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Descriptions of two new species of *Anomalosiphum* (Hemiptera: Aphididae, Greenideinae), including a winged ovipara with pedunculate eggs

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Of the Asian aphid genus *Anomalosiphum*, ***A. mendeli*** and ***A. essigi*** are described as new. Winged sexual forms of *A. mendeli* are reported here for the first time for an *Anomalosiphum*, featuring oviparae bearing pedunculate eggs. A key to the known species of *Anomalosiphum* is presented. Possible phylogenetic affinities between the Greenideinae, Neophyllaphidinae and Aiceoninae are discussed. © 2006 Government of Canada, Natural Resources Canada, *Zoological Journal of the Linnean Society*, 2006, **146**, 239–249.

ADDITIONAL KEYWORDS: *Aiceona* – *Allotrichosiphum* – *Cervaphidini* – *Chileaphis* – *Eutrichosiphum* – *Greenidea* – host plants – keys – *Neophyllaphis* – pedunculate eggs – *Schoutedenia*.

INTRODUCTION

Examination of a sample of small insects from a test operation for a programme of forest canopy insecticidal fogging at the Danum Valley Field Studies Centre, Sabah, Malaysia, revealed the presence of an unknown species of *Anomalosiphum*, a small Asian genus of aphid belonging to the tribe Cervaphidini, within the subfamily Greenideinae. All of the adults were alate, with only two (teneral) viviparae, the remaining adults being a mixture of males and oviparae with eggs that are clearly pedunculate. Fourth-instar alatoid nymphs were also present with either developing embryos or developing eggs. The first author was able to study, from the collection of the Essig Museum, University of California, Berkeley, a slide-mounted alate vivipara from China, previously identified by Essig (1951) as *A. pithecolobii* Takahashi, 1934. It was discovered, mainly by examination of the embryos and comparison with those contained in *A. pithecolobii* types in the C.C. Tao collection (Taiwan Agricultural Research Institute, Taichung, Taiwan), that Essig's sample did not represent this species, but rather an undescribed species somewhat related to *A. tiomanense* Martin & Agarwala, 1994. It appears desirable to give descriptions of the new taxa and to discuss some of their peculiarities.

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Abbreviations used in descriptions and keys

abd., abdomen/abdominal; ant., antenna/antennal; flag., flagellum/flagellar; ht2, second segment of hind tarsus; pt, processus terminalis of antenna; segm., segment(s); sens., sensoria; siph., siphunculi; tc1, first tarsal chaetotaxy; urs, ultimate rostral segment. All measurements are quoted in millimetres, unless stated otherwise.

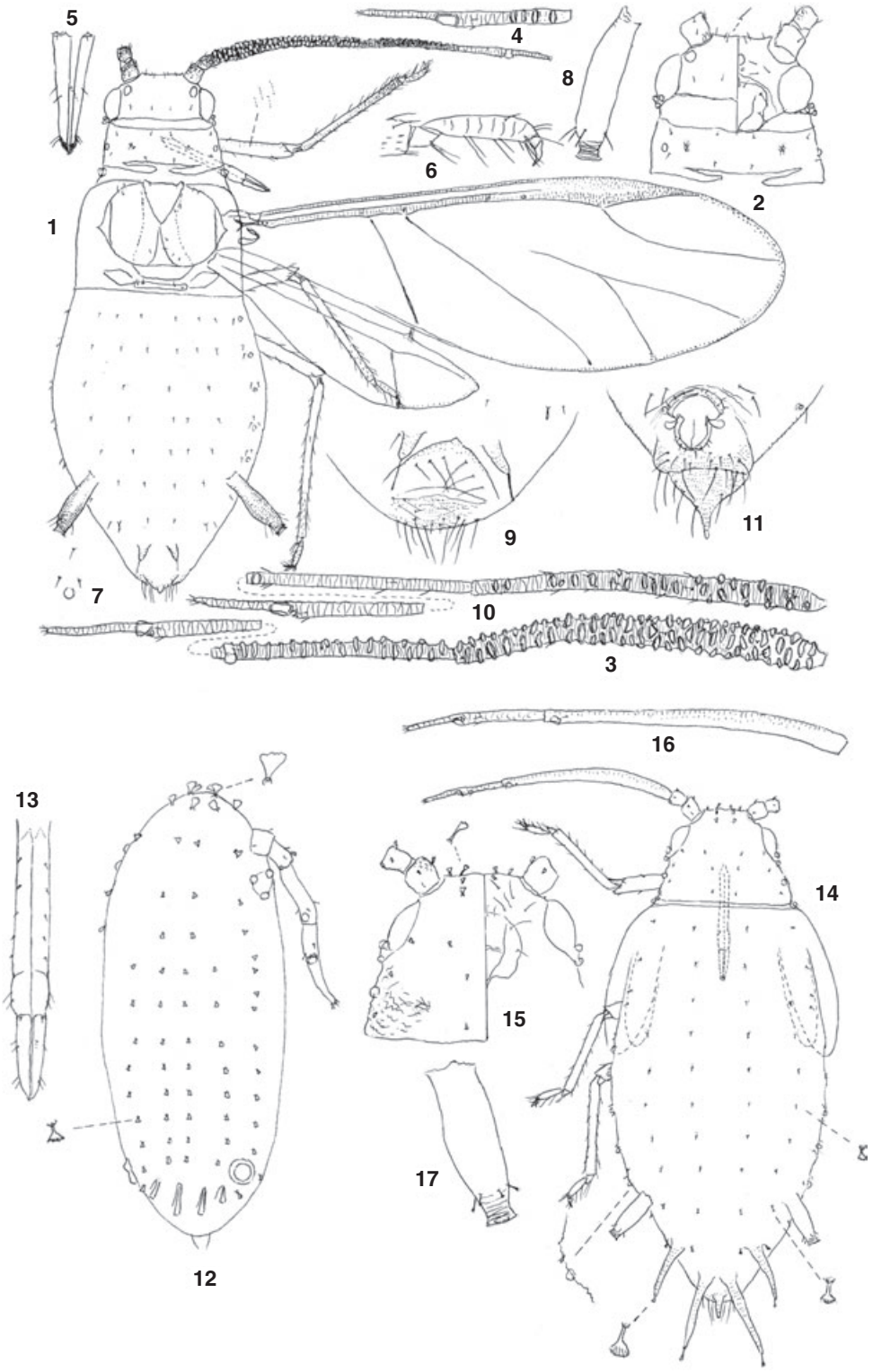
ANOMALOSIPHUM MENDELI SP. NOV.

(FIGS 1–27)

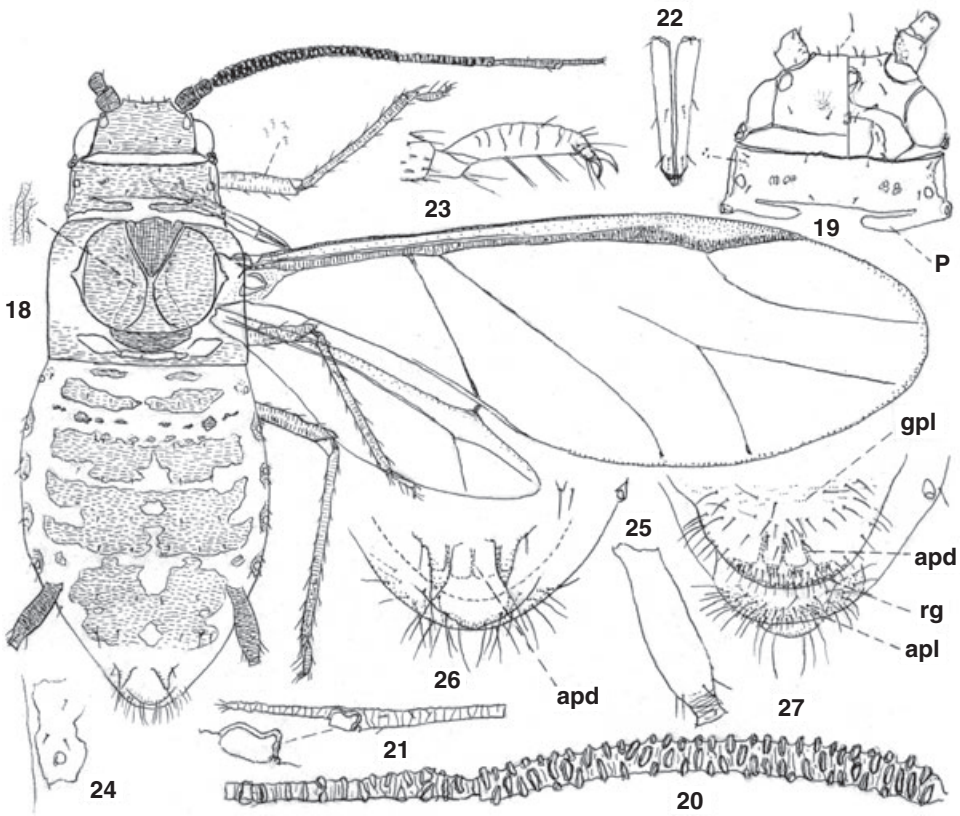
Description

Alate vivipara (from two teneral specimens). Slide-mounted specimens pale except for ant. segm. I and II, fore tibiae and siph. which are dusky; ant. segm. III and IV dark brown.

Morphology. Discal setae of vertex pointed, 15 μm long. Ant. 0.7 times body length, segm. III markedly



Figures 1–17. ***Anomalosiphum mendeli*** **sp. nov.**, paratypes. Figs 1–9, alate vivipara: 1, body; 2, head and pronotum; 3, ant. flagellum; 4, variant of ant. segm. V; 5, urs; 6, ht2; 7, marginal abd. setae and marginal papilla; 8, siph.; 9, posterior abd. Figs 10, 11, alate male: 10, ant. flagellum; 11, posterior abd., ventral view. Figs 12, 13, embryo: 12, body; 13, rostrum. Figs 14–17, alatoid nymph: 14, body; 15, head and pronotum; 16, ant. flagellum; 17, siph.



Figures 18–27. ***Anomalosiphum mendeli*** **sp. nov.**, alate ovipara, holotype: 18, body; 19, head and pronotum; 20, ant. segm. III & IV; 21, ant. segm. V; 22, urs; 23, ht2; 24, marginal abd. sclerites; 25, siph.; 26, posterior abd.; 27, posterior abd., ventral view. apd = apodeme of rudimentary ovipositor; apl = anal plate; gpl = genital plate; p = posttergite; rg = rudimentary gonapophyses.

swollen on basal half of segment, with about 7 pointed setae 11 μm long; segm. III, IV and base of V bearing 77–84, 20–21 and 0 (exceptionally 4 from an alatoid nymph) semiannular secondary sens., respectively; lengths of flag. segm., III 0.57, IV 0.37, V base 0.19, pt 0.12–0.13. Urs 0.099 long, 0.96 times ht2. Pronotum with 8 setae, with a marginal papilla on each side; sides of pronotum smooth. Mesoscutellum without setae. Metanotum with lateral membranous parts being without setae. Tc1 3 : 3 : 3, on second tarsomere lateroapical setae fine and thin, pointed. Dorsal surface of abdomen smooth, without sclerotization, possibly due to the teneral condition of the specimens. Dorsal abdominal setae sparse, blunt or pointed; paramedian setae on tergites I–VI 4–6 each, VII bearing 6 and VIII bearing 2–3 setae (2 borne on the processes); longest setae on tergites I, VII and VIII are 11, 19 and 38–45 μm, respectively. On tergite VII one pair of outer setae sometimes on a short, spiculose process about 8 μm long. Processes on tergite VIII 68 μm long. One conspicuous marginal papilla on each side of tergites I–V. Siph. swollen 0.21–0.23 long, 0.11 times body length, with a ring of 5 setae. Cauda rounded triangular, bearing 4 long and 2 shorter pointed setae and with an indistinct preapical process. Anal plate with about 15 setae. Rudimentary gonapophyses 2 or 3. Subgenital plate with 14 setae. Body 1.87–2.02 long.

Embryo. Eye a triommatidium. Ant. 4-segmented. Frontal and three pairs of anterior discal setae broad flabellate, expanding immediately from bases, 11 μm long; posterior discal setae 2 pairs, flabellate, 5 μm long. Dorsal body setae until tergite VI minute, flabellate with rather few jagged cusps. Pronotum with 2 pairs each of marginal and spinal setae. Meso- and metanotum each with 2 pairs of marginal and 1 pair each of spinal and pleural setae. Tergites I–VI each with 1 pair of spinal, pleural and marginal setae. Tergite VII with 4 setae, of which those of the inner pair 19 μm long, elongate flabellate, and on processes. Tergite VIII with 2 cylindrical setae with flabellate apices, 30 μm long, also on processes. Siph. well developed. Integument smooth. Chaetotactic formula of ant. segm: 1 + 1, 3, 3, 2. Chaetotactic formula of rostrum: 0, 5, 2, 1 + 4.

Alatoid nymph (from 1 specimen). Pale, legs, antennae and wing pads weakly pigmented. Ant. 0.6 times body length. Anterior discal setae of vertex 8–15 μm, flabellate, the longest with cylindrical basal half; posterior discals and remainder of dorsal body setae minute, 6–8 μm long, flabellate or with denticulate apices. On pronotum a pair of conspicuous marginal papillae, sides of pronotum weakly scabrous. Dorsal abdominal setae sparse, paramedian setae of tergites I–VI one pair of spinal and one pair of pleural setae, tergite VII bearing 6 (2 borne on the processes) and VIII 2 setae on processes. Processes on tergites VII and VIII 197 μm and 315 μm long, respectively, setae on processes 15 μm long. Siph. 0.21 long. Marginal papillae well developed from tergites I–V. Dorsal body integument smooth, except for sides of pronotum and for spicules on processes. Cauda with a dorsal process 64 μm long. Body 1.93 long.

Alate ovipara (from 6 specimens). In slide-mounted specimens head, thorax, legs and siphunculi brown, sclerotic parts of abd. pale brown; ant. flagellum and mesonotum more strongly pigmented; ventral abd. sclerites pale brown; pterostigma pale with dark inner bordering.

Morphology. Similar to the alate vivipara but differing as follows: Ant. segm. III, IV and base of V bearing 60–72, 10–21 and 0–1 semiannular secondary sens., respectively; lengths of flag. segm., III 0.43–0.61, IV 0.27–0.38, V base 0.17–0.21, pt 0.11–0.15. Urs 0.091–0.106 long, 0.86–1.08 times ht2. Pseudosensoria on tibia absent. Sides of pronotum with a few spicules; posterior part of pronotum with a pair of 'posttergites' (Wegierek, 2002) well developed. Dorsal sclerotization of abd. consisting of a free transverse paramedian band over tergite I and of ill-defined spinopleural bands that may fuse to form a large quadrate patch of irregular outline over tergites II–V and another medially indented patch over tergites VI–VII. Intersegmental sclerites developed in front of tergites I, II and VI. Marginal abd. sclerites present on tergites II–V, small, mutually free, sometimes poorly defined. On tergite VII pair of short processes up to 15 μm long. Tergite VIII bearing 4 setae, of which 2 at the base and 2 at the apex of the processes. Cauda semicircular without process. Anal plate large, rounded, spiculose, with about 50 setae. Subgenital plate large, bulging, with a few rows of spicules, with about 65 setae. Rudimentary gonapophyses 4. Apodemes of rudimentary ovipositor skeleton 3. Ventral abd. sclerites developed in pairs sublaterally on sternites III–VI, spiculose. Body 1.62–1.96 long.

Egg. Oblong elliptical, 0.40 × 0.18, translucent. A short peduncle 30 μm long on one pole. This appears to be an eversion of the chorion with a dark granulate surface of the exochorion (see Fig. 49).

Alate male (from 4 specimens). Colour when mounted on slides pale with dark brown ant.; legs, siph. and inner margin of pterostigma infuscated.

Morphology. Very similar to the alate vivipara with the following exceptions: Ant. segm. III bearing 19–31 semiannular secondary sens., other flag. segm. without secondary sens; lengths of flag. segm., III 0.53–0.60, IV 0.34–0.37, V base 0.20–0.22, pt 0.10–0.11. Sides of pronotum weakly spiculose. Tergite I and marginal lobes of tergites I–V weakly spiculose. Processes of tergite VIII 70–90 μm long excluding seta. Cauda with an apical process 42 μm long. Genital armature relatively small, weakly sclerotized; aedeagus of penis rounded, with a few minute setae. Subgenital plate developed as a narrow bar bearing about 10 minute setae. Body 1.49–1.62 long.

Host plant

Unknown (obtained from canopy fogging).

Material examined

HOLOTYPE alate ovipara, EAST MALAYSIA: Sabah, Danum Valley field station, 6.vi.1999 (H. Mendel *et al*.) (The Natural History Museum, London). PARATYPES: 2 alate viviparae, 7 alate oviparae, 6 males and 13 alatoid nymphs, of which 7 viviparous, same data as for holotype.

Comments

This species is easily recognized by the very great number of sensoria on the strongly swollen ant. segm. III, the presence of conspicuous marginal papillae on pronotum and tergites I–V, and the relatively sparse number of paramedian setae on the abdomen. Named after its collector Howard Mendel. This is the first record of alate oviparae in the genus *Anomalosiphum*, although they are also known to occur in genera of the Greenideini.

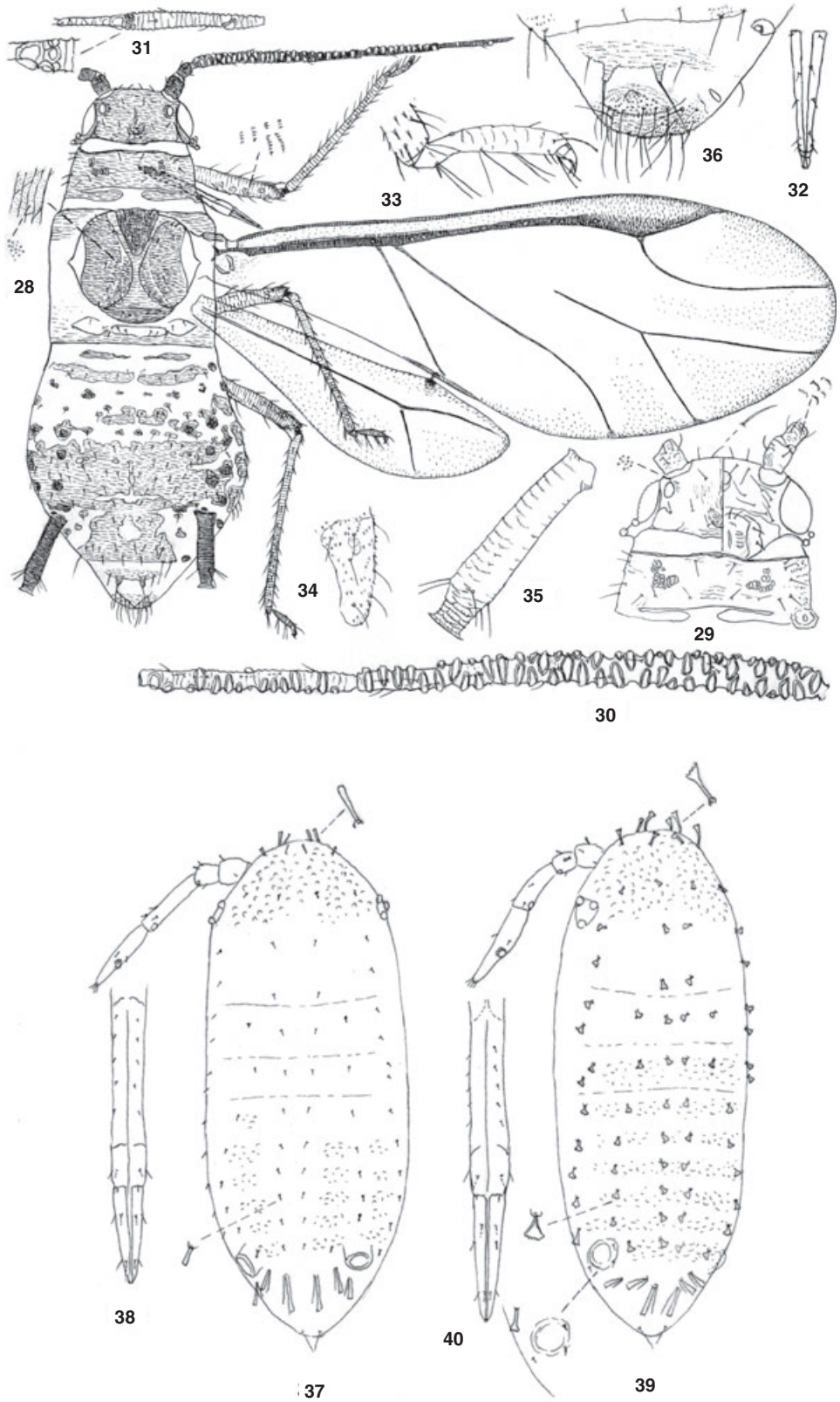
ANOMALOSIPHUM ESSIGI SP. NOV.

(FIGS 28–38)

Description

Alate vivipara (from 1 specimen). In slide-mounted specimens head, ant., legs and pronotum brown; mesonotum and siph. more strongly pigmented; sclerotic parts of abd. pale brown; pterostigma pale with dark inner bordering.

Morphology. Discal setae of vertex pointed, 19–26 μm long. Ant. 0.7 times body length, segm. III moderately swollen with 11 pointed setae 19 μm long; segm. III, IV and base of V bearing 58–61, 14–16 and



Figures 28–40. Figs 28–39. ***Anomalosiphum essigi* sp. nov.**, alate vivipara, holotype: 28, body; 29, head and pronotum; 30, ant. segm. III & IV; 31, ant. segm. V; 32, urs; 33, ht2; 34, marginal abd. sclerite; 35, siph.; 36, posterior abd.; 37–38, embryo: 37, body; 38, rostrum. Figs 39–40, *A. pithecolobii*, embryo: 39, body; 40, rostrum.

1 semiannular sec. sensoria, respectively; lengths of flag. segm., III 0.60, IV 0.26, base V 0.18, pt 0.06. Urs 0.129 long, 1.21 times ht2. Pronotum with about 15 setae, the longest 23 μm long, marginal setae in groups, marginal papillae absent; sides of pronotum spiculose; posterior part of pronotum with a pair of 'posttergites'. Mesocutellum with 2 setae. Lateral membranous parts of metanotum with 2 setae on each side. Tc1 3 : 3 : 3. Second tarsal segment with one pair of preapical setae conspicuous, weakly capitate, as long or longer than empodial setae. Dorsal surface of abd. with tergites I and VIII and marginal lobes of tergites I–V spiculose; a few spicules also on tergites V–VII. Dorsal sclerotization of abd. consisting of a band on tergite I, smaller sclerites on tergite II, a large, solid rectangular patch of irregular outline on tergites III–V, and another trapezoid patch on tergites VI and VII, almost coalescing with the former. Intersegmental sclerites developed in front of tergites I, II and VI (VII).

Marginal abd. sclerites developed on tergites II–V with 4–8 setae, the longest 34 μm long. Paramedian abd. setae numerous, pointed, tergite VII bearing 15 and VIII bearing 4 setae (2 on the processes); longest setae of tergites I, VII and VIII are 20, 76 and 102 μm, respectively. Processes on tergite VIII 34 μm long. Marginal papillae undeveloped. Siph. almost cylindrical, 0.27 long, 0.16 of body length, with a subapical ring of 5 setae. Cauda rounded, bearing 6 setae and a short preapical process. Anal plate with about 17 setae. Rudimentary gonapopyses 2. Subgenital plate with 8 setae. Body 1.77 long.

Embryo. Eye a triommatidium. Ant. 4-segmented. Frontal and anterior discal setae blunt, peg-like with barely expanded apices, 6–10 μm long. Dorsal body setae from pronotum to tergite VI minute, peg-like, about 6 μm long. Integument weakly variolose. Otherwise as normal for *Anomalosiphum*.

Host plant

Unknown (Metasequoia or Dawn Redwood region).

Material examined

HOLOTYPE alate vivipara, CHINA: Hupeh Province, Li-ch'uan, Siu Ho, 14.ix.1948, host unknown (Y.W. Djou) (Essig Museum of the University of California, Berkeley).

Comments. This species was described by Essig (1951) under the name *A. pithecolobii* Takahashi. However, the latter has a longer apical rostral segment (0.144 long, about 1.85 times ht2). In addition, a close comparison of the embryos revealed that Essig's specimen is different. The embryo of *A. pithecolobii* has flabellate dorsal body setae and the siph. bears two minute setae in addition (Fig. 39). In the embryo of *A. essigi* the dorsal body setae are blunt, peg-like and the siph. is without setae (Fig. 37). *Anomalosiphum essigi* somewhat resembles *A. scleroticum* Qiao & G.X. Zhang 2001 in having the sclerites of tergites VI/VII almost coalescing with those of tergites III/V, but differs by more and longer setae on the pronotum and the presence of a secondary sensorium on ant. segm. V. Epithet given in honour of the late professor E. O. Essig.

Anomalosiphum tiomanense was found again by the second author in China (Hong Kong Island, Pok Fu Lam Country Park) on *Dalbergia* sp., 21.xii.2001, 3 apterous, 5 alate viviparae and 3 alatoid nymphs. The apterae differ in having frontal setae 15–19 μm long (8–16 μm in the types) and in the alates submarginal setae on tergite VII are 45–57 μm long (15–19 μm in the types) and the apical setae on the processes of tergite VIII are 80–91 μm long (45–56 μm in the types). In addition, the embryos from the Hong Kong sample have dorsal body setae peg-like instead with incrassate, denticulate apices (Figs 41–48).

It appears premature to assign the Hong Kong material to a distinct subspecies because the nominate species is known from only a few specimens, all from one locality (north of Kampung Tekek, Pahang Province, West Malaysia) and intraspecific variation cannot be assessed.

Pedunculate eggs in the Greenideinae and other groups of aphids

As a chance observation, it was found that the oviparae of *Anomalosiphum mendeli* have eggs in their abdomen that are pedunculate. Apart from this species, stalked eggs were also found in the following oviparae of aphids mounted on slides: Subfam. Greenideinae: *Eutrichosiphum* sp., *Allotrichosiphum kashicola* (Kurisaki), *Greenidea* sp., *Schoutedenia lutea* (v.d. Goot), *S. ralumensis* Rübsaamen; Neophyllaphidinae: *Neophyllaphis araucariae* Takahashi, *N.* (*Chileaphis*) *podocarpini* Carrillo; Aiceoninae: *Aiceona himalaica* Miyazaki. The oviparae were all winged except wingless in the genus *Schoutedenia*. More examples could probably be given were it not for the fact that often the eggs have been removed in the preparations. A few types of pedunculate eggs are illustrated in Figs 49–56. It is noteworthy that the eggs of *S. ralumensis* have a smooth, short peduncle, whereas those of *S. lutea* have only a translucent bulging area on one pole of the egg. In *N.* (*C.*) *podocarpini* the stalk is cone-shaped, pigmented and smooth. In the other species examined the stalk has a dark granulate surface. The stalk of the egg of *A. himalaica* is strongly bent. Miyazaki (1977)

KEY TO *ANOMALOSIPHUM* SPECIES, ALATE VIVIPARAE

1. Ant. segm. III not much swollen, bearing up to 20 sens.; segm. IV and V without sec. sens. Embryo with setae from pronotum to tergite VI short flabellate. On unknown host. China.....*A. takahashii* Tao, 1947
– Ant. segm. III sometimes swollen on basal half, bearing more than 30 sens.; segm. IV and sometimes also segm. V with sec. sens. Embryo with dorsal body setae of various shapes. 2
2. Ant. segm. III strongly swollen, bearing 60–84 sens.; urs about 1.0 times ht2; marginal papillae on pronotum and tergites I–V conspicuous; tergite VII with 4–5 setae. In embryo setae from pronotum to tergite VI minute, flabellate, about 4 μm long. On unknown host. East Malaysia. .....***A. mendeli* sp. nov.**
– Ant. segm. III not much or only moderately swollen, bearing 33–61 sens.; urs mostly longer than 1.0 times ht2; marginal papillae often absent or indistinct; tergite VII mostly with more than 5 setae..... 3
3. Urs relatively long, about 1.85–2.00 times ht2. In embryo siph. with minute setae in addition to marginal seta of tergite VI. 4
– Urs relatively short, not more than 1.6 times ht2; in embryo siph. without setae, marginal seta of tergite VI minute or absent..... 5
4. Urs about 2 times ht2; ant. segm. III rather strongly swollen, bearing over 50 sens. In embryo setae from pronotum to tergite VI elongate flabellate, 19–22 μm long. On *Indigofera* sp. and possibly *Phyllanthus* sp. India. ..... *A. indigoferae* Ghosh, Ghosh & Raychaudhuri, 1971
– Urs about 1.85 times ht2; ant. segm. III weakly swollen, bearing about 30 sens. In embryo setae from pronotum to tergite VI short flabellate, 8 μm long. On *Pithecolobium lucidum*. Taiwan, Papua New Guinea. .....*A. pithecolobii* Takahashi, 1934
5. Urs 1.5–1.6 times ht2. In embryo setae from pronotum to tergite VI flabellate, 11–15 μm long. On *Rourea* sp. and *Xanthophyllum stipitatum*. Singapore. ..... *A. murphyi* Martin & Agarwala, 1994
– Urs at most 1.35 times ht2..... 6
6. Urs 1.20–1.35 times ht2. (Larger aphids, body length 1.50–1.85)..... 7
– Urs 1.05–1.13 times ht2. (Smaller aphids, body length 1.27–1.41)..... 8
7. Pronotum with about 15 setae, 19–23 μm long, marginals in groups. Patch on tergites VI/VII almost coalescing with sclerotic patch of preceding tergites. In embryo setae from pronotum to tergite VI minute, 6 μm long, peg-like, apices without cusps or indentations. On unknown host. China. .....***A. essigi* sp. nov.**
– Pronotum with about 9 setae, 8–15 μm long, marginals in single pairs. Patch on tergites VI/VII not coalescing with those of preceding tergites. In embryo setae from pronotum to tergite VI 15 μm long, flabellate. On *Dalbergia ferruginea*. Philippines.....*A. philippinense* Martin & Agarwala, 1994[1]
8. Ant. segm. V without secondary sens. On tergite VII a pair of short, sublateral processes 16 μm long. Sclerotic patch on tergites VI/VII almost coalescing with sclerotic patch of proceding tergites. In embryo setae from pronotum to tergite VI 6–8 μm long, flabellate.[2] On *Dalbergia hupeana*. China. .....*A. scleroticum* Qiao & G.X. Zhang, 2001
– Ant. segm. V with 1–3 secondary sens. Tergite VII without processes. Sclerites of tergites VI/VII not coalescing with those of preceding tergites. In embryo setae from pronotum to tergite VI minute, 4 μm long, peg-like or with incrassate denticulate apices. On *Dalbergia* spp. West Malaysia and China (Hong Kong). .....*A. tiomanense* Martin & Agarwala, 1994

[1]Martin & Agarwala (1994) named two new species as *A. tiomanensis* and *A. philippinensis*, respectively. However, the genus *Anomalosiphum* should be of neuter gender if we follow other generic names of aphids ending in *-siphum*, such as *Eutrichosiphum*, with *E. manipurense* Singh, D. Raychaudhuri & D.N. Raychaudhuri, for example.
[2]Type specimens of *A. scleroticum* were obtained on loan from the collection of the Academica Sinica, Beijing. Unlike figure 12 of the original description, the embryo has flabellate setae from pronotum to tergite VI.

has shown this on a photograph but does not give comments in his publication.

The function of the stalk remains unknown. It may serve for the fixation of the egg on foliage, but observations on egg-laying in *Anomalosiphum mendeli* could not be made. Takahashi (1959) states that the eggs of *Paratrichosiphum* (now *Allotrichosiphum*) *kashicola* are depressed and flat, but in his illustration no stalk is to be seen. Carver & Hales (1974) report on flat eggs in *Neophyllaphis brimblecombei* Carver laid in nature and in the laboratory but no mention is made of a stalk, which should occur in this group of aphids.

Similarities of oviparous female genitalia in Greenideinae, Neophyllaphidinae and Aiceoninae. Incidence of pseudosensoria

Miyazaki (1977) gave a description of the alate ovipara of *Aiceona himalaica*. The sclerotized genital

KEY TO *ANOMALOSIPHUM* SPECIES, APTEROUS VIVIPARAE

(Apterae of *A. pithecolobii*, *A. mendeli*, *A. essigi* and *A. scleroticum* unknown)

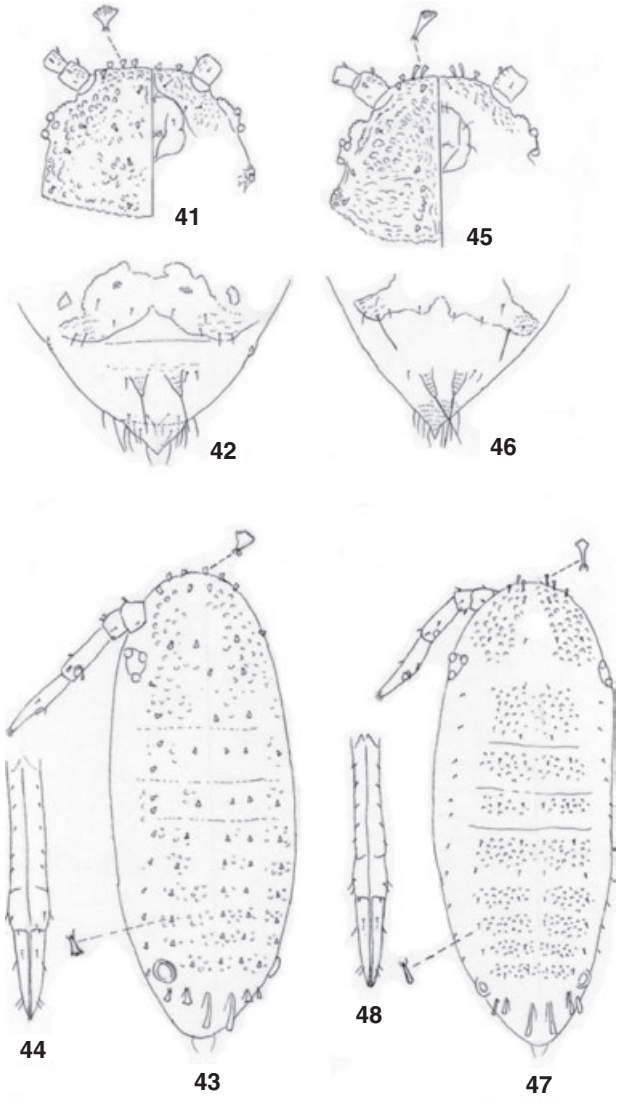
1. Dorsum of body weakly pigmented, aphids on slide appearing pale to the naked eye. Dorsal body integument mostly smooth or weakly sculptured. 2
– Much of dorsum of body pale brown to dark brown, at least on sides of abdomen. 4
2. Paired processes of tergite VII (minus setae) about 0.9 times as long as processes of tergite VIII; frontal setae about 34 μm long, pedunculate flabellate; dorsum of body almost smooth. In embryo dorsal body setae flabellate, about 15 μm long. ..... *A. philippinense* Martin & Agarwala, 1994
– Paired processes of tergite VII 0.50–0.75 times as long as processes of tergite VIII; frontal setae about 23 μm long or shorter, pedunculate or sessile flabellate; dorsum of body smooth or variolose. In embryo dorsal body setae short flabellate or peg-like, 4–6 μm long. 3
3. Urs 1.20–1.37 times ht2; dorsum of abdomen smooth. In embryo dorsal body setae flabellate. ..... *A. takahashii* Tao, 1947
– Urs 1.05–1.15 times ht2; dorsum of abdomen variolose or nodulose. In embryo dorsal body setae minute, peg-like or with incrassate, denticulate apices. ..... *A. tiomanense* Martin & Agarwala, 1994
4. Dorsum of body rather evenly pigmented. Dorsal body setae 19–38 μm long with at least half their lengths cylindrical before widening toward apices. Urs about 2 times ht2. Dorsal integument smooth or variolose. In embryo dorsal setae flabellate with elongate cylindrical basal part, siph. with 2 minute setae in addition to marginal seta of tergite VI. ..... *A. indigoferae* Ghosh *et al.*, 1971
– Median zone of abd. often markedly paler than the sides. Dorsal body setae 15–22 μm, flabellate, mostly expanding immediately from bases. Urs 1.38–1.58 times ht2. Dorsal integument strongly variolose or nodulose. In embryo dorsal setae short flabellate, expanding immediately from bases, siph. without setae. ..... *A. murphyi* Martin & Agarwala, 1994

plate is large, occupying nearly the whole width of sternites VII and VIII, which are almost completely separated by a transverse split, dividing the genital plate into an anterior and a posterior lobe. There are two types of setae on the posterior lobe, namely many pointed hair-like setae and less numerous peg-like setae (Fig. 61). Such a configuration is also known to occur in the genus *Neophyllaphis*. The transverse split is clearly observed in *N. grobleri* Eastop (Fig. 57), but it is almost obsolete in *N. araucariae* and *N.* (*Chileaphis*) *podocarpini* (Fig. 58) but the peg-like setae are always present on the posterior lobe of the genital plate. In the genus *Anomalosiphum* and some other genera of the Greenideini the genital plate of the winged ovipara is also large, but more bulging. In *A. mendeli* there is no subdivision and on the posterior part there are no peg-like setae, but setae are distinctly shorter than on the anterior part (Fig. 27). This seems to be the more advanced state, where the separation between sternites VII and VIII is no longer recognizable except for the different lengths of the setae, as in *Eutrichosiphum garhwalense* Maity & Chakrabarti (Fig. 60).

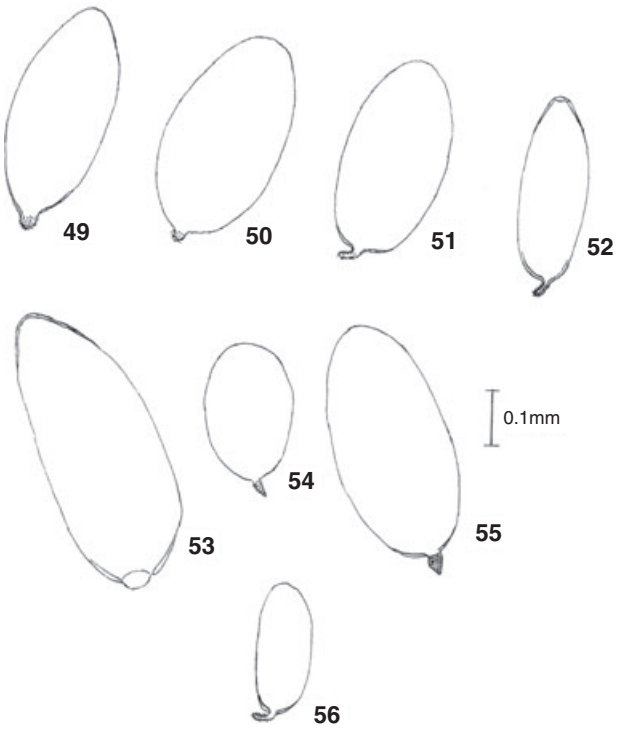
In the past the taxonomic position of the *Aiceoninae* was poorly understood. Takahashi (1921) originally placed *Aiceona* in the subtribe Anoecini of his tribe Lachnina. It now appears that this genus is not related to *Anoecia* but may have evolved from *Neophyllaphis*-like ancestors, which may also be the ancestors of primitive Lachninae, if one considers certain similarities between *Chileaphis* and Lachninae as monophyletic. Although the anal plate in *Aiceona* is not bilobate as in *Neophyllaphis*, the genital plate is quite similar in both groups. It also appears unlikely that stalked eggs have evolved several times independently in the aphids.

On the other hand, recent discoveries by Wegierek & Peñalver (2002) from the Miocene of Europe confirm that the Greenideinae are phylogenetically old. Both Greenideinae and Neophyllaphidinae oviparae have well-developed apodemes on rudiments of an ovipositor skeleton (Figs 57, 60). The presence of setae on the membranous lateral zones of the metanotum and the extended range of marginal abdominal setae (latero-sternal setae, Quednau & Remaudière, 1994) and other morphological characters make it highly probable that both groups may have evolved from the same ancestor. Recently, Wegierek (2002) pointed out that the drepanosiphine aphids and the Greenideinae show a marked resemblance with respect to head and thorax structure. In the Greenideinae we find striking examples of homoplasies with respect to *Drepanosiphum*, the Chaitophorinae and also the Saltusaphidinae.

Ghosh & Raychaudhuri (1973) report faintly indicated pseudosensoria-like structures on the hind tibiae of the oviparae of *Aiceona litseae* Basu & Hille Ris Lambers. In *A. himalaica* oviparae they are absent. The oviparae of Neophyllaphidinae have pseudosensoria on all or only the hind tibiae.



Figures 41–48. Variations observed in two populations of *Anomalosiphum tiomanense*. Figs 41–44, type specimens from West Malaysia: 41, aptera, head and pronotum; 42, alata, posterior abdomen; 43, 44, embryo with rostrum. Figs 45–48, specimens from Hong Kong: 45, aptera, head and pronotum; 46, alata, posterior abdomen; 47, 48, embryo with rostrum.

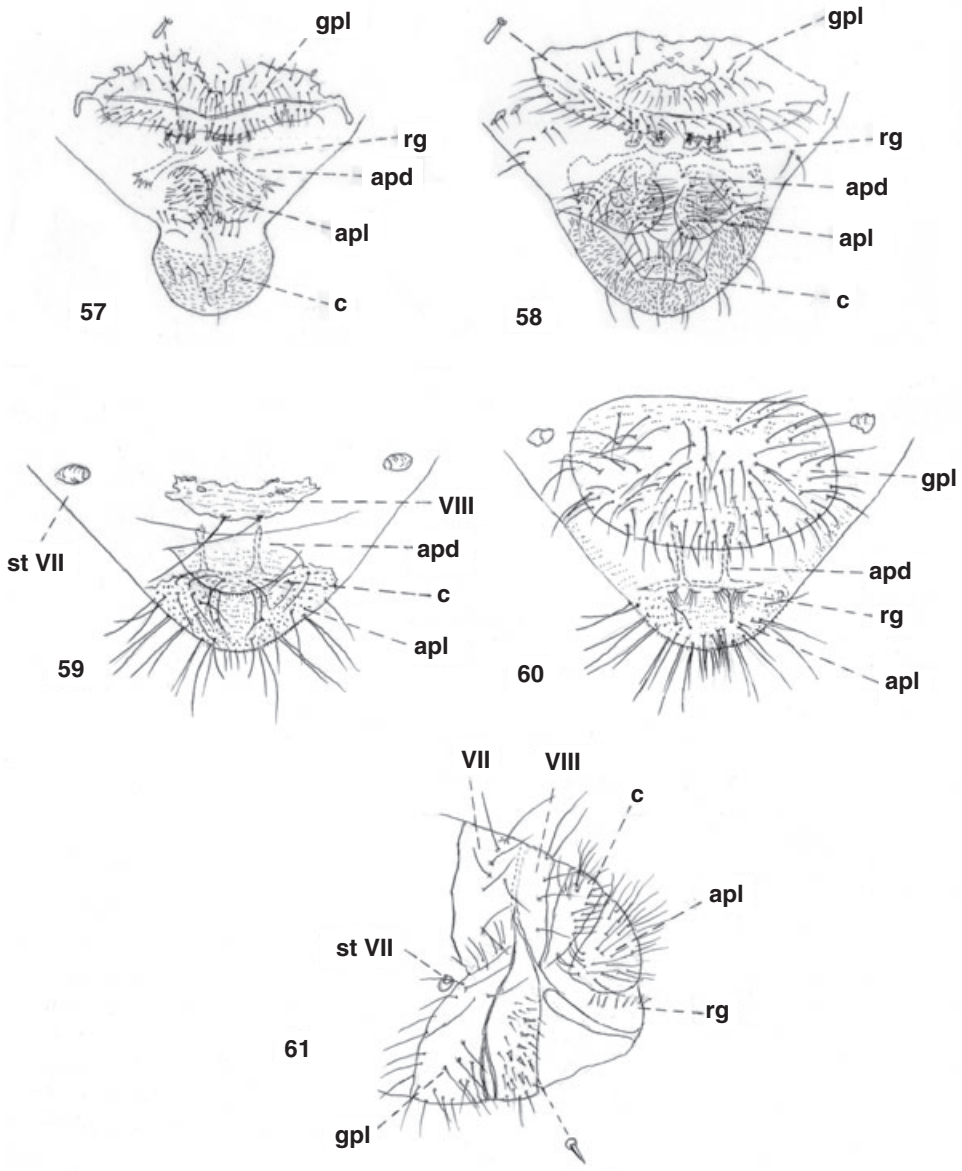


Figures 49–56. Pedunculate eggs of aphids: 49, *Anomalosiphum mendeli*; 50, *Eutrichosiphum* sp.; 51, *Greenidea* (*Trichosiphum*) *okajimai*; 52, *Allotrichosiphum kashicola*; 53, *Schoutedenia lutea*; 54, *Neophyllaphis podocarpi*; 55, *Neophyllaphis* (*Chileaphis*) *podocarpini*; 56, *Aiceona himalaica*.

Pseudosensoria are generally absent on the tibiae of oviparae in the Greenideinae, but the wingless oviparae of the Schoutedeniini have such organs on the hind femora. Pseudosensoria are commonly known to occur on the hind tibiae in all groups of the higher evolved Aphididae.

Occurrence of alate oviparae in the Aphididae

The alate condition of an ovipara is the primitive form in aphids and this was originally the case in all Aphididae (Mordvilko, 1934). In the extant fauna this condition is known only in the following subfamilies: Phloeomyzinae, Tamaliinae, Neophyllaphidinae, Greenideinae (except Schoutedeniini) and Aiceoninae. Mordvilko also pointed out that originally several bisexual generations existed. In the Greenideinae there is no particular time of the year for sexuales production within this group, even in temperate Japan. For instance, *Allotrichosiphum kashicola* (on *Quercus*) has only two generations a year in Osaka, where apterous fundatrices are sexuparae at the same time, and alate sexes emerge in the second generation in May. In a more northern region, in Tokyo, however, two or more generations are produced, the sexual forms appearing from the second generation (Takahashi, 1959). In the Neophyllaphidinae in Japan (on *Podocarpus*) winged oviparae and males appear from May until November, yet simultanously winged and wingless virgins develop. It is not clear whether the eggs laid by the oviparous females must necessarily hibernate or whether during the same summer fundatrices may develop from the eggs at the beginning of the sum-



Figures 57–61. Posterior abdomen of alate oviparous aphids: 57, *Neophyllaphis grobleri*, ventral view; 58, *Neophyllaphis* (*Chileaphis*) *podocarpini*, ventral view; 59, 60, *Eutrichosiphum garhwalense*, dorsal and ventral views; 61, *Aiceona himalaica*, lateral view. apd = apodeme of rudimentary ovipositor; apl = anal plate; c = cauda; gpl = genital plate; rg = rudimentary gonapophyses; st VII = stigma of abd. segm. VII; VII, VIII = tergites VII, VIII.

mer. In addition, in the Aiceoninae winged oviparae as well as males may be found in colonies at almost any time of the year (Blackman & Eastop, 1994). The sample of *Anomalosiphum mendeli* described here was collected in Malaysia in early June, i.e. in a tropical climate moderated by monsoonal effects. Phylogenetically old aphids which originally inhabited warmer climatic zones have found refuges in South East Asia after the pronounced climatic changes on other continents in recent times.

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