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New aquatic species of *Megaselia* Rondani from Bolivia (Diptera: Phoridae)

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Abstract
Ten aquatic species of *Megaselia* Rondani (1856) are reported from the internodes of the large bamboo *Guadua angustifolia* var. *chacoensis* in Bolivia. *Megaselia aquatica* sp. n., and *M. imitatrix* Borgmeier (1969) are named and seven species given code letters as their males remain unknown. Five of these species closely resemble the distinctive *M. imitatrix*. The eggs of species C, in addition to a subterminal plastron, uniquely have the rest of the egg covered in fine hairs. Three additional *Megaselia* species reported from bamboo or other phytotelms in the Americas, *Megaselia hansonix* Disney (2009), *M. rufipes* (Meigen) (1804) and *M. scalaris* (Loew) (1866) are illustrated. A key for *Megaselia* from the Americas reported from aquatic situations is presented.

Key words: Neotropical, new species, aquatic, phytotelms, bamboo, key.

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Introduction

The larvae of a diversity of species have long been known from aquatic container habitats (phytotelms) whose characteristics were reviewed by Frank & Lounibos (1983) and Kitching (2000). In the 20th Century the aquatic larvae of a number of species of scuttle fly (Diptera: Phoridae) were documented from phytotelms such as axil waters (e.g. of coconuts), bromeliads, bamboo internodes, coconut shells and husks, pitcher plants and rot-holes in trees and tree-stumps. These were reviewed by Disney (1994) and supplemented by records from bamboo internodes (Kovac 1993, 1994; Kovac & Streit 1996; Disney 1995), coconut shells and husks (Benton & Claugher 2000) and pitcher plants (Mogi & Yong 1992; Mogi & Chang 1996, 1997; Clarke & Kitching 1993).

During this Century the richest such fauna was confirmed and augmented for the Oriental Region (Disney 2004). Two species have been reported from the Nearctic Region (Disney et al. 2009; Murrell et al. 2014), with one of these also occurring in the northern Neotropical Region (in Dominica) (Borgmeier 1969). In addition the more northerly of these species, *Megaselia imitatrix* Borgmeier, was also reported from Brazil (Benton & Claugher 2000). However, a gravid female collected from a bathroom in Brazil, was seemingly neither of these species, and served to call into question the identity of Benton & Claugher's species (Disney et al. 2009). However, remounting the abdomen and improved imaging systems confirmed the identity of this female as being *M. imitatrix*.

Since then a series of samples from Uruguay, sent to RHLD by Maria Martínez (Universidad de la República, Facultad de Ciencias, Sección Entomología, Montevideo), have shown that *M. imitatrix* extends the length of the Neotropical Region.

Two other species, transported across the world by mankind, have larvae that feed on a range of decaying organic materials. Both occasionally breed in aquatic situations. *Megaselia rufipes* (Meigen) has been reported breeding in trickling filter sewage systems (Painter 1980). Likewise Kloter, Penner & Widmer (1977) report the larvae of *Dohrniphora cornuta* (Bigot) (1857) feeding on the sewage film of micro-organisms in trickling filter sewage beds. However, if competition for this resource becomes too great they become facultative predators on the eggs, larvae and pupae of *Psychoda alternata*. Jones (1918) reported it exploiting the dried remains of insects in the late summer pitchers of *Sarracenia flava*. However, as with *M. rufipes*, *D. cornuta* is better known for its occurrence in forensic cases (Disney et al. 2014).

In this paper we report on nine species reared by DK from larvae living in the waters of the internodes of a giant bamboo, *Guadua angustifolia* var. *chacoensis* (Poaceae). Unfortunately the reared adults included males for only

one species. Apart from *M. imitatrix* the other species are given code letters only until their males can be obtained.

Material and methods

The larvae and adults were sampled in the field by DK during a three-week stay in Buena Vista, Bolivia, about 100 km from Santa Cruz de la Sierra, as part of a general study on bamboo insects. The main study site was located near the road leading from Buena Vista to El Cairo in the vicinity of the Ichilo River (17.27.906S, 063.083W, altitude ca. 350 m). The collecting was conducted between 6 and 30 January 2011, i.e. during the month with the highest rainfall.

The larvae were obtained by using two methods: a) upright bamboo stems were felled and water-filled internodes possessing entrance holes created by moth larvae of the family Crambidae (diameter 2-3 mm) cut open using a machete, b) bamboo stems were felled, placed in a horizontal position about 1.5 m above ground and cut open in order to allow colonization by phorids. For that purpose a lid was created in the upper part of the internode, which could be opened and closed as needed (method after Kovac & Streit 1996). The flies arrived straight after the internodes were cut open and were present in the internode cavities for about 2-3 days.

Phorid larvae were sucked out using a large pipette, while adults staying in the dry part of the internode cavities were collected by using an aspirator. Larvae were collected ca. 1 week after the internodes were cut open, then transferred to the laboratory in plastic bags and reared to the adult stage in water-filled containers made of cut bamboo internodes sealed with gauze. Adults emerged 2-3 weeks after the bamboo stems were felled and colonized by phorids. Specimens of both adults and larvae were preserved in 70% ethanol. RHLD then mounted these on slides in Berlese Fluid (Disney 2001).

Holotypes, some paratypes and vouchers of species only known as females were posted for deposition in the Natural History Museum in Santa Cruz (NHMSC). However, the package arrived in Bolivia but was not delivered to the NHMSC and is presumed to have been intercepted by criminals. Other paratypes and vouchers are deposited in the University of Cambridge Museum of Zoology (UCMZ).

Results

Megaselia aquatica Disney **sp. nov.** (Figs 1a-j, 2a-j)

Material. Holotype male, **BOLIVIA**: Buena Vista, Santa Cruz, reared from internode of *Guadua angustifolia* var. *chacoensis*, 11 Jan 2011, (3/11, NHMSC, 40-37). Paratypes, 6 males, 9 females, as holotype except some (3/11, 14/11, UCMZ, 14-37-39), 5 larvae, 5 pupae/puparia.

Etymology. The name refers to the aquatic habit of the larvae.

Male. Frons as Fig. 1a and lacking microtrichia. Postpedicels, palps and proboscis as Fig. 1b, the postpediceles with more than a dozen subcutaneous pit sensilla. The palp with a concavity (Fig. 1b). Thorax mainly yellow, but scutum a little dusky and scutellum brown. Two notopleural bristles and no cleft in front of these. Mesopleuron bare. Scutellum with an anterior pair of hairs and a posterior pair of bristles. Abdominal tergite 1 brown, T2 and T3 mainly brown but with median regions yellow in anterior halves, T4 and T5 with much larger parts of median regions yellow and T6 with at least anterior third yellow. Venter yellow and with hairs on segments 3-6. Hypopygium as Figs 1c-g. Legs yellow apart from brown tip to hind femur. Fore tarsus with posterodorsal hair palisade on segments 1-5 and 5 longer than 4 (Fig. 1h). Dorsal hair palisade of mid tibia extends about 0.75 times its length. Hind femur as Fig. 1i. Hind tibia with 10-12 differentiated posterodorsal hairs, those of the distal half being more robust and the last longer and more robust than the rest; and spinules of apical combs simple. Wings (Fig. 1j) 1.6-1.7 mm long. Costal index 0.50-0.53. Costal ratios 5.1-7.5 : 3.9-5.6 : 1. Costal cilia (of section 3) 0.06 mm long. No hair at base of vein 3. With 5 axillary bristles, the outer being 0.10 mm long. Sc not reaching R1. Haltere knob pale gray.

Female. Head similar to male but labrum slightly wider than diameter of postpedicel. Otherwise head similar to male. Thorax as male. Abdominal tergites as Fig. 2a. And tip of abdomen as Fig. 2b. Apart from gray bands adjacent to tergites (Fig. 2a), venter yellow with hairs below segments 3-6. Sternite 7 and lobes at rear of sternum 8 as Fig. 2c. Dufour's crop mechanism pale, convex behind and about 0.06 mm long and 0.03 mm broad. Furca as Figs 2d-e. Legs similar to male. Wing as male except length 1.9-2.0 mm long and costal index 0.50-0.56. Otherwise it and haltere as male. None of the females were gravid.

Larva. Very similar to those of *M. hansonix* (Fig. 11 e) and *M. imitatrix.* Its details of the head end as Figs 1f-h. *M. aquatica* is most readily distinguished by the larger and darker thoracic spiracles (Figs 1f and h) compared with those of the other two species, which are much smaller and very pale (Figs 11 f and 13a).

Pupa. As Figs 1i-j.

Affinities. In the primary keys to Neotropical species of the giant genus *Megaselia* (Borgmeier 1962) the male of this species runs to page 310, couplet 72, lead 2, to *M. irene* Borgmeier, which is immediately distinguished from *M. aquatica* by its largely brown thorax, all brown abdominal tergites and the hairs of the proctiger not differentiated from those of the cerci. In his supplementary keys [Borgmeier (1969)] it runs to page 7, couplet 29, to the aquatic *M. imitatrix* Borgmeier. The latter also has yellow legs, apart from the dark tip to the hind femur. *M. aquatica* most closely resembles *M. imitatrix* but its male has half the number of hairs on each cercus (Fig. 3 a). However

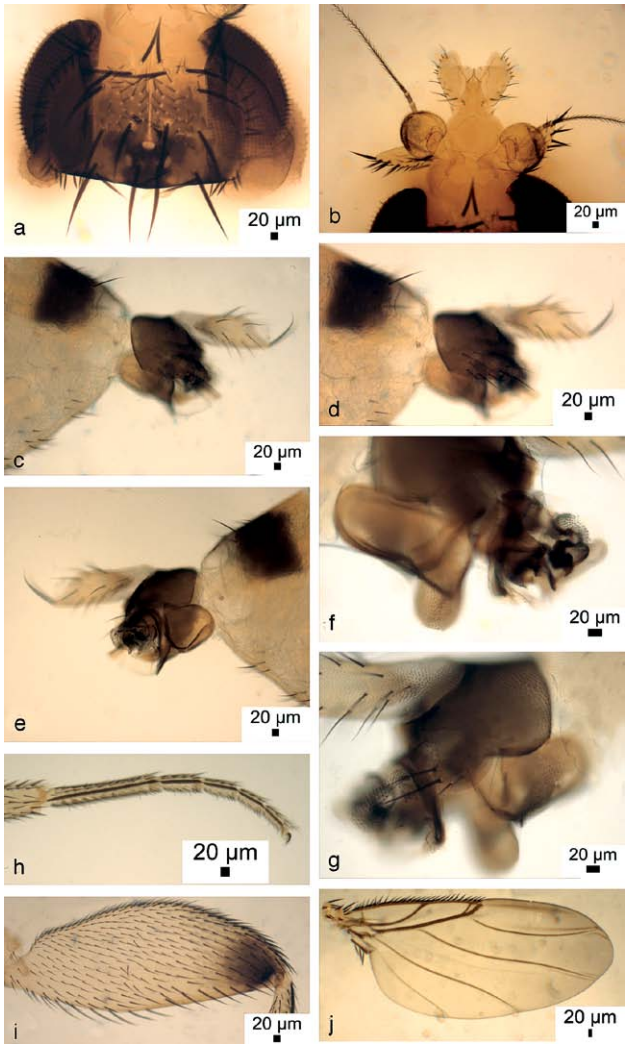

Fig. 1 – *Megaselia aquatica* male: **a**, frons; **b**, postpedicels palps and proboscis; **c-g**, hypopygium; **h**, front tarsus; **i**, hind femur; **j**, wing.

the female of *M. imitatrix* is immediately distinguished by abdominal tergite 6 being clearly wider than T5. In a later supplement [Borgmeier (1971)] the male runs to page 10, couplet 40, lead 1, to *M. plutei* Borgmeier, but it has a brown thorax and abdominal tergites. Three subsequently described species all have 3 bristles on the notopleuron.

Megaselia imitatrix Borgmeier, 1969 (Figs 3 a-n)

The holoype female remounted on a slide has confirmed the identification of this species given by Disney et. al. (2009). Details of the adults, egg, larva and pupa as Figs 3 a-n.

Material. A single teneral female was obtained in Bolivia but has been identified by comparison with several series of reared adults and larvae that were obtained in the waters of flower vases in cemeteries by Maria Martínez in Uruguay. Female, **BOLIVIA**: Buena Vista, Santa Cruz, reared from internode of *Guadua angustifolia* var. *chacoensis*, 13 Jan 2011, D. Kovac (16/11, NHMSC, 40-39).

Megaselia species B (Figs 4 a-n)

Material. 10 females, **BOLIVIA**: Buena Vista, Santa Cruz, reared from internode of *Guadua angustifolia* var. *chacoensis*, 11-13 Jan 2011, D. Kovac (14/11, 16 & 23, NHMSC, UCMZ, 40-37-39).

Female. Frons as Fig. 4 a and with dense but very fine microtrichia. Cheek with a dozen hairs and jowl with a single long bristle. Postpedicels, which lack SPS vesicles, palps

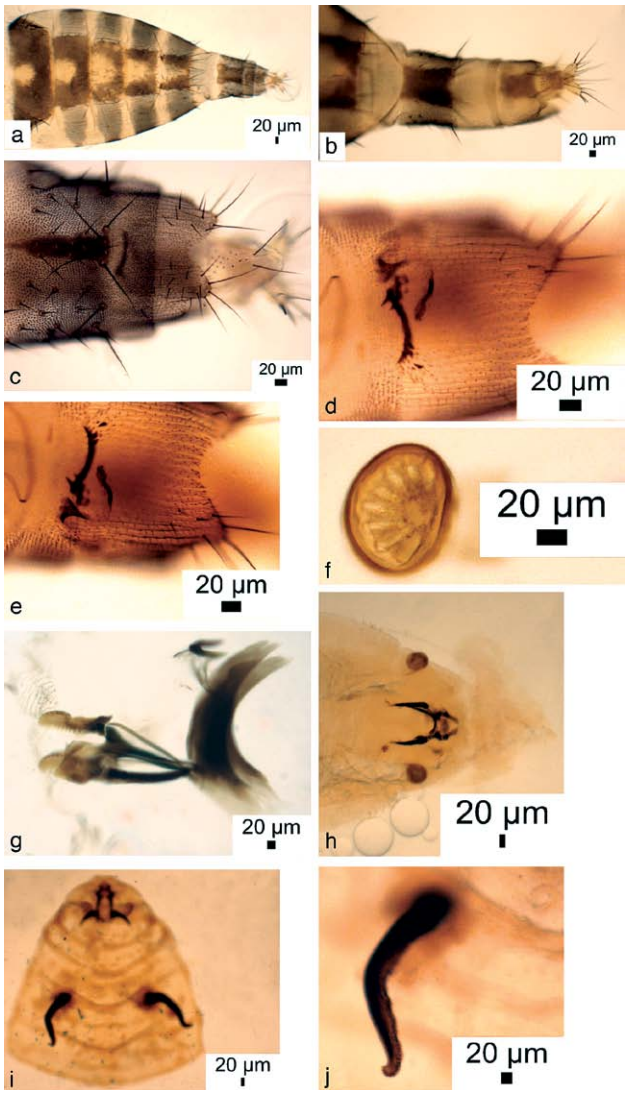

Fig. 2 – *Megaselia aquatica* female: **a**, abdominal tergites; **b**, tip of abdomen from above; **c**, abdominal sternites 7 and 8; **d**, furca from above; **e**, furca from below; **f-h**: details of larva: **f**, anterior spiracle; **g**, larval cephalopharyngeal skeleton and mandibles; **h**, anterior end of larva from above; **i**, pupal eclosion plate; **j**, pupal respiratory horn.

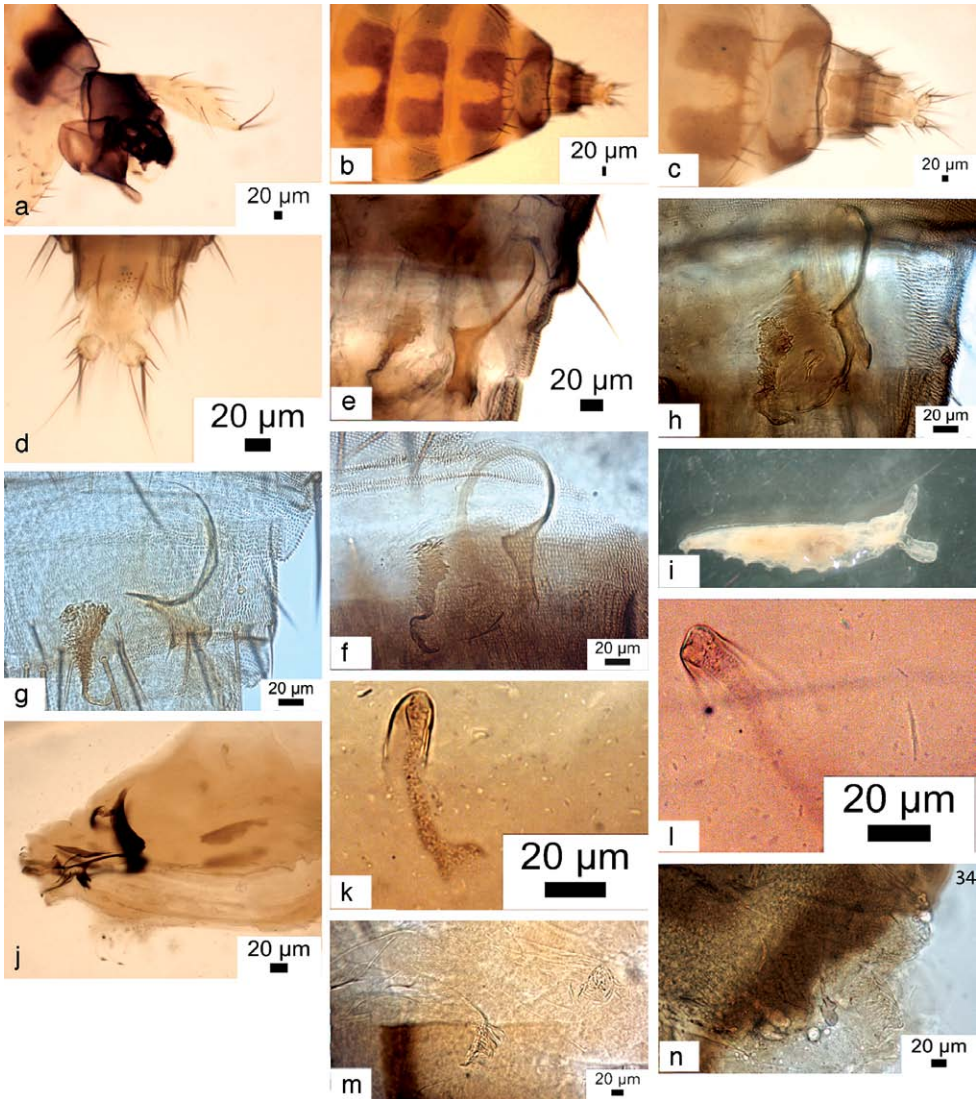

Fig. 3 – *Megaselia imitatrix*: **a**, male hypopygium; **b**-**h**, female. **b**-**c**, abdominal tergites; **d**, cerci; **e**-**h**, furca in different specimens; **i**, larva (photo by Bruno Canneva); **j**, anterior end of larva; **k**, anterior spiracle of larva; **l**, anterior spiracle of pupa; **m**-**n**, eggs in gravid females.

and proboscis as Fig. 4 b. The palps with an internal vesicle in outer half (Fig. 4 c). Thorax brown. Two notopleural bristles and no cleft in front of these. Mesopleuron bare. Scutellum with an anterior pair of hairs and a posterior pair of bristles. Abdominal tergites as Figs 4 d-e and rest of dorsal face as Fig. 4 f. Venter gray, and with numerous hairs below segments 3-6. Sternite 7 and beyond as Fig. 4 g. Furca as Fig. 4 h. Dufour's crop mechanism as Fig. 4 i. Legs yellow apart from brown tip of hind femur. Fore tarsus (Fig. 4 j) with posterodorsal hair palisades on segments 1-4 and half 5. Dorsal hair palisade of mid tibia extends almost two thirds of length. Hind femur as Fig. 4 k. Hind tibia with a dozen differentiated posterodorsal hairs, the most apical being longer than the rest, and spinules of apical combs simple. Wings (Fig. 4 l) 1.8-2.0 mm long. Costal index 0.52. Costal ratios 7.5 : 5.2 : 1. Costal cilia (of section 3) 0.07-0.08 mm long. No hair at base of vein 3. With 5 axillary bristles, the outer being 0.11-0.13 mm long. Sc not reaching R1. Haltere brown.

Eggs. As Fig 4 m, with a subterminal plastron surrounded by long processes (Fig. 4 n).

Affinities. In the primary keys to Neotropical species of the giant genus *Megaselia* (Borgmeier 1962) it runs to Group VII, couplet 72, lead 2 to *M. irene* Borgmeier, which differs in having brown postpedicels and brown thorax. Subsequently described species differ in having 3 notopleural bristles.

Megaselia species C (Figs 5 a-l)

Material. 5 females, **BOLIVIA**: Buena Vista, Santa Cruz, reared from internode of *Guadua angustifolia* var. *cha-*

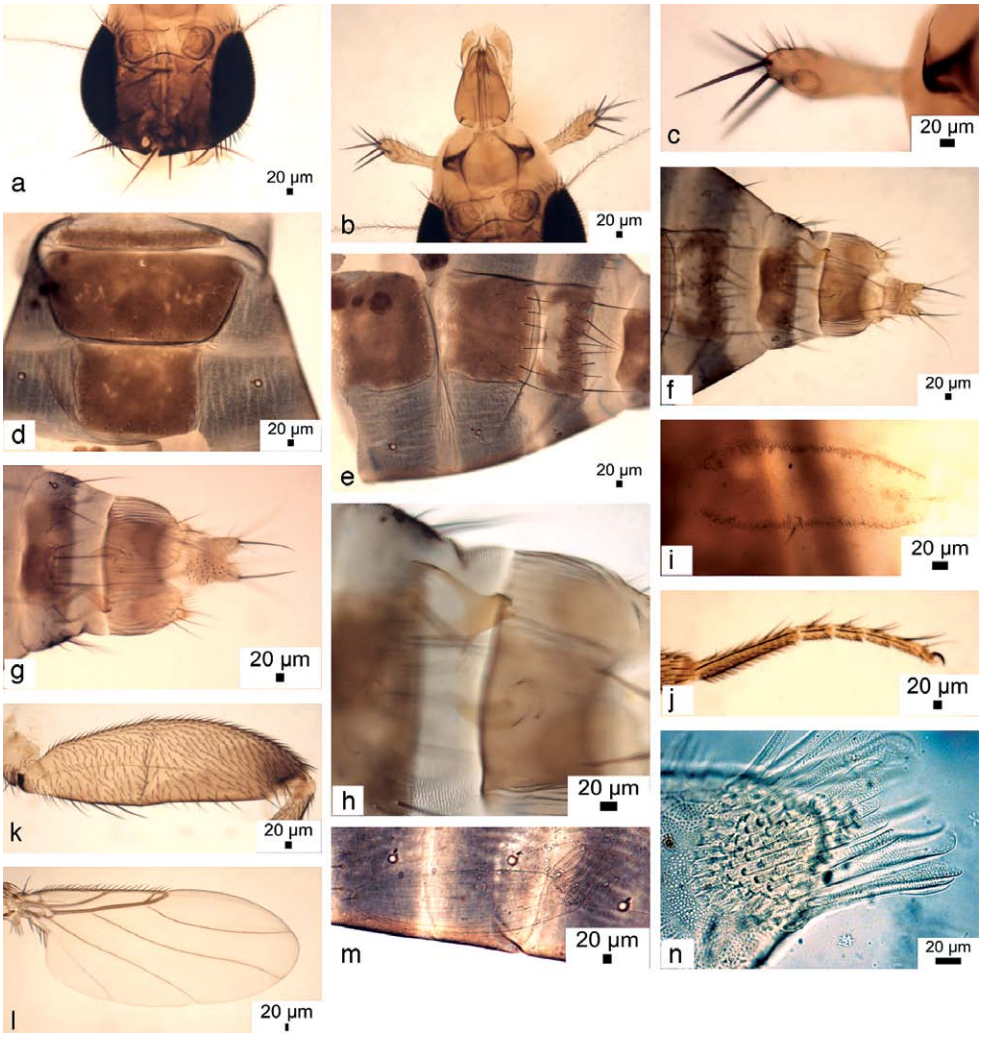

Fig. 4 – *Megaselia* Species B, female: **a**, frons; **b**, antennae, palps and proboscis; **c**, palp; **d**, abdominal tergites 1-3; **e**, tergites 4-6; **f**, T6 to tip of abdomen; **g**, sternite 7 to tip of abdomen; **h**, furca; **i**, Dufour's crop mechanism; **j**, front tarsus; **k**, hind femur; **l**, wing; **m**, egg; **n**, anterior end of egg.

coensis, Jan 2011, D. Kovac (14/11, 16/11, NHMSC, UCMZ, 40-37-39).

Female. Frons as Fig. 5 a and with dense but very fine microtrichia. Cheek with 6 bristles and jowl with two that are more robust. Postpedicels with SPS vesicles (Fig. 5 b). Palps and proboscis as Fig. 5 c. Thorax yellow. Two notopleural bristles and no cleft in front of these. Mesopleuron bare. Scutellum with an anterior pair of hairs and a posterior pair of bristles. Abdominal tergites as Fig. 5 d. Tergite 6 brown, wider than long and with hind margin clearly not as wide as front margin. Venter yellow but gray on flanks from edges of tergites, and with hairs below segments 3-6. Cerci as Fig. 5 e. Rear of sternum 8 as Fig. 5 f. Sternite 7 and furca present but not clearly seen in only available specimen. Dufour's crop mechanism as Fig. 5 g. Legs yellow apart from brown tip to hind femur. Fore tarsus (Fig. 5 h) with posterodorsal hair palisade on segments 1-5 and 5 longer than 4. Dorsal hair palisade of mid tibia extends about three quarters of its length. Hind femur and tibia as Fig. 5 i, the tibia with a dozen differentiated posterodorsal hairs, the most apical being the longest, and spinules of apical combs simple. Wings (Fig. 5 j) 2.0-2.7 mm long. Costal index 0.57-0.59. Costal ratios 4.8-7.1 : 3.8-5.7 : 1. Costal cilia (of section 3) 0.06-0.07 mm long. No hair at base of vein 3. With 5-6 axillary bristles, the outermost being 0.11-0.14 mm long. Sc not reaching R1. Haltere brown.

Eggs. Uniquely are hairy (Fig. 5 k), and with a subapical plastron (Fig. 5 l) that is very similar to that of species B.

Affinities. In the primary keys to Neotropical species of the giant genus *Megaselia* (Borgmeier 1962) it runs to Group VII, couplet 93, lead 1, to *M. cinerascens* Borgmeier, which differs in having brown postpedicels and only two axillary bristles. Subsequently described species have brown postpedicels and/or females with different abdominal tergites.

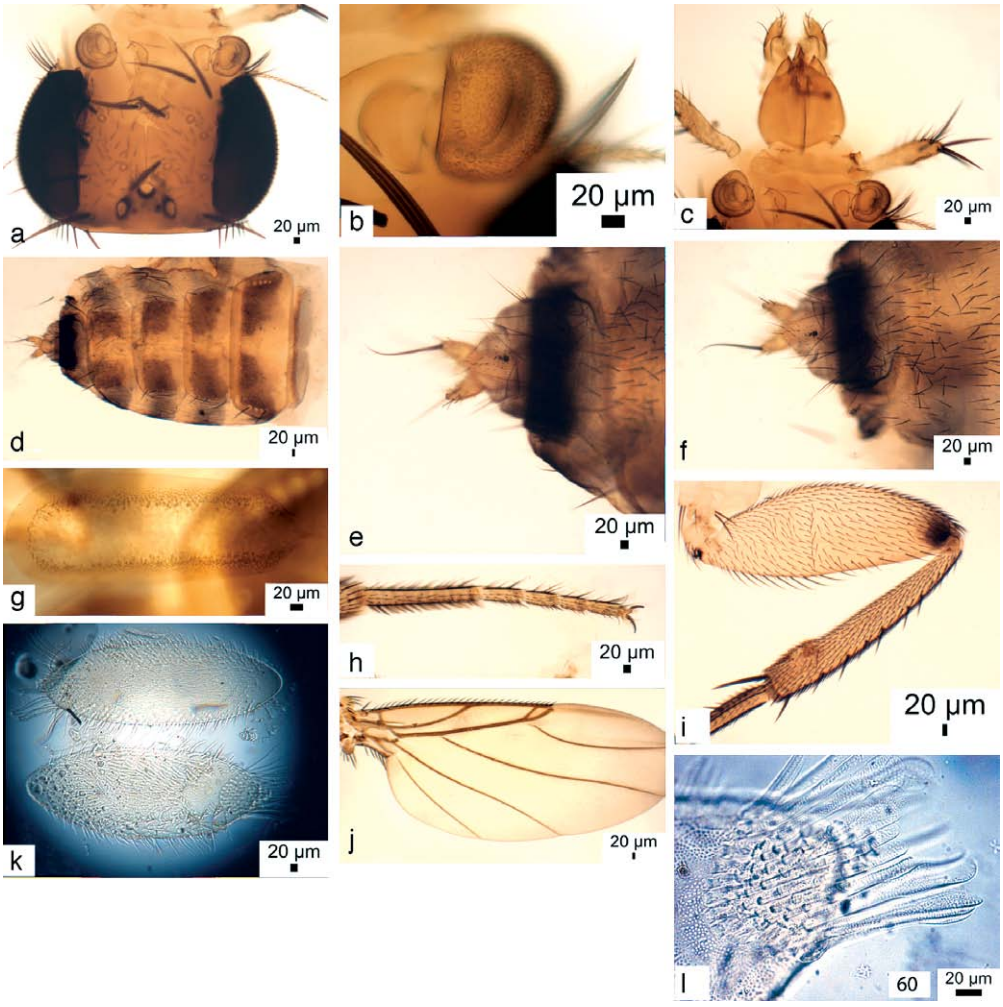

Fig. 5 – *Megaselia* Species C, female: **a**, frons; **b**, antenna; **c**, palps and proboscis; **d**, abdomen dorsal face; **e**, cerci; **f**, rear of sternum 8; **g**, Dufour's crop mechanism; **h**, front tarsus; i, hind femur and tibia; **j**, wing; **k**, two eggs; **l**, anterior end of egg.

Megaselia species D (Figs 6 a-k)

Material. Female, **BOLIVIA**: Buena Vista, Santa Cruz, reared from internode of *Guadua angustifolia* var. *chacoensis*, 13 Jan 2011, D. Kovac (16/11, NHMSC, 40-38).

Female. Head as Fig. 6 a, the frons having dense but very fine microtrichia. Postpedicels, palps and proboscis as Fig. 6 b, the palps having an enclosed pit. Thorax yellow, but scutellum brown. Two notopleural bristles and no cleft in front of these. Mesopleuron bare. Scutellum with an anterior pair of small hairs and a posterior pair of bristles. Abdominal tergites 1 and 2 brown, T3 to T6 as Fig. 6 c. Tergite 7 to tip of abdomen as Fig. 6 d. Cerci (Fig. 6 e) without a differentiated bristle that is clearly more robust than the hairs. Venter yellow but with grey bands dorsally from the lateral margins of the tergites, and with well developed hairs on segments 3 to 6 with those at rear of T6 clearly longer than the rest. Sternite 7 and lobes at rear of sternum 8 as Fig. 6 f. Furca complex (Fig. 6 g). Dufour's crop mechanism long and thin. Legs yellow apart from brown tip to hind femur. Front tarsus with a posterodorsal hair palisade on all five segments and segment 5 clearly longer than 4 (Fig. 6 h). Mid tibia and basitarsus as Fig. 6 i. Hind femur as Fig 6 j. Hind tibia with a dozen differentiated posterodorsal hairs, the most apical being the longest, and spinules of apical combs simple. Wings (Fig. 6 k) 1.7 mm long. Costal index 0.48. Costal ratios 5.3 : 4.2 : 1. Costal cilia (of section 3) 0.05 mm long. No hair at base of vein 3. With 5 axillary bristles, the outermost being 0.09 mm long. Sc not reaching R1. Haltere knob pale.
Eggs. With subterminal plastron similar to *M. imitatrix* (Fig. 3 m).
Affinities. In the primary keys to Neotropical species of the giant genus *Megaselia* (Borgmeier 1962) it runs to Group VII, couplet 72, lead 2 to *M. Irene* Borgmeier, which differs in having brown postpedicels and a brown thorax. Subsequently described species differ in having 3 notopleural bristles.

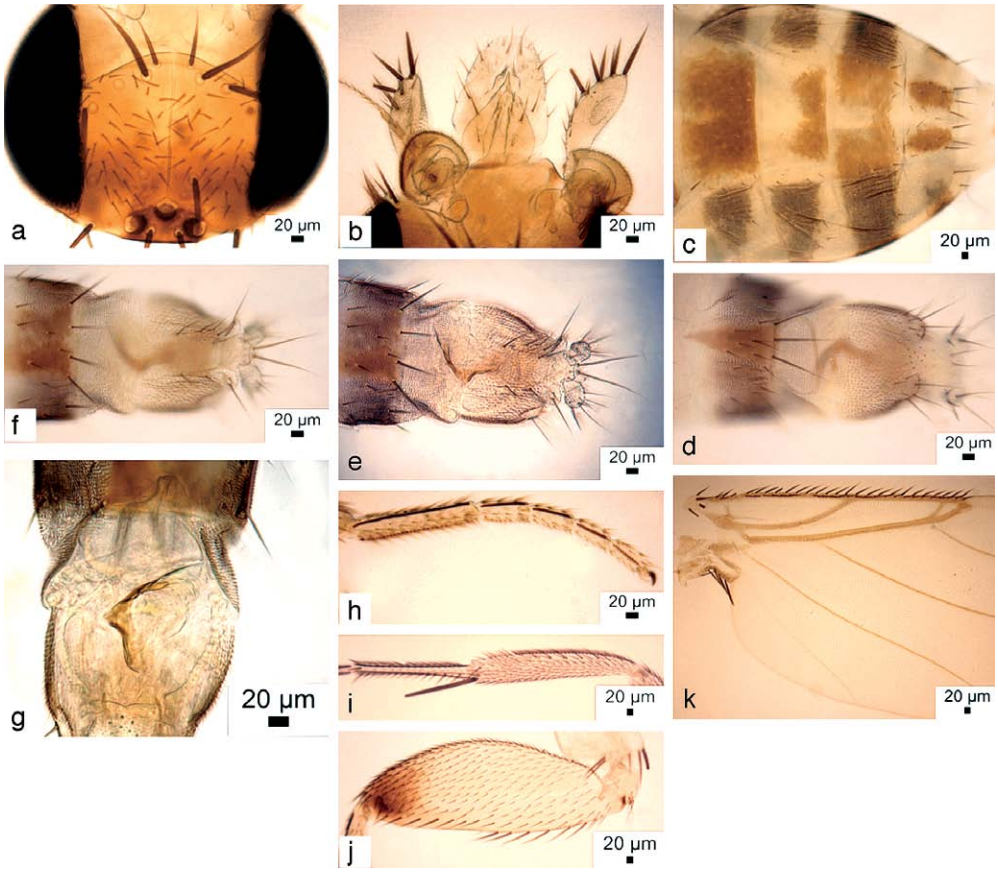

Fig. 6 – *Megaselia* Species D, female: **a**, head; **b**, postpedicels, palps and proboscis; **c**, abdominal tergites 3-6; **d**, tergite 7 to tip of abdomen; **e**, cerci; **f**, sternite 7 and lobes at rear of sternum 8; g, furca; **h**, front tarsus; **i**, mid tibia and basitasrsus; **j**, hind femur; **k**, wing.

Megaselia species E (Figs 7 a-m)

Material. Female, **BOLIVIA**: Buena Vista, Santa Cruz, reared from internode of *Guadua angustifolia* var. *chacoensis*, 13 Jan 2011, D. Kovac (16/11, NHMSC, 40-38).

Female. Frons as Fig. 7 a, and with dense but very fine microtrichia. Postpedicels, palps and proboscis as Fig. 7 b, the palps lacking a pit. Thorax yellow, but scutellum brown. Two notopleural bristles and no cleft in front of these. Mesopleuron bare. Scutellum with an anterior pair of hairs and a posterior pair of bristles. Abdominal tergites 1 to 5 brown, T4 to T7 as Fig. 7 c. Cerci (Fig. 7 d) without a differentiated bristle that is clearly more robust than the hairs. Venter yellow but with grey bands dorsally from the lateral margins of the tergites, and with well developed hairs on segments 3 to 6. Sternite 7 and lobes of sternum 8 as Fig. 7 e. Furca as Fig. 7 f. Dufour's crop mechanism as Fig. 7 g. Legs yellow apart from brown tip to hind femur. Front tarsus with a posterodorsal hair palisade on segments 1-4 (Fig. 7 h). Mid tibia as Fig. 7 i. Hind femur as Fig. 7 j. Hind tibia with about 10 differentiated posterodorsal hairs, the most apical being the longest, and the two spinules of apical combs between posteroventral spur and the long ventral bristle are forked (Fig. 7 k). Wings (Fig. 7 l) 1.5 mm long. Costal index 0.53. Costal ratios 4.1 : 3.1 : 1. Costal cilia (of section 3) 0.05 mm long. No hair at base of vein 3. With 3 axillary bristles, the outermost being 0.08 mm long. Sc ends in vein R1. Haltere knob gray.
Eggs. As Fig. 7 m.
Affinities. In the primary keys to Neotropical species of the giant genus *Megaselia* (Borgmeier 1962) it runs to Group VII, couplets 12 to 29 that cover females with modified abdominal tergites, but none fit. In his supplementary keys Borgmeier (1969) it runs to couplet 29, to the aquatic *M. imitatrix* Borgmeier, but differs in details such as abdominal tergites 2-5 being entirely brown. In addition the bifid spinules of the apical comb of the hind tibia (Fig. 7 k) distinguish it from most species.

Megaselia species F (Figs 8 a-g)

Material. Female, **BOLIVIA**: Buena Vista, Santa Cruz, reared from *Guadua angustifolia* var. *chacoensis*, 13 January 2011, D. Kovac (16/11, NHMSC, 40-39).

Female. Head as Fig. 8a, the frons having dense but very fine microtrichia. Postpedicels with a few SPS vesicles

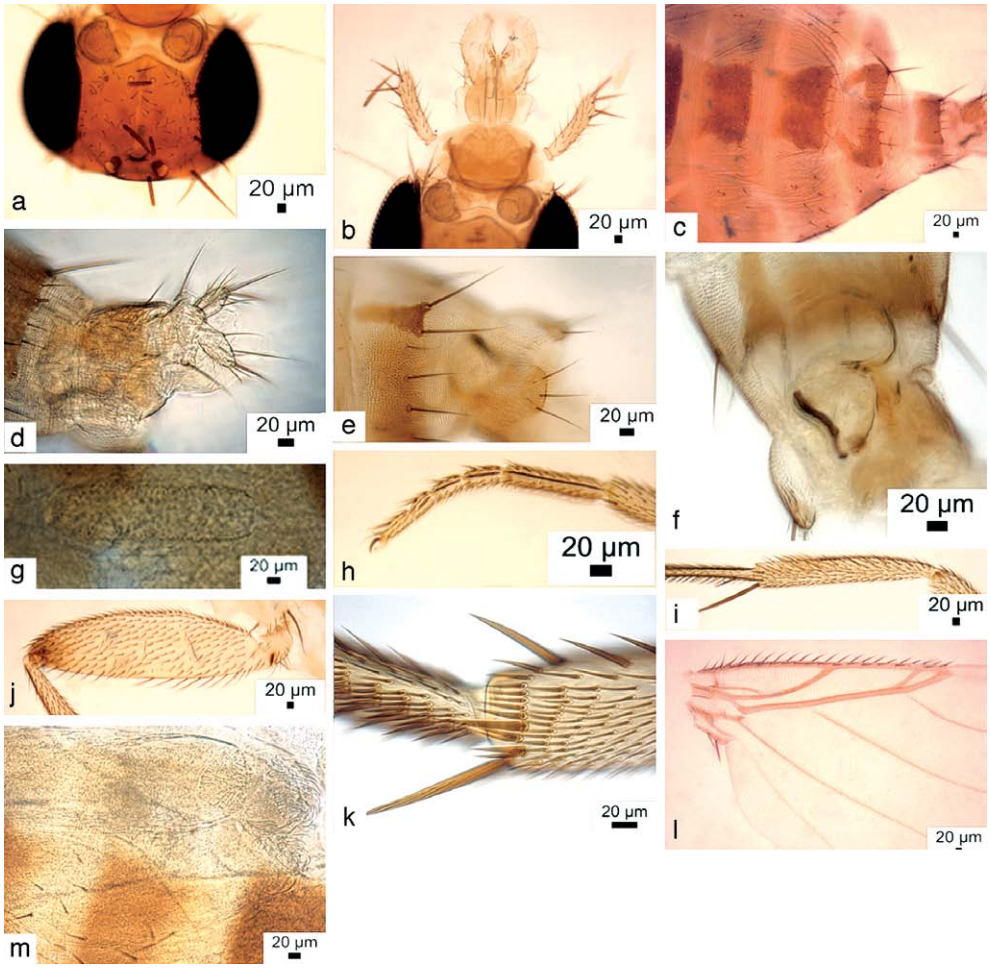

Fig. 7 – *Megaselia* Species E, female: **a**, frons; **b**, postpedicels, palps and proboscis; **c**, abdominal tergites 4-7; **d**, cerci; **e**, sternite 7 and right lobe at rear of sternum 8; **f**, furca; **g**, Dufour's crop mechanism; **h**, front tarsus; **i**, mid tibia; **j**, hind femur; **k**, tip of hind tibia; **l**, wing; **m**, eggs.

and the palps lacking a pit. Thorax yellow, but scutellum brown. Two notopleural bristles and no cleft in front of these. Mesopleuron bare. Scutellum with an anterior pair of hairs and a posterior pair of bristles. Abdominal tergites as Fig. 8b. Cerci with a differentiated bristle that is clearly more robust than the hairs (Fig. 8d). Walls of dorsal abdominal glands with a conspicuous sclerotized network (Fig. 8c). Venter yellow but with grey bands dorsally from the lateral margins of the tergites, and with well developed hairs on segments 3 to 6. Sternite 7 not evident due to retraction of terminal segments. Furca complex as Fig. 8 d. Dufour's crop mechanism not discerned. Legs yellow apart from brown tip to hind femur. Front tarsus with a posterodorsal hair palisade on segments 1-5 (Fig. 8e). Mid tibia with the dorsal hair palisade extending almost 0.8 times its length. Hind femur as Fig. 8f. Hind tibia with ten differentiated posterodorsal hairs, the most apical being the longest, and spinules of apical combs simple. Wings (Fig. 8g) 1.6 mm long. Costal index 0.48-0.49. Costal ratios 4.4 : 3.2: 1. Costal cilia (of section 3) 0.06 mm long. No hair at base of vein 3. With 5 axillary bristles, the outermost being 0.09 mm long. Sc not reaching R1. Haltere knob gray (Fig. 8b).

Eggs. With subterminal plastron similar to *M. imitatrix* (Fig. 3m)

Affinities. In the primary keys to Neotropical species of the giant genus *Megaselia* (Borgmeier 1962) it runs to Group VII, couplets 12 to 29 that cover females with modified abdominal tergites, but none fit. In his supplementary keys Borgmeier (1969) it runs to couplet 29, to the aquatic *M. imitatrix* Borgmeier, but its abdominal tergites 2-4 are only brown in their posterior thirds. In slide mounted specimens its dorsal abdominal glands will instantly distinguish it from other members of the *M. imitatrix* complex.

Megaselia species G (Figs 9 a-m)

Material. Female, **BOLIVIA**: Buena Vista, Santa Cruz, reared from internode of *Guadua angustifolia* var. *chacoensis*, 13 Jan 2011, D. Kovac (16/11, NHMSC, 40-39).

Female. Frons as Fig. 9 a, and with dense but very fine microtrichia. Postpedicels, palps and proboscis as Fig. 9 b the palps lacking a pit. Thorax yellow, but scutellum brown. Two notopleural bristles and no cleft in front of these. Mesopleuron bare. Scutellum with an anterior pair of hairs and a posterior pair of bristles. Abdominal tergites and cerci as Figs 9 c-d, the cerci with a ventral differentiated bristle that is clearly more robust than the hairs (Fig. 9 f). Venter yellow but with grey bands dorsally from the lateral margins of the tergites, and with well developed hairs on segments 3 to 6. Dufour's crop mechanism as Fig. 9 e. Sternite 7 divided into left and right portions (Fig. 9 f). Lobes at rear of sternum 8 as Fig. 9 f. Furca complex as Figs 9 f-g. Legs yellow apart from brown tip to hind femur. Front tarsus with a posterodorsal hair palisade on segments 1-4 (Fig. 9 h). Mid tibia with the dorsal hair palisade extending 0.62 times its length. Hind femur as Fig. 9 i. Hind tibia with a dozen differentiated posterodorsal hairs, the most apical being the longest, and spinules of apical combs with some that are forked (Figs 9 j-k). Wings (Fig. 9 l) 1.7 mm long. Costal index 0.55-0.56. Costal ratios 3.8 : 3.0: 1. Costal cilia (of section 3) 0.05 mm long. No hair at base of vein 3. With 4 axillary bristles, the outermost being 0.10 mm long. Sc reaching R1 but its tip pale. Haltere knob brownish gray.
Eggs. As Fig. 9 m.
Affinities. In the primary keys to Neotropical species of the giant genus *Megaselia* (Borgmeier 1962) it runs to Group VII, couplets 12 to 29 that cover females with modified abdominal tergites, but none fit. In his supplementary keys Borgmeier (1969) it either runs to couplet 29, to the aquatic *M. imitatrix* Borgmeier, but its abdominal 2-5 are entirely brown. Or else it runs to couplet 53, where its abdominal tergites differ from both species.

Megaselia species H (Figs 10 a-k)

Material. 6 Females, **BOLIVIA**: Buena Vista, Santa Cruz, reared from internode of *Guadua angustifolia* var. *chacoensis*, 13 Jan 2011, D. Kovac (16/11, NHMSC, UCMZ, 40-39).

Female. Frons as Fig. 10 a and with dense but very fine microsetae. Cheek with 8 bristles and jowl with 2 that are longer and more robust. Postpedicels, which have a few SPS vesicles, palps and proboscis as Fig. 10 b. Thorax yellow. Two notopleural bristles and no cleft in front of these. Mesopleuron bare. Scutellum with an anterior pair of hairs and a posterior pair of bristles. Abdominal tergites as Fig. 10 c. Venter yellow but with gray bands on flanks from edges of tergites, and with hairs below segments 3-6. Sternite 7 pale and marked by two strong bristles at rear margin (Fig. 10 e). Posterolateral lobes at rear of sternum 8 pale and each with 3 bristles at tip (Fig. 10e). Cerci as Fig. 10 d. Furca as Fig. 11 f. Dufour's crop mechanism exceptionally long and thin (Fig. 10 g). Legs yellow apart

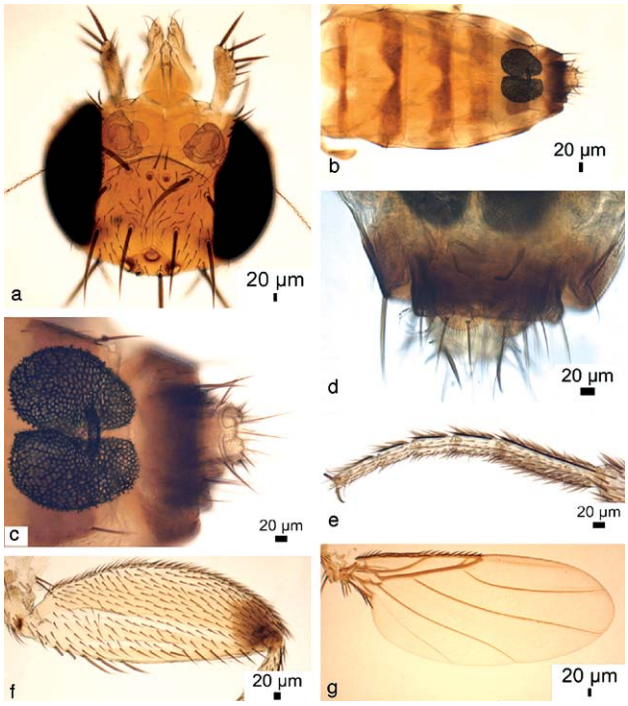

Fig. 8 – *Megaselia* Species F, female: **a**, head; **b**, dorsal face of abdomen; **c**, dorsal abdominal glands and cerci; **d**, furca and tips of lobes at rear of sternum 8; **e**, front tarsus; **f**, hind femur; **g**, wing.

from tip of hind femur. Fore tarsus with posterodorsal hair palisade on segments 1-5 and 5 longer than 4 (Fig. 10 h). Dorsal hair palisade of mid tibia extends about three quarters of its length. Hind femur as Fig. 10 i. Hind tibia with a dozen differentiated posterodorsal hairs and spinules of apical combs simple. Wings (Fig. 10 j) 0.9-2.6 mm long, with a very pale membrane and veins 4-6 very pale gray and 7 very pale. Costal index 0.48-0.51. Costal ratios 4.1-6.1 : 3.0-4.5 : 1. Costal cilia (of section 3) 0.04-0.10 mm long. No hair at base of vein 3. With 4-5 axillary bristles, the outer being 0.08-0.10 mm long. Sc not reaching R1. Haltere as Fig. 10 c.
Eggs. As Figs 10 k-l.
Affinities. In the primary keys to Neotropical species of the giant genus *Megaselia* (Borgmeier 1962) it runs to Group VII, couplets12 to 29 that cover females with modified abdominal tergites, but none fit. In his supplementary keys [Borgmeier (1969)] it either runs to couplet 29, to the aquatic *M. imitatrix* Borgmeier, but tergites 4 and 5 are more extensively yellow; or else it runs to couplet 53, where its abdominal tergites differ from both species.

Megaselia hansonix Disney, 2009 (Figs 11 a-g)

Details of the adults, egg and larva referred to above as Figs 11 a-g. The species is so far known from Texas.

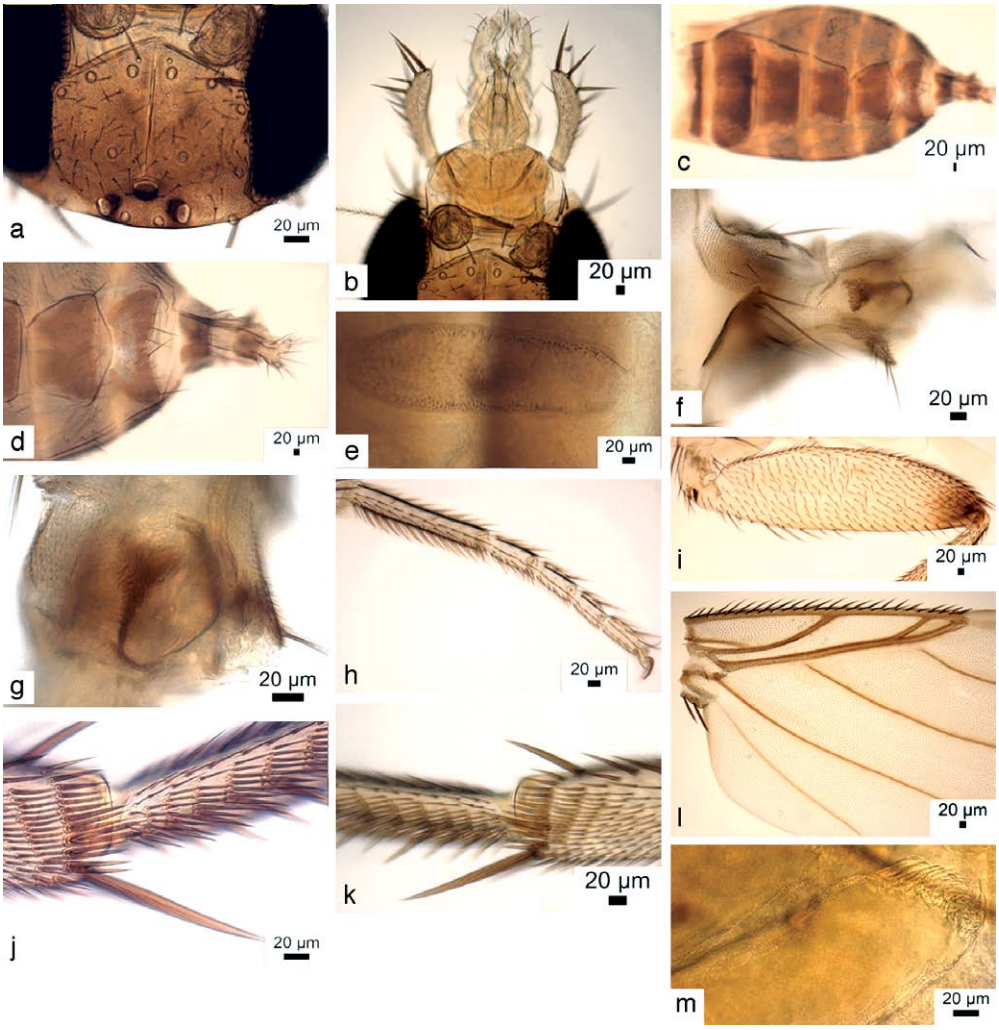

Fig. 9 – *Megaselia* Species G, female: **a**, frons; **b**, postpedicels, palps and proboscis; **c**, abdominal tergites; **d**, tergite 5 to tip of abdomen; **e**, Dufour's crop mechanism; **f**, lobes at rear of sternum 8; **g**, furca; **h**, front tarsus; **i**, hind femur; **j**-**k**, tips of hind tibiae; **l**, wing; **m**, anterior end of egg.

Megaselia rufipes (Meigen, 1804) (Figs 12 a-d)

Details of the adults, egg and larva as Figs 12 a-d.

This species has been transported around the world by man. The larvae are primarily breeders in a range of decaying materials and have frequently been obtained in human corpses. They are occasionally facultatively aquatic, for example being reported from trickling filter sewage systems (Painter 1980).

Megaselia scalaris (Loew, 1866) (Figs 13 a-d)

Details of the adults, egg and larva as Figs 13 a-d.

The larvae of this species are occasionally reported as being facultatively aquatic, having been recorded breeding in bamboo internodes and water filled shells of decaying coconuts (Disney 2004).

Key to the species of *Megaselia* from the Americas whose larvae have been reported from aquatic situations

1. Females 2
- Males (few only are known) 14
2. Thorax yellow to orange yellow 3
- Thorax dark brown to black. Abdominal tergites all dark and T4 to T7 as Fig. 12b. Dufour's crop mechanism as Fig. 12c ..... *M. rufipes*
3. Only T6 in part yellow (Figs 4e and 9c) 4
- Abdominal tergites 2-6 in part yellow 5
4. Palp with an internal vesicle in outer half (Fig. 4c). Abdominal tergites as Figs 4d-f ..... *M.* species B
- Palp lacks such a vesicle (Fig. 9b). Abdominal tergites as Fig. 9c ..... *M.* species G
5. Abdominal tergite 6 not as wide as T5 (Figs 2a and 6c) 6
- Abdominal T6 short but clearly wider than T5 (Figs 11b, 12 b and 13b) 7
6. T4 not as wide as T3 or T5 (Fig. 6c). T7 as Fig. 6d. Palp with pit as Fig. 6b ..... *M.* species D

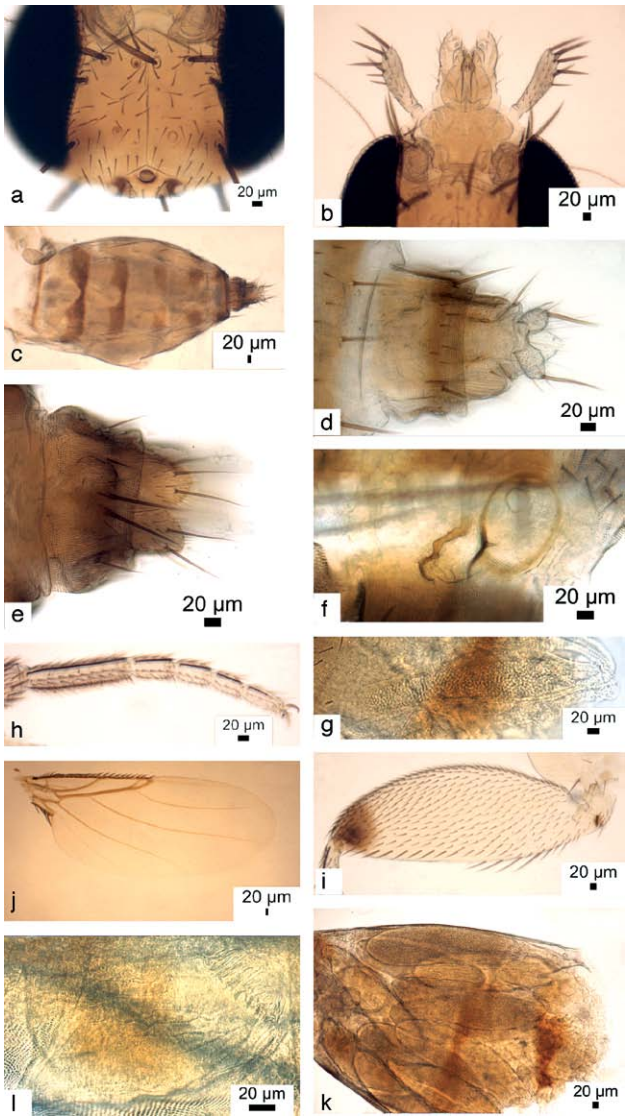

Fig. 10 – *Megaselia* Species H, female: **a**, frons; **b**, postpedicels, palps and proboscis; **c**, abdominal tergites and haltere; **d**, cerci; **e**, sternum 7 and lobes at rear of sternum 8; **f**, furca; **g**, Dufour's crop mechanism; **h**, front tarsus; **i**, hind femur; **j**, wing; **k**, eggs; **l**, an egg.

- Tergites progressively narrowing from T2 to T6 (Fig. 2a). T7 as Fig. 2b. Palp with pit as Fig. 1b ..... *M. aquatica*
7. Cercus with a bristle well differentiated from hairs (Figs 5e and 10d) 8
- Cercus lacks such a bristle (Fig. 7d) 13
8. Dorsal abdominal glands (DAGs) not evident 9
- DAGs strongly developed (Fig. 8c) ..... *M.* species F
9. Wing membrane lightly tinged grayish and veins 4-6 clearly evident (e.g. Fig. 5j) 10
- Wing membrane very pale and likewise veins 4-6 (Fig. 10j). (Palps and proboscis as Fig. 10b) ..... *M.* species H
10. Labrum larger and darker (Fig. 5c). Furca seemingly absent. (Cerci somewhat elongated - Fig. 5e) ..... *M.* species C
- Labrum smaller and paler (e.g. Fig. 3b). Furca evident ... 11

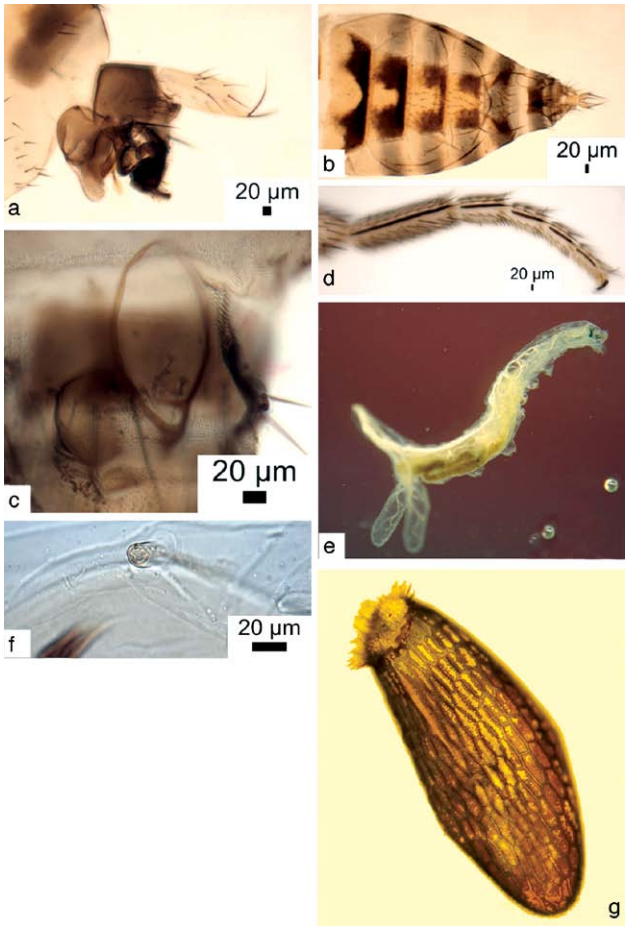

Fig. 11 – *Megaselia hansonix*: **a**, left face of male hypopygium; **b**, female abdominal tergites; **c**, female furca; **d**, female front tarsus; **e**, larva; **f**, anterior spiracle of larva; **g**, egg. (11e and g photographed by Harlin Hanson)

11. Furca in part hoop shaped (Figs 11c and 13c) 12
- Furca as Fig. 3h ..... *M.* species A
12. Abdominal tergites as Fig. 11b. Furca as Fig. 11c .... *M. hansonix*
- Abdominal tergites as Figs 3b-c. Furca as Figs 3e-h .... *M. imitatrix*
13. Abdominal tergites as Fig. 13b. Furca as Fig. 13c .... *M. scalaris*
- Abdominal tergites as Fig. 7c. Furca as Fig. 7f .... Species E
14. Thorax yellow to orange yellow 15
- Thorax dark brown to black. Abdominal tergites and epandrium with numerous robust bristles (Fig. 12a) ... *M. rufipes*
15. Bristles at tip of proctiger very robust (Fig. 13 a) and with microtrichia ..... *M. scalaris*
- Not so 16
16. The longer (right) paraphysis of the penis complex with a projecting hairy, finger like, process at its tip (Fig. 11a) .... *M. hansonix*
- Without this process 17
17. Hypopygium as Fig. 1c, with more numerous hairs on cercus ..... *M. aquatica*
- Hypopygium as Fig. 3a, with fewer hairs on cercus .... *M. imitatrix*

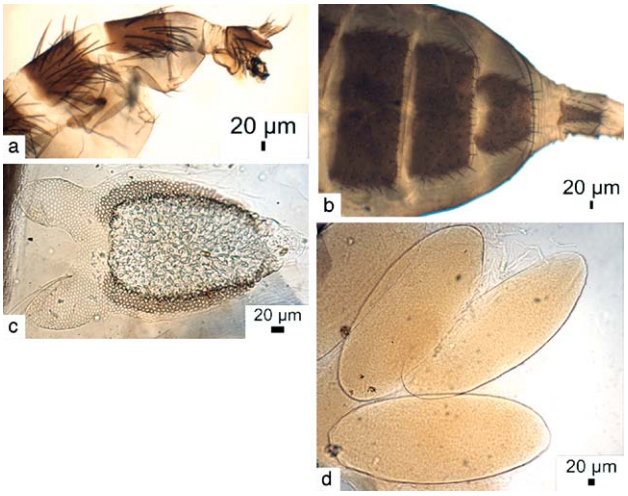

Fig. 12 – *Megaselia rufipes*: **a**, left face of male abdominal segments 5 and 6 and hypopygium; **b**, female abdominal tergites 4-7; **c**, female Dufour's crop mechanism; **d**, egg.

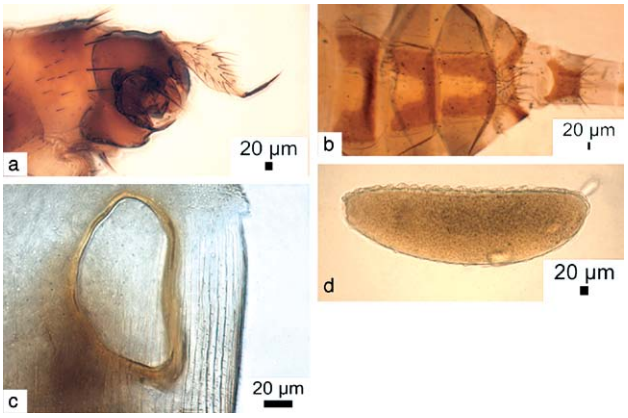

Fig. 13 – *Megaselia scalaris*: **a**, left face of male hypopygium; **b**, female abdominal tergites 3-7; **c**, female furca; **d**, side view of egg.

Key to known eggs

1. Without a plastron (Fig. 12d) ..... *M. rufipes*
- With a plastron (e.g. Figs 11g and 13d) 2
2. Plastron subterminal (e.g. Fig. 11g) 3
- Plastron dorsal, running the length of the egg (Fig. 13d) .... *M. scalaris*
3. Egg covered in fine hairs (Fig. 5k) ..... Species C
- Not so 4
4. Processes encircling plastron relatively long (Figs 4m-n) .... Species B
- These processes not as long (e.g. Fig. 11g) .... *M. hansonix* and Species E, F, G, H

Discussion

The Neotropical fauna of Phoridae with aquatic larvae is clearly richer than previously reported. The supposedly distinctive female of *Megaselia imitatrix* is now recognised as being one member of a sibling species complex. The egg of *M. scalaris,* with a plastron running the length of its dorsal face, is of the type that floats. The egg of *M. aquatica* remains to be described. The eggs of the other species, with their subapical plastrons, are of the type that is placed vertically on the sides of the container with the plastron uppermost close to the water surface. Two of these species have exceptionally long flattened process encircling the plastron. Such elongated processes have not been previously reported. In addition Species C uniquely has the rest of the egg covered in hairs. The different types of eggs and the observation that some larvae stayed in water and others in the wet zone above the water surface suggest that *Megaselia* species occupy different niches in bamboo internodes, as was observed in Southeast Asian species (Kovac & Streit 1996).

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References

Benton F., Claugher D. 2000. The structure and surface properties of the eggshell of *Megaselia imitatrix* Borgmeier (Diptera, Phoridae) in relation to the respiration of the embryo. Physiological Entomology, 25: 133–140.

Borgmeier T. 1962. Versuch einer Übersicht über die neotropischen *Megaselia*-Arten, sowie neue oder wenig bekannte Phoriden verschiedener Gattungen (Dipt. Phoridae). Studia Entomologica, Petropolis, 5: 289–488.

Borgmeier T. 1969. Bredin-Archbold-Smithsonian Biological Survey of Dominica: The Phoridae of Dominica (Diptera). Smithsonian Contributions Zoology, 23: 1–69.

Borgmeier T. 1971. Further studies on Phorid flies, mainly of the Neotropical Region (Diptera, Phoridae). Studia Entomologica, Petropolis, 14: 1–172.

Clarke C.M., Kitching R.L. 1993. The metazoan food webs from six species of Bornean *Nepenthes* species. Ecological Entomology, 18: 7–16.

Disney R.H.L. 1994. Scuttle Flies: The Phoridae. London, Chapman & Hall. [Archived by Springer Book Archives - https://www.springer.com]

Disney R.H.L. 1995. A new species of aquatic fly (Diptera: Phoridae) from the Temengor Forest Reserve, Hulu Perak, Malaysia. Malayan Nature Journal, 48: 271–279.

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, pp. 818–825. In Yule C.M., Yong H.S. (eds), Freshwater Invertebrates of the Malaysian Region. Kuala Lumpur: Academy of Sciences Malaysia. ISBN 983-41936-0-2.

Disney R.H.L., Copeland R.S., Murrell E. 2009. The true identity of Copeland's aquatic scuttle fly (Diptera: Phoridae) from Indiana and recognition of a sibling species from Texas. Proceedings of the Entomological Society of Washington, 111: 564–574.

Disney R.H.L., Garcia-Rojo A., Lindström A., Manlove J.D. 2014. Further occurrences of *Dohrniphora cornuta* (Bigot) (Diptera, Phoridae) in forensic cases indicate likely importance of this species in future cases. Forensic Science International, 241: e20–e22.

Frank J. H., Lounibos L.P. (eds) 1983. Phytotelmata: terrestrial plants as hosts for aquatic insect communities. Plexus Publishing Inc., New Jersey, vii + 293 pp.

Jones F.M. 1918. *Dohrniphora venusta* Coqu. in *Sarracenia flava*. Entomological News, 29: 299–302.

Kitching R.L. 2000. Food webs and container habitats. Cambridge University Press, Cambridge, xiii + 431 pp.

Kloter K.O., Penner L.R., Widmer W.J. 1977. Interactions between the larvae of *Psychoda alternata* (Dipt., Psychodidae) and *Dohrniphora cornuta* (Dipt., Phoridae) in a trickling filter sewage bed, with descriptions of the immature stages of the latter. Annals of the Entomological Society of America, 70: 775–781.

Kovac D. 1993. Abundant species in bamboo stems. Model for complex microecosystems. Reports of the Deutsche Forschungsgemeinschaft **3/93** German Research, 21–24.

Kovac D. 1994. Die Tierwelt des Bambus: ein Modell für komplexe tropische Lebensgemeinschaften. Natur und Museum, Frankfurt, 124: 119–136.

Kovac D., Streit B. 1996. The arthropod community in bamboo internodes in Peninsular Malaysia: microzonation and trophic structure. In: Edwards D.S. et al. (eds.). Tropical Rainforest research - Current Issues. Proceedings of tropical rainforest conference in Brunei, April 1993, pp. 85–99. Kluwer Academic Publishers: The Netherlands.

Mogi M., Chan K.L. 1996. Predatory habits of dipteran larvae inhabiting *Nepenthes* pitchers. The Raffles Bulletin of Zoology, 44: 233–245.

Mogi M., Chan K.L 1997. Variation in communities of Dipterans in *Nepenthes* pitchers in Singapore: predators increase prey community diversity. Annals of the Entomological Society of America, 90: 177–183.

Mogi M., Yong H.S. 1992. Aquatic arthropod communities in *Nepenthes* pitchers: the role of niche differentiation, aggregation, predation and competition in community organization. Oecologia ,90: 172–184.

Murrell E.G., Ives A.R., Juliano S.A. 2014. Intrinsic and extrinsic drivers of succession: effects of habitat age and season on an aquatic insect community. Ecological Entomology, DOI: 10.1111/een.12103

Painter H.A. 1980. A survey of filter fly nuisances and their remedies. Water Research Centre Technical Report, 155: 1–40.