant-lice, whiteflies, aphids, and scale insects) is one of the suborders of the order Hemiptera Linnaeus, 1758. The other five hemipteran suborders comprised being Paleorrhyncha Carpenter, 1931, Fulgoromorpha Evans, 1946, Cicadomorpha Evans, 1946, Coleorrhyncha Myers et China, 1929, and Heteroptera Latreille, 1810. The Sternorrhyncha comprises some 16,000 described species, divided into four major recent groups, and a few extinct ones, all entirely phytophagous and the suborder is usually thought to be monophyletic (Schlee, 1969c; von Dohlen and Moran, 1995; Gullan and Martin, 2003; Grimaldi and Engel, 2005; Cryan and Urban, 2012). However, according to opinions based on paleontological interpretation presented by Shcherbakov (1990, 2000a, 2005, 2007) and Shcherbakov and Popov (2002), the group is instead considered paraphyletic (diphyletic). The first lineage consists of Aphidina sensu Shcherbakov, 1990 — Pincombeomorpha Shcherbakov, 1990 and their descendants Coccinea Fallén, 1814 and Aphidomorpha Becker-Migdisova et Aizenberg, 1962 (united as Aphidiformes sensu Schlee, 1969b, or Aphidomorpha sensu Hennig, 1981), which was independently (and

earlier) separated from the stem of Archescytinoidea Tillyard, 1926 (suborder Palaeorrhyncha Carpenter, 1931). The second lineage—Psylliformes sensu Schlee 1969a (= Psyllinea sensu Shcherbakov, 2000a; = Psyllina sensu Shcherbakov and Popov, 2002; i.e. [Psyllomorpha Becker-Migdisova, 1962 + Aleyrodomorpha Heslop-Harrison, 1952])—derived directly from Archescytinoidea. The most recent interpretation of sternorrhynchan relationships was presented by Grimaldi (2003) and Ouvrard et al. (2010), in which the Protopsyllidiidae is the sister group of remaining sternorrhynchans, and the Psylloidea (extinct and extant) forms a separate lineage, being sister-group to aleyrodids, aphids and coccoids (Thao et al., 2004; Cryan and Urban, 2012). Forero (2008) in discussing the classification of the Hemiptera stated that the system for the Sternorrhyncha seems still not to be finally resolved.

2 Geological Setting

Lebanese amber with its unique taphonomical process is a valuable source of information on Early Cretaceous insects, especially those of small size. The presence of amber in Lebanon has been documented since the beginning of the 19th century; for a cursory review, see references in Azar et al., 2010. Concerning descriptions of trapped insects, the oldest publications are those of Willi Hennig (Hennig, 1970) and Dieter Schlee (Schlee, 1970;

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Schlee and Dietrich, 1970). Up to the present day, more than 300 amber deposits, ranging from Late Jurassic to the mid-Cretaceous (Cenomanian) have been found, of which 22 have yielded fossiliferous amber (Azar, 2012). The Lebanese amber outcrops are Early Cretaceous in age, estimated to be 125–135 million years old. Most of them are Neocomian (Berriasian through Valanginian to Hauterivian) or early Aptian in age (Azar et al., 2010).

The amber from Lebanon is associated with lignite and plant debris in layers of dark clay or shale, sometimes in a purely fluvial deposition system, i.e., channels or riverbanks. The deposition had sometimes been subjected to marine influences, as in a deltaic zone or in the littoral, intertidal area (Azar, 2007; Azar et al., 2010; Azar, 2012). Poinar and Milki (2001) described *Agathis leventensis*, thought to be the Lebanese amber-producing tree, based on fossils from Wadi Zerqua in Jordan (but never reported from the numerous localities in Lebanon) and on the comparative analysis of IR spectra of Lower Cretaceous ambers. This assertion was challenged by studies of fossilized wood, with gymnosperm trees of the families Araucariaceae – *Araucaroxylon* sp., or Cheirolepidiaceae – *Protocarpoxylon* sp., or a plant with cycad affinities, or even a new, postulated fossil family (Koteja and Azar, 2008; Azar et al., 2010).

Based on palynological studies and interpretations of the fossil amber inclusions, a paleoclimatic reconstruction of the Lebanese amber forest has been proposed. The amber-producing tree was definitively a gymnosperm, and the amber appears to have been produced in a tropical or subtropical, moderate to hot and very wet, dense forests in the North–East of Gondwanaland (Azar et al., 2010; Azar, 2012).

3 Material and Methods

Lebanese amber is brittle and soft, and resembles Alaskan, Canadian and some pieces of New Jersey ambers in general appearance and handling. The piece of amber containing the fossil described here as an inclusion was collected in the locality of Hammana / Mdeyrij, Central Lebanon [panoramic view of the site, the geological section and map are given in Azar et al. (2011: figs. 1 and 2, page 943; and fig. 3, page 944)]. It has been prepared, dissected, ground, polished and embedded in Canada balsam between two cover slips, as proposed by Azar (2000) and Azar et al. (2003). An Olympus SZH stereoscopic microscope, Olympus CK40 inverted microscope and Nikon microscope Microphot-FX (objectives from 4× to 40×) equipped with a camera lucida and changeable direct and transmitted light were used for microscopic examination.

The legs and body outline of the fossil may be deformed and optically shortened in the overview figures because of

the preservation within amber. Measurements are only approximate because of the taphonomic shriveling and various optical deformations.

Photographs have been taken using a Nikon Microphot-FX with a Nikon Eclipse E 600 digital camera using Lucia® software and an Olympus CK40 with Olympus Camedia C-5060 Wide Zoom camera using QuickPHOTO® 2.0 software; all images were adjusted using Combine ZP and Adobe® Photoshop Elements 6.0.

4 Systematics

Ordo Hemiptera Linnaeus, 1758

Subordo Sternorrhyncha Amyot et Serville, 1843

Infraordo Psylliformes sensu Schlee, 1969a

Hypordo Psyllomorpha Becker-Migdisova, 1962

Superfamilia Protopsyllidoidea Carpenter, 1931

1960b Protopsyllidoidea: Becker-Migdisova: 52.

1961 Protopsyllidoidea: Becker-Migdisova: 365.

Familia Protopsyllidiidae Carpenter, 1931

1926a Permopsyllidae: Tillyard (pars): 26.

1926b Permopsyllidae: Tillyard: 390.

1931 Carpenter: 115.

1931 Permopsyllinae: Martynov: 174.

1942 Permopsyllidae: Davis: 114.

1960b Permaphidopseidae: Becker-Migdisova (pars): 101.

1971 Permaphidopsidae: Szelegiewicz: 58.

Genus *Talaya* gen. nov.

Type species: *Talaya batraba* sp. nov.; by monotypy and present designation.

Diagnosis (nymph): Body dorsoventrally flattened, anterior and posterior portions distinctly elevated; laterally body strongly curved upwards; distinct median ecdysion line on dorsum, not reaching anterior margin of the body; line distinctly carinate, or roof-like on abdominal portion. Discs of head and thoracic segments fused in their median portions, suturae visible only in lateral portions; compound eyes placed on lateral eminences; rostrum very long, exceeding length of body; mandibular and maxillary stylets distinctly exceeding apex of rostral labium; clypeus swollen; preapical segment longest, reaching almost to level of pygidium and anal tube, apical segment shorter than preapical one; legs short, of clinging type, tarsi 1-segmented with double tarsal claw, wide arolium and long empodium; anal tube conical, with row of six long setae at apex, covered from above by dorsal lobe.

Remarks: *Talaya* gen. nov. is similar in general body shape to the protopsyllidiid species described based on Permian nymphs, i.e., *Permaleurodes rotundatum* Becker-Migdisova, 1960 and *Aleurnympha bibulla* Riek, 1974.

Unlike *Talaya*, the tergites of the pronotum are completely fused with the head in *Permaleurodes* and *Aleuonympha*, with no visible suturae separating head and prothorax and the compound eyes are in the dorsal position in *Permaleurodes* and *Aleuonympha*. *Talaya* gen. nov. is smaller than the nymphs of *Permaleurodes* and *Aleuonympha*, which seem to be 4th or 5th instars. We assume that *Talaya batraba* sp. nov. is in its 2nd or 3rd instar (see also discussion below).

Etymology: Generic name is derived from the Canaanite rain-goddess – Talaya. Gender: feminine.

Talaya batraba sp. nov.

Figs. 1–25

Diagnosis: As for genus, as it is the only included species.

Description: The specimen is a nymph of probably the 2nd or 3rd instar but see the discussion below. The body is dorsoventrally flattened, with anterior and posterior portions distinctly elevated; in lateral aspect the body is strongly curved upwards. The legs are short, but are not distinctly visible due to optical distortion in the piece of amber.

Body length is about 0.9 mm, with maximum body width is 0.4 mm, the anterior and posterior portions of the body being distinctly curved in a dorsal direction. There is an oval, dorsoventrally flattened head with segmentation visible. The cumulative length of the head and thoracic segments (c. 0.51 mm) exceeds the cumulative length of the

abdomen (c. 0.3 mm). The dorsal side of the body has a distinct median (ecdysion) line, not reaching the anterior margin of the body; this line is distinctly carinate, or roof-like in the abdominal portion. Wing-pads are not developed. The body is covered with distinct pits. The discs of the head and thoracic segments are fused in their median portions, with suturae visible only in the lateral portions.

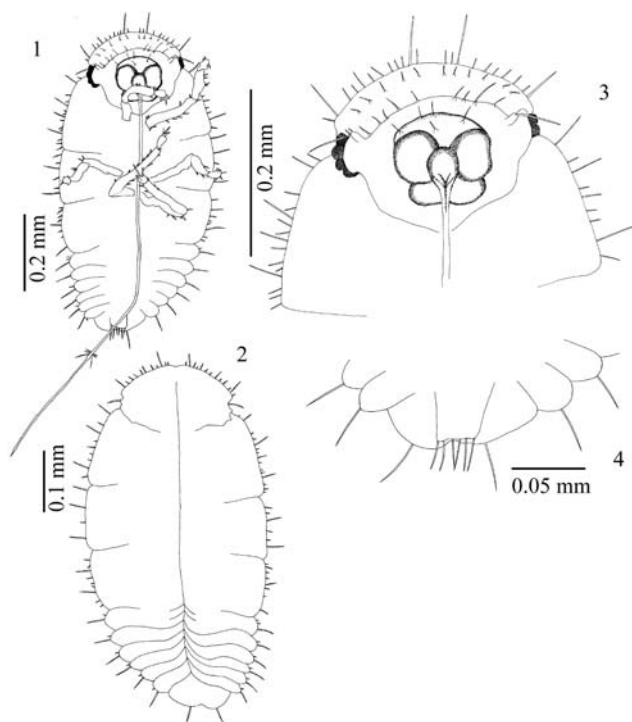
The anterior head segment (hypertrophied vertex) is about 0.14 mm long in the mid line, with the width of the anterior segment 0.20 mm. The anterior margin is arcuate, with a shallow median incision, and four longer setae, with an interspersed row of smaller setae. The lateral portion of the anterior segment (head, hypertrophied vertex) is shallowly incised, the suture not reaching the median portion of the body.

The suture separating the anteclypeus and postclypeus is visible in ventral aspect. The anteclypeus is distinctly swollen with two long setae, and distinct mandibular plates, separated from the anteclypeus by shallow suture; the maxillary plates are also distinct. The postclypeus is short, with a row of six long setae and two shorter setae. The rostrum is very long (0.72 mm), exceeding body length, with the preapical segment the longest (0.53 mm), reaching almost to the pygidium and the anal tube base. The apical segment is shorter (0.19 mm), with a few apical (sensory) setae. The mandibular and maxillary stylets are very long (exceeding 0.29 mm from rostrum apex), and the mandibular stylets have a few apical teeth. Both the mandibular and maxillary stylets distinctly exceed the apex of the rostral labium.

There are scattered ommatidia (probably six) placed on distinct ocular cones of the head. The antennae are short, and seem to be placed slightly in front of the ocular cones.

The pronotal segment is the longest (0.16 mm in lateral line, 0.19 mm in mid line), the lateral margins of which converge anteriad, with three longer setae and an interspersed row of shorter setae. The mesothoracic and metathoracic segments are of similar length (c. 0.14 mm and c. 0.14 mm in mid-line, 0.14 mm and 0.14 mm in the lateral lines, respectively).

The abdomen has nine homonomic segments, about 0.04 mm long in the lateral line; the lateral portion of abdomen has only six lateral lobes visible. The basal abdominal segments are fused in lateral lobes; the two basal segments are visible in the median portion of the abdomen. The lateral lobes of the abdominal segments are provided with long setae in the middle and short seta in front of the median seta. The last abdominal segment is lobe-like in dorsal view, with a shallow median incision and two distinct, long, caudal setae. The most distinctive feature of *Talaya* is a huge, conical, exposed, setiferous anal tube.



Figs. 1–4. Interpretation sketches of *Talaya batraba* gen. et sp. nov. 1. ventral view; 2. dorsal outline of body; 3. face; 4. tip of abdomen, ventral view (scale bars in respective figures).



Figs. 5–17. Photomicrographs of MNHN 1241, the holotype of *Talaya batraba* gen. et sp. nov. 5. dorsal view; 6. ventral view; 7. composed ventral view; 8. anterior portion of body in ventral view; 9. rostrum; 10. tip of rostrum; 11. tip of rostral stylets; 12. hind legs; 13. right hind leg tarsus; 14. hind leg tarsal claws and empodium; 15. hind legs; 16. fore leg tarsal claws and arolium; 17. abdomen, ventral view.

Both the last abdominal segment and the anal tube are about 0.05 mm long, conical, with a row of six long setae at the apex; the anal tube is covered from above by a dorsal lobe with a shallow median incision.

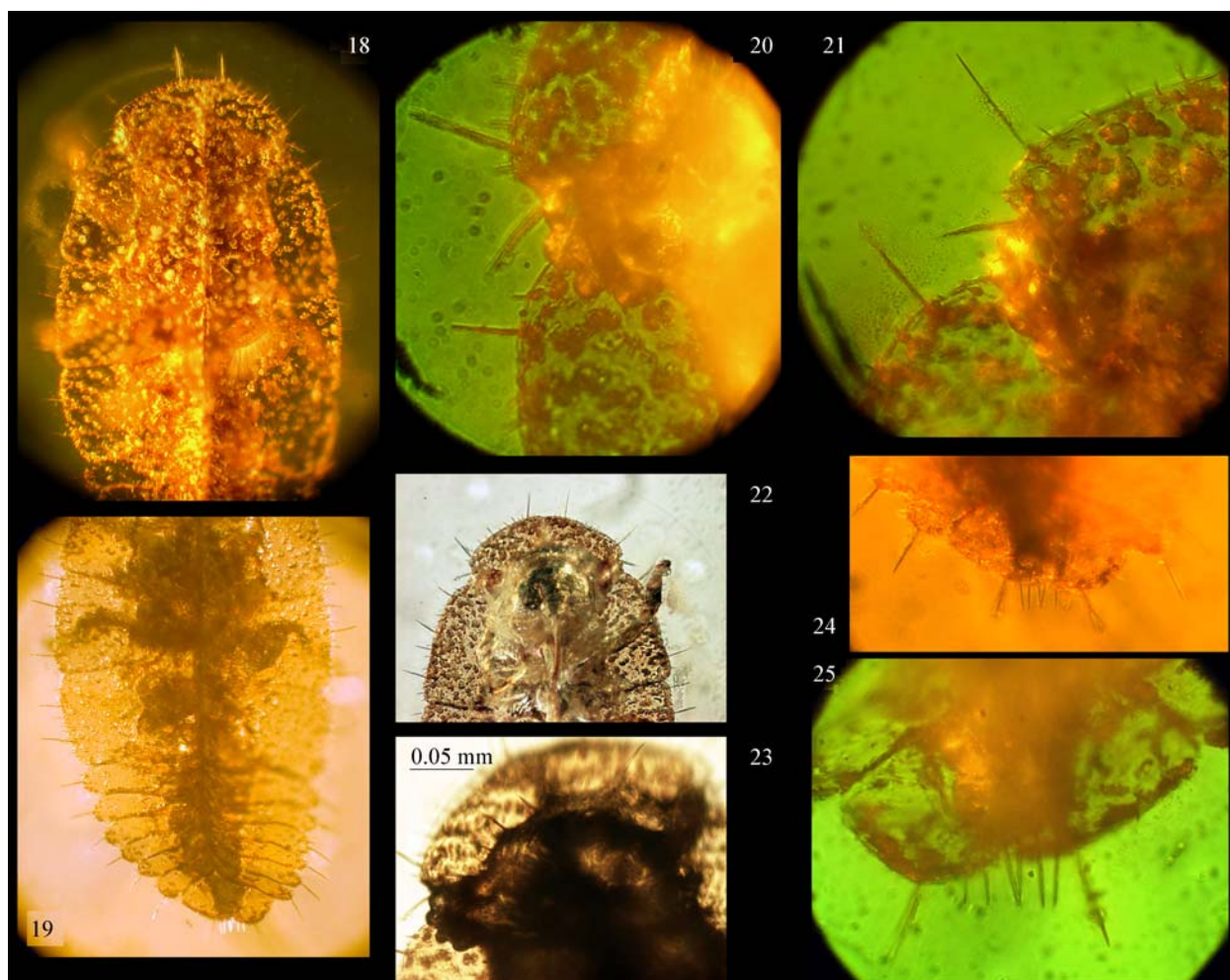
The legs are relatively short (about 0.23–0.3 mm), but of clinging type, with tarsi 1-segmented. The coxae are placed near the median axis of the body. The fore femur (about 0.13 mm) is merely thickened; the fore tibiae are rounded in cross section; the tarsal segment long, with distinct tarsal claws, wide arolium and a long empodium. The mid leg is similar to the fore leg. The hind femur (about 0.13 mm) is slightly thicker than the fore and mid femura; the hind tibia

(about 0.16 mm) is slightly longer than the fore and mid tibiae, with a few short setae. The tarsal segment is long (about 0.042 mm), about one-fourth of the hind tibia length.

Etymology: Specific name derived from an epithet of the goddess Talaya – ‘bat Rab’, meaning ‘Daughter of Rain’.

Age and occurrence: Early Cretaceous – early Aptian, Abeih Formation; (Azar et al., 2010); Mont Lebanon Governorate [Mouhafazit Jabal Loubnan]: Hammana / Mdeyrij, Caza Baabda, Lebanon.

Material. Holotype, a nymph, specimen number 1241, coll. Dany Azar, deposited in the Muséum national d’Histoire naturelle, Paris (MNHN).



Figs. 18–25. Photomicrographs of MNHN 1241, the holotype of *Talaya batraba* gen. et sp. nov. 18. anterior part of body, dorsal view; 19. posterior part of body, dorsal view; outline of body under widened tergal sclerites; 20. right eye, ventral view; 21. left eye, dorsal view; 22. face and prothorax, ventral view; 23. frons with setae; 24. tip of abdomen with anal tube, ventral view; 25. tip of anal tube with setae, dorsal view.

5 Discussion

The nymph described above is placed in the Protopsyllidiidae based on a combination of characters not found among other known Psylloidea nymphs. Unfortunately, the nymphal stages of the Jurassic and Cretaceous Malmopsyllidae and Liadopsyllidae are not known, so the only comparison possible is with known nymphs of the Protopsyllidiidae, Psylloidea and other Sternorrhyncha. In extant psyllids the head is not distinctly separated and elevated as seen in the *Talaya* nymph (White and Hodkinson, 1982, 1985). Also, among other sternorrhynchan nymphs (aleurodids, coccids), the head is not clearly separated from the thorax; among aphids separation of head and thorax is slightly more exposed (Shaposhnikov, 1980; Koteja, 1985). The swollen clypeus of *Talaya* resembles that portion of the imago head as seen in *Postopsyllidium*, the only other protopsyllidiid reported

from amber (Grimaldi 2003), and in imagines of *Liadopsylla* (Psylloidea: Liadopsyllidae) (Becker-Migdisova, 1985; Ouvrard et al., 2010). A slightly swollen clypeus is also observed in aphids, but is not seen in the other recent sternorrhynchan nymphs (White and Hodkinson 1982, 1985; Gill, 1990). Scattered ocelli placed on ocular cones are not recorded in any of the developmental stages known among psyllid nymphs (White and Hodkinson, 1982, 1985). In the other Sternorrhyncha (with exception of the aphids), the nymphal stages are highly modified and sedentary, with compound eyes reduced (White and Hodkinson 1982, 1985; Gill, 1990). The characteristic dorsal suture (ecdysion line?) found in *Talaya* is also found in recent psyllids as a membranous midline, and is recognizable also in the Permian and Triassic nymphs ascribed to Protopsyllidiidae (Evans, 1943; Becker-Migdisova 1985; Shcherbakov 2000a, b). In *Talaya*, the segments have no separated

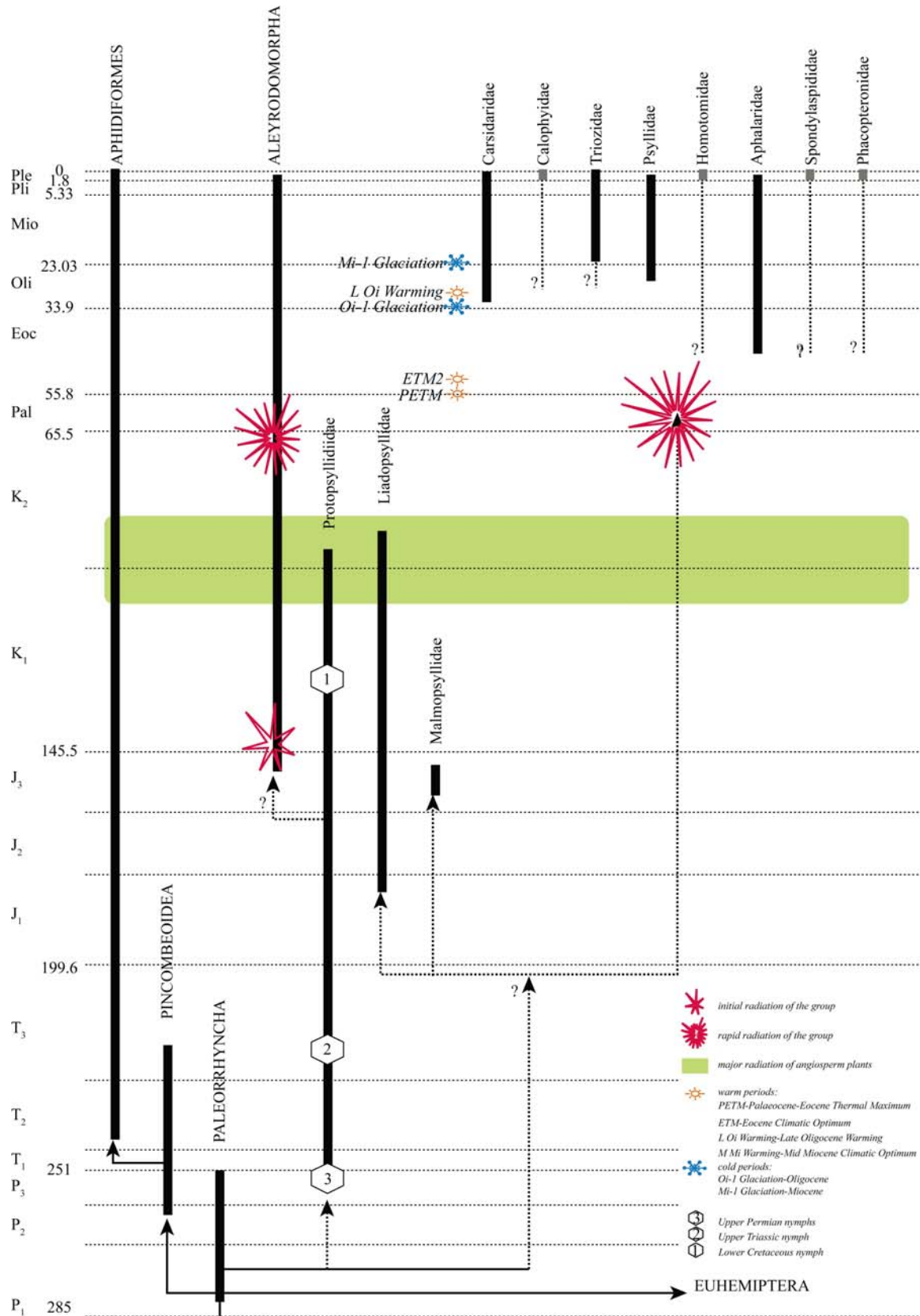


Fig. 26. Phylogram of the main groups of the Sternorrhyncha with a focus on the Psyllomorpha. Relationships between the groups based primarily on sources cited in the text, and modified by the present authors. Dashed lines indicate uncertainties at nodes and branch associations. Main events and radiations probably affecting the evolution of the Psylliformes are indicated. Stratigraphic positions of fossil nymphs ascribed to the Protopsyllidiidae are indicated. Families of the Psylloidea are presented according to White and Hodkinson (1985).

thoracic sclerites, similar to the situation found in the nymphs of Triozidae and Phacopterionidae (White and Hodkinson 1982, 1985; Loginova, 1981).

Nymphs of recent psylloids present scarce setation on their hind leg (White and Hodkinson 1982, 1985; Loginova, 1981), and a similar situation is observed in *Talaya*. Although the patterns of setation seen on other sternorrhynchan nymphs are still insufficiently studied, setation is usually also scarce (White and Hodkinson 1982, 1985; Loginova, 1981). Abdominal segments in recent psylloids present variously developed and arranged plates and sclerites (White and Hodkinson 1982, 1985; Loginova, 1981), whereas in *Talaya*, abdominal segments are regularly separated, without separated sclerites. The setation on the abdomen of recent psylloids is developed in various degrees, with number of setal types known (White and Hodkinson, 1985); in *Talaya*, there are regular major and minor hair-like setae on the lateral margins of each abdominal segment. The most distinctive feature of *Talaya* is the huge, conical, exposed, setiferous anal tube, the likes of which is unknown in any recent psylloid nymph. In the nymphs of psylloids and coccids, the anal ring is composed of specialised structures; the anal region in whitefly nymphs is composed of the vasiform orifice, operculum and lingula, whereas in aphids this area is transformed into cauda (Shcherbakov, 2007).

We assume that the nymph of *Talaya batraba* described above very probably represents a 2nd or 3rd instar because of the lack of wing-pads. However, it does present some features similar to those found in 4th and 5th instars of recent psylloids (White and Hodkinson 1982, 1985; Loginova, 1981). Last instars of recent psylloids are characterized by separation of the head, presence of a labial sheath, and separation of the tarsus from tibia. On the other hand, having the tarsus separated from the tibia is also found among other Sternorrhyncha nymphs in the younger instars (Klimaszewski, 1975; White and Hodkinson, 1982, 1985; Loginova, 1981; Koteja, 1985; Gill, 1990). The long rostrum of *Talaya*, with mandibular and maxillary stylets covered by a long labium, might indicate a rather older nymphal stage, as in recent psylloids where long stylets are placed as free coils (Klimaszewski, 1975). However, aphids with a very long rostrum, exhibit the mandibular and maxillary stylets concealed in the labial sheath (Grimaldi and Engel, 2005).

Becker-Migdisova (1973) suggested that at various geological times, under conditions of host plant specialization (monophagy), there have evolved specialized, 'streamlined' nymphs. In discussing nymphal characters of protopsyllidiids, she suggested that nymphs attained a high degree of specialization, despite having a tripartite tergal region of the thorax and 9-segmented abdomen. Klimaszewski (1995) commenting on the

evolution of Protopsyllidiidae, suggested that the failure of this group can be linked with extinction of their host plants, relating them with Peltaspermales and their descendants, the Caytoniales (Meyen, 1987; Taylor et al., 2009). The fossil nymph described in this paper seems to be a specialized form. The very long rostrum, with labium well developed and mandibular and maxillary stylets distinctly protruding, analogous to the elongate stylet coil of nymphs of recent psylloids, could be an adaptation for particular host plant and feeding habits (similar to some extinct aphids (Shaposhnikov, 1980; Shcherbakov and Popov, 2002)).

In all psylloids the last instar is characterized by the presence of distinct wing-pads, whereas *Talaya* has no wing-pads developed and, therefore, this lack of developed wing-pads suggests a 2nd or 3rd instar for the fossil taxon. This assumption may also be supported by the fossil's minute size. *Permaleurodes rotundatus* Becker-Migdisova, 1960 was described as a 'puparium', i.e., ultimate instar, and it is 3 mm long, with wing-pads developed. *Aleuromypha bibulla* Riek, 1974 is 4.8 mm long, with well-developed wing-pads (and eyes) and it is also thought to be an ultimate instar.

The cryptic features presented by *Talaya batraba* are also indicative of an adaptative nature. The lack of a meracanthus might be related to the lack of jumping abilities in this nymph. Ouvrard et al. (2010) showed that recent Psylloidea form a recently emerged group, very probably in relation to Mid-Cretaceous biotic reorganization and angiosperm radiation. The achievement of jumping abilities in psylloids probably occurred only once, and was triggered by these changes.

The recent Psylloidea retain some nymphal characters supposedly from their ancestral groups (e.g., 2-segmented tarsi, weakly developed articulation between coxa and trochanter and between tibia and basal tarsal segment; double empodium); however, they are highly specialised (Loginova, 1981; White and Hodkinson, 1982, 1985; Li, 2011). The Liadopsyllidae and Malmopsyllidae of late Early Jurassic to Early Cretaceous in age are thought to be ancestral to recent phylogenetic lineages of Psylloidea. Ouvrard et al. (2010) stated that the Mesozoic families probably do not form a monophyletic clade inside the Psylloidea. Therefore, the Liadopsyllidae and Malmopsyllidae are considered as paraphyletic stem groups in regard to the extant crown groups of the Psylloidea.

6 Taxonomic Position of Fossil Sternorrhynchan Nymphs

The taxonomy of recent and fossil Psyllomorpha is based on adult (alate) forms of both sexes, but the larvae

(nymphs) of extant psyllids are still inadequately known (Loginova, 1964; White and Hodkinson, 1985; Li, 2011). As mentioned above, the oldest known nymphs of Protopsyllidiidae (Permian, Triassic) were oval and flattened, presenting crypsis to various extents. These cryptic characters and probable lack of jumping abilities are also observable in the new taxon *Talaya*.

Nymphs ascribed to Protopsyllidiidae have only been reported from compression fossils (Fig. 26). The only other known amber inclusions (but imagines) placed in the Protopsyllidiidae are recorded from Lower Cretaceous Burmese amber (*Postopsyllidium rebecca* Grimaldi, 2003) and Upper Cretaceous New Jersey amber (*Postopsyllidium emilyae* Grimaldi, 2003) (Grimaldi, 2003), whereas the other protopsyllidiids are known from imprints and compression fossils (Becker-Migdisova, 1985; Klimaszewski, 1995).

Nymphs ascribed to the Protopsyllidiidae are known from the Permian deposits of Australia, South Africa and Russia (Evans, 1943; Becker-Migdisova, 1985; Shcherbakov, 2000a). The oldest remnants ascribed as the protopsyllidiid nymphs are known from the Upper Permian Isady locality, Vologda Region, Russia (Becker-Migdisova, 1985), whereas the oldest nymph ascribed to the family is known from the Upper Permian at Belmont, New South Wales, Australia (Evans, 1943).

The other Permian nymphs – *Permaleurodes rotundatum* Becker-Migdisova, 1960 from the Upper Permian of Surikovo-I, Ilinsk Horizon, Kemerovskaya Oblast, Kuznetskii Raion (District), Kuznetsk Basin, South Siberia, Russia (Becker-Migdisova, 1960a), and *Aleurnympha bibulla* Riek, 1974 from the Upper Permian Middle Beaufort Series in the vicinity of Mooi River, *Daptocephalus* reptile zone, Natal, South Africa (Riek, 1974a) – were assigned to a separate family Permaleurodidae Becker-Migdisova, 1960 and placed in the superfamily Aleyrodoidea. Evans (1963), Hennig (1969) and Schlee (1970) later regarded *Permaleurodes* as a doubtful member of Aleyrodomorpha, and Mound and Halsey (1978) and Carpenter (1992) treated this taxon as a cockroach nymph. *Aleurnympha* was also treated as a probable cockroach, representative of Blattoidea (Carpenter, 1992). Shcherbakov (2000a) argued against these proposals and placed both genera among the basal Hemiptera, stating that they most probably belonged to the Protopsyllidiidae or the related group of Psyllomorpha. Another nymph ascribed to the Protopsyllidiidae has been reported from the Upper Triassic Molteno Formation of South Africa (Riek, 1974b).

An extinct taxon, *Mesococcus asiaticus* Becker-Migdisova, 1960, from the Lower Jurassic Dzhil Horizon of Soguty, Issyk-Kul, Tonsk Raion (District), Kyrgyzstan (Becker-Migdisova, 1960a) is very probably

not a coccid (Koteja, 1990, 2000a, b; Shcherbakov 2007), but its placement remains doubtful, as this poor, minute, wingless impression (larva?; however, Becker-Migdisova, 1960a: 115, suggested that it is a female) is devoid of mouthparts, antennae and legs (reconstructed by Becker-Migdisova 1960a: Fig.10 as coccid-like in drawing). It may actually be a member of the aleyrodids, heteropterans or some other arthropod group (Koteja, 1990).

Another fossil taxon, *Hunanilarva micra* Lin, 1986, from Lower Jurassic rocks in Hunan Province, China was originally ascribed to Heteroptera: Lygaeidae (Lin, 1986), but it may also represent an early sternorrhynchan (Koteja, 1990).

Small, flattened nymphs, with short legs, ascribed to the Protopsyllidiidae, have also been found in Lower–Middle Jurassic Russian localities: Iya, in the Irkutsk Basin and Novospasskoe, in Buriatia (Shcherbakov, 1985). Shcherbakov (1985) noted that in the Krasnoyarsk, Novospasskoe and Uda fossil sites, the Protopsyllidiidae are the dominant group among hemipteran fossils and he related this predominance to an extreme decrease in remnants of larger insects, probably due to taphonomic reasons.

Among other Sternorrhyncha groups, the nymphs of true Coccinea are known since the Late Cretaceous (Koteja, 2000a). Aphids enter the fossil record in the Triassic (Wegierek, 2002; Hong et al., 2009; Heie and Wegierek, 2009a, b; Shcherbakov, 2010; Szwedo and Nel, 2011), with the earliest record of nymphs in the Upper Cretaceous Tajmyrian amber (Heie and Wegierek, 1998). Fossil aleyrodid nymphs are recorded from the Lower Cretaceous (Berriasian–Barremian) of the Purbeck and Wealden formations (Shcherbakov, 2000a) and from the Eocene/Oligocene of the Isle of Wight, England (Jarzembowski and Ross, 1993). The Psylloidea are known since the Early Jurassic (Becker-Migdisova, 1985), but there is only a single fossil nymph known – *Eogyropsylla* (last instar), recorded from the Middle Eocene Baltic amber (Klimaszewski, 1997). A single nymph placed in the Archescytinidae is known from the Upper Permian Usa Horizon in the Kuznetsk Coal Basin of Russia (Shcherbakov, 2000b). Only a few fossil nymphs ascribed to sternorrhynchans are known and, although they are formally described, often they are reported as nymphs of ‘probable whiteflies’, for example, from the Late Permian of South Africa (southern Pangaea/Gondwana) and Russia (Angara), as by Shear and Kukalová-Peck (1990) and Kukalová-Peck (1991).

Acknowledgements

We wish to express our sincere acknowledgements to Dr. Daniel Burckhardt (Naturhistorisches Museum, Basel,

Switzerland) for the discussions and very valuable comments on early drafts of this manuscript. We wish to express our thanks also to the reviewers of the paper and Dr Susan Turner (Brisbane) who all helped to improve the paper with very valuable comments and indications. This paper is a contribution to the research grant “Extinct and extant genus in the palaeontological record of recent families of insects” from the Ministry of Science and Higher Education of Poland/National Science Centre NN 303 2979 37 awarded to J.S. for years 2009–2012. It is also a contribution to the project “Insects in the Lower Cretaceous Lebanese amber: taxonomy, palaeobiodiversity and evolution”, under cooperative agreements between Lebanese University (Beirut); Museum, and Institute of Zoology, Polish Academy of Sciences, Warsaw; University of Gdansk; and the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow project “Origin and evolution of biodiversity of Europe and Middle East”. This paper is a contribution to the team project “Biodiversity: Origin, Structure, Evolution and Geology” awarded to D.A. by Lebanese University.

Manuscript received Jan. 8, 2012

accepted June 1, 2012

edited by Susan Turner

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