

A striking new species of *Megaselia* (Diptera, Phoridae) from Sulawesi, with re-evaluation of related genera

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Megaselia torautensis sp. n. from Sulawesi is described. In the light of its peculiar features the genus *Megaselia* is reviewed and the following Afrotropical genera synonymised with it: *Epimegaselia* Beyer, *Metaplastophora* Beyer, *Quasipseudacteon* Beyer, and *Tarsophoromyia* Beyer. The species included in these genera are related to the rest of *Megaselia* by indicating where they will key out in the existing keys to Afrotropical *Megaselia*.

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Traditionally the classification of species (i.e. the grouping of species into species-groups, subgenera, genera, tribes, etc) has been based on a straight forward typological/phenetic sorting. This, however, has tended to give rise to classifications ever at risk of revision as the morphological gaps between supra-specific taxa are bridged by newly discovered species. With the best estimates indicating that only about 10% of the world's fauna has been described and named by taxonomists, the prediction must be that the majority of supra-specific taxa proposed by traditional taxonomy must be at risk of revision.

While the Darwinian revolution initiated the process of freeing taxonomy from the dead hand of authoritative opinion and arbitrarily imposed classifications, it has required the clarifications of the Hennigian research programme to complete the process. Now, in principle, biological classification is an experimental science, which is seeking to discover the correct classification through a process of advancing testable hypotheses. Phylogenetic cladistics is truly heuristic. Such taxonomy can no longer be likened to biological philately. In four, of their five major tasks (see Disney

1983b), taxonomists can now truly claim to be engaged in science. Only in the solving of nomenclature problems is their task more akin to that of a lawyer than a scientist, in that precedence (the principle of priority) and typification are the key to arriving at a correct solution, rather than the critical evaluation of biological data.

The research programme that seeks to group species into a hierarchical scheme of monophyletic taxa may be causing a certain amount of instability in the short term, but in the longer term the resulting classification will more readily accommodate new species without the necessity for constant revisions of supra-specific taxa. While there is frequently controversy regarding the correctness of a claim to have identified a monophyletic group, such a claim constitutes a legitimate scientific hypothesis. As with all science such hypotheses cannot be proved. They can, however, be disproved; or at least the proposed autapomorphy of the characters, on which the hypotheses of monophyly are based, can be disproved by demonstration of homoplasy or reversed polarity of the homologous transformation series.

The giant genus *Megaselia* Rondani currently includes nearly 1400 valid species. It was previously estimated, from the ratios of known to unknown species in collections sent to the author, that the true total lies between 5000 and 20 000 species (Disney 1983a). Subsequent experience suggests the higher figure is more likely to be nearer the truth. Confronted with such an unmanageable mass of species there has been a strong temptation to lop off morphological segregates and to designate these as separate genera. With the description of new species, however, the gaps between such genera and the parent genus *Megaselia* have tended to be bridged again. Thus both *Endonepenthia* Schmitz and *Plastophora* Brues have had to be abandoned, and their included species returned to *Megaselia* (Disney 1978, 1981, 1986a).

A further complication confronts one when considering the legitimacy of the genus *Megaselia* and related genera. The ground plan of *Megaselia* appears to be close to the ground plan of the Phoridae in many respects (Disney 1988). Principal proposed apomorphic features are a mesopleural furrow, which serves to characterise the Metopininae, and the Dufour's crop mechanism in females, which serves to characterise the Megaseliini (Disney 1989). Within the Megaseliini the characterisation of the genera is far from being in terms of autapomorphic features. Even in terms of morphological gaps many of the proposed genera are so poorly characterised that they cannot be separated from *Megaselia* when attempting to construct a dichotomous key to genera, except when dealing with the fauna of a limited region. Even in the latter case the description of new species has tended to erode the distinctions proposed. Such a situation is only tolerable if one is confident that one is dealing with monophyletic genera. Where this is not yet the case then pragmatic criteria, such as designation of genera in terms of clear cut morphological distinctions, can be the only justification for maintaining parts of *Megaselia* s.l. as separate genera.

An additional complication in the Phoridae is that more than 50% of the genera (out of a current total around 235) are only known in one sex. Even when the female is known the past reliance on pinned specimens means it is frequently not known whether Dufour's crop mechanism is present or absent.

It is against the above background that a striking new species from Sulawesi is described. It is assigned to the genus *Megaselia*. By so doing the validity of several genera is called into question. The synonymising of some Afrotropical genera with *Megaselia* is proposed. Such action renders the latter genus even more unwieldy. However it is considered that the priority with the Megaseliini is to construct user-friendly identification keys to recognisable genera and their included species, as a first step in making progress in the classification of this mass of species. Segregates should only be removed and placed in separate genera when a case for their monophyly has been proposed and, at the same time, their placement in a subgenus been shown to be inappropriate on scientific grounds.

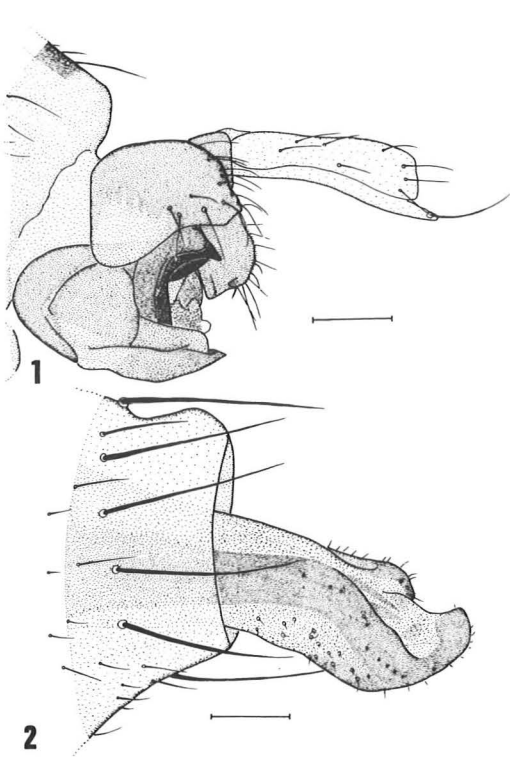
***Megaselia torautensis* sp. n.**

Figs. 1–4

Type material: Holotype ♀, Sulawesi-utara, Dumoga-Bone National Park, Toraut Forest, III.1985 (R. H. L. Disney) (in Cambridge University Zoology Museum). Paratypes: 1♀, 2♂♂ same data as holotype except ♀ 30–31.I.1985, and ♂♂ 23.VII–3.VIII.1985 (A. H. Kirk-Spriggs) (1♂ in National Museum of Wales, Cardiff)

Diagnosis: The combination of two longitudinal hair palisades on the mid-tibia, an unforked vein 3, two bristles and two hairs on the scutellum, and fine hairs and a pair of strong bristles on the mesopleuron, apart from distinctive male and female abdominal terminalia, will serve to distinguish this species from all other described *Megaselia* species except *M. bruesi* Disney, which has pale yellow halteres and only very short hairs on abdominal tergites 1–5.

Male: Frons about as wide as long, brown and with 70–80 hairs. Lower supra-antennal bristles a little shorter, weaker, and closer together than upper pair, which are situated about the same level as the antial bristles. The latter are clearly closer to the supra-antennals than to the antero-laterals, which are clearly higher on frons. In one specimen there is a weaker supernumerary supra-antennal bristle above the left upper supra-antennal. Preocellars a little further apart than upper supra-antennals, but closer to each other than either is from a medio-lateral bristle. The latter clearly lower on frons. Third antennal segment pale brown,

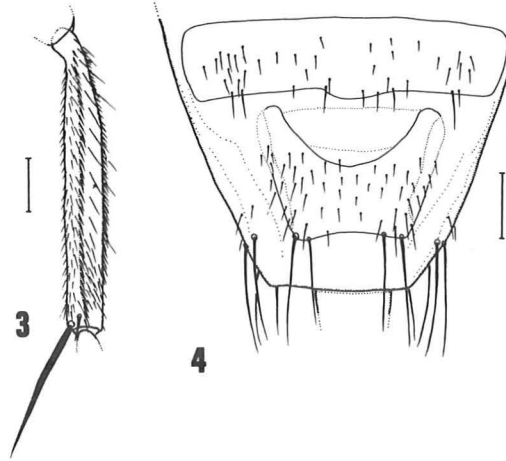


Figs. 1–2. *Megaselia torautensis* sp. n. — 1: male hypopygium viewed from left side; — 2: female ovipositor viewed from left side. — Scale bars = 0.1 mm.

spherical to ovoid, with a dorsal, pre-apical, shortish-haired, brown arista. Palps pale brownish with 4–5 apical bristles, the longest of which is no longer than greatest width of palp. Proboscis with pale brown labrum, simple labella lacking short pale spines below.

Thorax brown. Notopleuron with three bristles. A pair of humeral, intra-alar, post-alar and posterior dorso-central bristles on scutum. Scutellum with an anterior pair of short, fine hairs and a posterior pair of long bristles. Mesopleuron with 10–14 small hairs and a posterior pair of strong bristles, the lower of which is longer and stronger.

Abdomen with dark brown tergites and brownish venter. The latter with, mostly fine, hairs on segments 3–6 below, most obviously on segments 5 and 6, and a few on the flanks above. Tergite hairs short and fine, except for stronger postero-laterals. Hypopygium as Fig. 1, being brown with a dirty yellow anal tube.



Figs. 3–4. *Megaselia torautensis* sp. n. — 3: anterior face of male mid tibia; — 4: dorsal view of segments 5 and 6 of female abdomen. — Scale bars = 0.1 mm.

Front legs yellowish grey. Middle and hind legs more brownish, with apical third of hind femur progressively browner. With 5–7 of the hairs below basal half of hind femur as long as or clearly longer than those of antero-ventral row in apical half. Hind tibia with 12–18 postero-dorsal hairs, with those in lower half more robust and spine-like. Mid-tibia with both a dorsal and an anterior longitudinal hair palisade (Fig. 3). Fore tarsus with a postero-dorsal hair palisade on all five segments. The segments are long and slender, especially the metatarsus (the length ratios being 3.0 : 1.4 : 1.0 : 0.9 : 1).

Wings 1.8–1.9 mm long. Costal index 0.54–0.57. Costal ratios 1.01–1.18 : 1, vein 3 being unforked. Costal cilia 0.07–0.08 mm long. Vein Sc runs to R1, but is somewhat pale and subcostal cell is very narrow. A small hair at base of vein 3. All veins brownish, including vein 7. Axillary ridge with 3–5 bristles. Membrane distinctly brownish grey tinged. Haltere largely pale greyish brown.

Female: Frons and its chaetotaxy as in male. In one specimen there is a set of four small, supernumerary, supra-antennal bristles above the normal supra-antennals. Antennae as in male. Palps a little more slender than in male, and with bristles a little longer. Thorax as in male.

Abdomen with colouring and hairing as in male apart from development of bristles on venter at rear of segments 4–6. In particular segment 6 with a posterior row of long bristles encircling the segment (Figs 2 and 4). Ovipositor (Fig. 2) well developed. Dufour's crop mechanism weakly sclerotised.

Legs as male, except fore tarsus with postero-dorsal hair palisades on first four segments only.

Wings 1.8–1.9 mm long. Costal index 0.56–0.58. Costal ratios 0.94 : 1. Costal cilia 0.07 mm long. Otherwise as male.

A number of features of *M. torautensis* invite comment.

The presence of two hair palisades on the mid tibia (Fig. 3) is in contrast to the single dorsal hair palisade of most known *Megaselia* species. Double hair palisades on the hind tibia have been suggested as a ground-plan feature of the Phoridae (Disney 1988). In the undoubtedly monophyletic genus *Woodiphora* Schmitz there is a transformation series from two, to one, to no hair palisades on both the mid and hind tibiae (Disney 1989). The Platypezid *Plesioclythia argyrogyna* (De Meijere) not only has double hair palisades on both its hind and mid tibiae, but also has a single palisade on its front tibia. The simplest interpretation, on the principle of out-group comparison, is that the ground plan of the Phoridae included double hair palisades on its mid tibia. Table 1 summarises the recorded patterns. The most parsimonious interpretation of the double hair palisade on the mid tibia of *M. torautensis* is that this is a plesiomorphic, ground-plan, feature that has been retained. Furthermore the evidence suggests that the reduction from 2 to 1 palisade on both the mid and hind tibiae has taken place independently in *Woodiphora* and *Megaselia*.

Another feature interpreted as being plesiomorphic, in *M. torautensis*, is the distinct 'collar' between the epandrium and the anal tube. According to the most parsimonious interpretation of the homologies of the principal sclerites of the hypopygium this collar is the fused tergite and sternite of segment 10 (Disney 1986b, 1988, 1990). Other features considered to be plesiomorphic are the presence of 3 not 2 notopleural bristles, vein Sc terminating in R1, costal index exceeding 0.5, the short costal cilia, and vein 7 being distinct. Apo-

morphic features include the unforked vein 3, the modified ovipositor segments, and probably the elongated anal tube of the male.

The sexual dimorphism in the number of fore tarsal segments with a postero-dorsal hair palisade is unusual. The plesiomorphic state is probably the complete series of the male.

The supernumerary supra-antennal bristles in some specimens casts serious doubt on the taxonomic weight given to this character at the generic level. Indeed the taxonomic weight given to the number and inclination of the bristles at the front of the frons is undoubtedly misplaced. Mutants in both, on one side at least, are frequent in *Megaselia*. The cases reported above reinforce the grow-

Table 1. The numbers of longitudinal hair palisades on the tibiae.

	Hind	Mid	Front
PLATYPEZIDAE			
<i>Plesioclythia argyrogyna</i> (De Meijere)	2	2	1
SCIADOCERIDAE			
<i>Sciadocera rufomaculata</i> White	0	0	0
PHORIDAE			
<i>Aenigmatias lubbocki</i> (Verrall)	4–5	3	1
<i>Aenigmatistes foveolatus</i> Schmitz	1	1	0
<i>Cataclinusa pachycondylae</i> (Brues)	2	2	0
<i>Diplonevra abbreviata</i> (von Roser)	3	2	0
<i>D. bifasciata</i> (Walker)	3	2	0
<i>D. concinna</i> (Meigen)	2	2	0
<i>D. florea</i> (Fabricius)	2	2	0
<i>D. funebris</i> (Meigen)	2	2	0
<i>D. glabra</i> Schmitz	2	2	0
<i>D. watsoni</i> Disney	2	2	0
<i>Dohrniphora cornuta</i> (Bigot)	1	1	0
<i>Epicnemis flavidula</i> (Brues)	1	1	0
<i>Megaselia</i> spp. (most species)	1	1	0
<i>M. bruesi</i> Disney	1	2	0
<i>M. torautensis</i> sp. n.	1	2	0
<i>Multinevra macropygidia</i> Disney	5–7	3	1
<i>Myopiomyia harmani</i> Disney	1	1	0
<i>Palpiclavina tonkinensis</i> Silvestri	1	0	0
<i>Plectanochnema nudipes</i> (Becker)	4–5	2–3	0
<i>Woodiphora bilineata</i> Borgmeier	2	2	0
<i>W. bironi</i> (Brues)	1	0	0
<i>W. papuana</i> Disney	2	0	0
<i>W. parvula</i> Schmitz	2	1	0
<i>W. retroversa</i> (Wood)	0	0	0
<i>W. salomonis</i> Beyrer	1	1	0

ing evidence that these characters should be downgraded in terms of their taxonomic weight. Certainly the validity of some genera separated off from *Megaselia* must be called into question. Four such genera, from Africa, are re-assessed below.

***Megaselia bisetigera* (Beyer) comb. n.**

Tarsophoromyia bisetigera Beyer, 1965:198.

The genus *Tarsophoromyia* was erected for a species only known in the female sex. It has an ovipositor modified in a manner associated with parasitoid habits, combined with swollen fore-tarsal segments. Both characters are widespread in the genus *Megaselia*, the only unusual feature being that swollen fore-tarsal segments are normally restricted to the male sex. If *T. bisetigera* is to be placed in a separate genus then it must be inferred that there is a stronger case for transferring several hundred species from *Megaselia* to new genera. I conclude that Beyer failed to make out a case for placing *T. bisetigera* in a new genus, even in typological terms. I herewith transfer it to *Megaselia*, and synonymise *Tarsophoromyia* with the latter genus.

Megaselia bisetigera runs, allowing for eccentricities of construction that alternates couplets based on the female or the male sex only, to couplet 30 on page 54 of Beyer's (1965) keys.

***Megaselia caudalis* (Beyer) comb. n.**

Epimegaselia caudalis Beyer, 1959a:74.

The genus *Epimegaselia* was distinguished from *Megaselia* by the presence of an extra pair of bristles on the front margin of the frons, or at least by an extra pair of reclinate bristles. Beyer (1959a) reported only a single pair of proclinate supra-antennal bristles. The 'extra' pair of bristles could be a pair of supra-antennals that happen to be reclinate rather than porrect.

The porrect, as opposed to proclinate, inclination of the supra-antennal bristles is the basis for the recognition of the tribe Beckerinini (Schmitz 1956). In spite of this genera without supra-antennals were subsequently added to the tribe, without

any sustainable justification. Elsewhere (Disney 1989) it was concluded that a more satisfactory basis for recognition of tribes within the Metopininae is required. Certainly the inclination of bristles at the front of the frons is not adequate grounds for erecting a tribe. Information on variation in the placement and inclination of bristles in general would suggest that single gene mutations can bring about striking differences. Likewise supernumerary bristles are frequent, as evidenced by the supernumerary 'supra-antennal' bristles reported in two specimens of *M. torautensis* above. These must be due to simple gene mutations.

In view of the above considerations the concept of the genus *Epimegaselia* cannot be sustained. I thus transfer *E. caudalis* to the genus *Megaselia* and synonymise *Epimegaselia* with the latter.

Megaselia caudalis will run to couplet 5 on page 56 in Beyer's (1965) keys.

***Megaselia congrex* (Beyer) comb. n.**

Metaplastophora congrex Beyer, 1965:188

This species was placed in *Metaplastophora* along with the type species *M. rotundicauda* Beyer. The validity of the genus is called into question under the latter (see below).

If there were a case for placing this species in a separate genus to *Megaselia* then it would be difficult to justify placing it in the same genus as *M. rotundicauda*. Although Beyer (1965) stressed that both have a compressed ovipositor he gave less taxonomic weight to the obvious differences in the forms of the ovipositors. For example cerci are present in *M. congrex* but absent in *M. rotundicauda*.

In the keys to Afrotropical *Megaselia* (Beyer 1965) this species will run to couplet 4 on page 48.

***Megaselia furvicolor* (Beyer) comb. n.**

Quasipseudacteon furvicolor Beyer, 1959b:387.

The genus *Quasipseudacteon* was distinguished from *Megaselia* by a modified ovipositor, a supernumerary pair of reclinate bristles near the

front margin of the frons and a lack of proclinate supra-antennal bristles (Beyer 1959b).

The evidence suggests that the terminalia of the female abdomen have been independently modified in relation to the independent evolution of parasitoid habits in Phoridae in many clades, and in the genus *Megaselia* in particular (e.g. Disney 1978, 1986a). Thus "modified ovipositor" is not a single character, and certainly not a synapomorphic character. Until the different types of modification have been elucidated, and homologous transformation series identified, these characters cannot be used in classification.

The highlighting of the frontal bristle characters by Beyer rests on the assumption that reclinate or porrect bristles cannot be supra-antennals in the Metopinini, as opposed to the Beckerinini. This, however, is a circular argument. If the inclination of these bristles is given taxonomic weight at the species level only then the frontal chaetotaxy of *Quasipseudacteon* is best interpreted as being of the normal *Megaselia* type, except unlike most (but not all) *Megaselia* species there is only one pair of supra-antennals (which happen to be reclinate). As with *Epimegaselia* (see under *M. caudalis* above) we must discount the supposed difference from *Megaselia* in the frontal chaetotaxy.

Until at least one unambiguous apomorphic character is demonstrated, on which to base a generic distinction, the genus *Quasipseudacteon* cannot be sustained. I thus transfer *Q. furvicolor* to *Megaselia* and synonymise *Quasipseudacteon* with *Megaselia*.

Megaselia furvicolor will run to couplet 3, under "4 scutellaren", on page 48 of Beyer's (1965) keys.

***Megaselia rotundicauda* (Beyer) comb. n.**

Metaplastophora rotundicauda Beyer, 1965:186.

Beyer placed this species and *M. congrex* (see above) in a new genus *Metaplastophora* on the basis of the ovipositors being somewhat compressed. In his key to genera (Beyer 1965) he was unable to separate the male of this species from *Megaselia* and *Plastophora*. The latter genus has since been synonymised with *Megaselia* (Disney

1978, 1986a). Beyer's emphasis on the compression of the ovipositor tends to obscure the considerable difference in the structure of the ovipositor in these two species. For example there are no cerci in *M. rotundicauda*, but cerci are present in *M. congrex*.

Once again we are confronted with an attempt by Beyer to select part of the diverse radiation of ovipositor forms in *Megaselia*, on the basis of a single ill-defined characteristic (in this case the compression of the ovipositor), and to erect a new genus. This might be justified if detailed studies had been made of the adaptive radiation in the morphological modifications in the Metopininae, and monophyletic clades identified. Beyer, however, proposed a number of new genera on the basis of poor descriptions and uncritical evaluation of the structures used as a basis for erecting the proposed genera. He then adds to the confusion, in the case of *Metaplastophora*, by declaring that the males cannot be distinguished from *Megaselia*. I have no hesitation in synonymising *Metaplastophora* with *Megaselia*.

In the keys to Afrotropical *Megaselia* (Beyer 1965) this species will run to couplet 4 on page 48.

***Megaselia subulicauda* Schmitz**

Megasela subulicauda Schmitz, 1929:39

Hemiplastophora subulicauda (Schmitz) Beyer, 1965:186.
New synonym.

Beyer (1965) transferred *Megaselia subulicauda* to a new genus *Hemiplastophora* on the grounds that it has a somewhat elongated tubular ovipositor. It seems, from his choice of name, that he saw this as intermediate between *Megaselia* and *Plastophora*. With the synonymising of *Plastophora* with *Megaselia* (Disney 1978, 1986a) the genus *Hemiplastophora* cannot be sustained. I therefore return *H. subulicauda* to the genus *Megaselia*, and synonymise *Hemiplastophora* with *Megaselia*.

Megaselia subulicauda will run to couplet 20 on page 50 of Beyer's (1965) keys.

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