

Scuttle flies (Diptera : Phoridae) imprisoned by *Aristolochia baenzigeri* (Aristolochiaceae) in Thailand

Autor(en): **Bänziger, Hans / Disney, R. Henry L.**

Objektyp: **Article**

Zeitschrift: **Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society**

Band (Jahr): **79 (2006)**

Heft 1-2

PDF erstellt am: **28.04.2024**

Persistenter Link: <https://doi.org/10.5169/seals-402910>

Nutzungsbedingungen

Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern.

Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden.

Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss

Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

Scuttle flies (Diptera: Phoridae) imprisoned by *Aristolochia baenzigeri* (Aristolochiaceae) in Thailand

HANS BÄNZIGER¹ & R. HENRY L. DISNEY²

¹ Department of Entomology, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand. e-mail: sangda.h@chiangmai.ac.th

² University Museum of Zoology, Downing Street, Cambridge CB2 3EJ, England.
e-mail: rhld2@hermes.cam.ac.uk

Adults of 124 Phoridae, five Agromyzidae, and one Sphaeroceridae were found in the kettle-trap flowers of *Aristolochia baenzigeri* studied in N Thailand, 1995, 2004–2005. The Phoridae belong to 21 species in 8 genera. Eight new species are named and described in the genera *Anevrina* (1), *Conicera* (1), *Dohrniphora* (2), *Megaselia* (4). Seven species, only known in the female sex, are briefly described but remain unnamed. These belong to the genera *Borophaga* (*Godavaria*) (1), *Megaselia* (1) and *Woodiphora* (5). One species of *Puliciphora*, only known in the male sex remains unnamed, as the species recognition in this genus is based on the females.

Dohrniphora cornuta was by far the most common and, with only two failures, also the most efficient in acquiring pollen from sapromyiophilous *A. baenzigeri* (males slightly more than females) among 11 other phorid species carrying pollen. Only flowers in anthesis were visited although these were less smelly than fallen ones, the same having been observed with *Sarcophaga nathani* (Sarcophagidae), although these are far too large for being pollinators. Phorids flew to the red flower's central, yellow, patch where they fell off its slippery surface, down the funnel-like entrance of the trap. The flowers' sequestration, pollination and release of the pollinators was similar as found in other *Aristolochia*. It is considered as food-deceptive for male and female pollinators; it is not brood-site deceptive since only one in 65 females had mature eggs.

Keywords: *Aristolochia*, Diptera, new species, Phoridae, food-deceptive pollination, Thailand.

INTRODUCTION

Aristolochia is a genus of climbing plants in the family Aristolochiaceae with some 400 mainly tropical and subtropical species (Gonzales & Poncy 1999). They are of considerable interest for four main reasons. Some species are ornamentals cultivated for the bold shapes and colours of their flowers (e.g. *A. grandiflora* Swartz). Since ancient times several species have been used medicinally (e.g. the birthwort, *A. clematitis* L.). Other species, such as *A. debilis* Sieb. & Zucc., produce toxic substances in their leaves which are sequestered by butterfly caterpillars (e.g. by *Zerynthia polyxena* (Denis & Schiffermüller) and *Atrophaneura alcinous* Klug) as predator deterrents (Rothschild *et al.* 1972; Nishida & Fukami 1989). Finally, their flowers are of much ecological interest due to their complex pollination syndromes (e.g., Delpino 1867; Ule 1898; Cammerloher 1923, 1933; Knoll 1929; Daurmann 1959; Vogel 1965, 1993; Kugler 1970; Faegri & Pijl 1979; Hilje 1984; Endress 1994). Our study mainly deals with the taxonomy and ethology of the pollinators of *Aristolochia baenzigeri* Hansen & Phupathanaphong (Figs 27–29).

Aristolochia trap pollinators by various lures and keep them prisoners for a couple of days. Although the flowers are bisexual, they are not self-pollinating

because they are protogynous, i.e. they are in the female phase during the first day (when insects will deposit pollen from other flowers on the now receptive stigmas, while the anthers are closed). On the second day they are in the male phase (when insects will acquire pollen from the now dehiscent anthers while the stigmas are senescent). The insects are then released. Pollinators are mainly small Diptera, viz. Anthomyiidae, Ceratopogonidae, Chloropidae, Milichiidae, Otitidae, Phoridae, Sepsidae and, in some larger *Aristolochia*, Calliphoridae, Muscidae, Sarcophagidae, though the latter three may not be regular pollinators (e.g. Sprengel 1793; Cammerloher 1923, 1933; Lindner 1928; Havelka 1983; Wolda & Sabrosky 1986; Raz-zak *et al.* 1992; Hall & Brown 1993).

Intriguingly, there are also a number of Phoridae whose larvae feed upon the flowers of some species of *Aristolochia* in Brazil (Hime & Costa 1990) and Panama (Disney & Sakai 2001). However, the adult flies do not appear to be the flowers' pollinators, and at least some species oviposited on fallen, not anthetic flowers. Hence the relationship between such species of *Aristolochia* and Phoridae is basically different from the previously mentioned ones. The finding that some Phoridae develop in *Aristolochia* is additionally interesting in view of the fact that these plants often contain toxins, which need to be neutralized or may be sequestered as predator deterrents (*loc. cit.*).

MATERIALS AND METHODS

Field work was carried out by HB in N Thailand, Mae Hongson Prov., Pai Distr., Pang Mapha, site 1 (km 131.2), 910 m a.s.l., on 5 and 7 June, 2004; *ibid.* but site 2 (km 133.2), 820 m a.s.l., on 12 July, 1995, 31 July to 1 August, 1995, and 13 October, 1995; *ibid.* but site 4 (km 154.8), 720 m a.s.l., on 12 and 14 August, 2005. No *A. baenzigeri* were found with flowers on 30 January, 1996, but on 4 and 5 May, 1996, flower buds in all stages were seen at these sites. The habitat was mixed deciduous forest in limestone hills.

Generally, flowers were watched for several hours for insect visitors and their behaviour noted. For the collection of pollinators, flowers in various stages of anthesis and post-anthesis were placed in plastic boxes of 10 cm diameter and 7 cm height fitted with screw-on caps with brass mesh (mesh clearance 0.1–0.2 mm), fine enough to prevent adult scuttle flies escaping. Dead or euthanized (ethyl acetate) flies were dry-mounted or preserved in 70 % ethyl alcohol. The presence of pollen on the flies was checked by magnifying glass and its identity assessed under compound microscope (600x) by comparing pollen from the phorids (Fig. 29) to that obtained from anthers of *A. baenzigeri* flowers.

Identification of the Phoridae has been based on slide mounted specimens from collections made by HB (Disney 1994, 2001). For gravid females such mounts allow the determination of the number of eggs matured in an ovarian cycle. It also allows examination of the gut contents. None were found to have ingested pollen in the present study.

The identity of female Sarcophagidae (unidentifiable in most tropical species in the female sex) and their gravid status were assessed by forced parturition and the larvae reared to adults to identify their mothers through the male progeny, as detailed in Bänziger & Pape (2004).

Collected material is or will be deposited at Cambridge University Museum of Zoology (CUMZ) and at the Department of Entomology, Faculty of Agriculture, Chiang Mai University (DEFACU).

RESULTS

Systematics (by R. H. L. Disney)

Taxonomy and notes on scuttle flies (Diptera, Phoridae)

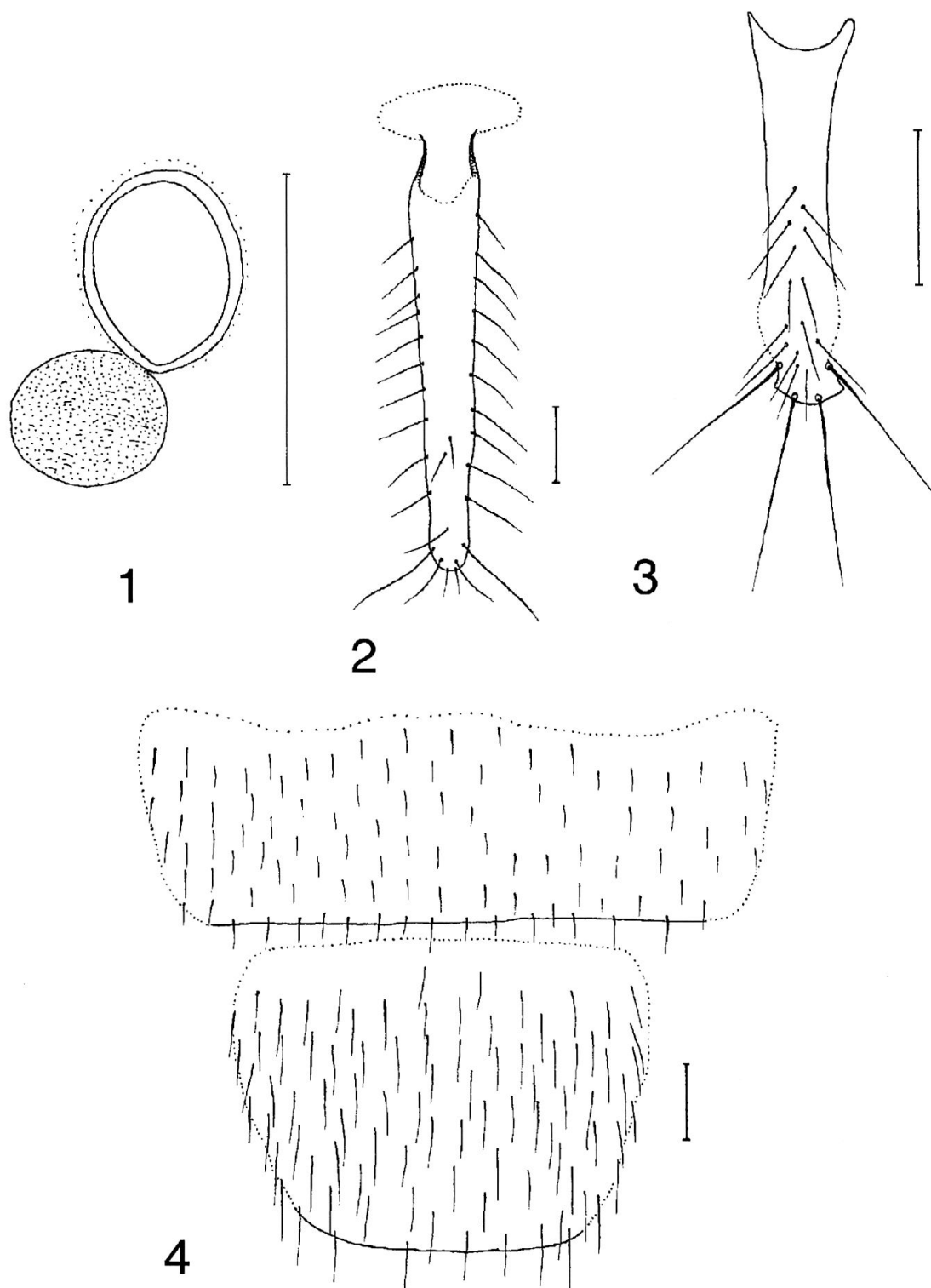
Anevrina Liroy

Brown (1995) provided a key to the eleven then known species, recorded from the Nearctic, Palearctic and Oriental Regions. Michailovskaya (1999) adds a further species from Russia, which runs to couplet 9 of Brown's key.

Anevrina wyatti Disney, n. sp. (Figs 1–4)

In the keys of Brown (1995) this species runs to couplet 4, lead 1, to *A. unispinosa* (Zetterstedt), but is immediately distinguished by its yellow legs and orange brown thorax and abdominal tergites, contrasting with these all being dark brown in *A. unispinosa*. Furthermore the row of hairs along the upper side of vein Rs are unusually pale and short. In other species, such as *A. unispinosa*, these hairs are black and exceed 0.05 mm in length.

Female. Frons brown, clearly broader than long, with 18–20 hairs and dense but very fine microsetae. Supra-antennal (SA) bristles robust. Antials about as far apart as pre-ocellars and clearly closer to anterolaterals than to each other. ALs slightly higher on frons. POs further apart than either is from a mediolateral bristle, which is level with or very slightly higher on frons. Cheek with a single bristle and jowl with 2 longer ones and some fine pale hairs. Postpedicels subglobose, pale brownish orange. Palps yellow, with four bristles and more than a dozen hairs. Labrum pale orange brown and very slightly wider than postpedicel. Labella straw yellow, and each with about twenty hairs on upper face and a submarginal row of about thirty small hairs below. Thorax mainly orange yellow, being paler on sides. Propleuron with three ventral bristles, the rearmost one being shortest; a long posterodorsal bristle preceded by a row of about eight pale fine bristles; 15–20 similar pale bristles away from margins plus one small and one long bristle near middle. Mesopleuron bare. Four notopleural bristles the second being smaller than the rest. Scutellum with two pairs of bristles. Abdominal tergites orange brown. T5–T6 as Fig. 4, The almost colourless T10 plus light brown epiproct as Fig. 3. Venter brown, and with numerous hairs below segments 3–6, those at rear of segment 6 (beyond T6, which does not extend the full length of the segment) are strongly differentiated as long bristle-like hairs (>0.3 mm long). Long pale hairs at rear of tergum 7. Sternite 7 pale brown and as Fig. 2. Tergum 8 with scattered hairs on outer thirds. Posterolateral lobes at rear of sternum 8 not developed, but with a row of long pale hairs at rear margin; in front of these a band of smaller hairs in posterior half; and anterior half with numerous minute hairs whose sockets only are visible at lower magnifications. Cerci almost colourless and about 2.3x as long as broad. The long-



Figs 1–4. *Anevrina wyatti* ♀, details of abdomen. – 1, furca plus possible spermatheca; – 2, sternite 7; – 3, tergite 10 and epiproct; – 4, T5–T6. Scale bars = 0.1 mm.

est (apical) hair at least 1.75x as long as cercus. Furca a very pale hoop alongside a darker body that is possibly a spermatheca (Fig. 1). Legs pale orange yellow. Front tibia with a near-dorsal bristle near mid point and 8–9 small spinules below it. Fore tarsus with posterodorsal hair palisade on segments 1–3 only plus a vestigial palisade in basal third of 4. Mid tibia with the normal basal pair of bristles and a pre-apical anterior bristle. Hairs below basal half of hind femur not differentiated from adjacent hairs of anterior face and thus clearly shorter than those of anteroventral row of outer half. Hind tibia with an anterior bristle in middle of second quarter and a pre-apical anterior bristle. Spinules of apical combs all simple. Wings 3.2 mm long. Costal index 0.65. Costal ratios 6.2 : 4.7 : 1. Costal cilia (of section 3) 0.05–0.06 mm long. The 19–21 hairs along upper side of vein 3 (Rs) are pale and minute (0.03 mm long) and the most basal not differentiated. Fork of vein 3 narrow. With one long, pale, feathered axillary bristle. Sc reaching R1. Veins yellowish brown. Membrane tinged yellowish grey (evident to naked eye when viewed against a white background). Haltere straw yellow, but knob partly a little darker, and in addition to normal hairs on basal third of knob there are a few smaller hairs on distal part.

Material examined. Holotype ♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m, in flower of *A. baenzigeri*, 1.viii.1995, H. Bänziger (CUMZ, 30–12).

Etymology. Named for Nigel Wyatt (Natural History Museum, London) who has identified Calliphoridae and Syrphidae for HB and arranged many loans of critical specimens of Phoridae for RHL D.

***Borophaga* Enderlein**

Brown (1992) proposed splitting up this genus into a number of separate genera (*Godavaria*, *Latiborophaga* and *Peromitra*, in addition to *Borophaga* in a more restricted sense). The polarities of a number of the postulated transformation series advanced in support of this proposal are in contention. For example, the presence of vein 2 is proposed as an autapomorphy of *Godavaria*. However, this character state is undoubtedly part of the groundplan of the family, so Brown's proposal assumes the loss and subsequent reacquisition of this vein. In view of the tentative nature of such speculations, it was considered more sensible to treat these taxa as subgenera, at least until a consensus is achieved (Disney 1994). Despite this suggestion it has not been followed by other authors. I therefore offer the following key to these genera/subgenera:

1. Tip of vein 3 swollen *Borophaga*
- Tip of vein 3 not swollen 2
2. Vein 2 present and strongly developed *Godavaria*
- Vein 2 weak or absent 3
3. Anterior ocellus broader than high. Vein Rs more-or-less straight. (Abdominal sternites 5 and 6 present in male) *Peromitra*
- Anterior ocellus subcircular. Vein Rs deflected near middle. (Female costa thickened. Male hypandrium with dense pubescence) *Latiborophaga*

The two specimens procured in the present study are both females that belong to *Godavaria*, which can only be named in the male sex in our present state of knowledge. The males of the four known species are keyed by Brown (1992) supplemented by Liu (2001).

Borophaga (Godavaria) sp.

Material examined. 2 ♀♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 910 m, in flower of *A. baenzigeri*, 7.vi.2004, H. Bänziger (CUMZ, 30–52).

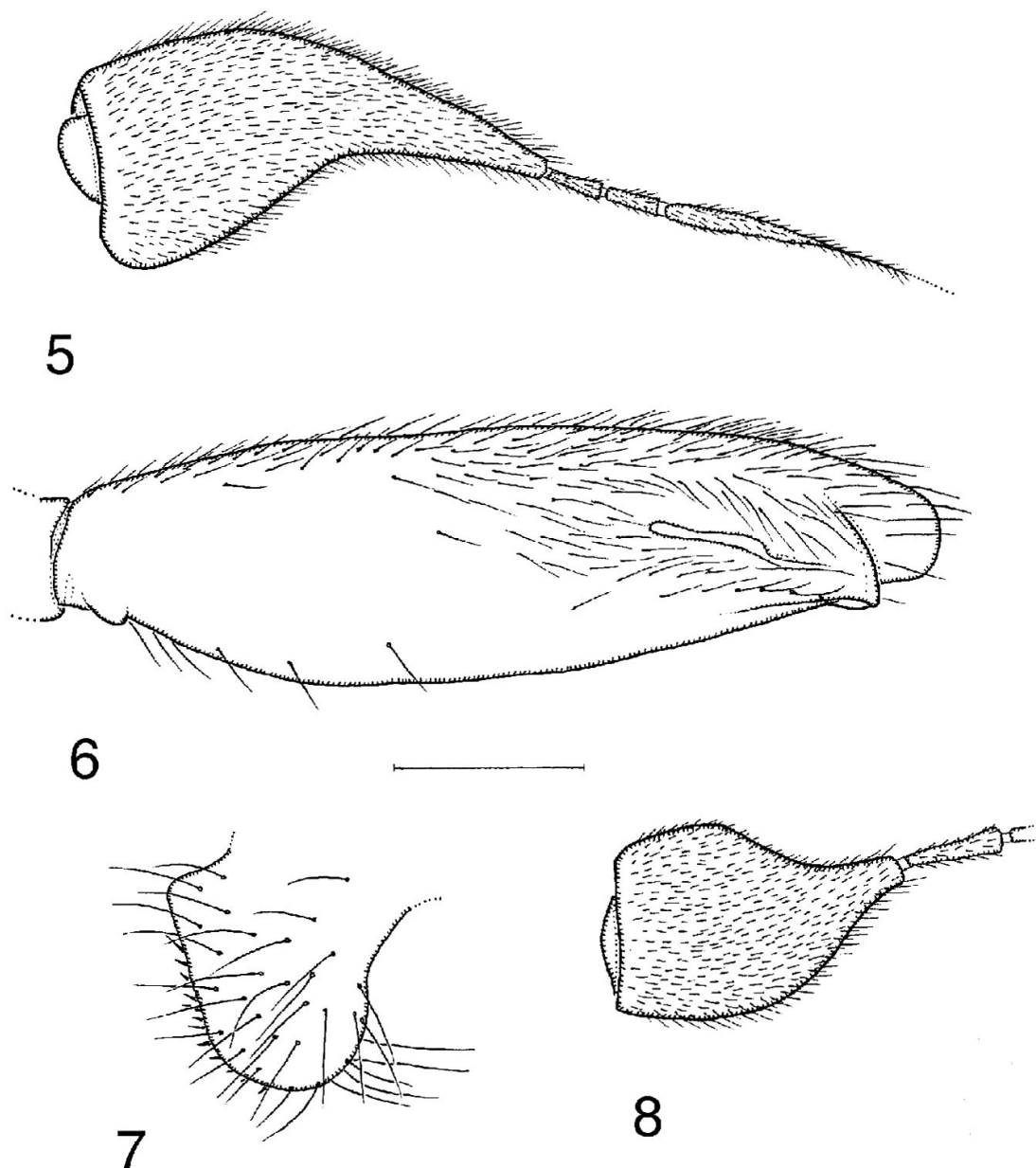
Conicera Meigen

The Oriental species cannot be named in the female sex in our present state of knowledge unless associated with their males, which have been keyed by Disney (1990c) and supplemented by Liu (2001). A male and a female recorded in this study prove to belong to a new species that is described below.

***Conicera thailandiae* Disney, n. sp. (Figs 5–11)**

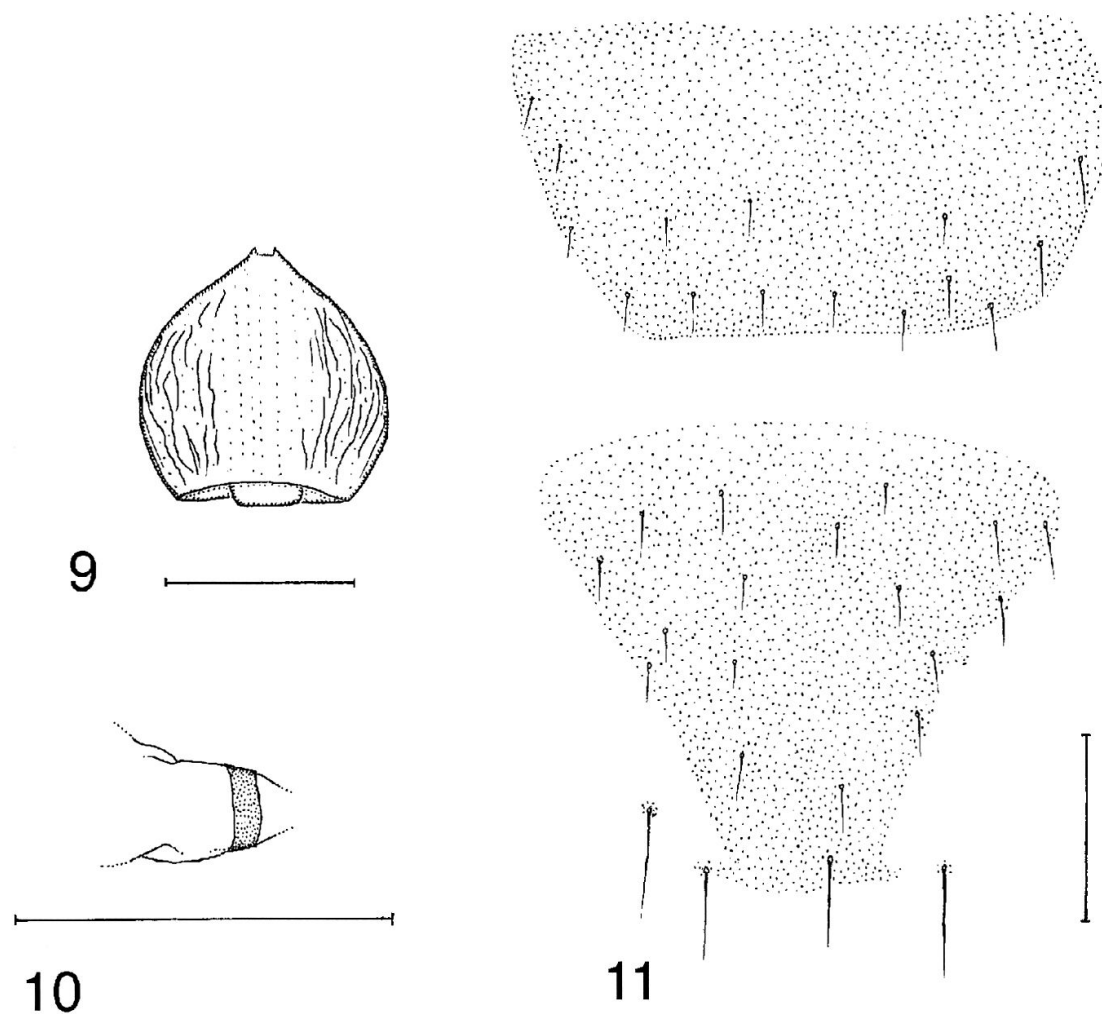
In the keys of Disney (1990c) the male runs to couplet 6, but is immediately distinguished from both species of this couplet by the darker legs. The postpedicel of *C. flavipalpus* Beyer is much narrower than that of the new species. *C. procericornis* Schmitz is not only a much yellower species but its costal section 1 is shorter than section 2. In the new species 1 is clearly longer than 2. The female of *C. procericornis* is immediately distinguished by its subglobose postpedicels, which are typical for females of the genus. In the new species they are apically tapered (as is typical of males) but this apical extension is still much shorter than that of its male. In the keys of Liu (2001) the male runs to couplet 2, but details of the mid femur and right clasper of the hypopygium exclude both species (which are also keyed in Disney 1990c).

Male. Frons brown, clearly broader than long, with 13–14 hairs and dense but very fine microsetae. The single pair of SAs robust but much shorter than antials, which are a little closer together than pro-ocellars. POs closer together than either is from the much shorter mediolateral bristles, which are very slightly lower on frons. Cheek with 2–3 bristles and jowl with 2 longer ones. Postpedicels brown and as Fig. 5. Palps a little paler, with five short bristles and as many hairs. Labrum about 1.3x wider than palps and of similar shade of brown. Labella more straw yellow and with at most a row of a dozen short spinules below each. Thorax brown, being paler on sides. Mesopleuron bare. Four notopleural bristles, the second being out of line and closer to margin. Scutellum with an anterior pair of small hairs (smaller than hairs at rear of scutum) and a posterior pair of bristles. Abdominal tergites brown with small hairs, including those at rear of T6. Venter pale grey, and with a few small hairs below segments 3–6. Hypopygium brown, with the right clasper as Fig. 7. The left clasper is more elongated and both have almost two dozen dark spinules along their inner rear margins. Hind femur brown, mid femur partly brown and partly pale straw yellow. Front femur mainly pale straw yellow, as are the tibiae and tarsi on all legs. Front tibia with ten small near-dorsal spines, the uppermost being longer than the rest. Fore tarsus with posterodorsal hair palisade on all five



Figs 5–8. *Conicera thailandiae*. – 5, ♂, antenna; – 6, ♂, posterior face of mid femur; – 7, ♂, external face of right clasper; – 8, ♀, antenna. Scale bar = 0.1 mm.

segments. Mid femur with long narrow pit organ terminating in a broad subtriangular projection (Fig. 6). Mid tibia with the normal basal pair of bristles, a short pre-apical and one short and one very long apical spur. Hairs below basal half of hind femur not differentiated from the adjacent hairs of anterior face and thus clearly shorter than those of anteroventral row of outer half. Hind tibia with an anterior and an anterodorsal bristle near end of basal quarter, an anterodorsal just below middle, a short anterior bristle in last quarter and a long and a short apical spur. Spinules of apical combs simple. Wings 1.3–1.4 mm long. Costal index 0.45. Costal ratios 1.8 : 1. Costal cilia (of section 3) 0.02–0.03 mm long. No hair at base of vein 3. With



Figs 9–11. *Conicera thailandiae* ♀. – 9, labrum; – 10, sclerotised ring of spermathecal duct, with anterior end to right; – 11, abdominal tergites 5–6. Scale bars = 0.1 mm.

a single long, but fine, feathered axillary bristle. Sc not reaching R1. Veins greyish brown, apart from the very pale vein 7. Membrane lightly tinged grey. Haltere brown.

Female. Frons similar to male. Postpedicels as Fig. 8. Palps similar to male but paler and with longer but finer bristles and much longer and more numerous hairs. Labrum darker, larger and much more robust (Fig. 9). Labella paler, with fewer spinules but with long pale teeth on inner margins. Thorax as male. Abdominal tergites brown, with small hairs apart from a longer posterolateral on T2 and a smaller one on T3 and those at rear of T6. T5–T6 as Fig. 11. Venter greyish brown and with hairs below segments 3–6, those at the rear of 6 being longer. Cerci pale but very lightly tinged brown and about 3x as long as broad. Internally the sclerotised ring of spermathecal duct as Fig. 10. Legs similar to male but mid femur lacks pit organ and process. Wing 1.7–1.8 mm long. Costal index just over 0.5. Costal ratios 1.5–1.6 : 1. Costal cilia (of section 3) 0.03 mm long. Otherwise it and haltere as male.

Material examined. Holotype ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 910 m, in flower of *A. baenzigeri*, 7.vi.2004, H. Bänziger (CUMZ, 30–53). ♀ paratype, as holotype except 820 m, 1.viii.1995 (30–12). The latter had six almost mature eggs present.

Etymology. Named after the country of the type locality.

***Diplonevra* Lioy**

Only the males of the Oriental species have been keyed (Disney 1990a).

***Diplonevra peregrina* (Wiedemann, 1830).**

This is a widespread species that is known to breed in the corpses of bats in caves (McClure *et al.* 1967).

Material examined. 2 ♂♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m and 910 m, in flower of *A. baenzigeri*, 31.vii.1995, 7.vi.2004, H. Bänziger (CUMZ, 30–12 & 52); 2 ♂♂, the same except 720 m, 12.viii.2005 (DEFACU, 30–54).

***Dohrniphora* Dahl**

There is a key to the males only of the Oriental species (Disney 1990b). Apart from a cosmopolitan species (see below), and a few myrmecophilous and termitophilous species, most females of the Oriental species cannot be named in our present state of knowledge unless associated with their males.

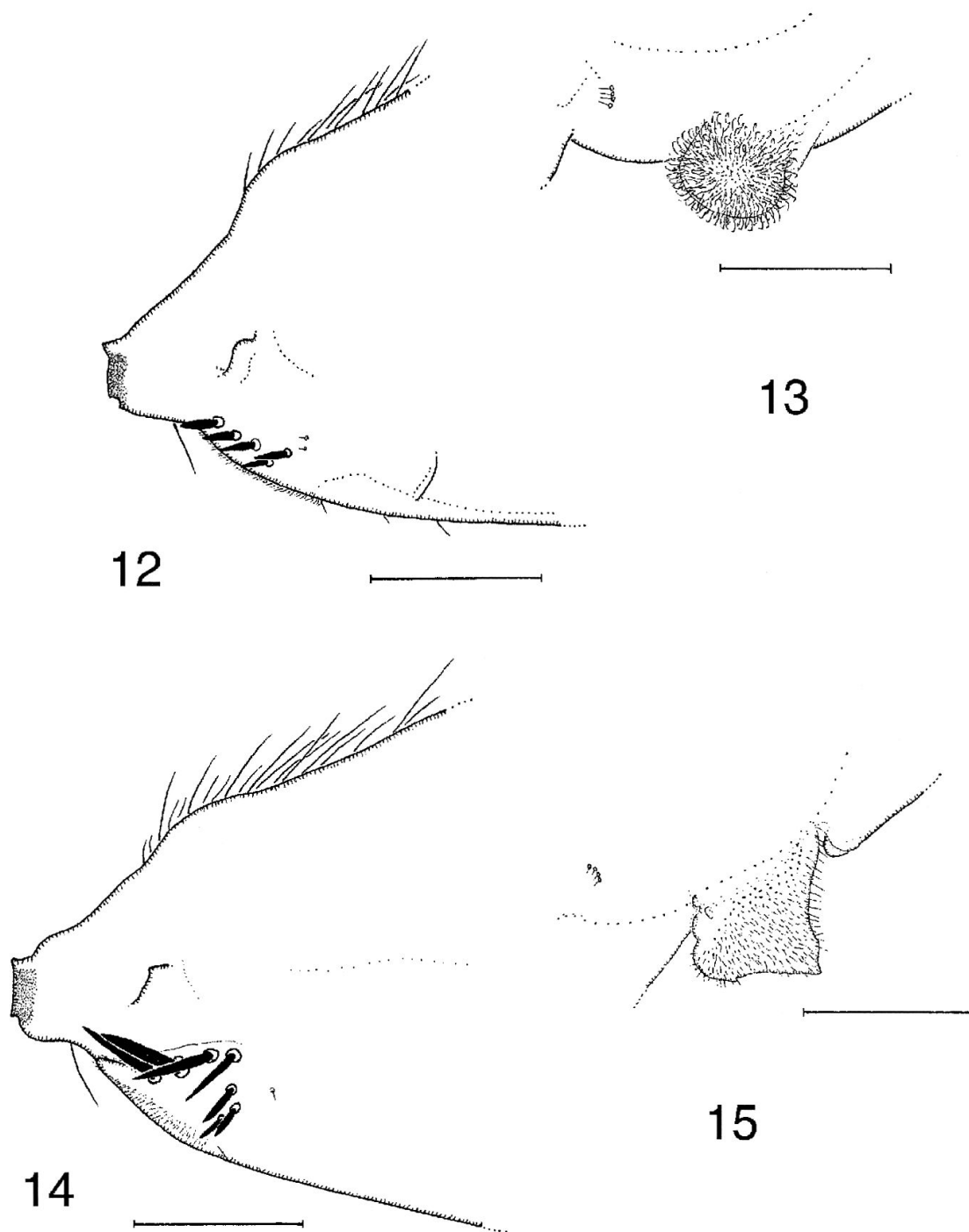
***Dohrniphora cornuta* (Bigot, 1857)**

This is a widespread species through the agency of man, but it probably originates in the Oriental Region. It breeds in a wide range of decaying organic materials (Disney 1994). It has been reported visiting flowers of *Aristolochia elegans* (Brues 1928). It was the commonest species visiting *A. baenzigeri* in our study.

Material examined. 28 ♂♂, 19 ♀♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m and 910 m, in flower of *A. baenzigeri*, 31.vii.1995, 1.viii.1995, 7.vi.2004, H. Bänziger (Some CUMZ, 30–12–14 & 52–53); 2 ♂♂, the same except 720 m, 12.viii.2005 (CUMZ, 30–54).

***Dohrniphora sorora* Disney, n. sp. (Figs 12–13)**

In the key to males (Disney 1990b) this species runs to couplet 46, where it is intermediate between *D. barroni* Disney and *D. georgei* Disney. The former has a patch of microsetae on the posterior face (similar to those on the anterior face) of the hind femur just beyond the row of spinules (as depicted in Fig. 17A in Disney, 1990b). *D. georgei* and the new species lack this patch of microsetae. Abdominal tergites 3–5 are almost entirely brown in *D. georgei*, with only small, short, yellow median emarginations of the front margins of the tergites. By contrast in *D. sorora* the yellow patches extend more than half the length of each tergite and are evident as descending wedges of yellow when viewed from the side. A subsequently described species, *D. malaysiae* Green (1997), also runs to this couplet. It resembles *D. georgei* and *D. sorora*. Its yellow regions of T3–T5 only extend more than half the lengths along the median line and are not evident when viewed from the side.



Figs 12–15. *Dohrniphora* ♂♂, posterior faces of details of hind legs. 12–13. *D. sorora*. – 12, base of femur; – 13, coxal lobe. 14–15, *D. thailandensis*. – 14, base of femur; – 15, coxal lobe. Scale bars = 0.1 mm.

Otherwise it differs from *D. sorora* in having a large patch devoid of hairs on the anterior face of the hind femur opposite and beyond the row of spinules on the posterior face. In *D. sorora* this patch is much smaller (with only 2–3 hairs missing).

The females of *D. malaysiae* and *D. sorora* are immediately distinguished by the hairs on segments 2–4, and the anterior half of 5, of the abdominal venter. In

the former these hairs are reduced in size, being smaller than those on tergites 1–4. In *D. sorora* these hairs are not reduced and are clearly larger than those on the tergites. The females also resemble those of *D. cornuta*, but its abdomen has a darker venter and at least tergite 2 is partly yellow. In addition the dorsal hair palisade of the mid tibia is longer, extending about half its length (compared with only about a third in *D. cornuta*).

Male. Frons brown, broader than long, with 60–80 hairs and dense but very fine microsetae. SAs almost as long as antials, which are about twice as far from each other as either is from an anterolateral, all four bristles being at about the same level on the frons. Pre-ocellars about as far apart as antials and clearly further apart than either is from a mediolateral bristle, which is slightly lower on frons. Cheek with only one bristle and jowl with 2 longer ones. Postpedicels a little longer than greatest breadth and brown but not dark. Palps yellow, the small basal segment being paler and the second segment darker. The latter is about twice as long as its greatest breadth and has 15–25 hairs plus four apical bristles. Proboscis a little darker than palps, with the labrum about as wide as segment 2 of a palp but only about three fifths of its length. Labella relatively narrow. Thorax with dirty straw yellow to light brown scutum, a light brown scutellum, and pale straw yellow pleural regions. Mesopleuron with a dozen hairs below and behind the anterior spiracle. No humeral bristle. Three notopleural bristles, the front one being longer and more robust than those behind, and no cleft in front of it. Scutellum with an anterior pair of small hairs (only as long as those in middle of scutum) and a posterior pair of bristles. Abdominal tergites part brown and part yellow. On each tergite the yellow extends from the middle of the anterior margin in a triangle extending more than half the length. On T2 and T6 the yellow extends to the lateral margins each side. On T3–T5 the yellow is largely restricted to the median third, but in side view is evident as a wedge of yellow in the anterior half. The hairs are small and sparse, but are a little longer and more numerous on T6. Venter pale straw yellow, and with hairs below segments 4 and 5 and 3–4 long bristles at the rear of 5. Hypopygium typical of the genus, with dusky straw yellow epandrium and brown hypandrium, apart from the posterior lobe, and the anal tube is straw yellow. Legs entirely straw yellow. Front tibia with 4–5 near dorsal spines. Fore tarsus with posterodorsal hair palisade on segments 1–5. Dorsal hair palisade of mid tibia extends about half its length. Base of hind femur as Fig. 12, there being 4–5 spinules. Hind coxal lobe as Fig. 13. Hind tibia with 10–11 fine, but clearly differentiated, posterodorsal hairs and some smaller differentiated short hairs behind these in the basal half to two thirds. Apart from the dorsal apical spine and ventral spurs the tibia lacks bristles. Spinules of apical combs all simple. Wings 1.5–1.8 mm long. Costal index 0.48–0.49. Costal ratios 7.9–8.2 : 1.6–1.7 : 1. Costal cilia (of section 3) 0.04 mm long. Hair at base of vein 3 subequal to costal cilia of dorsal row. With the normal single, feathered, axillary bristle characteristic of the genus. Sc fading away as its tip approaches R1. Veins brown, apart from very pale vein 7. Membrane tinged greyish brown (evident when viewed with hand lens against a white background). Haltere straw yellow.

Female. Very similar to male but with upper part of mesopleuron and propleuron brown and abdominal venter is brown. Otherwise it differs as follows. Postpedicels more nearly globose. Palps broader, being only about 1.8x as long as greatest breadth, with at least two dozen hairs and five longer bristles at apex. Probos-

cis with labrum about three times as long as greatest breadth, which is about 1.2x as broad as a palp. The hypopharynx ends in a pair of mandible-like, toothed, appendages; but the labella are reduced. Abdominal tergites 1–4 present, but T3 is narrower than T2 and T4 narrower than T3. T1 is brown but yellow at the sides. T2 is largely yellow, but brown laterally and along the hind margin. T3 and T4 are brown with anteromedian wedges of yellow that variably extend laterally and posteriorly along the midline. Venter brown with hairs below from segment 3 onwards, and a pair of bristles at the rear of segment 6. The cerci and rest of segment 10 are straw yellow. Legs similar to male but hind femur lacks spinules but has a row of hairs below basal half similar to those of anteroventral row of outer half. No hind coxal lobe. Wing as male except 2.0–2.1 mm long. Costal index 0.53–0.54. Costal ratios 7.6–8.9 : 2.4–2.9 : 1. Costal cilia (of section 3) 0.05 mm long. Otherwise it is as male. Haltere as male but knob more dusky.

One female retained four mature eggs, each measuring 0.4–0.5 x 0.2–0.3 mm.

Material examined. Holotype ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 720 m, in flower of *A. baenzigeri*, 12.viii.2005, H. Bänziger (CUMZ, 30–54). Paratypes, 3 ♂♂ as holotype; 3 ♀♀ as holotype except 910 m, 7.vi.2004 (CUMZ, 30–53).

Etymology. Soror means sister, and refers to this being a sibling species of *D. malaysiae*.

***Dohrniphora thailandensis* Disney, n. sp. (Figs 14–15)**

In the key to males (Disney 1990b) this species runs to couplet 43, lead 1, to *D. palawanensis* Disney; but it is immediately distinguished from the latter by its abdominal tergites being entirely brown and having six spinules at the base of the hind femur. In Liu's (2001) key it runs to couplet 8, lead 2, to *D. insulana* Liu; but the spinule complex at the base of the hind femur differs and the latter has a yellow postpedicel.

Male. Frons brown, broader than long, with 64–62 hairs and dense but minute microsetae. SAs almost as long as antials, which are almost twice as far from each other as either is from an anterolateral, all four bristles being at about the same level on the frons. Pre-ocellars about as far apart as antials and a little further apart than either is from a mediolateral bristle, which is a little lower on frons. Cheek with only one bristle and jowl with 2 longer ones. Postpedicels a little longer than greatest breadth and light brown. Palps yellow, the small basal segment being paler and the second segment darker. The latter is about 2.4x as long as its greatest breadth and has 12–13 hairs plus 4–5 apical bristles. Proboscis a little darker than palps, with the labrum almost as wide as segment 2 of a palp but only about two thirds of its length. Labella relatively narrow. Thorax brown with paler pleural regions. Mesopleuron with 6–9 hairs below and behind the anterior spiracle. No humeral bristle. Three notopleural bristles, the front one being longer and more robust than those behind, and no cleft in front of it. Scutellum with an anterior pair of small hairs (only as long as those in middle of scutum) and a posterior pair of bristles. Abdominal tergites brown with small and sparse hairs except on T6, there they are more numerous and clearly longer at rear margin. Venter dusky straw yellow, and with hairs below segment 4 and several bristles at rear of 5. Hypopygium typical of the genus, with brown epandrium and hypandrium, and a straw yellow anal tube.

Legs entirely straw yellow apart from brown dorsal edge of hind femur. Front tibia with 4 nearly dorsal spines. Fore tarsus with posterodorsal hair palisade on segments 1–5. Dorsal hair palisade of mid tibia extends about a third of its length. Base of hind femur as Fig. 14. Hind coxal lobe as Fig. 15. Hind tibia with 11 fine, but clearly differentiated, posterodorsal hairs and some smaller differentiated short hairs behind these in the basal half to two thirds. Apart from the dorsal apical spine and ventral spurs the tibia lacks bristles. Spinules of apical combs all simple. Wings 1.6–1.7 mm long. Costal index 0.48–0.49. Costal ratios 7.3 : 2.1–2.2 : 1. Costal cilia (of section 3) 0.04–0.05 mm long. Hair at base of vein 3 subequal to costal cilia of dorsal row. With the normal single, feathered, axillary bristle characteristic of the genus. Sc fading away as its tip approaches R1. Thick veins brown, thin veins more greyish apart from very pale vein 7. Membrane lightly tinged grey. Haltere straw yellow.

Material examined. Holotype ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 720 m, in flower of *A. baenzigeri*, 12.viii.2005, H. Bänziger (CUMZ, 30–54).

Etymology. Named after the country of the type locality.

Megaselia Rondani

This giant genus has more than 1400 described species and this is probably only around 10 % of the total in the world today. The taxonomy of this genus is currently largely a task for specialists. Disney (1994) provides a guide to the identification literature, but this is rapidly becoming out of date. Eight species were recorded. Four new to science are described and named. One female specimen is probably an undescribed species, but it cannot be named until associated with its male.

***Megaselia deningi* Disney, 1982**

The scavenging larvae of this species are primarily aquatic in the waters of pitcher plants (*Nepenthes* L.) and the internodes of giant bamboos (*Gigantochloa scortechini* Gamble). They have also been reported in takuwan (Japanese garden radishes pickled with rice bran and salt) and in a case of urinary myiasis (Disney 2004).

Material examined. 1 ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 720 m, in flower of *A. baenzigeri*, 12.viii.2005, H. Bänziger (CUMZ, 30–54).

***Megaselia hanseni* Disney, n. sp. (Fig. 16)**

In the keys of Borgmeier (1967b) this species will run to couplet 79 on page 90, to *M. bisecta* Brues. It is immediately distinguished by the lack of a hair at the base of vein 3, the postpedicels being yellowish brown (those of *M. bisecta* being pale yellow) and vein 4 originating close to vein 3. The subsequently described *M. robinsoni* Disney will also run to this couplet and lead. Its male is distinguished from *M. hanseni* by its enlarged and densely spinose labella, its abdominal tergites 2–6 being partly yellow and by the bifid spinules of the hind tibial apical comb being restricted to the region dorsal to the posteroventral spur (in *M. hanseni* they are restricted to the pair of spinules between the PVS and the longer ventral spur).

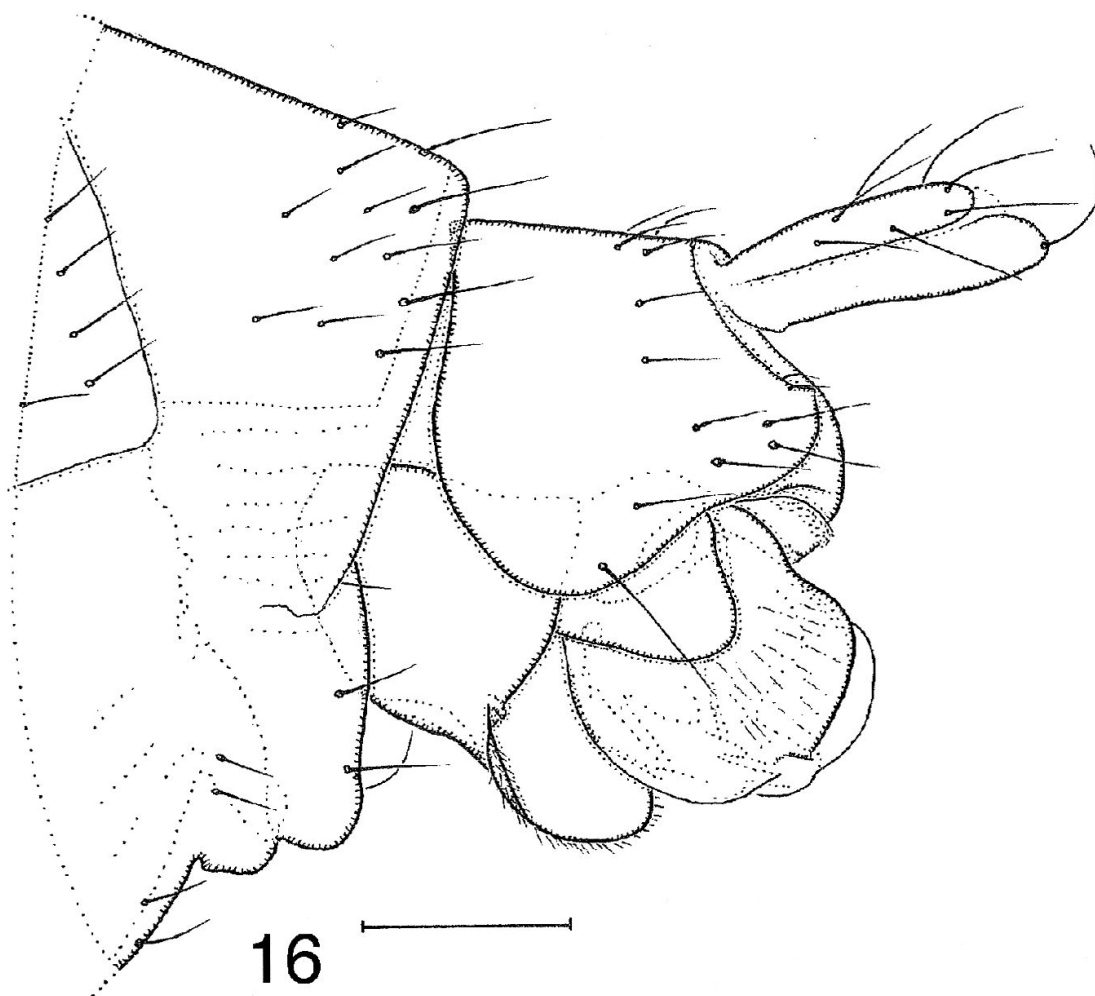


Fig. 16. *Megaselia hanseni* ♂, left face of hypopygium. Scale bar = 0.1 mm.

Male. Frons yellowish brown to brown, broader than long, with 48–68 hairs and dense but fine microsetae. Lower supra-antennal bristles clearly smaller than upper pair, which are closer together than pre-ocellars. Antials about level with upper SAs, which are distinctly higher on frons. POs and mediolaterals equidistant or a little further apart than either is from an ML bristle, which is slightly higher on frons. With two short bristles on cheek and a longer pair on jowl. Subglobose yellowish brown to light brown postpedicel lacks SPS vesicles. Straw yellow palps with 5–6 bristles, which are short apart from the longer apical one, and 2–4 hairs. Labrum straw yellow and about 0.6x as broad as postpedicel. Labella a little paler and with only a few small spinules below (mainly restricted to tips). Thorax orange brown to brown but paler on sides. Each side of scutum with a humeral bristle, three notopleurals, an intra-alar, a postalar, a prescutellar dorsocentral and a small bristle between the last two. Mesopleuron bare. Scutellum with an anterior pair of small hairs (subequal to those in middle of scutum) and a posterior pair of bristles. Abdominal tergites brown, with fine hairs apart from longer ones at rear of T6. Venter straw yellow lightly tinged brown and with hairs below segments 3–6. Hypopygium with brown epandrium and straw yellow lightly tinged brown hypandrium and anal

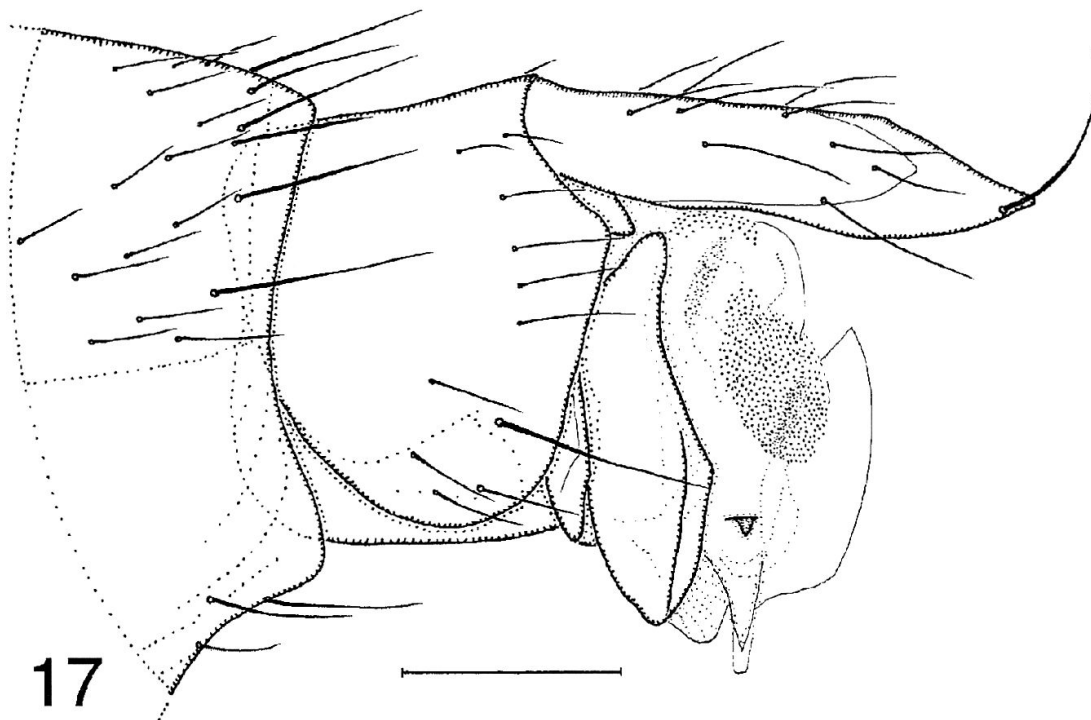


Fig. 17. *Megaselia leucopleuralis* ♂, left face of hypopygium. Scale bar = 0.1 mm.

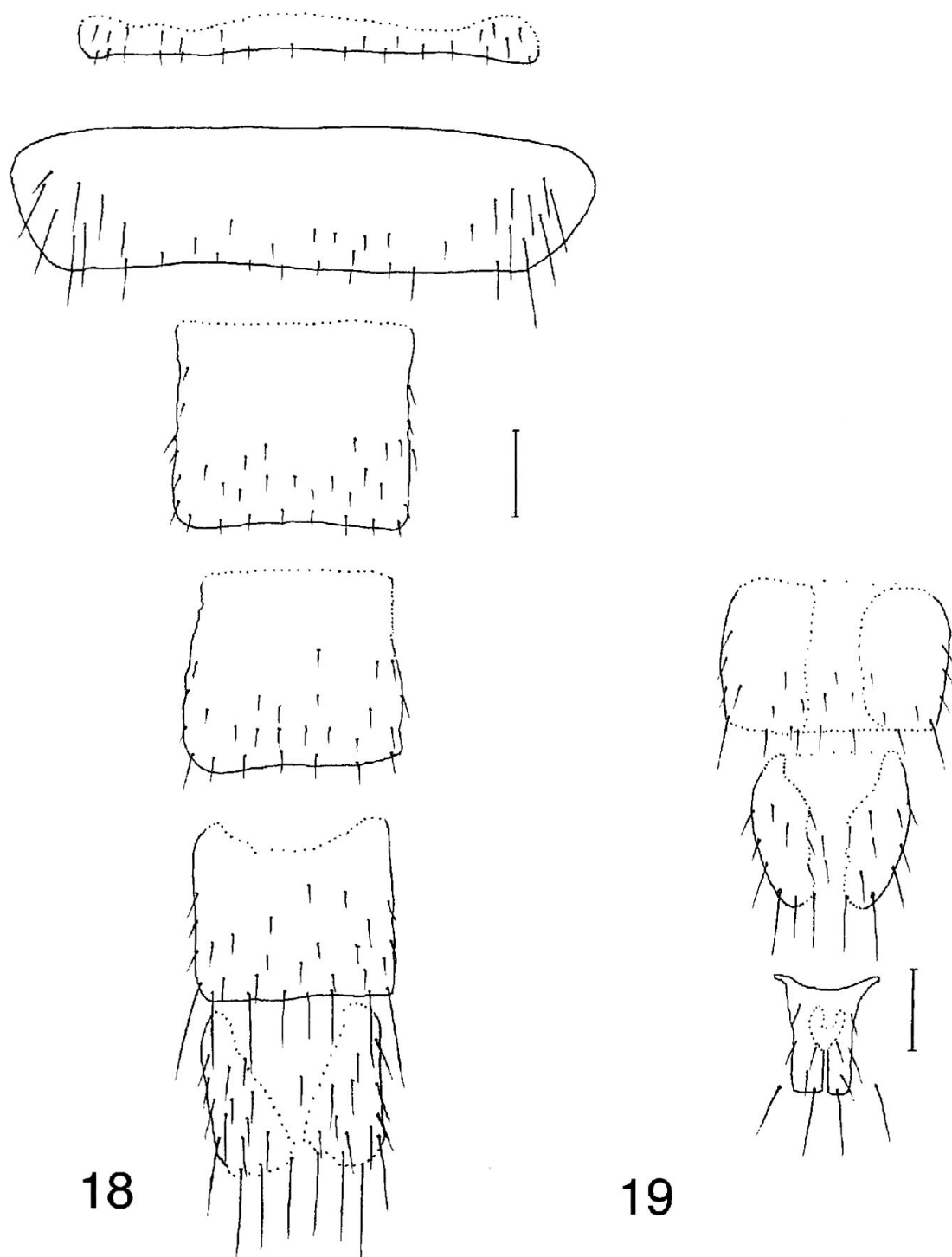
tube, and as Fig. 16. The right lobe is broadly rounded apically and a little shorter than the left lobe, which lies in a more ventral position. Legs straw yellow apart from brown tip of hind femur and narrowly along dorsal edge of hind tibia. Front tarsus slender with posterodorsal hair palisade on segments 1–4 only, and 5 is a little longer than segment 4. Mid tibia with dorsal hair palisade extending about 0.7x length. Hind femur with most of hairs below basal half distinctly longer than those of the anteroventral row in outer half. Hind tibia with 12–13 clearly differentiated posterodorsal hairs. Apical comb of posterior face with the pair of spinules between the posteroventral spur and the longer ventral spur bifid, the rest being all simple. Wings 1.3–1.5 mm long. Costal index 0.50–0.53. Costal ratios 3.6–4.3 : 2.3–2.8 : 1. Costal cilia, of anterior row of section 3, 0.05–0.07 mm long. Vein Sc ends before reaching R1. No hair at base of vein 3. Two axillary bristles, the outermost being longer than costal cilia. Veins yellowish brown, 7 being paler. Membrane lightly tinged yellowish grey to grey. Halteres brown.

Material examined. Holotype ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m, in flower of *A. baenzigeri*, 1.viii.1995, H. Bänziger (CUMZ, 30–12). 2 paratype ♂♂, as holotype (30–12, 30–14).

Etymology. Named after Dr Bertel Hansen, who not only named the host plant but during two decades identified scores of plants collected by HB.

***Megaselia leucopleuralis* Disney, n. sp. (Figs 17–18)**

In the keys of Borgmeier (1967b) the male runs to couplet 81 on page 90, to the female of *M. chipensis* (Brues), whose male is unknown. In this couplet the thorax is stated to be yellow, but in the original description it is described as having



Figs 18–19. *Megaselia* ♀♀, abdominal tergites. – 18, *M. leucopleuralis* T1–T6; – 19, *Megaselia* sp. TH8, T5–7. Scale bar = 0.1 mm.

reddish brown pleurae and a darker dorsum. Either way it differs from the brown dorsum and contrasting pale straw yellow of the pleurae of the new species. However, the female runs to couplet 21 on page 84, to the female of *M. brevisecta* Brues, whose male is also unknown. The latter's female has a yellow abdominal venter and

the tergites are only gradually narrowed, in contrast to the new species.

Male. Frons chestnut brown, broader than long, with 35–42 hairs and dense but fine microsetae. Upper SAs robust and at least twice as long as lower pair. Upper SAs a little higher on frons than antials, which are about midway between upper SAs and anterolaterals, which are slightly higher on frons. Pre-ocellars almost twice as far apart as upper SAs and a little further apart than either is from a mediolateral bristle, which is level with or very slightly higher on frons. Cheek with two small bristles and jowl with two much longer ones. Postpedicels subglobose, pale brownish yellow, with about two dozen SPS vesicles that are subequal to the diameters of sockets of bristles on palps. The latter pale straw yellow, with six bristles and as many hairs. Labrum straw yellow and about 1.8x as broad as palps and about 0.6x as wide as postpedicel. Labella also pale, each being about as wide as a palp, and with only a few, widely spaced, short spinules below. Thorax brown on top, but largely whitish yellow on sides. Mesopleuron bare. Two notopleural bristles and no cleft in front of these. Scutellum with an anterior pair of hairs subequal to hairs in middle of scutum and a posterior pair of bristles. Abdominal tergites brown with some of the posterolateral hairs on T2–T5 differentiated from the rest and those at rear of T6 longer (Fig. 17). Venter very pale grey, and with hairs below segments 4–6. Hypopygium brown, apart from whitish yellow anal tube, and as Fig. 17. Right lobe of hypandrium shorter than that of left side (which is distally obscured in Fig. 17 by the extruded penis complex). With two rectal papillae. Legs whitish yellow, except for brown apical quarter of hind femur. Fore tarsus with posterodorsal hair palisade on segments 1–5, and segment 5 a little longer than 4. Dorsal hair palisade of mid tibia extends almost 0.8x of length. 4–5 hairs below basal half of hind femur clearly longer than those of anteroventral row of outer half. Hind tibia with ten differentiated posterodorsal hairs, the last being more spine like. Spinules of apical combs simple. Wings 1.4–1.5 mm long. Costal index 0.51–0.52. Costal ratios 3.4–3.5 : 4.1 : 1. Costal cilia (of section 3) 0.05–0.06 mm long. No hair at base of vein 3. With three axillary bristles, the outermost one being longer than costal cilia. Sc reaching R1. Veins brown, but 7 paler. Membrane tinged brownish grey (evident to naked eye when viewed against a white background). Haltere brown.

Female. Frons similar to male but paler. Postpedicels with fewer SPS vesicles. Palps with seven bristles and twice as many hairs. Labrum darker and 1.1–1.2x wider than diameter of postpedicel. Otherwise head similar to male. Thorax as male but a little paler on top and the anterior scutellars are almost as strong as the posterior notopleural bristles. Abdominal tergites brown. T1–T6 as Fig. 18. T7 with concave anterior margin as wide as T6 but tapering to half this width at hind margin, from which a narrow unpigmented median wedge extends forwards for almost half the length of the tergite. T8 is a paler rectangle (a little longer than broad). Venter grey with yellowish intersegmental bands, and with conspicuous hairs below segments 3–6. Sternite 7 narrow, being widest in the middle third and with the anterior fifth strongly tapered to a pointed process. The rear margin has a pair of long bristles and there are half a dozen hairs in the posterior three fifths. Posterolateral lobes at rear of sternum 8 project about 0.05 mm and bear three long bristles and twice as many hairs in front of these. Cerci very pale, at least twice as long as broad, and with one very long bristle and several shorter hairs. Epiproct with a pair of long bristles and a pair of short hairs. With two rectal papillae. Furca a sclerotised hoop about 0.13 mm in diameter. A paler, ill-defined, scaly, vaginal sclerite is also pres-

ent. Dufour's crop mechanism broadly rounded behind and measuring 0.25–0.26 mm in length and 0.18 mm in its greatest breadth. Legs similar to male. Wing as male except length is 1.7–1.8 mm. Costal index 0.58. Costal ratios 4.0 : 5.0 : 1. Costal cilia 0.06 mm long. Otherwise it and haltere as male.

This female was gravid, with six eggs measuring about 0.63–0.65 x 0.22–0.24 mm. The dorsal face of each egg comprises a demarcated plastron consisting of sub-parallel, irregular and repeatedly interrupted, ridges running the length of the egg.

Material examined. Holotype ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 720 m, in flower of *A. baenzigeri*, 12.viii.2005, H. Bänziger (CUMZ, 30–54). Paratype ♀, same data as holotype.

Etymology. The name refers to the pale thoracic pleura.

***Megaselia malaisei* Beyer, 1958**

This species was described from a series of females from Burma.

Material examined. 1 ♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 720 m, in flower of *A. baenzigeri*, 12.viii.2005, H. Bänziger (CUMZ, 30–54).

***Megaselia martensi* Disney, 1999**

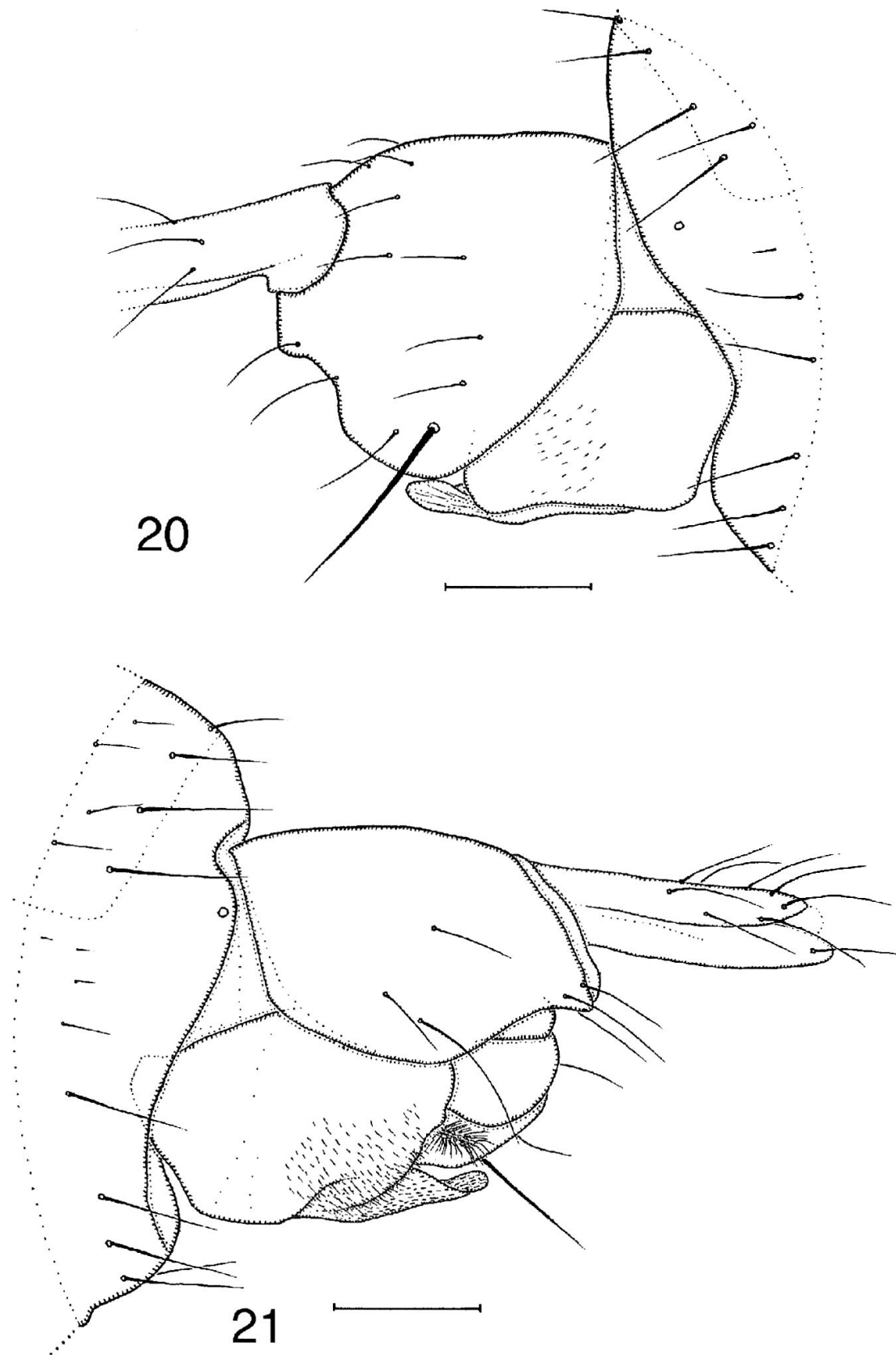
This species was described from a single male from Nepal (Disney, 1999a). In Borgmeier's (1967b) key it will run out at couplet 59 on page 89 or couplet 105 on page 92.

Material examined. 1 ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 720 m, in flower of *A. baenzigeri*, 12.viii.2005, H. Bänziger (CUMZ, 30–54).

***Megaselia pangmaphae* Disney, n. sp. (Figs 20–21)**

In the keys of Borgmeier (1967b) this species runs to couplet 68 on page 90, but clashes with both leads; because the hind femora are entirely yellow, the first costal section is longer than 2+3, and abdominal tergites 5 and 6 are largely yellow. Subsequently described species running to this couplet have different hypopygia and the tip of the hind femur is brown and/or some of the spinules of the apical comb of hind tibia are bifid.

Male. Frons orange brown (but darker around ocelli), clearly broader than long, with 40–44 hairs and dense but very fine microsetae. Lower SAs clearly shorter and less robust than upper pair and closer together. Upper SAs are level with or slightly higher on frons than anterolaterals but distinctly further from antials than latter are from ALs, which are higher on frons. Pre-ocellars clearly further apart than upper SAs and slightly further from each other than either is from a mediolateral bristle, which is about the same level on frons. Cheek with 1–4 bristles and jowl with two longer ones. Postpedicels subglobose, straw yellow, without SPS vesicles. Palps similar colour, with seven bristles (four long and three short) and 4–5 hairs. Labrum coloured as palps and about 0.8x as wide as postpedicel. Labella also coloured as palps and with very few short spinules at tips. Thorax mainly orange yellow apart from brown on pteropleuron. Mesopleuron bare. Three notopleural bristles. Scutellum with an anterior pair of hairs (at most as long as hairs at rear of



Figs 20–21. *Megaselia pangmaphae* ♂, hypopygium. – 20, right face of epandrium and hypandrium; – 21, left face of hypopygium. Scale bars = 0.1 mm.

scutum) and a posterior pair of bristles. Abdominal tergites partly yellow: T1 brown, at least anterior half of T2 yellow, T3 brown with a yellow anteromedian patch, T4 brown with a broad yellow median band in anterior half, T5 yellow but a little darker towards rear margin, and T6 yellow with a narrowly brown hind margin. All tergites with short sparse hairs, but T2 with some longer hairs at sides, T3–T5 with some moderately longer hairs posterolaterally and with the hairs at rear of T6 clearly longer than rest (Figs 18–19). Venter whitish straw yellow and with hairs below segments 3–6, but those at rear of segments 5 and 6 as strong as those at rear of T6 (Fig. 21). Hypopygium orange brown, with straw yellow anal tube, and as Figs 20–21. Legs straw yellow apart from brown patch on mid coxa. Fore tarsus with a posterodorsal hair palisade on all five segments. Dorsal hair palisade of mid tibia extends about three quarters of length and tarsal segment 5 is almost 1.5x as broad as 4 and about 1.7x as long. The longest hairs below basal half of hind femur at most about as long as those of anteroventral row of outer half. Hind tibia with 12–13 differentiated posterodorsal hairs, the lowest 5–6 being distinctly more robust. Spinules of apical combs all simple. Wings 1.5–1.6 mm long. Costal index 0.48–0.49. Costal ratios 4.7 : 3.1 : 1. Costal cilia (of section 3) 0.05–0.06 mm long. No hair at base of vein 3. With two axillary bristles, the outer one being longer than costal cilia. Sc clearly not reaching R1. Veins yellowish brown, but 7 is obscure. Membrane only very lightly tinged grey. Haltere brown but not dark.

Material examined. Holotype ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m, in flower of *A. baenzigeri*, 1.viii.1995, H. Bänziger (CUMZ, 30–12).

Etymology. Named after the type locality.

***Megaselia prachavali* Disney, n. sp. (Fig. 22)**

In the keys of Borgmeier (1967a) this species will readily run to couplet 38 on page 204, where the choice is between halteres with ‘yellow’ or ‘dark’ knobs. The yellowish brown knobs of this species means one needs to follow both leads, but dark knobs is the preferred option. The first option takes this male to couplets 41 and the second to couplet 52. All four leads do not fit. Two subsequently described species will run to the same couplets, *M. weissflogi* Disney to 41 and *M. chlumetiae* Disney to couplet 52. Both differ in the details of the hypopygia and the former has a much narrower frons and the latter has brown, as opposed to yellowish, postpedicels. Indeed both species are generally darker than the new species.

Male. Frons brown, a little broader than long (1.2 : 1), with 76–80 hairs and dense but fine microsetae. Lower SAs much shorter and finer than upper pair and a little closer together. Upper SAs about level with antials, which are clearly closer to them than to anterolaterals, which are clearly higher on frons. Pre-ocellars distinctly further apart than upper SAs and a little further apart than either is from a mediolateral bristle, which is very slightly higher on frons. Cheek with two bristles and jowl with two longer ones. Postpedicels subglobose, straw yellow lightly tinged brown, and lacking SPS vesicles. Palps straw yellow with six bristles and 1–2 strong hairs. Labrum slightly darker than palps and about 0.5–0.6x as wide as postpedicel. Labella coloured as palps and with a few short spinules around apical margins. Thorax orange to yellowish brown, being paler on sides. Mesopleuron with 4–5 hairs and a differentiated bristle subequal to middle notopleural bristle. Three

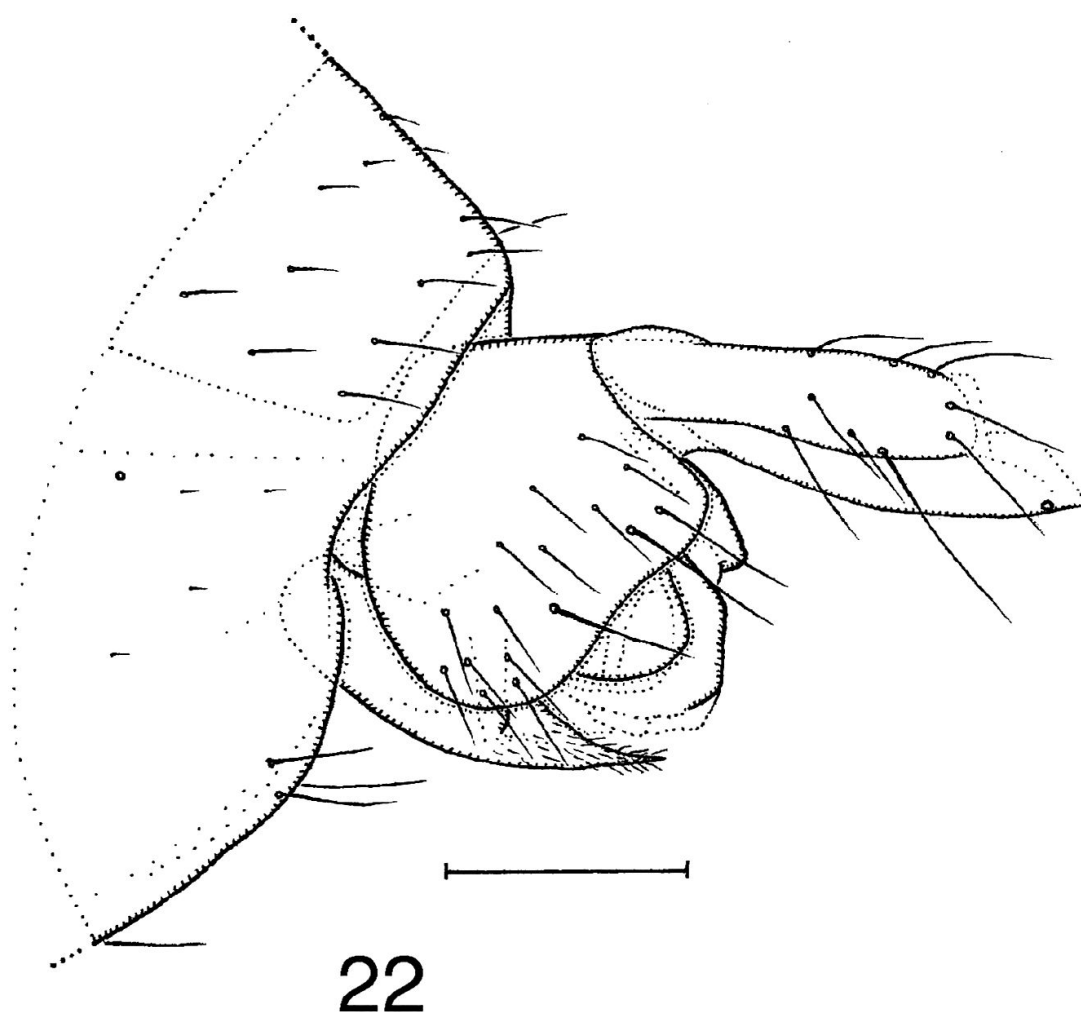


Fig. 22. *Megaselia prachavali* ♂, left face of hypopygium. Scale bar = 0.1 mm.

notopleural bristles, the middle one being a little shorter than the other two. Scutellum with an anterior pair of hairs (subequal to hairs on scutum adjacent to notopleuron) and a posterior pair of bristles. Abdominal tergites mainly brown but T2–T5 with paler regions along front and rear margins and also front margin of T6. The hairs mainly minute and sparse but a little longer posterolaterally on T2–T5 and at rear of T6 (Fig. 22). Venter pale straw yellow, with hairs below segments 3–6. Hypopygium brown, with straw yellow anal tube, and as Fig. 22. (The hairs at the tip of the proctiger are missing from the only available specimen. Their sockets are distinctly larger than those of the hairs on the cerci). Right side of epandrium emarginate in anterior half. Right lobe of hypandrium not developed. Legs straw yellow, apart from brown on tip of hind femur and mid coxa. Fore tarsus with posterodorsal hair palisade on all five segments. Dorsal hair palisade of mid tibia extends about 0.7x length. Hairs below basal half of hind femur subequal to or a little longer than those of anteroventral row of outer half. Hind tibia with 11–12 differentiated posterodorsal hairs, the lowest 5–6 being more robust than the rest. Spinules of apical combs all simple. Wings 1.2 mm long. Costal index 0.47–0.48. Cos-

tal ratios 7.0 : 3.7–3.8 : 1. Costal cilia (of section 3) 0.05–0.06 mm long. Hair at base of vein 3 minute (easily overlooked at low magnifications). With two axillary bristles, which are longer than costal cilia. Sc fading away just before reaching R1. Veins yellowish brown. Membrane only very lightly tinged grey. Haltere with brown stem and paler brown knob.

Material examined. Holotype ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m, in flower of *A. baenzigeri*, 1.viii.1995, H. Bänziger (CUMZ, 30–12).

Etymology. Named after Mr Prachaval Sukumalanand who supported Dr Hans Bänziger's projects for more than two decades.

***Megaselia* sp. TH8 (Fig. 19)**

This species cannot be named until linked to its male. In the keys of Borgmeier (1967a) it runs to couplet 30, lead 1, on page 201, to *M. destructor* (Malloch), which is only known in the female sex. However, the latter has even shorter costal cilia than sp. TH8.

Female. Frons orange brown, broader than long, with 98–102 hairs and dense but very fine microsetae. Lower SAs clearly shorter than upper pair and closer together. Upper SAs are level with or slightly lower on frons than antials which are about midway between them and anterolaterals, which are higher on frons. Pre-ocellars a little further apart than upper SAs and slightly further from each other than either is from a mediolateral bristle, which is about the same level on frons. Cheek with 4–6 bristles and jowl with two longer ones. Postpedicels subglobose, brownish yellow, with about two dozen irregularly shaped SPS vesicles that are subequal in diameters to those of sockets of lower SAs. Palps straw yellow, with seventeen bristles that get progressively smaller towards base. Labrum slightly darker than palps and at least as wide as postpedicel. Labella very much paler and with very few short spinules below. Thorax orange to orange brown, being paler on sides. Mesopleuron with 7–8 hairs and 1–2 moderate bristles at rear margin. Two notopleural bristles and no cleft in front of these. Scutellum with four bristles, the anterior pair being shorter than the posterior pair. Abdominal tergites largely yellowish brown but T1, the hind margins of T2 and T3 and T6 and T7 are darker, but the anterior half of T5 and the whole of T6 are divided along the median band (Fig. 19). With small sparse hairs except for longer ones at sides of T2 and at rear of T6 and T7 (Fig. 19). Venter brown with pale intersegmental bands, and with hairs below segments 3–6. Sternite 7 narrow, tapering to an anterior point, with 3–4 hairs and a longer pair at rear margin. Posterolateral lobes at rear of sternum 8 not quite as long as basal breadth and with three long hairs, two medium ones and six short ones further forward. Cerci very pale and about 1.7–1.8x as long as broad, with three fine hairs, three more robust hairs at tip and one very long hair. Rectal papillae not observed. Furca an oval, sclerotised loop about 0.3 mm long and 0.2 mm wide. Dufour's crop mechanism 0.8–0.9 mm long and 0.6–0.7 mm wide and rounded behind. Legs straw yellow except for brown patch on mid coxa and tip of hind femur. Fore tarsus with posterodorsal hair palisade on all five segments, and 5 a little longer than 4. Dorsal hair palisade of mid tibia extends about 0.8x of length. Hairs below basal half of hind femur a little longer than those of anteroventral row of outer half. Hind tibia with 9–11 differentiated posterodorsal hairs, the first two being fine and the rest robust. Spinules of apical combs all simple. Wings 1.5–1.6 mm

long. Costal index 0.51–0.52. Costal ratios 4.7 : 3.5 : 1. Costal cilia (of section 3) 0.06 mm long. No hair at base of vein 3. With five axillary bristles, the outer ones being clearly longer than costal cilia. Sc reaching R1 and its tip fusing with it. Thick veins straw yellow tinged brown, 4–6 yellowish brown and 7 only discerned with critical lighting. Membrane scarcely tinged grey (not evident to naked eye when viewed against a white background). Haltere with straw yellow knob.

Material examined. ♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m, in flower of *A. baenzigeri*, 1.viii.1995, H. Bänziger (CUMZ, 30–12).

***Puliciphora* Dahl**

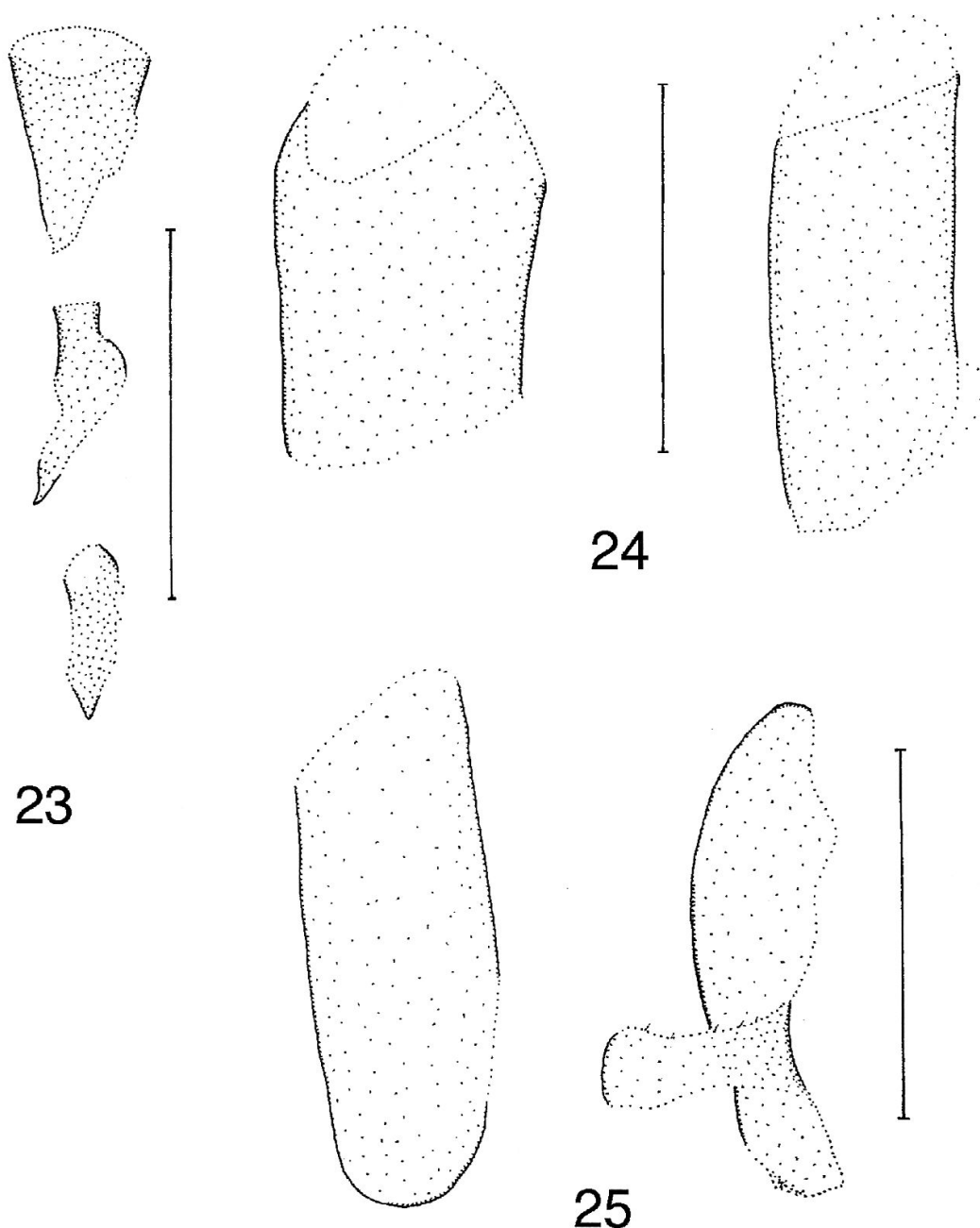
The flightless females of the Oriental species are keyed by Disney (1999b). Most males, including that noted below, cannot be named in our present state of knowledge.

Material examined. 1 ♂, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 720 m, in flower of *A. baenzigeri*, 12.viii.2005, H. Bänziger (CUMZ, 30–54).

***Woodiphora* Schmitz**

Both sexes of the Australasian and Oriental species have been keyed, but some females remain unknown or not yet linked to their males (Disney 1989). This key needs supplementing by Liu (2001). A series of females collected from *Aristolochia baenzigeri* flowers evidently belong to five species. In the keys below one runs out as *W. parvula* Schmitz, but is an undescribed sibling species. Four species resemble *W. santoshi* Disney and related species, but all appear to be undescribed. However, several related species are only known in the male sex. These females cannot be named until their males are procured. The five species, here given code letters, can be separated by the following key:

1. Hind tibia with a dorsal and an incomplete anterior longitudinal hair palisade. Mid tibia with a dorsal hair palisade. Furca (internalised abdominal sternite 9) as Fig. 23 Species TH-A
 - All tibiae lack longitudinal hair palisades. Furca otherwise 2
2. Furca an enormous pale hairy capsule (Fig. 26) Species E
 - Furca much smaller and with few or no hairs (Figs 24–25) and sometimes obscure (being largely unsclerotised) 3
3. Anterolateral bristles distinctly higher on frons than upper supra-antennal bristles. (Hind femur brown) Species C
 - ALs level with or only very slightly higher on frons than upper SAs 4
4. All femora brown, apart from pale streak on front femur. Labrum brown and at least 1.3x as wide as postpedicel. The irregular triangular sclerite embraced by the antero-median emargination of the abdominal tergite 6 is about as broad as long Species D
 - Front and mid femora straw yellow, hind femur yellowish brown in distal third or more. Labrum a dusky straw yellow and subequal in width to postpedicel. The irregular triangular sclerite embraced by the antero- median emargination of T6 is clearly longer than greatest breadth and tapers to an anterior point Species B



Figs 23–25. *Woodiphora* species, ♀ furcas (internalised sternites 9), with anterior ends to top of page and viewed from above. – 23, Species TH-A, three different views; – 24, Species B, two different views; – 25, Species C, two different views. Scale bars = 0.1 mm.

***Woodiphora* species TH-A (Disney, 2005) (Fig. 23)**

In the keys of both Disney (1989) and Liu (2001) these females run out as *W. parvula* Schmitz. However, this ‘distinctive’ species is now known to be a sibling species complex (Disney 2005), and this species has been designated Species TH-A.

Material examined. 4 ♀♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m, in flower of *A. baenzigeri*, 1.viii.1995, H. Bänziger (CUMZ, 30–12 & 14).

Woodiphora species B to E.

In the primary key (Disney 1989) these females run down to *W. santoshi* Disney, or similar species in subsequent couplets, but all four species differ in the forms of their abdominal furcas. Furthermore, it was noted in the key that the unknown females of two other species would be likely to run out at the same couplet. In Liu's (2001) key these females run to his couplets 11–13, but all differ in the shapes of their T7 from his four species. It would seem that about a dozen species have very similar females. Until associated males are obtained it will not be possible to resolve the identities of species B–E.

Woodiphora species B (Fig. 24)

Furca as Fig. 24.

Material examined. 8 ♀♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m and 910 m, in flower of *A. baenzigeri*, 31.vii.1995, 1.viii.1995, 7.vi.2004, 9.vi.2004, H. Bänziger (CUMZ, 30–52–53); 2 ♀♀, the same except 720 m, 12.viii.2005 (DEFACU, 30–54).

Woodiphora species C (Fig. 25)

Furca as Fig. 25.

Material examined. 2 ♀♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m, in flower of *A. baenzigeri*, 1.viii. 1995, 13.x.1995, H. Bänziger (CUMZ, 30–14 & 54).

Woodiphora species D

The single specimen is somewhat damaged. The furca is similar to Fig. 24 but is about twice as large and with some small hairs, but it is less than half as large as Fig. 26, which has larger hairs.

Material examined. 1 ♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m, in flower of *A. baenzigeri*, 1.viii.1995, H. Bänziger (CUMZ, 30–14).

Woodiphora species E (Fig. 26)

The furca is large and hairy at its posterior end (Fig. 26) and with more and longer hairs on the ventral face towards rear. This furca thus resembles that of *W. malaysiae* Disney (Figs 7–9 in Disney 1989).

Material examined. 8 ♀♀, North Thailand: Pai District, Mae Hongson Province, Pang Mapha, 820 m and 910 m, in flower of *A. baenzigeri*, 1.viii.1995, 7.vi.2004, H. Bänziger (CUMZ, 30–14, 53–54).

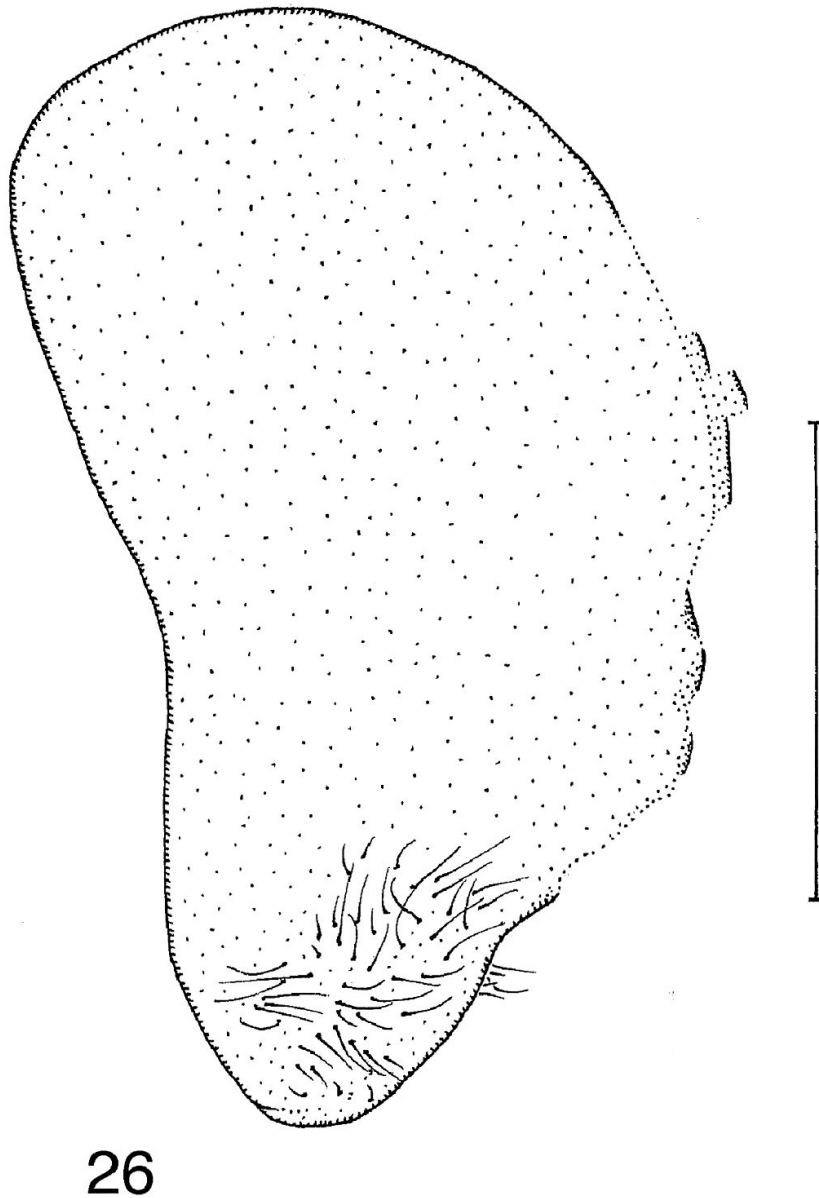


Fig. 26. *Woodiphora* species E, ♀ furca, with anterior end to top of page and viewed from above. Scale bar = 0.1 mm.

Natural history (by H. Bänziger)

Functional morphology of Aristolochia baenzigeri (Figs 27, 28)

The liana is cauliflorous, often on the typically long, procumbent stretches of the stem. Thus, the flowers often lie directly on the ground, or on the procumbent parts of the stem, only few being higher up (highest: 3 m). Fruits from the previous year's flowering and tiny fruitlets of the study year's flowering indicate that pollination had been successful at least in some flowers.

The expanded part of the flower perianth (ep) is up to 9x9 cm wide, inside dark red, shiny but not slippery, with a central blotch about 1.5 cm in diameter,



Figs 27–29. *Aristolochia baenzigeri*. – 27. Two flowers in anthesis. Scale bar = 3.5 cm. – 28. Longitudinal section showing the right half of the flower; a = ascending tube, e = entrance to the falling tube, ep = expanded part of the perianth, f = falling tube, g = gynostemium, p = pollination chamber, w = window pane. Scale bar = 5 cm. – 29. Three euthanized *Dohrniphora cornuta* carrying pollen of *Aristolochia baenzigeri*. Scale bar = 2.5 mm. Photographs by H. Bänziger.

brightly yellow, dull and slippery. The position of the perianth of the urceolate (kettle trap) flower is nearly vertical, the upper part of the perianth functioning like a roof to shelter it from rain. At the center of the yellow blotch is the funnel-like entrance of the trap (e). The entrance is connected to a descending, narrow tube (f) leading down vertically to an expanded «J-shaped» tube, namely to the short leg of the «J». About two thirds up the long leg (a) of the «J» there is a constriction which leads into the pollination chamber (p) containing anthers and stigmas (in form of a

gynostemium) (g). The descending tube is dark and slippery. The «J-shaped» tube is not completely dark but somewhat translucent and its walls are lined by a net-like carpet of hairs, except where the walls are overhanging near the top of the small leg of the «J». At the ceiling of the pollination chamber is an annular, translucent window pane (w). Further details have been published in related studies (Bänziger 1989; Hansen & Phupathanaphong 1999).

The odour is difficult to describe as it is neither typically cadaveric, nor excrement-like, the ones generally found in sapromyiophilous *Aristolochia*. Odour of fresh flowers is quite weak to the human nose, even at close quarters, and only slightly unpleasant. Towards the end of anthesis, when flowers become flabby and the colours darken, it is more smelly. Once fallen, it smells rather offensively rotten but, when it starts to decompose into a slimy mess, the smell progressively disappears. Therefore, the scent production is unusual for *Aristolochia*, generally being described as strongest while in anthesis (e.g. Cammerloher 1923). Also in similarly sapromyiophilous flowers, such as *Rhizanthus infanticida* Bänziger & Hansen (Rafflesiaceae) the smell is strongest while in anthesis (Bänziger 1996b, mentioned as *R. zippelii* (Blume) Spach, Bänziger & Hansen 2000).

Insect species involved in pollination and their behaviour

Twelve of the 21 species of scuttle flies found imprisoned in *A. baenzigeri* had acquired pollen from the flower (Tab. 1). However, of the 9 species lacking pollen, six were caught from a flower in the female phase (first day of anthesis) when anthers are still closed, hence no inference can be made as to whether they are pollen vectors. Of the remaining three species, only one or two specimens were found, too meagre data for excluding them as pollinators. With 70 specimens *Dohrniphora cornuta* was more common than all other species taken together. Both sexes were involved in *D. cornuta*, in comparable numbers, while in the other species only one of the sexes was.

When approaching a flower, Phorids often zig-zagged for a few moments (indicating olfactory attraction), then generally flew straight (indicating visual attraction) to the yellow patch. Here they instantly fell off the slippery surface and tumbled into the tube. Less often, they first settled on the red perianth, on which they crawled without losing their grip, to the yellow patch, from which they often fell in a moment, though sometimes they managed to crawl for some distance before tumbling. But in some other cases the fall was so sudden after flying straight to the yellow patch that it seemed to be due to their having hit it unexpectedly.

Fallen *A. baenzigeri* flowers were not visited by these phorids, only the more faintly and less malevolent smelling flowers in anthesis. Interestingly, the same was observed with 12 female *Sarcophaga nathani* (Lopes) (Sarcophagidae) which, intriguingly, were not attracted to the smelly, rotting flowers but to the weak-scented flowers in anthesis. They settled on the flowers and some attempted to enter the tube but were far too big to penetrate. None larviposited on the flower, though the four specimens caught were all highly gravid, as evidenced by manipulative parturition of larvae.

On a few fallen flowers many tiny larvae belonging to the Cecidomyiinae (Cecidomyiidae) were found. They were seen feeding from flower tissue, but then did not develop further. It is not clear whether this was due to the flower's possible

Tab. 1. Phoridae¹ imprisoned by *Aristolochia baenzigeri*. In parentheses additional records from a flower in first-day anthesis when pollen is not yet released.

	With pollen		Without pollen	
	males	females	males	females
<i>Anevrina wyatti</i>		1		
<i>Borophaga</i> sp.		2		
<i>Conicera thailandiae</i>		1	1	
<i>Diplonevra peregrina</i>	2		(2)	
<i>Dohrniphora cornuta</i> ²	20	15	2 (2)	
<i>Dohrniphora sorora</i>		1	(4)	2
<i>Dohrniphora thailandensis</i>			(1)	
<i>Megaselia deningi</i>			(1)	
<i>Megaselia hansenii</i>	3			
<i>Megaselia leucopleuralis</i>			(1)	(1)
<i>Megaselia malaisei</i>				(1)
<i>Megaselia martensi</i>			(1)	
<i>Megaselia pangmaphae</i>			1	
<i>Megaselia prachavali</i>			1	
<i>Megaselia</i> species TH8				1
<i>Puliciphora</i> sp.			(1)	
<i>Woodiphora</i> species TH-A		4		
<i>Woodiphora</i> species B		7		1 (2)
<i>Woodiphora</i> species C		2		
<i>Woodiphora</i> species D		1		
<i>Woodiphora</i> species E		7		1

¹ In addition, five Agromyzidae, two of which carrying pollen of *A. baenzigeri*, and one Sphaeroceridae were caught from the flower.

² An additional 16 males and 15 females, many carrying pollen of *A. baenzigeri*, were caught on 31.vii and 1.viii.1995. However, the number of pollen carriers could not be reliably assessed, as pollen presumably became detached in some specimens while floating in the alcohol vials.

content of toxic substances (cf. Rothschild *et al.* 1972; Nishida & Fukami 1989), or because they were representatives of a guild which are predators on small invertebrates such as mites.

DISCUSSION

The most basic aspect of our study, the taxonomy, was typically difficult as often found in tropical habitats due to their high biodiversity. Thus, it took several years before it was established that the liana *A. baenzigeri* was new, and then described (Hansen & Phupathanaphong 1999). Of the 21 species of Phoridae found in *A. baenzigeri* (Tab. 1), only five were previously known. Eight are described as new, six are briefly described or keyed but remain unnamed because caught only in the female sex, while two are not described. The other adult dipterans found in *A. baenzigeri*, Agromyzidae and Sphaeroceridae, were not further identified. With only

five and one specimens caught, respectively, they at best play only a very minor role as pollinators. Only two of the Agromyzidae carried pollen. Nevertheless, the Agromyzidae and Sphaeroceridae are herewith recorded for the first time from any *Aristolochia*. The Phoridae numbered 124, some 90% with pollen of the flower. A number of larval Cecidomyiidae from the flower played no role in the pollination.

The behaviour of the pollinators inside *A. baenzigeri* could not be observed but is deduced from its morphology (Fig. 28). From the entrance of the trap, the flies fall through the tube to the bottom. Escape up the descending tube is precluded (slippery, no hairs to get hold on for climbing) and unattractive (dark). At the top end of the other leg of the tube, light suffuses through the window panes into the pollination chamber, down the ascending tube, so the flies climb towards the light on the network of hairs. The flies pass through the narrow passage between wall and stigmatic surface, where pollen (if any carried) is removed from the back of their thorax onto the sticky stigma. When the following day the anthers dehisce, pollen is acquired, probably in a similar way. The sticky pollen grains remain stuck mainly on and between the long bristles of the scutum and scutellum of the thorax (Fig. 29).

Once the flower dropped to the ground, the descending tube lies more or less horizontally, thus the flies will no more skid and can leave the flower.

With 35 successful pollen acquisitions (53 % of all phorid acquisitions) but only two failures, *D. cornuta* was the most common and most efficient of the twelve pollinator species (Tab. 1). If the unreliable data from the additional 31 *D. cornuta* were considered at the same acquisition efficiency, some 64 specimens could have been expected with pollen. The next most common pollen carriers were *Woodiphora* species B and E, each with just 7 acquisitions.

With 20 (57 %) males against 15 (43 %) females, *D. cornuta* males were carrying pollen slightly more frequently than females. This is the opposite of most of the other species, though this is likely to be so by chance due to the low numbers of specimens found. Indeed, Hall & Brown (1993) reported a preponderance of *Megaselia* spp. males visiting the flowers of *A. littoralis* Parodi in Florida.

While *A. baenzigeri* may well offer nectar, like many *Aristolochia* (Cammerloher 1923; Daumann 1959), by definition the flower should be termed as deceptive since it does not offer what its odours promise when in anthesis, viz. decomposing organic substances. Generally, female and to a lesser extent also male adults of detritivore Diptera require such substances for reproduction, evidently what they were seeking in the flower. Hence the flower is food-deceptive. If any nectar is present in foul-smelling *Aristolochia*, it is only for keeping the flies alive while being prisoners. However, in female pollinators the flower may additionally act by brood-site deception. Gravid females may be misleadingly attracted by the faked presence of rotting substances as a breeding ground for their young. This seems to be the case with the attraction of the highly gravid flesh flies, *S. nathani*, although these are not pollinators. Evidently some of the flower's odour components must be related to those emanating from a corpse. As a necrobiotic species (Bänziger & Pape 2004) these flies lay on, and their larvae develop in, cadavers. However, with one exception (one *Dohrniphora sorora*; the only other fly with eggs was *Conicera thailandiae*, but these were not yet mature) none of the total 65 female scuttle flies caught had mature eggs, so *A. baenzigeri* did not act by brood-site deception in these species. *D. sorora* was probably seeking food rather than a breeding site.

In the case of Phoridae, though, caution is required because, unlike *S. nathani* which does not develop in decomposing plant material, at least some phorid species can develop in the flowers of some species of *Aristolochia*. Namely, the scuttle fly *Megaselia aristolochiae* Prado upon *A. labiata* Willd. in Brazil (Hime & Costa 1990), *M. metropolitanoensis* Disney upon *A. maxima* Jacqu., *M. sakaiae* Disney and *Puliciphora pygmaea* (Borgmeier) upon *A. maxima* and *A. inflata* H. B. K. in Panama (Disney & Sakai 2001). However, the adult flies of these species do not appear to be the flowers' pollinators, at least none was reported to carry pollen of *Aristolochia*, and *M. metropolitanoensis* and *P. pygmaea* oviposited on fallen, not anthetic flowers (Disney & Sakai 2001). Hence, whether these flowers offer a real breeding site as a reward for these flies or whether the flowers act by brood-site deception, does not apply. An example of the former relationship are *Yucca* spp. (Agavaceae), the ovary of which flowers is partly eaten by the larvae of the moth *Pronuba yuccasella* which hatch from the eggs laid by the pollinator (Kugler 1970). The larvae develop to adulthood causing only limited damage to the ovary which is adapted to this trade-off.

The mechanism triggering the trapping of flies in *A. baenzigeri* appears less sophisticated than in other comparable kettle trap flowers such as the lady slipper orchids *Paphiopedilum villosum* (Lindl.) Stein, *P. callosum* (Rchb. f.) Stein and *Cypripedium guttatum* Sw. (Bänziger 1996a, 2002; Bänziger *et al.* 2005). However, the liana's flower captures more flies (up to a dozen or more) in a shorter time (about 12 hours) and keeps them prisoner and alive for longer periods (some 48 hours or more). *P. villosum* only occasionally, if at all, entraps a hover fly pollinator during its anthesis lasting 2–3 months, keeps them prisoner for just 0.5 to 32 min and, in the case of *P. callosum*, entrapment results in the death of the progeny of the pollinator which, a moment before tumbling into the trap, is tricked into laying an egg although the hatchling cannot survive there.

ACKNOWLEDGMENTS

HB extends his sincerest thanks to Mr. P. Sukumalanand for his unfailing support for all the authors' projects; to Mr. F. Richter who sent very relevant references; to Ms. S. Panthi for her assistance in the field and computer matters. RHLD was funded by the Professor Hering Memorial Research Fund (British Entomological & Natural History Society). The authors are grateful to the Escher funds for financing additional printing costs.

ZUSAMMENFASSUNG

Während Studien über die Bestäubungsökologie von *Aristolochia baenzigeri* Hansen & Phuphathana-phong (Osterluzeigewächse, Aristolochiaceae) in Thailand (1995, 2004–2005) wurden Imagines von 124 Phoriden, 5 Agromyziden und einer Sphaeroceride in den Kesselfallenblüten dieser Liane gefunden. Unter den Phoriden wurden 21 Arten in 8 Gattungen lebend eingesperrt gefunden, aber nur 5 Arten waren bekannt. 8 neue Arten werden beschrieben: *Anevrina wyatti* Disney, *Conicera thailandiae* Disney, *Dohrniphora sorora* Disney, *D. thailandensis* Disney, *Megaselia hansenii* Disney, *M. leucopleuralis* Disney, *M. prachavali* Disney, *M. pangmaphae* Disney. 7 Arten, die nur als Weibchen bekannt sind, werden kurz beschrieben, aber nicht benannt: 1 *Borophaga*, 1 *Megaselia* und 5 *Woodi-phora*. Eine *Puliciphora*, die nur als Männchen bekannt ist, bleibt unbeschrieben, da die Bestimmung der Arten in dieser Gattung auf Weibchen beruht.

Mit 37 Individuen war *D. cornuta* bei weitem die häufigste Art und, abgesehen von zwei Misserfolgen, auch die erfolgreichste im Aufnehmen von Pollen der sapromyiophilen *A. baenzigeri*, die Männchen leicht häufiger als die Weibchen. 11 weitere Phoridenarten hatten ebenfalls Pollen aufgenommen, machten aber zusammen weniger als die Hälfte aller Pollenaufnahmen aus. Agromyziden und Sphaeroceriden werden zum ersten Male als Bestäuber/Besucher einer *Aristolochia* erwähnt.

Nur anethetische Blumen wurden besucht, obwohl diese weniger stark rochen als abgefallene. Dasselbe galt für die Fleischfliege *Sarcophaga nathani* (Sarcophagidae), welche jedoch viel zu gross war, um in die Blume hinein zu fallen. Phoriden flogen auf den zentralen, hellgelben Fleck der dunkelroten Blüte, wo sie von der schlüpfrigen Oberfläche abrutschten und in den trichterförmigen Schlund der Falle stürzten. Die komplexen Vorgänge der Gefangenhaltung, Bestäubung und Freilassung der Häftlinge waren denen anderer *Aristolochia*-Arten ähnlich. *A. baenzigeri* wird als Futtertätuschblume für Männchen und Weibchen gedeutet; sie ist keine Brutsubstrattätuschblume, da nur eines der 65 weiblichen Häftlinge reife Eier trug.

REFERENCES

- Bänziger, H. 1989. Lardizabalaceae: New plant family for Thailand «predicted» by rare moth on Doi Suthep. — Natural History Bulletin of the Siam Society 37: 187–208.
- Bänziger, H. 1996a. The mesmerizing wart: the pollination strategy of epiphytic lady slipper orchid *Paphiopedilum villosum* (Lindl.) Stein (Orchidaceae). — Botanical Journal of the Linnean Society 121: 59–90.
- Bänziger, H. 1996b. Pollination of a flowering oddity: *Rhizanthus zippelii* (Blume) Spach (Rafflesiaceae). — Natural History Bulletin of the Siam Society 44: 113–142.
- Bänziger, H. 2002. Smart alecks and dumb flies: natural pollination of some wild lady slipper orchids (*Paphiopedilum* spp., Orchidaceae). In: Clark, J., Elliott, W.M., Tingley, G. & Biro, J. (editors), Proceedings of the 16th World Orchid Conference 1999, pp. 165–169 & 461–463 [plates 45–57]. — Vancouver Orchid Society, Vancouver.
- Bänziger, H. & Hansen, B. 2000. A new taxonomic revision of a deceptive flower, *Rhizanthus* Dumortier (Rafflesiaceae). — Natural History Bulletin of the Siam Society 48: 117–143.
- Bänziger, H. & Pape, T. 2004. Flowers, faeces and cadavers: natural feeding and laying habits of flesh flies in Thailand (Diptera: Sarcophagidae, *Sarcophaga* spp.). — Journal of Natural History 38: 1677–1694.
- Bänziger, H., Sun, H. & Luo, Y.-B. 2005. Pollination of a slippery lady slipper orchid in south-west China: *Cypripedium guttatum* (Orchidaceae). — Botanical Journal of the Linnean Society 148: 251–264.
- Borgmeier, T. 1967a. Studies on Indo-Australian Phorid flies, based mainly on material of the Museum of Comparative Zoology and the United States National Museum (Diptera, Phoridae). — Studia Entomologica, Petropolis 9: 129–328 (1966).
- Borgmeier, T. 1967b. Studies on Indo-Australian Phorid flies, based mainly on material of the Museum of Comparative Zoology and the United States National Museum. Part II. — Studia Entomologica, Petropolis 10: 81–276.
- Brown, B.V. 1992. Generic revision of Phoridae of the Nearctic Region and phylogenetic classification of Phoridae, Sciadoceridae and Ironomyiidae (Diptera: Phoridae). — Memoirs of the Entomological Society of Canada 164: 1–144.
- Brown, B.V. 1995. Review of the species of *Anevrina* Lioy (Diptera: Phoridae), with a new species and a revised world key. — Entomological Problems 25 (2): 1–10 (1994).
- Brues, C.T. 1928. Some Cuban Phoridae which visit the flowers of *Aristolochia elegans*. — Psyche 35: 160–161.
- Cammerloher, H. 1923. Zur Biologie der Blüte von *Aristolochia grandiflora* Swartz. — Österreichische Botanische Zeitschrift 72: 180–198.
- Cammerloher, H. 1933. Die Bestäubungseinrichtungen der Blüten von *Aristolochia lindneri* Berger. — Planta 19: 351–365.
- Daumann, E. 1959. Zur Kenntnis der Blütennektarien von *Aristolochia*. — Preslia 31: 359–372.
- Delpino, F. 1867. Sugli apparecchi della fecondazione nelle piante antocarpee (Fanerogame). Sommario di osservazioni fatte negli anni 1865–1866. — M. Cellini & Co., Firenze, 39 pp.
- Disney, R.H.L. 1989. A key to Australian and Oriental *Woodiphora* (Diptera: Phoridae), affinities of the genus and descriptions of new species. — Journal of Natural History 23: 1137–1175.
- Disney, R.H.L. 1990a. A key to *Diplonevra* males of the Australasian and Oriental Regions, including two new species (Diptera, Phoridae). — Entomologica Fennica 1: 33–39.
- Disney, R.H.L. 1990b. Key to *Dohrniphora* males (Diptera: Phoridae) of the Australasian and Oriental Regions, with descriptions of new species. — Zoological Journal of the Linnean Society 99: 339–387.
- Disney, R.H.L. 1990c. A revised key to Australasian and Oriental *Conicera* (Diptera: Phoridae), with three new species. — Entomologica Scandinavica 21: 339–344.
- Disney, R.H.L. 1994. Scuttle Flies: The Phoridae. — Chapman & Hall, London, xii + 467 pp.
- Disney, R.H.L. 1999a. A troublesome sibling species complex of scuttle flies (Diptera: Phoridae) revisited. — Journal of Natural History 33: 1159–1216.

- Disney, R.H.L. 1999b. New species and a new key to Oriental *Puliciphora* (Diptera: Phoridae). — *Entomologica scandinavica* 30: 243–248.
- Disney, R.H.L. 2001. The preservation of small Diptera. — *Entomologist's Monthly Magazine* 137: 155–159.
- Disney, R.H.L. 2004. Insecta: Diptera, Phoridae. In: Yule, C.M. & Yong, H.S., *Freshwater Invertebrates of the Malaysian Region*, pp. 818–825. — *Academy of Sciences of Malaysia*.
- Disney, R.H.L. 2005. The 'distinctive' *Woodiphora parvula* Schmitz (Dipt., Phoridae) is a sibling species complex. — *Entomologist's Monthly Magazine* 141: 143–150.
- Disney, R.H.L. & Sakai, S. 2001. Scuttle flies (Diptera: Phoridae) whose larvae develop in flowers of *Aristolochia* (Aristolochiaceae) in Panama. — *European Journal of Entomology* 98: 367–373.
- Endress, P.K. 1994. *Diversity and evolutionary biology of tropical flowers*. — Cambridge University Press, Cambridge, xiv + 511 pp.
- Faegri, K. & Pijl, L. van der, 1979. *The principles of pollination ecology*. — Pergamon Press, Oxford, 244 pp.
- Gonzalez, F. & Poncy, O. 1999. A new species of *Aristolochia* (Aristolochiaceae) from Thailand. — *Brittonia* 51: 452–456.
- Green, D.M. 1997. A new record and a new species of *Dohrniphora* (Diptera: Phoridae) from Malaysia. — *Malayan Nature Journal* 50: 159–165.
- Hall, D.W. & Brown, B.V. 1993. Pollination of *Aristolochia littoralis* (Aristolochiales: Aristolochiaceae) by males of *Megaselia* spp. (Diptera: Phoridae). — *Annals of the Entomological Society of America* 86: 609–613.
- Hansen, B. & Phuphathanaphong, L. 1999. Two new species of *Aristolochia* (Aristolochiaceae) from Thailand. — *Nordic Journal of Botany* 19: 575–579.
- Havelka, P. 1983. Die Ceratopogonidenfauna der Osterluzei (*Aristolochia clematidis*). — *Mosquito News* 42: 524.
- Hilje, L. 1984. Fenología y ecología floral de *Aristolochia grandiflora* Swartz (Aristolochiaceae) en Costa Rica. — *Brenesia* 22: 1–44.
- Hime N. da C. & Costa E. de L. 1990. Dípteros ocorrentes nas aristolóquias brasileiras – levantamento preliminar. — *Ciência e Cultura* 42: 832–834.
- Knoll, F. 1929. Die Gleitfalle als Blumentypus. — *Verhandlungen der Zoologisch-Botanischen Gesellschaft* 79: 9–12.
- Kugler, H. 1970. *Blütenökologie*. — Gustav Fischer, Stuttgart, xi + 345 pp.
- Lindner, E. 1928. *Aristolochia lindneri* Berger und ihre Bestäubung durch Fliegen. — *Biologisches Zentralblatt* 48: 93–101.
- Liu, G. 2001. A Taxonomic Study of Chinese Phorid Flies Diptera: Phoridae (part 1). — China: Neupress.
- McClure, A.W.R., Lim, B.-L. & Winn, S.E. 1967. Fauna of the Batu Cave, Batu Caves, Kuala Lumpur, Malaysia. — *Pacific Insects* 9: 399–428.
- Michailovskaya, M. V. 1999. A review of the genera *Triphleba* Rondani, *Phora* Latreille and *Anevrina* Lioy (Diptera, Phoridae) from Russian Far East. — *Far Eastern Entomologist* 70: 1–16.
- Nishida, N. & Fukami, H. 1989. Ecological adaptation of an Aristolochiaceae-feeding swallowtail butterfly, *Atrophaneura alcinous*, to aristolochic acids. — *Journal of Chemical Ecology* 11: 1989.
- Razzak, M.A., Ali, R. & Ali S.I. 1992. The pollination biology of *Aristolochia bracteolata* Lamk. (Aristolochiaceae). — *Pakistan Journal of Botany* 24: 79–87.
- Rothschild, M., Euw, J.V. & Reichstein, T. 1972. Aristolochic acids stored by *Zerynthia polyxena* (Lepidoptera). — *Insect Biochemistry* 2: 334–343.
- Sprengel, C.K. 1793. *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen*. — F. Vieweg, Berlin, 442 + 8 pp, 25 Tafeln.
- Ule, E. 1898. Ueber Blütheneinrichtungen einiger Aristolochien in Brasilien. — *Berichte der Deutschen Botanischen Gesellschaft* 16: 74–91.
- Vogel, S. 1965. Kesselfallen-Blumen. — *Umschau in Wissenschaft und Technik* 65: 12–17.
- Vogel, S. 1993. *Betrug bei Pflanzen: Die Täuschblumen*. — Akademie der Wissenschaften und der Literatur, Mainz, F. Steiner, Stuttgart, 48 pp.
- Wolda, H. & Sabrosky, C.W. 1986. Insect visitors to two forms of *Aristolochia pilosa* in Las Cumbres, Panama. — *Biotropica* 18: 295–299.

(received Januar 10, 2006; accepted March 27, 2006)