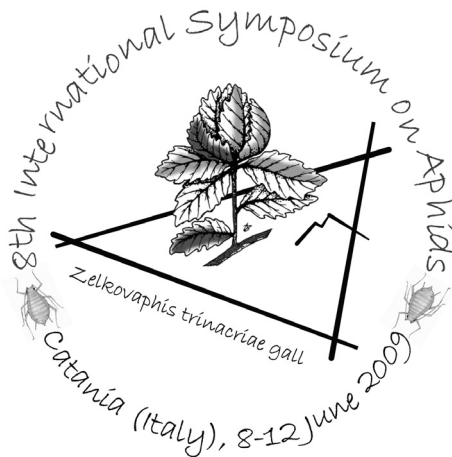


PROCEEDINGS

8TH INTERNATIONAL SYMPOSIUM ON APHIDS

Catania, Italy, 8-12 June 2009



on behalf of

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PHYLOGENETIC ASPECTS OF THE SALTUSAPHIDINAE

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Quednau F.W. – Phylogenetic aspects of the Saltusaphidinae.

Based on detailed studies of the morphological characters of adults and embryos, the probable course of evolution of the Saltusaphidinae is elucidated on account of development of leaping legs which show reduction in one lineage (the Tripsaphidini), but remained relatively stable in the other (the Saltusaphidini). In the group without leaping legs, as a result of reduction, a split occurred giving rise to forms with setiform empodial setae and with both oblique veins in the hind wing, as compared with the normal condition of spatulate empodial setae and loss of one oblique vein in the hind wing. It is contended that the Saltusaphidinae have probably originated from *Neophyllaphis*- or *Phyllaphis*-like ancestors of which the fossil genus *Balticaphis* may be taken as an example.

A previously published hypothesis by EASTOP (1958) assuming that it may be possible that the leaping habit would have arisen twice in this group of aphids is refuted. It is also mentioned that some species of the Thripsaphidini produce stalked eggs, a form of egg known from Mindarinae, Neophyllaphidinae, Greeideinae and also Aphidina Ovipara including the fossil genus *Elektraphis*.

KEY WORDS: Aphids, monophyletic lineage, evolutionary trends, leaping legs.

The Saltusaphidinae stand apart from other drepanosiphine aphids because of certain traits that are only found in this particular subfamily. These features are: multilensed eyes without triommatidium in all morphs and immature stages (except for *Neosaltusaphis*, where the ocular tubercle is poorly developed); front of head often with a median protrusion of various heights, but antennal tubercles absent or poorly developed. The legs of the aphids are normal or saltatorial in all stages, with fore and middle legs, or, more rarely, all legs modified for leaping. The first tarsal segments always have 5 ventral and no dorsal setae like in Israelaphidinae. The rostrum is always short with a short, blunt, apical segment and almost always bearing 1 pair of secondary setae, already in the embryo, and on the second rostral segment a wishbone-shaped stiffening has been developed. In the alate morph the head is flattened and on the ventral side without an epicranial suture, the median ocellus nearly in frontal position far removed from the clypeus, and on the mesonotum a foramen is absent, but the mesoscutellum often has a few setae. Wings are usually elongate, the venation in the fore wing normal, in the hind wing mostly with only 1 oblique vein, and cubital veins are always widely separated at their bases.

There is a characteristic elongate shape of the body in many species, the dorsum of the body in the more pear-shaped forms sometimes highly arched and the leading setae on low, conical elevations somewhat similar to those of the Macropodaphidinae. Antennae are often quite long. In the adult the dorsal body setae are usually numerous or even excessively numerous. These setae, at first hair-like, become spatulate, fan-shaped, mushroom- or inverted umbrella-shaped in the more highly evolved genera. Siphunculi are on tergite VI or on the border between tergites V and VI, with all transitions from poriform to short cylindrical. The eighth tergite is rounded or there may be a pair of short processes on the posterior margin in some species. The cauda has a short globular or sub-

quadrate knob and the anal plate is bilobed also in the ovipara.

In the more primitive genera wax gland pore elements in form of cribriform discs around setae occur on all tergites. In the more highly evolved genera they are present only on posterior abdominal tergites or entirely lacking, but often wax gland pores persist on the integument in form of minute scattered pits. In the more advanced genera the dorsal integument, originally adorned with rows of fine spicules, may become variolose or nodulose. Spiculose areas are also found on legs and antennae (Fig. I).

In the Saltusaphidinae the male is always apterous and dwarfish. The oviparae have 1 pair of subventral wax gland plates with mostly 2 perforations and pseudo-sensoria are present only on the hind tibiae. It is noteworthy that in several genera of the Saltusaphidinae stalked eggs were found, a form of egg that is also known in *Mindarus* and *Neophyllaphis*.

A peculiarity of the Saltusaphidinae is the double filter chamber of the mid-gut (PONSEN, 1992). A double filter chamber is also known to occur in the Panaphidini. The Saltusaphidinae live on Cyperaceae and Juncaceae. They are not host-alternating. We know about 60 species contained in 15 genera and subgenera. Their geographical distribution is at present holarctic, with a few species also occurring in the Ethiopian, Australian and Neotropical regions.

The origin of the more primitive Saltusaphidinae could probably be traced back to *Phyllaphis*-like forms which have abundant waxy secretions. The comparison with Phyllaphidinae seems justified because the alate morphs of *Phyllaphis* and *Machilaphis* are very similar to *Thripsaphis* and *Trichocallis*. Also in the phyllaphidinae genera *Machilaphis* and *Diphylaphis* we find the ocular tubercle undeveloped in the alate morph, and in *Stegophylla* we find empodial setae varying from rod-shaped of flabellate to being hairlike.

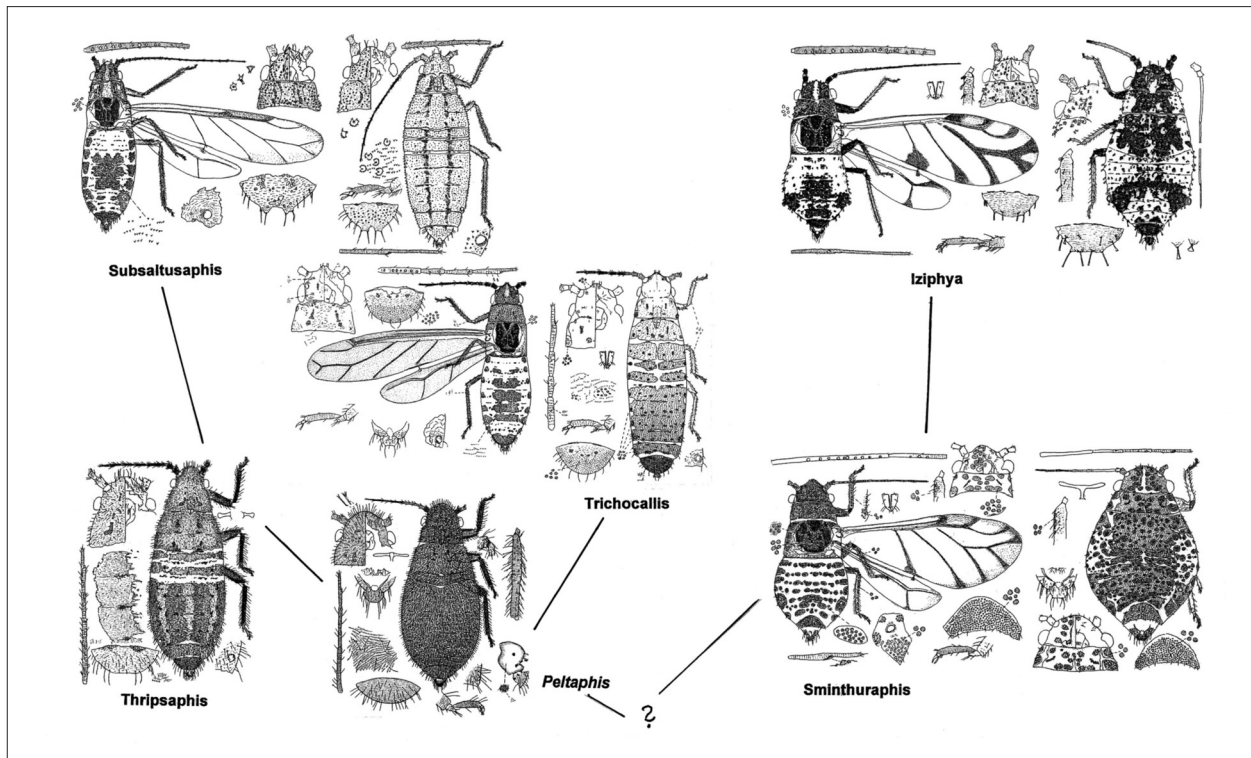


Fig. I – Main morphological forms of Saltusaphidinae and their relationships.

It must be assumed, however, that the development of leaping legs in the Saltusaphidinae occurred differently and independently from the one found in the *Lizerius-Spicaphis-Drepanosiphum*-lineage. It is conceivable that the primitive Saltusaphidinae were a leaping group and that there are two distinct branches with a major splitting in one of these. The two branches roughly correspond to the original non-leaping and leaping tribes of the author (1953). He improved on the classification by BÖRNER (1949) in first removing *Saltusaphis* sensu Börner from the Iziphyni (now Saltusaphidini). Börner's *Saltusaphis* had been misinterpreted at that time and has since been considered as the same genus as *Subsaltusaphis* Quednau, which has no leaping legs. Quednau had discovered the leaping ability of several European genera having the enlarged femora and shovel-shaped tibial bases on fore and middle legs, which led him to an alternative classification with non-leaping and leaping forms in the Saltusaphidinae (*Thripsaphidini* and *Iziphyni*, now Saltusaphidini, respectively). However he could not consider *Peltaphis* for lack of material available for study.

In the first lineage, the *Thripsaphidini*, the most primitive forms were most likely endowed to jump with all six legs (*Sechsbeinspringer* of Börner), a condition found in the North American genus *Peltaphis* and also in the fossil aphid *Balticaphis hauniaie* HEIE, 1967, which both have all femora enlarged. The latter aphid was subsequently placed by HEIE (1972) into the genus *Megapodaphis*, together with another species *M. frontalis*, which has the typical bulging of the front of the head of the Saltusaphidinae, absence of the ocular tubercle and enlarged femora of all legs. HEIE & WEGIEREK (1998) considered *Megapodaphis* as belonging to the Saltusaphidini, but it is conceivable that only the apterae described as *B. hauniaie* and the species *frontalis* qualify for being related to this group. The alate morph which Heie

described as *Megapodaphis monstrabilis* appears to belong to another group of fossil aphids related to the Macropodaphidinae. The leaping legs of the primitive Saltusaphidinae as demonstrated by *Peltaphis* and the two apterous fossil morphs are not the same type as those found in the genera of the *Iziphya*-group. Their tibial bases are not shovel-shaped and the lower side of the base of the tibiae is not hollowed, which is different from the normal saltatorial form of a tibial flector. It is here assumed that the leaping ability of the *Peltaphis-Thripsaphis*-lineage was lost during later evolution, but transitional types of legs have not been found (Fig. II).

The genus *Peltaphis* is distinguished by a carapace formation from the fusion of tergites 2-7 which, on the abdomen, extends ventrally and includes most sternites which are sometimes incompletely fused mesally. From *Peltaphis* the genus *Thripsaphis* may have arisen. One *Thripsaphis* species, to be described as new in the near future, also has a carapace, although to a lesser degree. It is noteworthy that in the remaining *Thripsaphis* species the thoracic nota and abdominal tergites are mutually free, which BÖRNER (1949) considered as a primitive condition. Such free nota and tergites are also found in the genus *Neobacillaphis*. The higher evolved genera of the *Thripsaphidini*, viz. *Neosaltusaphis* and *Subsaltusaphis* have, in the apterous vivipara, thoracic nota 2/3 and tergites 3/6 fused. The oviparae, however, retain the free tergites. In the genus *Thripsaphis* cribriform wax gland discs or minute wax gland pores occur on the dorsum of the body, and these gland pores have been lost in many species of the *Thripsaphidini* during later evolution. The eighth tergite is rounded in the primitive genera but assumes a bipartite form in *Neosaltusaphis* and *Subsaltusaphis*. The dorsal body integument has rows of spicules in the primitive forms and becomes variolose or nodulose in the more highly evolved genera. Also the integument of the antennal segments passes

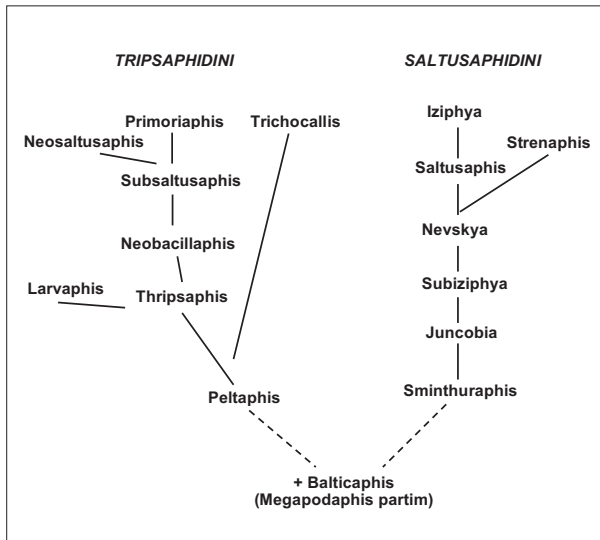


Fig. II – Phylogenetic tree of the Saltusaphidinae.

from being imbricated to densely spiculate. It is noteworthy that *Neosaltusaphis* still has vestiges of an ocular tubercle, the only such case known in the Saltusaphidinae. In *Neobacillaphis*, *Neosaltusaphis* and *Subsalsusaphis* we notice the gradual change from pointed dorsal body setae into the spatulate, mushroom- or umbrella-shaped form, these setae sometimes occurring in mixed association (*S. intermedia*, *S. aquatilis*).

The genera of the Thripsaphidini so far discussed, all have spatulate empodial setae as normal for the whole subfamily, and in the alate morph there is loss of one cubital vein (cu1b) in the hind wing. The embryos are, with the exception of those in *Neosaltusaphis* of a rather hairy type with respect to the arrangement of dorsal body setae. As in the genera *Symydobius* and *Clethrobius* of the Calaphidini, the embryos of *Peltaphis*, *Thripsaphis* and *Subsalsusaphis* have rows of spinal, pleural and marginal setae on the tergites, often supplemented by additional setae in the marginal and pleural body zone. These setae are pointed in the primitive, and spatulate or umbrella-shaped in the more advanced genera. In the embryos of some species an augmentation of setae on the antennal segments is observed. Only the embryo of *Neosaltusaphis* has assumed a protopattern of arrangement of dorsal body setae, with pleural setae absent and spinal and marginal seta present only as 1 pair per tergite. In the adults of the subgenus *Primoriaphis* of *Subsalsusaphis*, paramarginal setae are developed on the sides of the head and the accessory sensoria of the last antennal segment are scattered, both highly apomorphic traits which will appear also in some genera of the *Iziphyha*-group, the Saltusaphidini (Plate I).

An early splitting has occurred in the Thripsaphidini in so far that in the genus *Trichocallis* the empodial setae have become secondarily setiform and that the original two oblique veins in the hind wing are retained. The embryonic chaetotaxy of *Trichocallis* is almost always a protopattern, only in *Trichocallis scabra* there are also single pairs of pleural setae. In *Trichocallis* the dorsal body setae remain pointed, paramedian setae are absent on the head and the accessory sensoria of the last antennal segment are adjacent to the primary sensorium. A reversal from normally spatulate empodial setae to hair-like ones is also observed in some species of subgenus *Pasekia* in *Myzocallis* and in *Cranaphis* of the Panaphidini.

It is conceivable that the so far discussed forms of the Saltusaphidinae represent one monophyletic lineage.

In the second lineage, the Saltusaphidini, formerly called Iziphyni, all forms including the embryo are provided with leaping legs based on swollen femora and shovel-shaped tibial bases of only fore and middle legs. This development of leaping legs is distinctly different from the one found in *Peltaphis* and also from that of the Lizeriinae, Spicaphidinae and Drepanosiphinae, although functionally based on comparable organs. It is not impossible that the *Iziphyha*-group evolved from ancestor forms with 3 pairs of jumping legs, but no evidence exists.

The most primitive genus in the Saltusaphidini is undoubtedly the genus *Sminthuraphis* which has large, polyfaceted wax gland plates on the dorsum of body. The arrangement of these wax gland plates on sclerites is very similar to those found in the genus *Ceriferella* of the Lizeriinae.

In the genus *Sminthuraphis* the embryo or first instar nymph is interesting because it forecasts the protopattern type of rod-shaped or flabellate dorsal body setae that is characteristic for most species of the Saltusaphidini. However already the second instar of *Sminthuraphis* reverts to the original short pointed setae. *Sminthuraphis* has the processus terminalis of the last antennal segment shorter than the base of that segment, there is very little spiculation on legs and antennae, siphunculi are poriform tergite VIII is rounded and accessory sensoria not scattered, all primitive features. In the remaining genera of the Saltusaphidini a number of apomorphic traits develop: dorsal body setae become spatulate, rod-shaped or umbrella-shaped, the sub-basal setae of the tibiae different from the other tibial setae, paramarginal setae appear on the sides of the head, as well as scattered accessory sensoria, there are dense rows of spicules on legs and antennae, processes on posterior margin of tergite VIII, furthermore short, seta-bearing processes on dorsum of body and in the alate morph bordered or spotted wing veins. In the embryos modifications concern the addition of pleural setae on some of the thoracic nota or on some of the posterior tergites, rarely pleural setae appear on all tergites or even marginal thoracic setae in double pairs are developed (*Subiziphyha clauseni*, *Juncobia leegei*). The most advanced genus is *Iziphyha*.

It is not conceivable that the loss of leaping became a major trend in the *Iziphyha*-group, and it would not be possible to derive from it genera of the Thripsaphidini. In an earlier publication EASTOP (1958) made a comment on QUEDNAU's (1953, 1954) writings, stating that the latter author implied that in the Saltusaphidinae it would be unlikely that the leaping habit could have arisen twice in the same group, and that this would result in his placement of otherwise similar aphid species in different tribes because of different degrees of development of the fore-femora. However, in the extant Saltusaphidinae the evidence for gradual degrees of strengthening of these femora is most scanty. A slight diminishing of the sizes of the leaping legs is observed in the genera *Strenaphis* and *Nevskya*, but this may have little significance and may represent merely extreme variation.

There is also no possibility to derive *Trichocallis*, belonging to the tribe without leaping legs, from members of the Saltusaphidini. Although this genus has a protopattern in the embryonic stage, the wax gland pore elements in *Trichocallis* are different from those found in *Sminthuraphis* and do not assume the form of polyfaceted areas on sclerites.

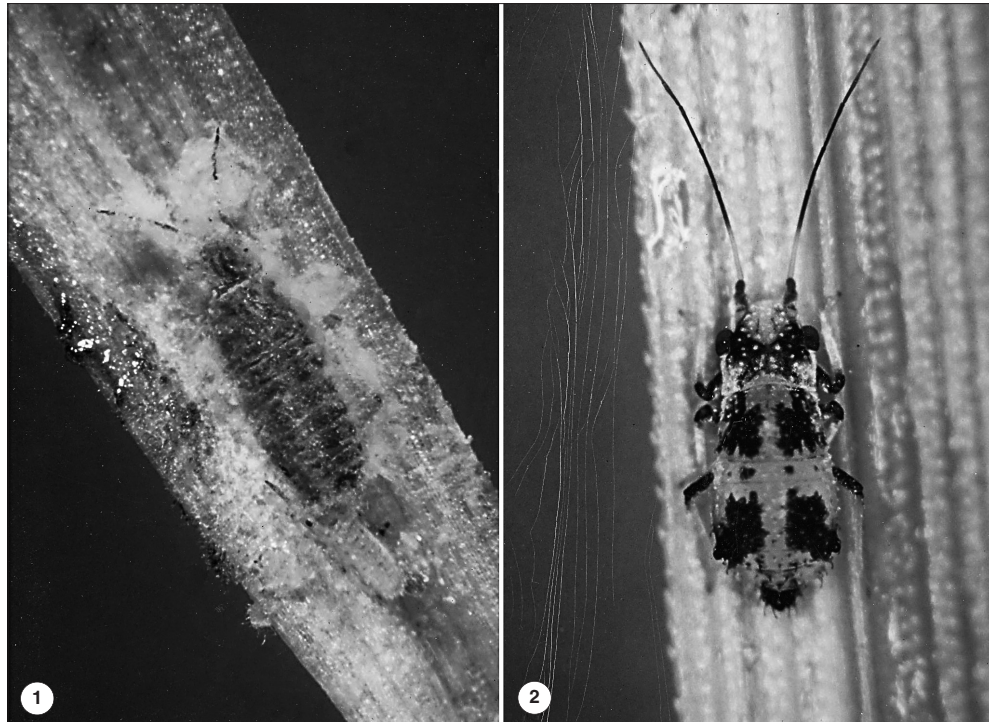


Plate I

Examples of Saltusaphidinae (apterous viviparae): 1. *Trichocallis ossianilssoni* (H.R.L.); 2. *Iziphyba bufo* (Walk.).

An intriguing question is whether the genus *Subsaltusaphis* is a derivate of *Thripsaphis* in adopting the apomorphic umbrella-shaped dorsal body setae, or whether it should be considered as a derivate of *Strenaphis* or *Nevskya*-like forms by the complete loss of leaping legs but retention of the modified dorsal body setae, imputing that *Nevskya* and *Strenaphis* have relatively weakly developed leaping legs so that eventually forms like *Subsaltusaphis*, *Primoriaphis* or *Neosaltusaphis* would result. But this is difficult to accept. Against the latter hypothesis speaks the hairy condition of the embryos in *Subsaltusaphis* which is unknown in the Saltusaphidini, and the non-scattered condition of the accessory sensoria in the majority of the species of the *Thripsaphis* group. Also *Subsaltusaphis* would not develop the pairs of large pigmented sclerotic spots on the dorsum of the body as observed in *Nevskya* and *Iziphyba*. There is, however, an intriguing superficial resemblance between the aptera of *Strenaphis elongata* and *Neosaltusaphis bodenheimeri*, which RICHARDS (1971) considered to belong to the same genus, but the presence of leaping legs in *Strenaphis* which are absent in *Neosaltusaphis*, and the segmentally separated tergites in *Strenaphis* which are solidly fused in *Neosaltusaphis*, proves him wrong.

On the other hand, EASTOP (1958) rightly concluded that the primitive Saltusaphidinae were a leaping group and that the ability to leap has become lost by several genera independently. Even if Quednau's classification is accepted it would not necessarily place similar species in different tribes or place heterogenous elements in the same tribe. Meanwhile a number of new genera and species were discovered in the Saltusaphidinae and their study gave support to Quednau's classification.

It thus appears that the system of the Saltusaphidinae is best represented by the alternative situation Thripsaphidini – Saltusaphidini which goes back monophyletically to ancestor forms like *Balticaphis*.

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