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A revision of the *Philoliche aethiopica* species complex (Diptera: Tabanidae)

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ABSTRACT

The *Philoliche aethiopica* (Thunberg) species complex has a history of being taxonomically difficult. This group of pollinating flies is of particular interest to botanists and pollination biologists. This paper reviews its taxonomy and redescribes its species with the aid of new morphological and molecular data. Molecular evidence supports the group's monophyly, with two sister-clades, the "*aethiopica*" clade (= *P. aethiopica*) and the "*rondani*" clade (= *P. elegans* (Bigot), *P. rondani* (Bertoloni), *P. rubiginosa* Dias, and *P. umbratipennis* (Ricardo) stat. rev.). These clades correspond to two species groups defined by male morphology ("*aethiopica*" group = *P. aethiopica* and *P. formosa* (Austen); "*rondani*" group = *P. elegans*, *P. rondani*, *P. rubiginosa*, and *P. umbratipennis* stat. rev.). Molecular evidence also reveals a new character, the index of frons divergence, which is diagnostic for the two clades, and is thus a tool for separating previously indistinguishable females of *P. aethiopica* from *P. rondani*. Additionally, I show that some of the longest proboscis specimens, previously confused with *P. rondani* and *P. aethiopica*, are actually *P. umbratipennis* (Ricardo) stat. rev. *P. rubiginosa*, previously known only from Mozambique, is shown to occur in South Africa, and the male of this species is described for the first time. Furthermore, I show that the distribution of morphotypes within species with differing proboscis lengths is geographically structured, with long-proboscis species occurring only in the Albany Centre of Endemism.

KEY WORDS: Tabanidae, *Philoliche*, horse flies, Afrotropical, taxonomy, phylogeny, identification key, pollinators.

INTRODUCTION

Philoliche Wiedemann, 1820 (often cited as 1828) is an Old World genus of horse flies (Diptera: Tabanidae) including nine subgenera and 119 species, most of which are found in Africa (Oldroyd 1957; Chainey & Oldroyd 1980). This genus represents almost all horse flies in the subfamily Pangoniinae found in sub-Saharan Africa, and constitutes all but one species of the tribe Philolichini. About a dozen of the species in the subgenera *Philoliche* (24 species) and *Stenophara* Enderlein, 1922 (22 species) have proboscis 1–3 times as long as their body. These proboscides are specialised for extracting nectar from flowers (Oldroyd 1957; Jobling 1976), and although questioned by some (McKeever & French 1999), females of these species feed on blood (Mitter 1918; Tetley 1918; Sen 1931; Usher 1972; Morita pers. observ.). In southern Africa, several species groups in the subgenus *Philoliche* are involved in pollinator-mediated speciation of flowering plants (Goldblatt & Manning 1996; Johnson & Steiner 1997). In particular, the *P. (P.) aethiopica* species complex exhibits proboscis length variation that is assumed to be due to local adaptation to floral resources (Oldroyd 1957; Johnson & Steiner 1995; Johnson 2000; Johnson *et al.* 2002; Johnson & Morita 2006; Morita 2006, in press *b*).

The *P. (P.) aethiopica* species complex is taxonomically difficult. Previously, the group included five nominal species, *P. aethiopica* (Thunberg, 1789), *P. rondani* (Bertoloni, 1861 [1862]), *P. elegans* (Bigot, 1892), *P. formosa* (Austen, 1920), and *P. rubiginosa* Dias, 1966. The complex is distributed along the Great Escarpment and

Lowveld of south-eastern Africa, from southern South Africa to the Eastern Highlands of Zimbabwe. *P. rubiginosa* was not previously recognised as occurring in South Africa, and has been systematically misidentified as the more common *P. elegans*. This is because they share the only diagnostic character previously available in any key, a grey hind margin on the mesothorax (Fig. 1). The two most common species, *P. aethiopica* and *P. rondani*, appear to have the longest proboscides, and are frequently observed visiting flowers. Historically, these two species have been difficult to separate (Oldroyd 1957; Usher 1972). Prior to this work, *P. rondani* was distinguishable from *P. aethiopica* based on three characters found only in males (J. Chainey, pers. comm.). I now provide characters to distinguish female *P. rondani* from *P. aethiopica*, and I show that the longest proboscis specimens previously assigned to *P. rondani*, and confused with *P. aethiopica*, are actually *P. umbratipennis* (Ricardo) stat. rev.

The species in this complex were placed in *Philoliche* by Oldroyd (1957) following Mackerras (1954). Mackerras (1954) revolutionised tabanid systematics when he used genital morphology to reorganise Tabanidae into three currently accepted subfamilies and their constituent tribes. This had the consequence of placing all but a few African pangoniines into the tribe Philolichini. When Oldroyd (1957) revised the Afrotropical tabanids, he found that all except questionable species records of Pangoniinae in sub-Saharan Africa belonged to Philolichini. Unfortunately, genital characteristics in tabanids are not distinctive below the tribal level (Cole 1927; Mackerras 1954; Burger 2002). Oldroyd (1957) proclaimed the status of African pangoniine genera as chaotic, due to a

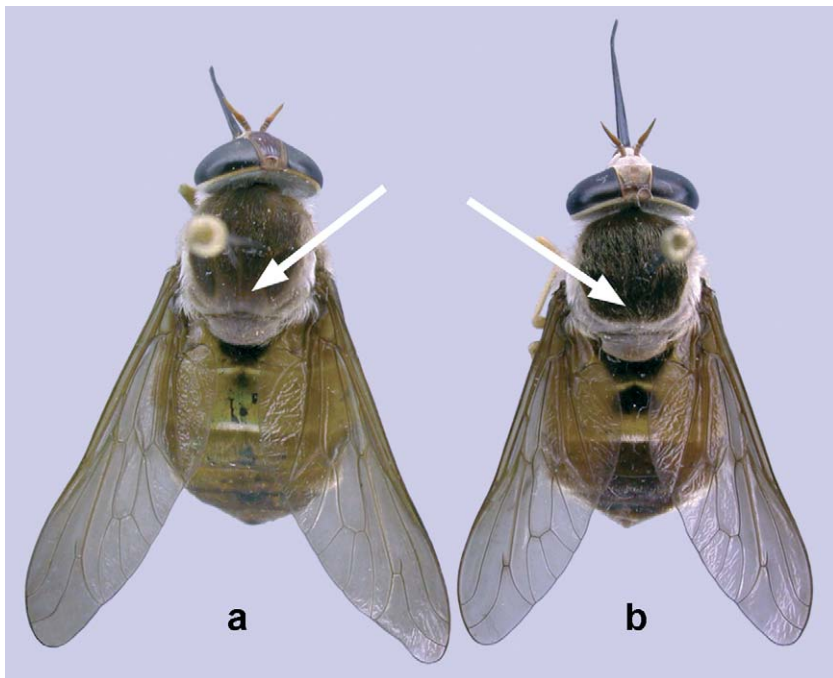


Fig. 1. Dorsal view of (a) *Philoliche rubiginosa* and (b) *P. elegans* showing differences in patterning of the mesoscutum and frons. White arrows point to the transition between colouring of the grey hind margin of the mesoscutum and the main part of the mesothorax.

lack of consistent characteristics. Subsequently, he reclassified all recognised Afrotropical Philolichini as *Philoliche*, placing the species among nine subgenera. This brought all the members of the *P. aethiopica* species complex from various generic placements into the subgenus *Philoliche* (*Philoliche*).

The purpose of this investigation is to clarify species and species groups within the *P. aethiopica* species complex using novel molecular (Morita, in press *a*) and new morphological data in a phylogenetic framework. Redescriptions are provided, as well as notes on geographic variants. Molecular evidence places all members of this complex into one clade, with two constituent sister-clades, hereinafter referred to as the “*aethiopica*” clade (= *P. aethiopica* and hypothetically the rare *P. formosa*), and the “*rondani*” clade (= *P. elegans*, *P. rondani*, *P. rubiginosa*, and *P. umbratipennis* stat. rev.). These clades correspond to two morphologically defined species groups—*aethiopica* group (= *P. aethiopica* and *P. formosa*) and *rondani* group (= *P. elegans*, *P. rondani*, *P. rubiginosa*, and *P. umbratipennis* stat. rev.)—that have differences in male morphology, previously used to separate *P. aethiopica* from *P. rondani*. This organisation also facilitated the discovery of a morphological character in females. This character, the index of frons divergence (IFD; sensu Usher 1965), reliably separates these two species groups. Both molecular, and morphological data support the species status of *P. umbratipennis* (Ricardo, 1900) stat. rev. Finally, I contribute to the known distribution of *P. rubiginosa*, and describe the male of the species for the first time.

MATERIAL AND METHODS

Specimen collection

Seventy-three specimens of the *P. aethiopica* species complex were collected from across its range over a two-year period (2002–2004) in South Africa using an aerial net or an H-trap (Kappmeier 2000). Additionally, six specimens suitable for DNA extraction were provided by Craig Peter and Donald DeKlerk. Collected specimens were stored in 95–100% ethanol for future DNA extraction (see protocol in Morita 2006, in press *a*). Three hundred and eleven specimens were borrowed from museums and other collections, and examined as detailed below.

Location of specimens examined

The four letter codens used for each collection follow Arnett *et al.* (1993). Other personal collections have abbreviations that are based on the first and last initial of the owner of the collection followed by “PC” for “personal collection,” where they do not conflict with Arnett *et al.* (1993). All specimens cited here under Shelah Morita Personal Collection (SMPC) will be deposited either in the Bohart Museum of Entomology or in the Natal Museum.

- AEIC – The American Entomological Institute, 3005 SW 56th Ave., Gainesville, Florida, 32608-5047 USA. Curator, D. Wahl.
- BMNH – The Natural History Museum, Department of Entomology, Cromwell Road, London, SW7 5BD United Kingdom. Curator, D. Notton.
- CASC – California Academy of Sciences, Department of Entomology, Golden Gate Park, San Francisco, California, 94118 USA. Curator, Ch. Griswold.
- IEGG – Museo di Zoologia, Università di Bologna, Via Selmi, 3 – 40126 Bologna, Italy. Curator, B. Sabelli.

- MHNE – Museu da Historia Natural, Universidade Eduardo Mondlane, Praça Travessia do Zambeze, 104 Maputo, Mozambique C.P. 257. Curator, A. Cabral.
- MNHN – National Collection of Insects, Museum National d’Histoire Naturelle, 45, Rue Buffon, Paris 75005, France.
- NMSA – The Natal Museum, Department of Arthropoda, Jabu Ndlovu Str., Pietermaritzburg, 3201 South Africa. Curator, M. Mostovski.
- OXUM – University Museum of Natural History, University Museum Parks Rd., Oxford OX1 3PW, United Kingdom. Curator, D.J. Rogers.
- SAMC – The Iziko Museums of Cape Town, Department of Entomology, Queen Victoria St, Cape Town 8000, Western Cape, South Africa. Curator, M. Cochrane.
- UCDC – The Bohart Museum of Entomology, Department of Entomology, 1 Shields Ave., University of California, Davis, California, 95616 USA. Curator, S. Heydon.
- ZMHB – Museum für Naturkunde der Humboldt-Universität zu Berlin, Invalidenstraße 43, D-10115 Berlin, Germany. Curator, J. Ziegler.

Geographic areas covered

All species discussed in this paper occur in South Africa, Mozambique, Zimbabwe and Zambia. Specific regions of South Africa are given after Van Wyk and Smith (2001). The Albany Centre of Endemism is located at the transition between winter and summer rainfall area in the Eastern Cape of South Africa. The Maputaland Centre of Endemism covers the northeast section of KwaZulu-Natal into the southern portion of Mozambique.

Molecular data and phylogenetic relationships used for this study

Phylogenetic relationships amongst the taxa described here were inferred from the results of previous analyses of molecular data described by Morita (Morita 2006, in press *a*). This work was based on the combined analysis of 907 bp of the protein-coding nuclear gene CAD (carbomoylphosphate synthase (CPS) domain of carbamoylphosphate synthetase 2, aspartate transcarbamylase, and dihydroorotase, Moulton & Wiegmann 2004) and 886 bp of the mitochondrial gene COI (Brady *et al.* 2000; Hasegawa *et al.* 2002). Other South African members of the subgenus *P. (Philoliche)*, exemplars from all other subgenera of *Philoliche*, all tribes of the horse fly subfamilies Chrysopsinae and Tabaninae, and to a sample of the family Pelecorhynchidae, serve as outgroups to the *P. aethiopica* species complex (Morita 2006, in press *a*).

Morphological characters

I searched for morphological characters that had state differences capable of separating species, based on clades suggested by the molecular data. In particular, I sought diagnostic characters for females of these species. Genitalia of male and female tabanids are not diagnostic below tribal level, because of their uniformity (Mackerras 1954; Burger & Chainey 2000), so external skeletal characters were examined. All morphological characters were measured to the nearest 0.1-millimeter using a binocular microscope with an ocular micrometer, and documented photographically using an EntoVision Imaging Suite (GT Vision LLC, MD, USA), with an LED illumination dome. Body

length was not measured, due to its pliable nature. Proboscis length was not considered as a diagnostic character because of potential plasticity related to its adaptive value or allometry. However, because of its ecological significance, proboscis lengths were mapped over each species range.

Terminology

Morphological terminology used in this paper follows McAlpine *et al.* (1981). This terminology differs specifically from that of previous workers on this group in the following way: the mesonotum includes the prescutum, scutum and scutellum (not just the prescutum and scutum); the fifth radial cell = first posterior cell *auct*; the third medial cell = fourth posterior cell *auct*; tergites 1 and 2 = segment 1 (they are fused and have been considered as “tergite 1” by some authors), with tergite 3 = segment 2, etc.

RESULTS

Summary tree based on previous phylogenetic analyses

A summary tree, showing the relationships of taxa in this species complex and statistical support of all reconstruction methods, is shown in Fig. 2. All species were sampled, with the exception of *P. formosa*, which was not collected during this study. Also discussed, but not sampled in the molecular analysis, is the Zimbabwean form of *P. aethiopica*.

The relationships of taxa in the *P. aethiopica* species complex were consistent between Maximum Parsimony, Maximum Likelihood and Bayesian phylogenetic inference methods (Morita 2006: figs 1.4–1.6; Morita in press *a*: figs 4–6). All reconstructions

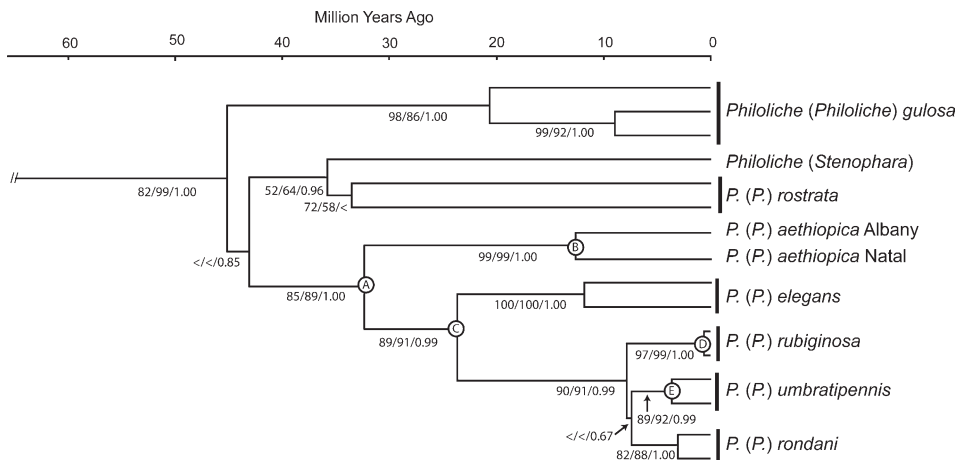


Fig. 2. Phylogenetic relationships in the subgenus *Philoliche* (*Philoliche*) from southern Africa. Relationships and chronographic data are based on Morita (2006, in press *a, b*). Numbers under branches represent clade support from maximum parsimony (bootstrap proportions from 1000 replicates, MP), maximum likelihood (bootstrap proportions from 1000 replicates, ML), Bayesian (posterior probability from 20 million generations of MCMC, PP) analyses presented as MP/ML/PP (Morita in press *a*). Branch lengths are proportional to millions of years (MYA) (Morita in press *b*). Major clades are marked with letters in circles: A – *P. aethiopica* species complex, B – *aethiopica* species group, C – *rondani* species group, D – *rubiginosa*, E – *P. umbratipennis*.

placed the monotypic subgenus *P. (Subpangonia) Surcouf, 1908* within the clade containing *P. rondani* and *P. rubiginosa*. However, results of separate analyses of each gene partition and partition homogeneity tests (Morita 2006: table 1.3; Morita in press a: table 3) show that the placement of this taxon is disputable. *P. (Subpangonia)* was therefore not considered to be a true member of the *P. rondani* + *P. rubiginosa* clade, and was excluded from this study.

The *P. aethiopica* species complex is strongly evidenced as monophyletic (Fig. 2, Clade A: MP/ML/BP=85, 89, 1.00). Two strongly supported subclades (Fig. 2, Clades B: MP/ML/BP=99, 99, 1.00 and C: MP/ML/BP=89, 91, 0.99) correspond to the morphologically defined species groups, the *aethiopica* species group (Fig. 2, Clade B) and the *rondani* species group (Fig. 2, Clade C). *P. rubiginosa* (Fig. 2, Clade D: MP/ML/BP=97, 99, 1.00) and *P. umbratipennis* (Fig. 2, Clade E: MP/ML/BP=89, 92, 0.99) also show a strong support, but the relationships between them remain unclear. The species previously referred to as *P. rondani* ‘Albany form’ (Morita 2006), was found to be *P. umbratipennis* (Ricardo, 1900) based on morphological examination, and it is redescribed below.

Morphological characters

The index of frontal divergence (as used by Usher 1965) is diagnostic in separating females between the *aethiopica* and *rondani* species groups (Fig. 3, see Clades B and C in Fig. 2). Usher (1965: 43) defines the index of frontal divergence as:

$$\text{index of frons divergence} = \frac{\text{frons width at callus base (at clypeal suture)}}{\text{frons width at vertex}}$$

This may differ from the “frons index” or “divergence index” of other authors, as the formulae are not always defined. The measurements for each species and morphotype are presented in Table 1. The index of frons divergence differs significantly between the *rondani* and *aethiopica* species groups (Wilcoxon/Kruskal-Wallis one-way rank-sums test for non-normal distributions: $\chi^2=33.7333$, $p<0.0001$). These species groups correspond to the *aethiopica* and *rondani* clades (Fig. 2, Clades B and C). The division between the species groups occurs at about a ratio of 2.1 (Fig. 4).

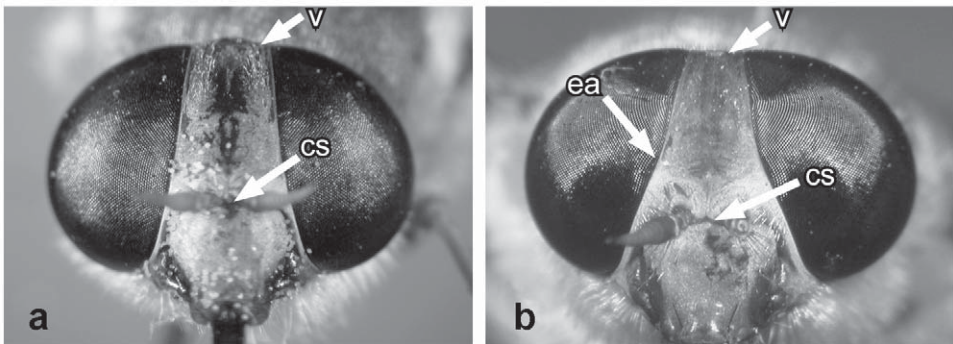


Fig. 3. Frons divergence in females of (a) *P. rondani* and (b) *P. aethiopica*. The index of frons divergence is the ratio of the width of the frons at the clypeal suture (cs) to the width of the frons at the vertex (v). Note also that most *P. aethiopica* also have an obtuse angle in the inner eye margin (ea), though this is variable.

TABLE 1
Morphological measurements for species and species groups.

taxon	species group	N	proboscis length		vertex width		base width		frons height		index of frons divergence (base/vertex)	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>aethiopica</i> group		22	17.02	1.5871	0.83	0.0255	2.00	0.0378	2.74	0.0389	2.43	0.0496
<i>rondani</i> group		24	10.70	1.2759	1.03	0.0242	1.77	0.0240	2.82	0.0336	1.74	0.0282
<i>aethiopica</i> Albany form	<i>aethiopica</i>	9	23.12	0.9607	0.88	0.0447	2.10	0.0649	2.82	0.0795	2.41	0.0721
<i>aethiopica</i> Natal form	<i>aethiopica</i>	13	12.27	1.1923	0.79	0.0276	1.92	0.0351	2.68	0.0307	2.45	0.0696
<i>elegans</i>	<i>rondani</i>	7	9.01	0.2978	1.10	0.0445	1.78	0.0278	2.75	0.0647	1.63	0.0503
<i>rondani</i>	<i>rondani</i>	6	9.97	0.4114	0.96	0.0361	1.73	0.0328	2.90	0.0809	1.81	0.0464
<i>umbratipennis</i>	<i>rondani</i>	4	23.42	0.8886	1.11	0.0195	1.92	0.0527	2.90	0.0408	1.72	0.0211
<i>rubiginosa</i>	<i>rondani</i>	7	5.76	0.9683	0.96	0.0397	1.71	0.0475	2.80	0.0555	1.80	0.0553

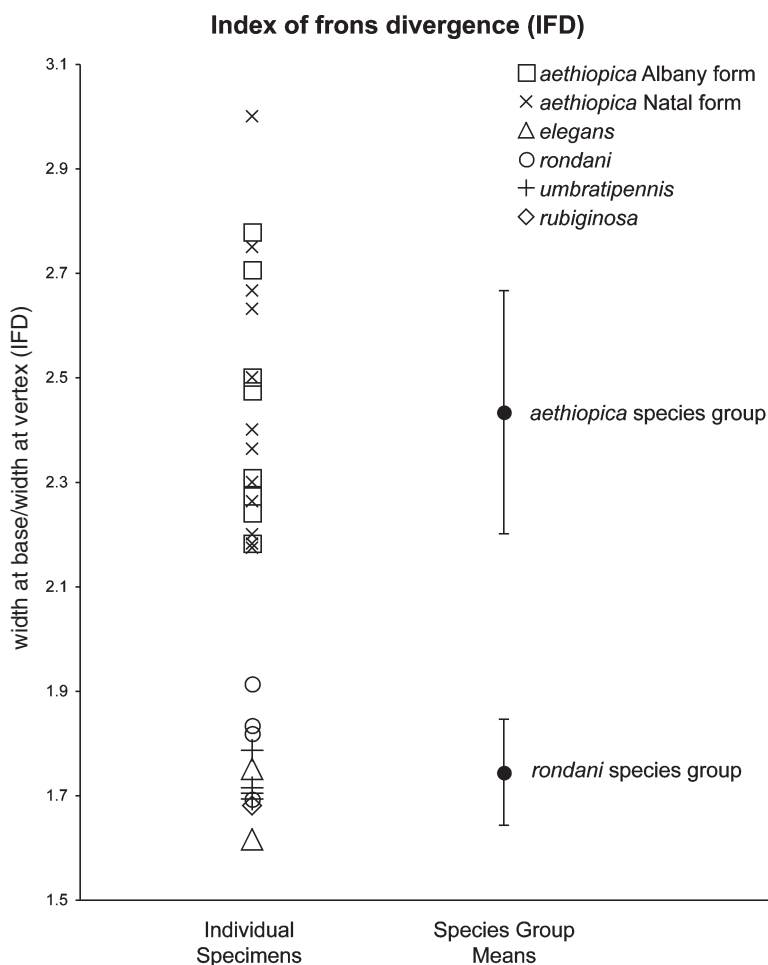


Fig. 4. Graph showing variation in the index of frons divergence (IFD) for the *Philoliche aethiopica* species complex. On the right, markers indicate the arithmetic mean for each species group with error bars for the standard deviation. The index of frons divergence differs significantly between the *rondani* and *aethiopica* species groups (Wilcoxon/Kruskal-Wallis one-way rank-sums test for non-normal distributions: $\chi^2=33.7333$, $p<0.0001$). The distinction between the *rondani* and *aethiopica* species groups occurs around an index of frons divergence of 2.1.

Images of all characters discussed in this paper have been deposited in Morphbank and can be viewed at <http://www.morphbank.net/myCollection/?id=195765>.

Species redescrptions

The following are redescrptions of species in the *Philoliche aethiopica* species complex, with clarification of the limits of each. Literature citing species names in which no nomenclatural action was taken have been omitted from the synonymies.

TAXONOMY

Philoliche (Philoliche) aethiopica (Thunberg, 1789)

Figs 3a, 5a, 6, 7

Tabanus aethiopicus Thunberg, 1789: 91. Cape of Good Hope [South Africa] (UZIU). Type series re-designated as type series for *Tanyglossa aethiopica* by Thunberg 1827.

Tanyglossa aethiopica (Thunberg): Thunberg 1827: 65, 67, table 1, fig. 6. Cape of Good Hope [South Africa] (UZIU).

Pangonia (Philoliche) varicolor Wiedemann, 1828: 98. Cape [South Africa] (ZMHB). Syn. by Surcouf 1921: 133. Accepted here.

Pangonia appendiculata Macquart, 1837 [1838]: 430, 434 [1838: 101 (97)]. The Cape [South Africa] (MNHN). Syn. by Austen 1920: 139. Accepted here, type missing from MNHN.

Diatomineura (Corizoneura) appendiculata (Macquart): Rondani 1864: 85.

Mycteromyia ensata Bigot, 1892: 608. Cape of Good Hope [South Africa]. Syn. by Oldroyd 1957: 337. Accepted here, type depository unknown—not in BMNH, MNHN or OXUM.

Diatomineura (Corizoneura) varicolor (Wiedemann): Ricardo 1900: 110.

Corizoneura aethiopica (Thunberg): Austen 1920: 139.

Pangonius varicolor (Wiedemann): Surcouf 1921: 129. [Lapsus]

Siridorhina aethiopica (Thunberg): Enderlein 1925: 265.

Nuceria aethiopica (Thunberg): Bequaert 1930: 887.

Philoliche (Philoliche) aethiopica ssp. *aethiopica* (Thunberg): Oldroyd 1957: 337.

Philoliche (Philoliche) aethiopica (Thunberg): Dias 1966: 1176.

Diagnosis: *P. aethiopica* is distinguished from all species in the *rondani* species group as follows: ♂ eye facets of similar size, longer lappets with the dorsal process of tarsus 2 extending beyond proximal margin of tarsus 4; ♀ index of frons divergence greater than 2.1 (Fig. 3). *P. aethiopica* differs from *P. formosa* by lacking distinct, narrow, grey sublateral stripes on the scutum.

Redescription:

Female.

Head: Eyes dichoptic; facets of similar size throughout. Frons strongly divergent towards antennae, eye margin with slightly angular curve; covered with yellow or golden pruinescence (pollinosity); slightly convex. Face conically produced forward a distance just greater than sagittal depth of eye. Antennae with first two segments brown or red-brown with black hairs; flagellum dark orange-brown to bright orange, sometimes with dark apex. Palps slender; distal segment wider with black hairs and tapering to a point just after a sensory groove. Proboscis equal to or almost twice body length.

Thorax: Mesonotum dark brown with faint or absent sublateral stripes; if sublateral stripes are distinct, they are not narrow and grey, but instead, broad and brown or brownish red. Supra-alar areas of scutum sharply contrasting with white-grey pruinescence beginning at postpronotal lobes and ending at post-alar calli. Pleura light grey with numerous white to yellow hairs.

Wings: Slightly smoky, becoming clearer posteriorly; darkened slightly at cross-veins. Fifth radial cell usually open although closed at margin, or even closed and stalked in some specimens; third medial cell always open.

Legs: Coxae grey, paler dorsally and with white hairs; trochanters black; femora orangish red. Tibia of foreleg and midleg paler dorsally than femora; returning to colour of femora distally. Hind tibia same colour as femora, but with black hairs dorsally, so appearing darker. Tarsi concolourous with tibia of same leg. Tarsomeres 3–5 with black hairs on foreleg; tarsomeres 2–4 and tip of tarsomere 1 with black hairs on mid and hind legs.

Abdomen: Bright reddish orange dorsally with black medial spot on segments 1 and 2; segments 3 and 4 also darkened medially. Central posterior margin of segment 2 sometimes with white or yellow hairs. Posterior margin of segment 4 with dark hairs interrupted medially with white hairs forming a spot, or entirely white or black haired. Posterolateral margin of segments 3–7 with tufts of black or white hairs as follows: 3 – black, 4 – white, 5 – black, 6 – white, 7 – white.

Male as female except:

Head: Eyes holoptic; facets of similar size throughout. Frons small and triangular, pruinose, covered with long, silky yellow, golden or white hairs; eye margins beginning to diverge a distance from vertex similar to length of first two segments of antennae. Face conically produced, but not as prominent as in female, clypeus highly reduced. Palps reduced compared to female. Clypeus reduced to frontoclypeal membrane.

Thorax: Mesonotum with longer, more dense, golden or yellow hairs.

Legs: Distally projecting dorsal process on tarsomeres 1 and 2 (lappet). Lappet of tarsomere 2 extending beyond proximal margin of tarsomere 4.

Abdomen: Narrower and often more brightly coloured.

Variation: This species is divisible into three morphotypes that overlap in distribution (Fig. 6) and differ distinctly in proboscis length (Fig. 7). The Albany form is larger and consistently has a spot of white hairs in the center of the hind margin of the fourth segment of the abdomen (Fig. 5a). The Natal form is slightly smaller and may have a white fringe along the entire hind margin of the fourth segment of the abdomen, or a spot (like the Albany form) or no white hairs at all. The Zimbabwe form is similar in size to *P. rondani*, and consistently has a white fringe along the entire hind margin of the fourth abdominal segment.

Type material examined:

Tabanus aethiopicus Thunberg. Syntypes: 2 ♀ “Cape” [South Africa: without precise locality], [C. Thunberg], Thunbergsaml., #22082, #28315 (UZIU).

Pangonia (Philoliche) varicolor Wiedemann. Syntype: 1 ♀ “*Pr. b. sp.*” [= Cape of Good Hope, South Africa], M.H.K. Lichtenstein, #321 (ZMHB).

Additional material examined:

Albany form

SOUTH AFRICA: *Western Cape*: 1 ♀ George (33°48'S:22°27'E), 10.ii.1913, Dr Brauns (NMSA); 1 ♂ Robinson Pass Mossel Bay (33°54'S:22°01'E), 30.ix.1921, Dr Brauns (NMSA); Seweweekspoort (33°24'S:21°25'E), G. van Son: 1 ♀ 1 ♂ 17.xi.1940 (NMSA); 2 ♂ 30.x.1941 (NMSA); Willowmore (33°18'S:23°29'E): Dr Brauns: 1 ♂ 15.x.1920 (NMSA); 1 ♀ 11.xi.1920 (NMSA); 1 ♀ 1.xi.1921 (NMSA); 1 ♀ 2 ♂ xi.1922 (NMSA); 4 ♂ 1–7.x.1923 (NMSA); 1 ♀ 1 ♂ [no date] (NMSA); G. Kobrow: 1 ♂ [no date] (NMSA); collector unknown: 1 ♂ 1 ♀ 11.xi.1920 (NMNH, det. as *varicolor* by Kroeber 1921); 1 ♀ 15.xi (NMSA). *Eastern Cape*: Grahamstown (33°18'S:26°32'E): 4 ♀ 1 ♂ 11–18.xi.1958, C. J.-Guillarmod; 1 ♂ 10.xii.1960, E. McCallan; 1 ♀ 2.iv.1957, F. Lock; 1 ♀ 22.x.1969, J.G.H. Londt; 1 ♀ iv.1954, K. Norval (all NMSA); 1 ♀ 12 mi. NW of Grahamstown, 21.xi.1970, H.V., B.B. and D.D. Daly (CASC, det. as *aethiopica*

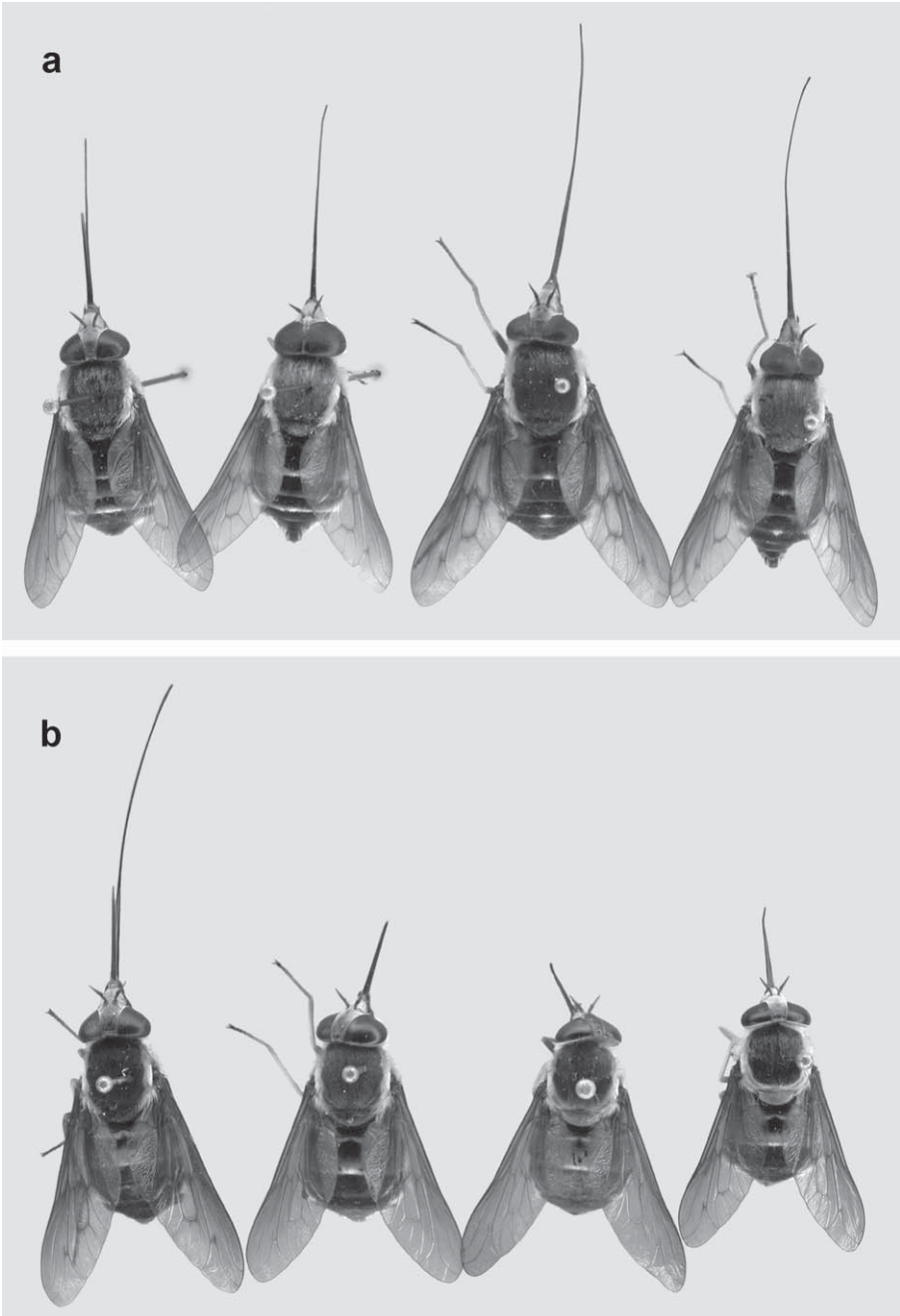


Fig. 5. (a) Morphotypes of *Philoliche aethiopica*. From left to right: *Philoliche aethiopica* Natal (female and male), *P. aethiopica* Albany (female and male). Note that the Natal form pictured here has a white stripe formed by a continuous fringe of white hairs on the posterior margin of the fourth abdominal segment. (b) Females of the *rondani* species group. From left to right: *Philoliche umbratipennis* stat. rev., *P. rondani*, *P. rubiginosa*, and *P. elegans*.

by Chainey 1987); 1♂ Faraway Found, 10 km W Grahamstown (33°17'S:26°22'E), 6.xii.1976, R.M. Miller (NMSA); 1♀ "Albany [Dist.]" [nr. Grahamstown], 3.x.1952, N.J. Myers (UCDC, det. as *aethiopica* by Oldroyd 1956); Hamburg (33°18'S:27°28'E): 1♀ 1♂ 3.xii.1956, P.E. Hulley (NMSA); 2♀ 1.i.1959, P.E. Hulley (NMSA); 2♀ Kenton On The Sea (33°41'S:26°40'E), 21.xi.1970, J.G.H. Londt (NMSA); 1♀ Kleinmond (34°21'S:19°02'E), ii.1957, J. Bradish (NMSA); 1♀ 1♂ Koega Reserve Nursery, 30 km N of Port Elizabeth (33°43'S:25°41'E), 30.x.2003, C. Peter (SMPC); 1♂ Kowie (33°36'S:26°54'E), 28.x.1919, H.E.I. (NMSA); 1♀ Kwelera R. mouth (28°55'S:28°03'E), 31.xii.1995, C. Peter (NMSA); 1♂ Oldenburgia Trail (33°20'S:26°30'E), 1.xii.2003, C. Peter (SMPC); 1♀ Otto du Plessis Pass (31°15'S:28°00'E), 26.xii.1999, S.D. Johnson (NMSA); 1♂ Port Alfred (33°36'S:26°54'E), 7.ii.1955, F.J. Junor (NMSA); 1♀ same locality, 20.xii.1956, PE Hulley (NMSA); Port Elizabeth (33°58'S:25°35'E): 1♀ 1.i.1950, B. Stuckenberg (NMSA); 1♂ 16.xi.1953, J.S. Taylor (NMSA); 1♂ 24.xi.1960, J.S. Taylor (NMSA); 1♂ 24.vii.1943, M.F. Todd (NMSA); 1♂ 10.i.1954, Y. Clark (NMSA); 1♀ 2♂ Port Elizabeth, Zwartkops (33°52'S:25°36'E), 25.xi.1921, Dr Brauns (NMSA); 3♀ R102 E of Jeffery's Bay (33°54'S:25°02'E), 9.ii.2004, S.I. Morita (SMPC); 4♂ R102 nr Gamtoos R. mouth (34°00'S:24°55'E), 9.ii.2004, S.I. Morita (SMPC); 1♀ R67 nr Bathurst (33°33'S:26°60'E), 18.ii.2004, S.I. Morita (SMPC); 1♀ road to Glen Craig Farm at Bosberg (32°41'S:25°40'E), 6.ii.2004, S.I. Morita (SMPC); Resolution (33°10'S:26°43'E): 2♀ 17–20.xi.1928, A. Walton (NMSA); 1♀ 21.i.1929, A. Walton (NMSA); 1♀ Trappes Valley (33°27'S:26°54'E), xi.1924, H. Cronwright (NMSA); 1♀ Van Stadens Pass (33°55'S:25°12'E), 1.i.1924, Dr Brauns (NMSA); 3♀ 1♂ Van Stadens Pass (33°54'S:25°12'E), 2–8.ii.2004, S.I. Morita (SMPC); 1♀ Van Stadens R. Mts (33°58'S:25°13'E), 1.i.1980, J.G.H. Londt (NMSA). *Free State*: 2♂ Welbedacht (29°08'S:25°49'E), xi.1940, G. van Son (NMSA). *Mpumalanga*: 1♀ Gladdespruit R. Headwaters at Kaapsehoop (25°31'S:30°51'E), 3.xi.1970, Stuckenberg (NMSA). *KwaZulu-Natal*: 1♀ Amatikulu (29°08'S:31°35'E), 20.xi.2001, C. Peter (NMSA); 1♀ Eshowe (28°53'S:31°28'E), xii (NMSA); Ladismith (33°29'S:21°16'E): 1♀ 2♂ 5.x.1912, Dr Brauns (NMSA); 1♀ 3♂ Dr Brauns, 15.ix.1923 (NMSA); 2♀ 1♂ 15.xii.1923, Dr Brauns (NMSA); 1♀ xi.1943, C. J.-Guillarmod (CASC, det. as *aethiopica* by Oldroyd 1972: labelled "*c.f. appendiculata*"); 1♀ Port Shepstone (30°45'S:30°27'E), ix.1919, H.K. Munro (NMSA).

Natal form

LESOTHO: 1♀ Bushmans Pass, Maloti Mts (29°26'S:27°51'E), 8.i.1963, B. & P. Stuckenberg (NMSA); 1♀ Mahlatsa (29°13'S:27°59'E), 1.i.1953, C. Jacot-Guillarmod (NMSA). SOUTH AFRICA: *Limpopo*: 4♀ 1♂ Hoenertsburg, 14.ii.1938, G.v. Son (NMSA). *Eastern Cape*: 1♀ Dangerhoek on Telle R. 35 km E Sterkspruit (30°32'S:27°40'E), 10.i.1979, J.G.H. Londt & B. Stuckenberg (NMSA); 1♂ East London (33°02'S:27°55'E), 14.ii.1922, H.K. Munro (NMSA); 1♀ 2♂ same data but 21–29.xii.1924 (NMSA); 3♀ Hogsback (32°35'S:27°05'E), 26–28.xii.1952, J.S. Taylor (NMSA); 1♀ Kleinmonde (34°21'S:19°02'E), i.1955, Omer-Cooper (NMSA); 2♂ Port Elizabeth (33°58'S:25°35'E) [no date, collector unknown] (NMSA); 1♂ Port St Johns (31°37'S:29°33'E), 20.xi.1961, B. Stuckenberg (NMSA); 1♀ Qxulu R. (33°05'S:27°43'E), 15.xii.1970, J.G.H. Londt (NMSA); 1♀ R67 nr Bathurst (33°33'S:26°60'E), 18.ii.2004, S.I. Morita (SMPC); 1♂ Umzimkulu (30°16'S:29°56'E), 19.xii (NMSA). *Mpumalanga*: 1♀ Barberton, Lomati R. Headwaters, Havelock Rd (25°51'S:31°11'E), 7.xi.1970, Stuckenberg (NMSA); 3♀ 1♂ Gladdespruit R. Headwaters at Kaapsehoop (25°31'S:30°51'E), 3.xi.1970, Stuckenberg (NMSA); 1♀ 1♂ Kastrol Nek (27°17'S:30°17'E), i.1922, G.v. Dam (NMSA); 2♂ Mariepskop (24°32'S:30°52'E), G.v. Son, i.1926 (NMSA); 5♀ 8 km W of Luneberg (27°19'S:30°35'E), 15.xii.1971, T.B. Oatley (NMSA); 1♀ RSA side of Josefsdal (25°56'S:31°06'E), 9.iii.2004, S.I. Morita (SMPC). *KwaZulu-Natal*: 1♀ Cathedral Peak Area (29°02'S:29°15'E), 24.i.1990, I. Pajor (NMSA); 3♂ nr Giant's Castle (29°12'S:29°35'E), 28.xii.2002–2.i.2003, S.I. Morita (SMPC); 1♀ 3♂ Sani Pass Rd (29°37'S:29°22'E), 13.i.2003, S.I. Morita (SMPC); 2♂ "Nat. Pk" [Drakensberg?], 10.i.1951 (NMSA); 4♂ nr Underberg (29°51'S:29°45'E), 18.i.2003, S.I. Morita (SMPC); 1♀ NE of Underberg, B.C. Anderson (SMPC); 1♂ Eshowe, Dhlizna Forest Nat. Res. (28°53'S:31°28'E), 20.xi.1978, J.G.H. Londt (NMSA); 1♀ Eshowe, Entumeni Nat. Res. (28°51'S:31°19'E), 7.xii.1977, J.G.H. Londt (NMSA); 1♂ Giants Castle Game Reserve (29°14'S:29°29'E), ii.1962, K. Tinley (NMSA); 1♂ Hilton (29°26'S:30°06'E), 7.i.2003, S.I. Morita (SMPC); 1♂ Hilton Rd (29°33'S:30°18'E), i.1954, P. Graham (NMSA); 11♀ Karkloof range nr Mt Alida (29°11'S:30°22'E), 24.xii.1961, B. & P. Stuckenberg (NMSA); 2♀ Shaw Farm, Karkloof (29°18'S:30°19'E), 21.xii.2002, S.I. Morita (SMPC); 2♂ Karkloof falls (29°42'S:30°16'E), 6.xi.1960, T. Schofield (NMSA); 1♀ Merrivale Heights, xii (NMSA); 2♀ 4♂ Mt Gilboa (29°17'S:30°17.5'E), 5.i.2003, S.I. Morita (SMPC); 1♀ Ketelfontein (29°34'S:30°19'E), xi.1969, T.B. Oatley (NMSA); 1♂ 2 mi. ESE of Grahamstown, 26.xi.1970, H.V. Daly & F. Farguharson (CASC, det. as *aethiopica* by Chainey, 1987); 1♀ Pietermaritzburg (29°37'S:30°23'E), 21.xii.1917, Hardenberg (NMSA); 1♀ 1♂ Tongaat (29°35'S:31°08'E), H.C. Burnup (NMSA); 1♀ Roselands Farm E of Richmond (29°55'S:30°09.5'E), 29.ii.2004, S.I. Morita (SMPC); 1♂ Park Rynie, x.1951, A.J. Duke (CASC, det. as *rondani* by Philp, 1962); 1♀ Scottburgh (30°17'S:30°45'E), 15.xi.1963, B. & P. Stuckenberg (NMSA); 1♀ Lovedale Lookout, Weza Forest (30°40'S:29°39.5'E), 28.ii.2004, S.I. Morita (SMPC); 17♀ 1♂ Umtamvuna Nat. Res. (31°03.5'S:30°10.5'E), 11–18.xi.2000, S. van Noort (SAMC); 1♀ Umtamvuna Nat. Res. (31°00'S:30°10'E), 26.ii.2004, S.I. Morita (SMPC); 1♀ Bizana, 1912, J.B. Goodall (CASC); 1♀ "Natal", J.F. Quekett (CASC, det. as

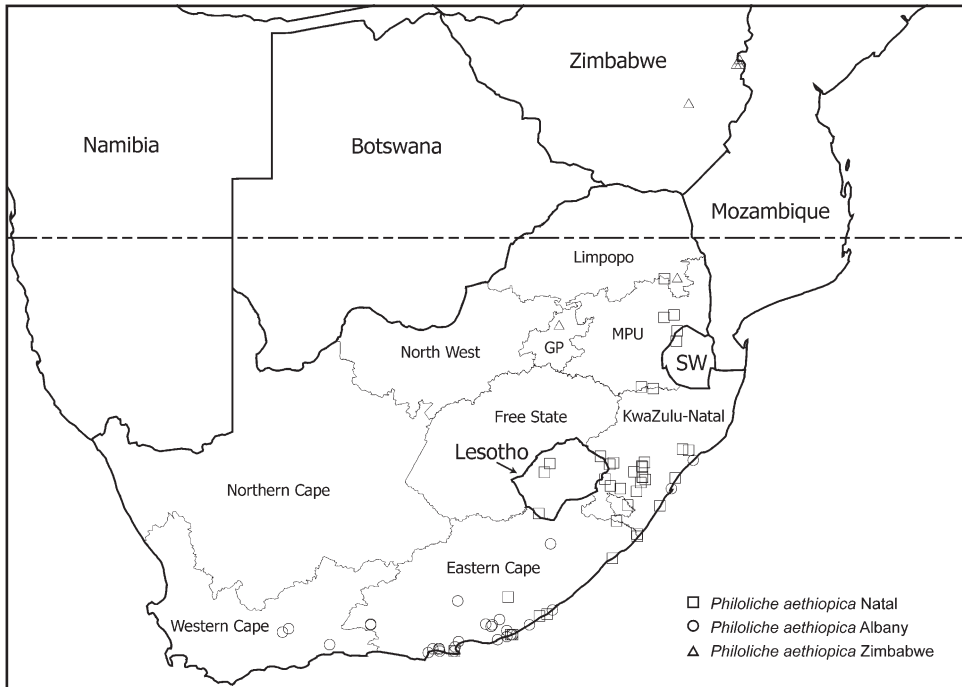


Fig. 6. Distribution of *Philoliche aethiopica* forms over South African provinces (GP – Gauteng, MPU – Mpumalanga) and in neighbouring countries (SW – Swaziland). Note that Albany and Natal forms overlap in distribution in the Eastern Cape and along the south coast of KwaZulu-Natal. Collections from Willowmore and those in the Western Cape Province are doubtful. Most of these specimens were collected by Dr Brauns (in particular, those from Willowmore) and probably did not come from the stated localities.

aethiopica by Austen 1934: labelled “genotype species”). SWAZILAND: 1 ♀ Ntabambomvu Hills, Piggs Peak Rd (26°07'S:31°10'E), 26.ii.1971, B. & P. Stuckenberg (NMSA).

Zimbabwe form

ZIMBABWE: *Manicaland*: “Umtali [Mutare] District”, P.A. Sheppard: 1 ♀ 3♂ 5–26.x.1930, 2 ♀ 3♂ 23.ix–1.xi.1931, 1 ♀ 12.x.1932; 1 ♀ 3♂ N Vumba Mts (19°05'S:32°45'E), 13–27.ix.1965, D.M. Cookson (NMSA); Laurenceville (19°05'S:32°40'E), D.M. Cookson: 4 ♀ 1♂ 24.ix–5.x.1962, 6 ♀ 1♂ 18.ix–1.x.1963, 3 ♀ 8♂ 23.ix–12.x.1964; 1 ♀ Chirinda Forest (20°05'S:31°28'E), 1926, Zimbabwe Museum Exp. (all NMSA). SOUTH AFRICA: *Limpopo*: 1 ♀ Hoedspruit 30 km SE (24°30'S:31°11'E), 30.ix.1978, D. Brothers & J. Guillardom (NMSA). *Gauteng*: 1 ♀ Pretoria (25°42'S:28°13'E), 13.x.1914, H.K. Munro (NMSA).

Distribution: South Africa, Mozambique, Zimbabwe, Zambia (Fig. 6). The Albany form occurs in South Africa from the Eastern Cape, with older records from the Cape Fold Mountains of the Western Cape. The Natal form occurs from southern Mozambique and Zimbabwe down to the eastern edge of the Albany Centre in the Eastern Cape. The Zimbabwe form occurs from Gauteng Prov., South Africa, and north and east along the mountains into Zimbabwe. A record of this species from Tanzania is extremely unlikely based on the distribution of other collections and the ambiguity of the identification as stated by the author (Johnson 1898: 157).

Remarks: There are three recognised junior synonyms of *P. aethiopica*: *Pangonia varicolor*, *Pangonia appendiculata*, and *Mycteromyia ensata*. Thunberg (1789) first

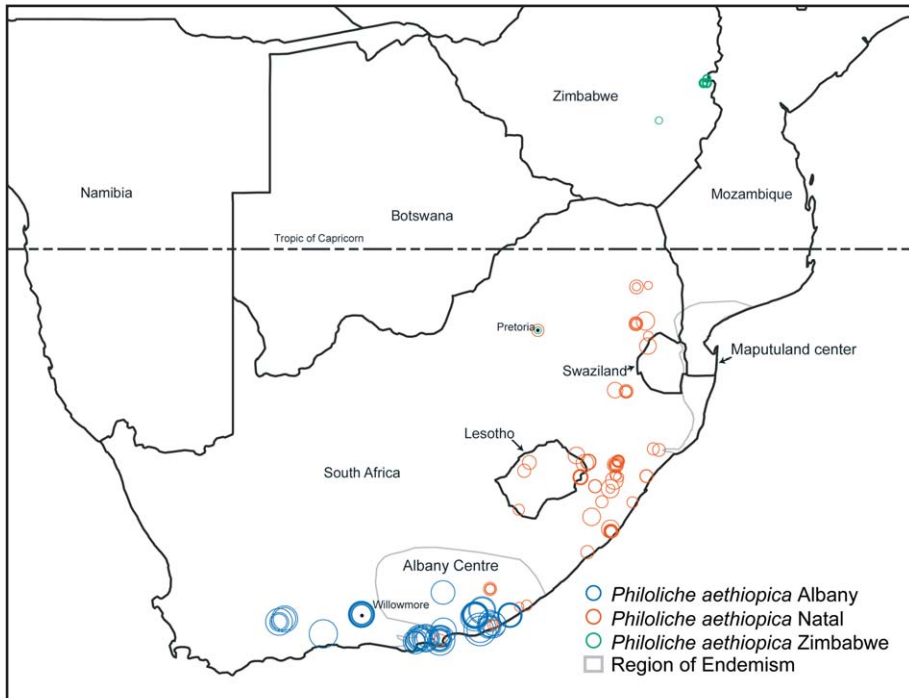


Fig. 7. Map showing geographic and taxonomic variation in proboscis length for forms of *Philoliche aethiopica*. Circle diameter is proportional to the proboscis length of the individual specimen collected at that site. Colours indicate the different morphotypes. Note the overlap in distribution of the forms. Collections from Willowmore and those in the Western Cape Province are doubtful. Most of these specimens were collected by Dr Brauns (in particular, those from Willowmore) and are unlikely to have come from the stated localities.

described *aethiopica* under *Tabanus* L., 1758, and subsequently redescribed it in the genus *Tanyglossa* Meigen, 1804 (Thunberg 1827). It appears that Thunberg re-labelled the *Tabanus aethiopicus* type specimens and types of *Tanyglossa aethiopica*, such that the types for each description are identical and are no longer labelled as *Tabanus aethiopicus*. *Tanyglossa* was found later to be a junior synonym of *Pangonius* Latreille, 1802, the history of which is confounded by its misspelling as *Pangonia* by Latreille in 1804 (Sabrosky 1999). Both *Pa. varicolor* and *Pa. appendiculata* were originally described in *Pangonia*. Subsequently, Rondani (1864) divided *Pangonia* into two genera, each with two subgenera as follows: *Pangonia* (*Pangonia* Latreille), *Pangonia* (*Erephrosia* Rondani), *Diatomineura* (*Diatomineura* Rondani), and *Diatomineura* (*Corizoneura* Rondani); with most African species, including *Pa. varicolor* and *Pa. appendiculata*, falling into *Pa.* (*Pangonia*) and *D.* (*Corizoneura*). Ricardo (1900) followed Rondani's rubric in her description of *D. (C.) umbratipennis*, which was later incorrectly synonymised under *Ph. aethiopica* by Oldroyd (1957). However, Ricardo (1900) was uncertain as to where to place *Mycteromyia* Philippi, 1865, which included *M. ensata* as described by Bigot (1892); therefore the affiliation of African *Mycteromyia* with other African pangoniines was not recognised until Oldroyd (1957). After *Diatomineura* was synonymised by Brethes (1914) with *Oscia* Walker, 1850, Austen (1920) raised the

subgenus *D.* (*Corizoneura*) to generic status and divided it into *Corizoneura* and a new genus, *Buplex* Austen, 1920. At the same time, he synonymised *D. (C.) appendiculata* under *C. aethiopica*. One year later, Surcouf (1921) also synonymised *Pa. varicolor* with *C. aethiopica*, although in the same volume he also incorrectly listed *Pa. varicolor* as a valid species under *Pangonius*. Enderlein (1925) reclassified *C. aethiopica* under his new genus *Siridorhina* Enderlein, selecting *Pangonia longirostris* Hardwicke, 1823, as type species for the genus. He also dealt with *Pangonius* and *Pangonia* by dividing it into *Pangonius* Latreille, 1802 (which he restricted to Palaearctic species) and *Nuceria* Enderlein, 1925 (for the remaining, African species). For *Nuceria*, he chose the type *Tabanus rostratus* L., 1764. Unfortunately, he failed to take into account Coquillett's (1910) designation of types. As pointed out by Bequaert (1930), Coquillett's type selection makes *Siridorhina* a junior synonym of *Nuceria* Walker, 1850, and its junior homonym, *Nuceria* Enderlein, 1925, a junior synonym of *Philoliche* Wiedemann, 1820. This caused Bequaert (1930) to classify *S. aethiopica* as *Nuceria* Walker and the African species of *Pangonia* as *Philoliche*.

When Oldroyd (1957) transferred all of the Afrotropical species of Philolichini to *Philoliche* based on the placement of oldest type, *Tabanus rostratus*, he made *Nuceria* Walker a junior synonym of *Philoliche*, and placed *Nuceria aethiopica* under the subgenus *Philoliche* (*Philoliche*). Additionally, Oldroyd (1957) made *P. (P.) rondani* a subspecies of *P. (P.) aethiopica*. While doing so, he synonymised *Mycteromyia ensata* and *Corizoneura umbratipennis* with *Philoliche (P.) aethiopica* ssp. *aethiopica*, and *Pangonia rondani* and *Diatomineura (Corizoneura) pallidipennis* under *P. (P.) aethiopica* ssp. *rondani*. Following Oldroyd's (1957) division, when Dias (1966) restored *P. (P.) rondani* to species status (see below) he left *C. umbratipennis* in synonymy with *P. aethiopica*. This paper shows that the suite of male characters in *C. umbratipennis* (Ricardo) places it within the *rondani* species group, rejecting its synonymy with *P. aethiopica*.

Philoliche (Philoliche) rondani (Bertoloni, 1861)

Figs 3b, 5b, 8, 9

Pangonia rondani Bertoloni, 1861: 29 [1862: 56]. Inhambane, Mozambique (IEGG). Type unavailable.

Diatomineura (Corizoneura) pallidipennis Ricardo, 1900: 110. Delagoa Bay [Maputo Bay], Mozambique (BMNH). Syn. by Oldroyd 1957: 339. Accepted here.

Corizoneura pallidipennis (Ricardo): Austen 1920: 140.

Pangonius rondanii (Bertoloni): Surcouf 1921: 128. [incorrect subsequent spelling of *rondani*].

Corizoneura rondanii (Bertoloni): Enderlein 1925: 266. [incorrect subsequent spelling of *rondani*].

Siridorhina pallidipennis (Ricardo): Enderlein 1925: 266.

Nuceria pallidipennis (Ricardo): Dias 1955: 176.

Philoliche (Philoliche) aethiopica ssp. *rondanii* (Bertoloni): Oldroyd 1957: 331. [incorrect subsequent spelling of *rondani*].

Philoliche (Philoliche) rondanii (Bertoloni): Dias 1966: 1182. [incorrect subsequent spelling of *rondani*].

Philoliche (Philoliche) rondani (Bertoloni): Chainey & Oldroyd 1980: 289.

Diagnosis: *P. rondani* is distinguished from *P. aethiopica* as follows: ♂ eye facets distinctly larger dorsally than ventrally; shorter lappets on foretarsi with the dorsal process of tarsomere 2 never extending beyond proximal margin of tarsomere 4; ♀ index of frons divergence less than 2.1. Its lack of whitish grey pruinescence on the posterior margin of the scutum separates *P. rondani* from *P. elegans* and *P. rubiginosa*. In contrast to its close relative, *P. umbratipennis*, *P. rondani* has all coxae similar in colour and both black and white tufts of hair posterolaterally on segment 5 instead of segment 4.

Description:*Female.*

Head: Eyes dichoptic; facets of similar size throughout. Frons slightly divergent towards antennae, almost parallel; covered with yellow-grey or golden pruinescence (pollinosity), very slightly convex. Face conically produced forward, distance no longer than length of antennae. Antennae with first two segments light brown to brown with black hairs; flagellum orange-brown to bright orange, sometimes with dark apex. Palps slender; distal segment only slightly wider, with black hairs and shallow sensory groove; tip not ending in sharp point. Proboscis length varies from length of head and thorax combined to almost twice body length.

Thorax: Mesonotum yellow-brown to dark brown with faint or no sublateral stripes. If sublateral stripes are more distinct, they are not narrow and grey, but broad and brown or brownish red. Supra-alar areas of scutum sharply contrasting with white-grey pruinescence beginning at postpronotal lobes and ending at post-alar calli. White-grey pruinescence may continue in a very thin band just anterior to scutoscutellar suture, but never more anterior than pre-scutellum. Pleura light grey with numerous white to yellow hairs.

Wings: Slightly smoky, becoming clearer posteriorly; rarely darkened slightly at cross-veins. Fifth radial cell usually open although closed at margin or even closed and stalked in some specimens; third medial cell always open.

Legs: Coxae grey, paler dorsally and with white hairs; trochanters black; femora orange. Tibia of foreleg and midleg paler dorsally than femora. Hind tibia same colour as femora with a few to many black hairs. Tarsi concolourous with tibia of same leg; darkened at apex of fifth tarsomere. Tarsomeres 3–5 with black hairs on foreleg; tarsomeres 2–4 and tip of tarsomere 1 with black hairs on mid and hind legs.

Abdomen: Bright orange-yellow with black medial spot on segments 1 and 2; segments 3 and 4 may also be slightly darkened medially, but are most often darker throughout. Central posterior margin of segment 2 sometimes with white or yellow hairs. Posterior margin of segment 4 with black hairs (as rest of segment), except on posterolateral margin. Posterolateral margin of segments 3–7 with tufts of black or white hairs as follows: 3 – black, 4 – white, 5 – black and white, 6 – white, 7 – white.

Male as female except:

Head: Eyes holoptic; facets increasing in size from ventral to dorsal very abruptly. Frons extremely small and triangular, pruinescent, covered with long, silky yellow, golden or white hairs; eye margins beginning to diverge a distance from vertex similar to length of antennae. Face conically produced, but not as prominent as in female, clypeus highly reduced. Palps reduced compared to female.

Thorax: Mesonotum with longer, more dense, golden or yellow hairs.

Legs: With short distally projecting dorsal process on tarsomeres 1 and 2 (lappet). Lappet of tarsomere 2 never extending beyond proximal margin of tarsomere 4.

Abdomen: Abdomen narrower and often more brightly coloured.

Variation: This widely collected species shows some variation in body size and proboscis length.

Type material examined:

Diatomineura (Corizoneura) pallidipennis Ricardo

Holotype: 1 ♀ MOZAMBIQUE: Delagoa Bay [Maputo Bay], R.W. Plant, #242037 (BMNH).

Additional material examined: LESOTHO: 2 ♀ “Caffraria”, J. Wahlberg (NMNH, labelled Riksmuseum Stockholm). MOZAMBIQUE: 1 ♀ Maputo [“Lourenço Marques”], C.W. Howard (NMNH). SOUTH AFRICA: *North West*: 1 ♀ Rustenburg (24°56'S:27°09'E), 3.xi.1967 (NMSA). *Limpopo*: 3 ♀ 2♂ Entabeni Forest Station Zoutpansberg Range (23°00'S:30°14'E), i.1975, B. Stuckenberg (NMSA); 1 ♀ Mkhado, “Mountain View Rst.” (22°59'S:29°55'E), 7.iii.2003, S.I. Morita (SMPC); 1 ♀ Mkhado (23°03'S:29°54'E): 5.iv.1948, A.B. (NMSA); 1 ♀ 1.i.1920, Dr Breyer (NMSA); 1♂ Masekwaspoort, 10 km N Mkhado, 22.ii.1980, J. Londt & L. Schoeman (NMSA); 1 ♀ Blouberg Motlakeng (23°07'S:28°59'E), 6.i.1955, Tvl Museum Exp. (NMSA); 2 ♀ Grootdraai Olifants River (24°08'S:31°01'E), x.1927, H. Lang (NMSA); 2 ♀ 1♂ Malta Forest, 15 km W Ofcolaco (24°10'S:30°14'E), 21.ii.1980, J. Londt & L. Schoeman (NMSA); 1 ♀ Moorddrift (24°15'S:28°57'E), i.1925, G.v. Dam (NMSA); 1 ♀ Abel Erasmus Pass (24°26'S:30°39'E), 26.ii.1980, J. Londt & L. Schoeman (NMSA). *Gauteng*: Pretoria (25°42'S:28°13'E): 1♂ 31.xii.1923, A. Roberts (NMSA); H.K. Munro: 1 ♀ 25.xii.1912 (NMSA); 1 ♀ 16.xii.1914 (NMSA); 1 ♀ 19.x.1915 (NMSA); 1 ♀ v.1950, no collector (NMSA); 2 ♀ Fountains, Pretoria, 31.x.1951, A.L. Capener (CASC); 2 ♀ Groenkloof (25°49'S:28°13'E), 6.i.1922, G. v. Dam (NMSA). *Mpumalanga*: 1 ♀ Hoedspruit 30 km SE (24°30'S:31°11'E), 30.ix.1978, D. Brothers & J. Guillardarm (NMSA); 1 ♀ Sabie Caravan Park (25°06'S:30°47'E), 27.ii.1980, J. Londt & L. Schoeman (NMSA); 1 ♀ Long Tom Pass W of Sabie (25°10'S:30°38'E), 9.iii.2004, S.I. Morita (SMPC); 1 ♀ Kruger National Park, Skukuza (24°58'S:31°36'E), Zumpt (NMSA); 2 ♀ Kruger National Park, Crocodile Bridge (25°21'S:31°54'E), ii.1969, Zumpt (NMSA); 2 ♀ Mt Carmel NW Side (25°22'S:30°44'E), 6.xi.1970, B. Stuckenberg (NMSA); 1 ♀ Hectorspruit (25°26'S:31°41'E), 17.x.1927, J.S. Taylor (NMSA); 1♂ Nelspruit (25°28'S:30°58'E), x.1917, H.G. Breijer (NMSA); 5 ♀ Louws creek (25°38'S:31°17'E), iii.1920, G.v.D./A. Rob (NMSA); Barberton (25°47'S:31°03'E): 1♂ x.1922, G.v. Dam (NMSA); 3 ♀ 19.iii.1920, G.v.D./A. Rob (NMSA); 1 ♀ Mt Emlembe Near Havelock Mine on Barberton Road (25°55'S:31°07'E), 7.xi.1970, B. Stuckenberg (NMSA); 1 ♀ Tzaneen, 1.x.1954 (NMSA). *KwaZulu-Natal*: 1 ♀ 1♂ Ndumu Nat. Res. (26°55'S:32°15'E), 19.x–1.xi.1961, T. Oatley (NMSA); Ingwavuma (27°08'S:31°59'E): 1 ♀ 10.xii.1963. B. & P. Stuckenberg (NMSA); 1 ♀ 7.iv.1961, D.W. Rorke (NMSA); 1 ♀ P. Reavell (NMSA); 1 ♀ no collector: i.1957 (NMSA); 1 ♀ iv (NMSA); 1♂ 10 mi. N of Ubombo, 4.iv.1958, E.S. Ross & R.E. Leech (CASC, det. as *rondani* by Chainey, 1987); 5 ♀ 30 mi. N of Empangeni, xii.1927–i.1928, M.C. Mossop (NMNH, det. as *pallidipennis* by Fairchild, 1938); 1 ♀ “Tete Pan Zululand” (27°08'S:32°16'E), 7.x.1955, Paterson (NMSA); 1♂ 20 mi. S Ndumu Game Res. Camp (27°10'S:32°10'E), 29.xi.1971, M.E. & B.J. Irwin (NMSA); 1♂ Ndumu, xi.1967 (NMSA); 1 ♀ Pongola R. (27°22'S:31°35'E), x.1929, Marley (NMSA); 1 ♀ Jozini 10 mi. (27°26'S:32°04'E), xii.1971, M.E. & B.J. Irwin (NMSA); 1 ♀ Hluhluwe (28°07'S:32°20'E), x.1930, Marley (NMSA); 1 ♀ Umfolosi (28°20'S:31°50'E) (NMSA); 1 ♀ Ulundi (28°20'S:31°25'E), 18.xii (NMSA); 1 ♀ 20 km W of Tugela Ferry (28°45'S:30°15'E), 26.ii.1977, R.M. Miller (NMSA); 1 ♀ Ngoye Forest (28°50'S:31°40'E), ii.1957, B. Stuckenberg (NMSA); 1 ♀ 1♂ Weenen (28°51'S:30°04'E), xii.1923, H.P. Thomasset (NMSA); 1 ♀ Zimbaba Forest Middeldrift Rd nr Kranskop (28°55'S:30°52'E), 4.ii.1970, T.B. Oatley (NMSA); 1 ♀ 4♂ Kranskop, Die Kop (28°55'S:30°56'E), 10.ii.2003, S.I. Morita (SMPC); 1 ♀ 1♂ Kranskop, Rd to Tugela R. (28°56'S:30°57'E), 10.ii.2003, S.I. Morita (SMPC); Wartburg, Bruyn's Hill (29°26'S:30°39'E): 1♂ 4.iv.1980, A.C.B. (NMSA); 1♂ 27.iii.1978 (NMSA); Pietermaritzburg (29°37'S:30°23'E): B. Stuckenberg: 1 ♀ 5.iv.1954 (NMSA); 1♂ 30.iii.1956 (NMSA); 1 ♀ 13.iii.1961 (NMSA); 1♂ 31.x.1932, F. Abraham (NMSA); 1 ♀ 16.iii (NMSA); 1 ♀ Mkondeni (29°40'S:30°24'E), 7.iv.1968, P.F. Tempest (NMSA); 1♂ Ashburton, xi (NMSA); 1 ♀ Hilton, Midmar Dam, 26.iv.1968, T. Oatley (CASC, det. as *rondani* by Usher, 1973); 1♂ Durban (29°51'S:31°02'E), 16.vii.1910, G.F. Leigh (NMSA); 1 ♀ Roselands Farm E of Richmond (29°55'S:30°09'E), 29.ii.2004, S.I. Morita (SMPC); 1 ♀ Bizana, 1912, J.B. Goodall (CASC); 5 ♀ Ixopo Dist., Mackston (30°01'S:30°18'E), 16.iv.1977, R.M. Miller (NMSA); 1 ♀ Kununata Highflats (30°16'S:30°15'E), 10.iv.1981, A.C.B. (NMSA); 1♂ Glendale Police Station nr Umhlali, 8.x (NMSA); 1 ♀ Hatherley, 16.xii (NMSA). *Eastern Cape*: 1 ♀ Elandshoek (25°30'S:30°43'E), 3.xi.1946, A.L. Capener (NMSA); 1 ♀ Umzimkulu (30°16'S:29°56'E), 6.i.1981, A.C.B. (NMSA); 3 ♀ 1♂ R63 E of Bedford (32°40'S:26°01'E), 5.ii.2004, S.I. Morita (SMPC); 1 ♀ Qxulu R. (33°05'S:27°43'E), 15.xii.1970, J.G.H. Londt (NMSA); 1 ♀ “Albany [Dist.] ” (33°10'S:26°43'E), v.1950, B. Stuckenberg (NMSA); Grahamstown (33°18'S:26°32'E): 1♂ E. McC. Callan, 17.xi.1957 (NMSA); J.G.H. Londt: 1 ♀ 3.iv.1965 (NMSA); 1 ♀ 1♂ 5.iv.1970 (NMSA); 1 ♀ 1♂ 22.iii.1973 (NMSA); 1♂ 30.xi, no collector (NMSA); 2 ♀ Old Woman's R. Mouth (33°29'S:27°08'E), 20.xi.2003, B.S. Ripley (SMPC); 1 ♀ Port Alfred (33°36'S:26°54'E), 27.ii.1956, P.E. Hulley (NMSA); 1 ♀ Port Alfred, ii.1956, R. Phillips, (NMSA). *Unknown Province*: “Waterkloof”: 1 ♀ 25.xii.1919, A. Roberts (NMSA); 2 ♀ 25.xii.1919, W. Impey (NMSA); 3 ♀ “Garstfontein”, 3.i.1922, A. Roberts (NMSA); 1♂ “Woodbush”, xii.1924, G.v. Dam (NMSA); 1♂ “Prospect”, 19.iii.1923, H.K. Munro (NMSA). ZIMBABWE: *Masvingo*: 2♂ Lundi (21°02'S:31°10'E), 23.ix.1961, G. van Son (NMSA).

Distribution: South Africa, Mozambique, Zimbabwe, Zambia (Fig. 8).

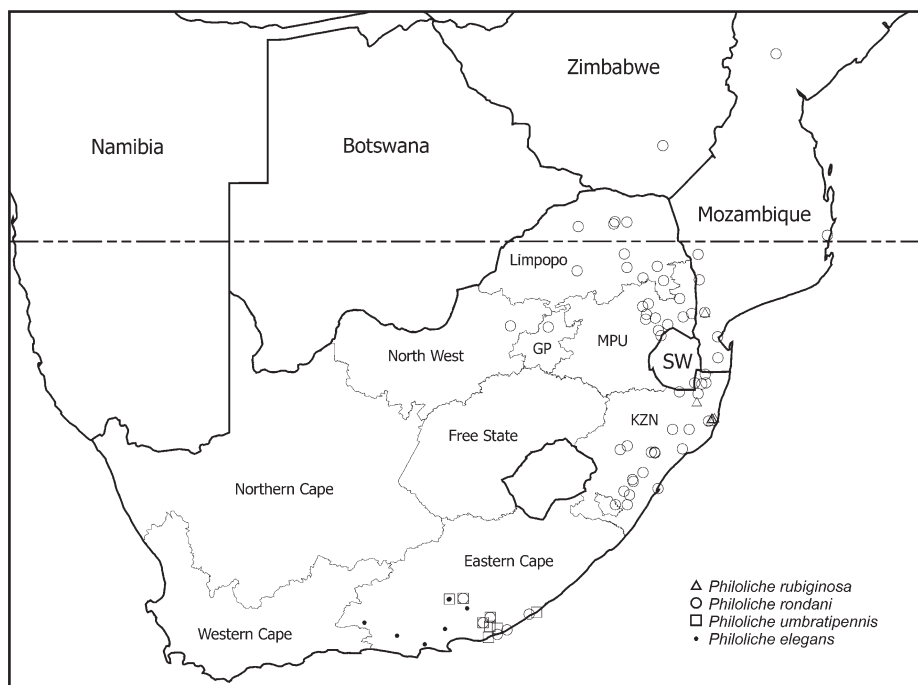


Fig. 8. Geographic distribution of the *rondani* species group over South African provinces (GP – Gauteng, MPU – Mpumalanga, KZN – KwaZulu-Natal) and in neighbouring countries (SW – Swaziland). Note that all taxa overlap in distribution in the Eastern Cape, with the exception of *Philoliche rubiginosa*.

Remarks: This species is closely related to *P. umbratipennis* with which it overlaps in distribution (Figs 8, 9), and has distinct differences in proboscis length (Fig. 9). Molecular evidence supports the monophyly of the long proboscid *P. umbratipennis*, but recognition of *P. umbratipennis* may render *P. rondani* paraphyletic based on preliminary molecular analysis (data not shown, see discussion).

Pangonia rondani was described first by Bertoloni (1861) based on one female specimen from Mozambique. When Surcouf (1921) reclassified it as *Pangonius* Latrielle, he changed the spelling to *Pangonius rondanii* to create Latin gender agreement with the new genus. Since the epithet was honorific for Prof. Camillio Rondani, this correction was unjustified (IZCN articles 31.2.1, 33.4, and 34.2.1). The incorrect subsequent spelling continued until its correction in the Afrotropical catalog of Diptera (Chainey & Oldroyd 1980). Ricardo (1900) first described *Diatomineura (Corizoneura) pallidipennis* under Rondani's (1864) subgenus based on a female from Maputo Bay, Mozambique. Later it was placed within *Siridorhina* Enderlein, and then in *Nuceria* Walker (see Remarks for *P. aethiopica*). Oldroyd (1957: 339) synonymised *N. pallidipennis* with *P. (P.) rondani* and made *P. (P.) rondani* a subspecies of *P. (P.) aethiopica* stating:

“This common fly of south-eastern Africa is distinguished from the typical *aethiopica* by its shorter face in both sexes, by the reduced abdominal markings, and by the absence of dark brown spots on the wings. I have found that in Natal these two forms merge into one another, and I conclude that they should be regarded as subspecies.”

Dias (1966) disagreed and resurrected *P. (P.) rondani*, based on the overlapping distribution of the two forms, and what he considered to be differences in their ecology. Due to taxonomic uncertainty, Usher (1972) chose to ignore *P. (P.) rondani* as a separate entity in her review of the South African horsefly fauna, and did not mention that Dias had revised its status. She discussed Oldroyd's decision to separate *P. (P.) aethiopica* into "two geographically separable subspecies", and stated, "This is a highly complex problem badly in need of further study. For the present, I have treated *aethiopica* as a single, very variable species" (Usher 1972: 467).

Philoliche (Philoliche) umbratipennis (Ricardo, 1900), **stat. rev.**

Figs 5b, 8, 9

Diatomineura (Corizoneura) umbratipennis Ricardo, 1900: 111. Annshaw [ECP], South Africa (BMNH).

Corizoneura umbratipennis (Ricardo): Austen 1920: 140.

Philoliche (Philoliche) aethiopica ssp. *aethiopica* (Thunberg): Oldroyd 1957: 337. Syn. rejected here.

Philoliche (Philoliche) aethiopica (Thunberg): Dias 1966: 1176.

Diagnosis: *P. umbratipennis* can be distinguished from *P. rondani* by its relatively paler hind coxa and hind femur, by the third abdominal segment which is relatively paler than the other segments, and by having both black and white tufts of hair posterolaterally on segment 4. This species appears to occur only in the Albany Centre of endemism. It usually has a proboscis 2 times greater in length than *P. rondani*.

Description:

Female.

Head: Eyes dichoptic; facets of similar size throughout. Frons only slightly divergent towards antennae, almost parallel; covered with yellow-grey or golden pruinescence (pollinosity) with shiny, reddish surface visible underneath; convex. Face conically produced forward, distance just greater than sagittal depth of the eye. Antennae with first two segments light brown to brown with black hairs; flagellum orange-brown to bright orange, sometimes with dark apex. Palps slender; distal segment wider with black hairs and sensory groove leading to an aperture; tip ending in a point. Proboscis length usually 1.5–2× body length.

Thorax: Mesonotum dark brown with faint or no sublateral stripes. If sublateral stripes are evident, they are not narrow and grey but instead broad and brown or brownish red. Supra-alar areas of scutum sharply contrasting with white-grey pruinescence beginning with the postpronotal lobes and ending at the post-alar calli. Pleura light grey to pinkish grey with numerous white to yellow hairs, also with very few dark hairs.

Wings: Smoky, becoming clearer posteriorly; darkened at cross-veins. Fifth radial cell usually open but closed at margin or even closed and stalked in some specimens; third medial cell always open.

Legs: Fore and mid coxae grey to pinkish grey, paler dorsally and with white and a few black hairs; hind coxa yellow, trochanters orange; fore and mid femora orange; hind femur yellow, same as hind coxa. Tibia of foreleg and midleg paler than femora. Hind tibia darker than hind femur with black hairs. Tarsi concolourous with tibia of same leg; darkened at apex of fifth tarsomere in fore and midtarsi. Tarsomeres with black hairs.

Abdomen: Orange-yellow with black medial spot on segments 1 and 2; segments 3 orange-yellow with scattered spots of pigment, but no true spot; segments 4–7 dark

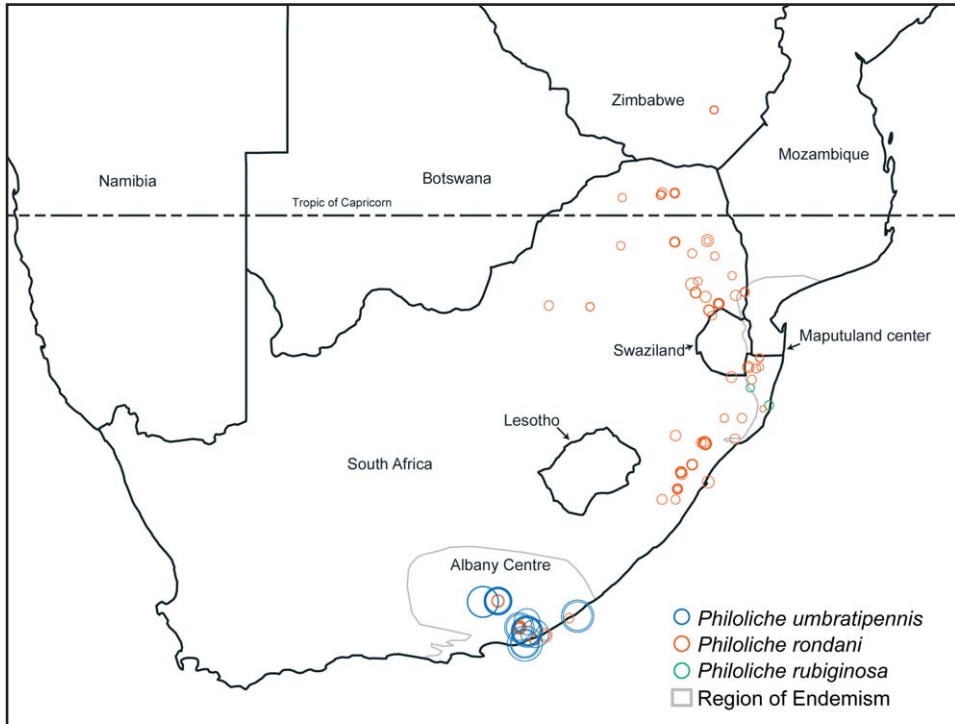


Fig. 9. Map showing geographic and taxonomic variation in proboscis length for *Philoliche rubiginosa*, *P. rondani* and *P. umbratipennis*. Circle diameter is proportional to the proboscis length of the individual specimen collected at that site.

yellow-brown. Central posterior margin of segment 2 sometimes with white or yellow hairs. Posterior margin of segment 4 with black hairs (as rest of segment), except on posterolateral margin. Posterolateral margin of segments 3–7 with tufts of black or white hairs as follows: 3 – black, 4 – black and white, 5 – black, 6 – white, 7 – white.

Male as female except:

Head: Eyes holoptic; facets increasing in size from ventral to dorsal very abruptly. Frons extremely small and triangular, pruinose, covered with long, silky yellow, golden or white hairs; eye margins beginning to diverge a distance from vertex similar to length of antennae. Face conically produced, but not as prominent as in female, clypeus highly reduced. Palps reduced compared to female but with sensory pit. Clypeus reduced to frontoclypeal membrane.

Thorax: Mesonotum with longer, more dense, golden or yellow hairs.

Legs: With short, distally projecting dorsal process on tarsomeres 1 and 2 (lappet). Lappet of tarsomere 2 never extending beyond proximal margin of tarsomere 4.

Abdomen: Abdomen narrower and often more brightly coloured.

Type material examined:

Diatomineura (Corizoneura) umbratipennis Ricardo

Syntypes: 1♀ 1♂ SOUTH AFRICA: *Eastern Cape*: “Annshaw” [Mission], [Rev.] Barrett, #242033, #242036 (BMNH).

Additional material examined: SOUTH AFRICA: *Eastern Cape*: 2 ♀ 2♂ R63 E of Bedford (32°40'S:26°01'E), 5.ii.2004, S.I. Morita (SMPC); 3 ♀ 11♂ Rd to Glen Craig Farm at Bosberg (32°41':25°39'E), 6.ii.2004, S.I. Morita (SMPC); East London (33°02'S:27°55'E), H.K. Munro: 1♂ 29.x.1922 (NMSA), 1 ♀ 15.xi.1924 (NMSA); 1 ♀ Resolution (33°10'S:26°43'E), 23.iii.1928, A. Walton (NMSA); Grahamstown (33°18'S:26°32'E): 2 ♀ 5.iv.1970, J.G.H. Londt (NMSA); 1♂ "Albany [Dist.]", 11.v.1949, B. Stuckenberg (NMSA); 3 ♀ 2♂ R67 N of Port Alfred (33°23'S:26°42'E), 18.ii.2004, S.I. Morita (SMPC); 1 ♀ Trappes Valley (33°27'S:26°54'E), xi.1924, H. Cronwright (NMSA); 3 ♀ Kenton On The Sea (33°41'S:26°40'E), 21.xi.1970, J.G.H. Londt (NMSA).

Distribution: Southern Africa; known only in the Albany Centre.

Remarks: Ricardo (1900) described *D. (C.) umbratipennis* based on a series of specimens collected by Rev. Barrett at the Annshaw Mission in the former Ciskei (currently Eastern Cape). It was later reclassified as *Corizoneura* by Austen (1920), and then synonymised under *P. aethiopica* ssp. *aethiopica* by Oldroyd (1957). It was left in synonymy with *P. aethiopica* when Dias separated *P. rondani* as a species (1966).

The molecular (Morita 2006, in press *a*) and morphological evidence presented here show that *Corizoneura umbratipennis* (Ricardo) was incorrectly synonymised with *P. aethiopica*. Examination of the type material reveals clear dimorphism in eye facets from dorsal to ventral, only short lappets on the fore tarsi of the male, and the index of frons divergence less than 2.1 in the female. These characters place *P. umbratipennis* in the *rondani* species group. Additionally, molecular data resolve *P. umbratipennis* as a monophyletic clade within the *rondani* clade (Fig. 2). However, the sister clade of *P. umbratipennis* is still unclear. It forms a strongly supported clade with both *P. rondani* and *P. rubiginosa*, which is itself a sister one to *P. elegans*. Strong support for monophyly of *P. umbratipennis* and its morphological distinctness, even where it overlaps geographically with *P. rondani*, testifies to this entity's species status (see discussion).

Philoliche (Philoliche) elegans (Bigot, 1892)

Figs 1b, 8, 9

Mycteromyia elegans Bigot, 1892: 608. Cape of Good Hope [South Africa] (BMNH).

Philoliche (Philoliche) elegans (Bigot): Oldroyd 1957: 335.

Diagnosis: *P. elegans* is the only species of *Philoliche* with a band of white-grey pruinescence which forms a sharply contrasting border along the sides and posterior margin of the scutum. It is separated from *P. rubiginosa* by this sharp contrast in colour, whereas in *P. rubiginosa* the white-grey pruinescence on the posterior margin of the scutum blends gradually into the brown of the scutum. Also, the frons in females of *P. elegans* is yellow-grey pruinose, versus the shining, dark red frons of *P. rubiginosa*.

Description:

Female.

Head: Eyes dichoptic; facets of similar size throughout. Frons parallel-sided from vertex towards antennae, covered with grey to yellow-grey pruinescence (pollinosity), slightly convex. Face conically produced forward a distance not more than length of antennae. Antennae with first two segments light brown to brown with black hairs; flagellum orange-brown to bright orange sometimes with dark apex. Palps slender; distal segment wider, with black hairs and sensory groove leading to an aperture; apex blunt. Proboscis length rarely longer than length of head and thorax combined.

Thorax: Mesonotum dark brown with faint or no sublateral stripes. If sublateral stripes are more evident, they are not narrow and grey but instead broad and brown or brownish red. Supra-alar areas of scutum sharply contrasting with white-grey pruinescence beginning at postpronotal lobes and continuing along the sides and in band across posterior margin of scutum. Scutellum colour ranging from white-grey to slightly pink. Pleura light grey to pinkish grey with numerous white to yellow hairs.

Wings: Slightly smoky, becoming clearer posteriorly; can be slightly darkened at cross-veins. Fifth radial cell usually open although closed at margin or even closed and stalked in some specimens; third medial cell always open.

Legs: Coxae pinkish grey with white hairs; trochanters orange to brown; fore and mid femora orange; hind femur yellow. Tibia of foreleg and midleg paler than femora. Hind tibia with black hairs; colour darker than hind femur towards apex. Tarsi concolourous with apex of tibia of same leg; darkened at apex of fifth tarsomere in all tarsi.

Abdomen: Bright orange-yellow with black medial spot on segments 1 and 2; segments 3 and 4 may also be slightly darkened medially, but are most often darker throughout. Central posterior margin of segment 2 sometimes with white or yellow hairs. Posterior margin of segment 4 with black hairs (as rest of segment), except on posterolateral margin. Posterolateral margin of segments 3–7 with tufts of black or white hairs as follows: 3 – black, 4 – white, 5 – some black but mostly white, 6 – white, 7 – white.

Male similar to female except:

Head: Eyes holoptic; facets increasing in size from ventral to dorsal very abruptly. Frons extremely small and triangular, pruinescent, covered with long, silky yellow, golden or white hairs; eye margins beginning to diverge a distance from vertex similar to length of antennae. Face conically produced, but not as prominent as in female, clypeus highly reduced. Palps reduced compared to female, but with sensory pit. Clypeus reduced to frontoclypeal membrane.

Thorax: Mesonotum with longer, more dense, golden or yellow hairs.

Legs: With short distally projecting dorsal process on tarsomeres 1 and 2 (lappet). Lappet of tarsomere 2 never extending beyond proximal margin of tarsomere 4.

Abdomen: Narrower and often more brightly coloured.

Type material examined:

Mycteromyia elegans Bigot

Syntypes: 1 ♀ 1 ♂ Cape of Good Hope [South Africa], J. Bigot & G.H. Verrall, #240246, #240247 (BMNH).

Additional material examined: SOUTH AFRICA: *Western Cape*: Willowmore (33°18'S:23°29'E), Dr Brauns: 1 ♀ 1 ♂ 1.xii.1918 (SAMC), 1 ♀ 1 ♂ 1.xii.1918, iii.1920, 20.xii.1921, 20.i.1922, 3.i.1926 (all NMSA). *Eastern Cape*: Sundays River Valley (33°43'S:25°51'E), 29.xii.1977–12.i.1978, J.G.H. Londt (NMSA); 5 ♀ Bavianskloof (33°38':24°19'E), 9–10.ii.2004, S.I. Morita (SMPC); Clifton, 18 km SW of Grahamstown (33°27'S:26°20'E), 21.i.1986, F.W. & S.K. Gess (AMGS); 1 ♂ Drainage on R67 (32°56'S:26°07'E), 6.ii.2004, S.I. Morita (SMPC); Dunbrody (33°28'S:25°33'E): 2 ♀ 1897 and 1900, O'Neil (both SAMC); V. Powers (AMGS); Grahamstown (33°18'S:26°32'E): 22.iii.1973, J.G.H. Londt (NMSA); Martin, iii, xii.1956 (AMGS); Strowan, 5 km W of Grahamstown (33°18'S:26°27'E), 30.xi.1970, F.W. Gess (AMGS); Hilton, 20 km NW of Grahamstown (33°15'S:26°21'E), 21–18.x.1970, F.W. Gess (AMGS); 1 ♀ Loerie (33°52'S:25°02'E), i.1960 (SAMC); 2 ♀ 4 ♂ Rd to Glen Craig Farm at Bosberg (32°41'S:25°39'E), 6.ii.2004, S.I. Morita (SMPC); Resolution, 20 km NNE of Grahamstown (33°10'S:26°43'E), A. Walton: 7–30.i.1928 (NMSA); 8.i.1928 (AMGS); Somerset East Boschberg (32°42'S:25°39'E), 17.i.1986, K. Steiner (NMSA); 1 ♂ Stream Crossing, Bosberg (32°42'S:25°39'E), 6.ii.2003, S.I. Morita (SMPC); 1 ♀ Zwartkops (Swartkops) Port Elizabeth Cape Colony, 20.xii.1922, Dr Brauns (NMSA).

Distribution: Limited to the western portion of the Eastern Cape Province, South Africa (Fig. 8).

Remarks: Bigot (1892) described both the male and female of *Mycteromyia elegans*. This species was later transferred to *Philoliche (Philoliche)* by Oldroyd (1957: 336), where he comments that “Apart from the grey thoracic border, *elegans* is closely related to *rondanii* [sic]”. This is noteworthy, since on the next page Oldroyd (1957: 337) classifies *P. (P.) rondani* as a subspecies of *P. (P.) aethiopica*.

Philoliche (Philoliche) formosa (Austen, 1920)

Corizoneura formosa Austen, 1920: 142. Cape Province, South Africa (BMNH).

Philoliche (Philoliche) formosa (Austen): Oldroyd 1957: 334.

Diagnosis: *P. formosa* is distinguished from all species in the *rondani* species group as follows: ♂ eye facets of similar size; longer lappets with the dorsal process of tarsomere 2 extending beyond proximal margin of tarsomere 4. *P. formosa* is similar to *P. aethiopica*, but is differentiated by having a pair of narrow, grey sublateral stripes on the scutum.

Description (only male known):

Similar to *Philoliche aethiopica* except:

Thorax: With pair of narrow, grey sublateral stripes on the scutum.

Abdomen: Posterior margin of segment 4 has a spot or widening of white hairs in the centre.

Variation: In some specimens, dark hairs along the posterior margin flank the white spot on segment 4.

Type material examined:

Corizoneura formosa Austen

Paratype: 1♂ SOUTH AFRICA: Northern Cape: Deelfontein [SW of De Aar], Colonel Sloggett, 7.xii.1902, #242038 (BMNH).

Additional material examined (all NMSA): SOUTH AFRICA: *Limopopo*: 1♂ Entabeni, Soutpansberg, xi. 1931, G. van Son; 1♂ ix.1952 [collector unknown]. *KwaZulu-Natal*: 1♂ Hluhluwe G.R. [Game Reserve] (28°05'S:32°04'E), [Zumpt]. *Eastern Cape*: 1♂ Malowi [Malowe] Umzimkulu (30°18'S:29°50'E), 9.xii.1968.

Distribution: South Africa: Northern Cape, Limpopo, KwaZulu-Natal, Eastern Cape.

Remarks: *C. formosa* was described based on four male specimens with distinct longitudinal sublateral stripes on the thorax. Oldroyd (1957: 334) reclassified it as *Philoliche (Philoliche)* and surmised that it might be a “mere local race of *aethiopica*”. However, he was not confident enough to synonymise these species, due to the small number of specimens available. Very few specimens of this species have ever been collected, and based on the variation in thoracic stripes present within *P. (P.) aethiopica*, *P. (P.) formosa* may be a variant of *P. (P.) aethiopica*. However, the sublateral stripes in the few existing specimens, that I have seen, are quite distinct. I contend that more collections are required to make a definitive decision on this issue (see discussion).

Philoliche (Philoliche) rubiginosa Dias, 1966

Figs 1a, 5b, 8, 9

Philoliche (Philoliche) rubiginosa Dias, 1966: 1189. Sabié, “Lourenço Marques” [Maputo], Mozambique (MHNE). Type not available.

nec *Corizoneura rubiginosa* Bigot, 1892: 617. “Australie.”

Diagnosis: *P. rubiginosa* is the only species of *Philoliche* with white-grey pruinescence that gradually blends from the scutellum, across the posterior margin of the scutum, into the brown colour of the scutum. It is separated from *P. elegans* by this lack of sharp contrast in colour, whereas in *P. elegans* the white-grey pruinescence on the posterior margin of the scutum is sharply demarcated from the brown of the scutum. Also, the frons in *P. elegans* is yellow-grey pruinose, versus *P. rubiginosa*, which is shining and dark red.

Description:

Female.

Head: Eyes dichoptic; facets of similar size throughout. Frons very slightly divergent towards antennae, almost parallel; reddish brown and shining, if yellow-grey pruinescence present, then only on ridges along eye margin. Face conically produced forward a distance not more than length of the antennae. Antennae with first two segments orange to brown with black hairs; flagellum orange-brown to bright orange. Palps slender; distal segment wider and short with black hairs and sensory groove leading to an aperture; apex blunt. Proboscis length rarely much longer than length of head and thorax combined.

Thorax: Mesonotum brown to reddish brown with faint, paler brown or red-brown sublateral stripes. Supra-alar areas of scutum gradually blending into white-grey pruinescence beginning with postpronotal lobes and continuing across the posterior margin of the scutum; pruinescence continues anteriorly beyond the pre-scutellum. Scutellum same white-grey colour that may be slightly pink. Pleura light grey to pinkish grey with numerous white to yellow hairs.

Wings: Slightly smoky and slightly tinted yellow, usually without darkening at cross-veins. Fifth radial cell usually open, although closed at margin or even closed and stalked in some specimens; third medial cell always open. Darker yellow pterostigma, subcostal cell and costal cell.

Legs: Fore coxae brown, mid and hind coxae yellow with white and some black hairs; trochanters orange to brown; fore and mid femora yellow-orange; hind femur paler yellow. Tibia of foreleg and midleg paler than femora. Hind tibia darker than hind femur towards apex; tarsi concolourous with apex of tibia of same leg; darkened at apex of fifth tarsomere in all tarsi.

Abdomen: Orange-yellow with black medial spot on segments 1 and 2; segments 3–7 slightly darker than 1 and 2 and with coat of small, black hairs. Central posterior margin of segment 2 sometimes with white or yellow hairs. Posterior margin of segment 4 with black hairs (as rest of segment), except on posterolateral margin. Posterolateral margin of segments 3–7 with tufts of black or white hairs as follows: 3 – black, 4 – mostly white, 5 – mostly white, 6 – white, 7 – white.

Male as female except:

Head: Eyes holoptic; facets abruptly increasing in size from ventral to dorsal margin. Frons extremely small and triangular, pruinose, covered with long, silky yellow, golden or white hairs; eye margins beginning to diverge a distance from vertex similar to length of antennae. Face conically produced, but not as prominent as in female, clypeus highly reduced. Palps reduced compared to female but with sensory pit. Clypeus reduced to frontoclypeal membrane. Antennae and proboscis similar to female.

Thorax: Legs with short distally projecting dorsal process on tarsomeres 1 and 2 (lappet). Lappet of tarsomere 2 never extending beyond proximal margin of tarsomere 4.

Abdomen: Abdomen narrower and often more brightly coloured.

Holotype (not examined): 1 ♀ MOZAMBIQUE: *Maputo*: nr Dingue, i.1955, H. Gonçalves Vocente (MHNE).

Additional material examined: SOUTH AFRICA: *KwaZulu-Natal*: Fanie's Island (28°19'S:32°25'E): 1 ♀ 19.ii.2003, S.I. Morita (SMPC), 1 ♀ 19.ii.2003, D. DeKlerk (SMPC); HellsGate Tsetse Fly Res. St. (28°07'S:32°23'E): 15 ♀ 16–21.ii.2003, S.I. Morita (SMPC); J. Esterhuisen: 12 ♀ 17–24.ii.2003, 1 ♀ 3.iii.2003, 19 ♀ no date (all SMPC); 2 ♀ Mkhuzi (27°37'S:32°02'E), xii.1960, P. de Moor (NMSA); St Lucia (28°23'S:32°25'E): 1 ♀ 16.xii.1983, J. Manning (NMSA, det. as *elegans* by Manning, 1983); 1 ♀ 20.xii.1970, H.V. & B.B. Daly (CASC, det. as *elegans* by Chainey, 1987); 1 ♂ St Lucia Estuary, 13.xi.1970, H. & M. Townes (AEIC).

Distribution: Southern Mozambique and north-eastern KwaZulu-Natal, South Africa (Maputaland Centre) (Figs 8, 9).

Remarks: *P. (P.) rubiginosa* was described by Dias (1966) based on one female specimen. This species has not been mentioned by any subsequent author other than its appearance in the Afrotropical catalogue of Diptera (Chainey & Oldroyd 1980). Dias (1966) gives its distribution as the southern parts of Mozambique. Based on my own collections and a few specimens in NMSA, CASC, AEIC, and a long series of females collected by J. Esterhuisen, I can extend the species range to the Maputaland region of South Africa near St Lucia, KZN. It is likely due to the previously understood distribution (Dias 1966), that Usher (1972) did not record this species in her review of the South African tabanids. The lack of recognition of this species by Usher (1972) probably also explains why no subsequent researchers have considered *P. rubiginosa*, and have therefore misidentified this species as *P. (P.) elegans*, based on the grey colouration of the scutellum in both species (Fig. 1).

Key to species in the *Philoliche (Philoliche) aethiopica* species complex

- 1 Holoptic: eyes meeting or nearly meeting in front (males) 2
 - Dichoptic: eyes clearly separated, not touching or close to touching at any point (females) 3
- 2 Fore tarsi with long process on first and second segments (lappets); eye facets all of similar size or only gradually increasing in size from ventral to dorsal; eyes meeting until slightly above antennae leaving a small triangle of a frons (**aethiopica** group) 4
 - Fore tarsi without long process on first and second segments; if process exists, it does not extend beyond the distal margin of the third tarsomere; eye facets abruptly increasing in size from ventral to dorsal forming a demarcating, horizontal line; eyes contiguous to near the base of antennae, no vestige of frons remaining (**rondani** group) 5
- 3 Ratio of frons width at base to frons width at vertex greater than or equal to 2.1 (Fig. 3b) (**aethiopica** group) 4
 - Ratio of frons width at base to frons width at vertex less than 2.1 (Fig. 3a) (**rondani** group) 5
- 4 Dorsum of mesothorax with distinct, narrow, grey sublateral stripes. Females: females are not yet known for this species; this is their provisional outcome in this

- key as predicted by the distribution of other characters in the group
 **formosa** (Austen)
- Dorsum of mesothorax without stripes, or with indistinct, broad, dull reddish or greyish ones **aethiopica** (Thunberg)
- 5 Dorsum of mesothorax with grey band on lateral margins and with grey on posterior margin; scutellum greyish pink (Fig. 1) 6
- Dorsum of mesothorax with grey band on lateral margins, but not on posterior margin; scutellum concolourous with centre of mesothorax, not greyish pink 7
- 6 Grey posterior margin of mesothorax sharply contrasting with brown at centre; frons generally light coloured and pollinose, not wholly shiny (Fig. 1b) **elegans** (Bigot)
- Grey posterior margin of mesothorax gradually blending into brown anteriorly; frons generally dark and shiny. If frons pollinose, then only along eye margin (Fig. 1a) **rubiginosa** Dias
- 7 All legs similarly coloured on proximal segments: coxae grey, paler dorsally and with white hairs; trochanters black; femora orange. Posterolateral margin of segments 4 and 5 with tufts of black or white hairs as follows: 4 – white only, 5 – black and white **rondani** (Bertoloni)
- Fore and mid legs similarly coloured, hind legs different: fore and mid coxae grey to pinkish grey, paler dorsally and with white and a few black hairs, trochanters black; hind coxa yellow, trochanters orange; fore and mid femora orange, hind femur yellow, same as hind coxa. Tibia of foreleg and midleg paler than femora. Hind tibia darker than hind femur, with black hairs. Posterolateral margin of segments 4 and 5 with tufts of black or white hairs as follows: 4 – black and white, 5 – black only. Third abdominal segment relatively paler dorsally than the other abdominal segments. Proboscis usually 2× greater in length than *P. rondani*. Known from the Albany Centre of endemism only.....**umbratipennis** (Ricardo) stat. rev.

DISCUSSION AND CONCLUSIONS

The majority of workers interested in species of *Philoliche* are not exclusively insect systematists, but pollination biologists (Johnson & Steiner 1995, 1997, 2000, 2003; Johnson 1997, 2000; Goldblatt & Manning 1999, 2000, 2006; Manning *et al.* 1999; Johnson *et al.* 2002; Morita 2006, in press *b*). The previous inability to separate *P. aethiopica* and *P. rondani* females, with consistent misidentification of *P. rubiginosa* as *P. elegans*, highlights the importance of a clear redescription of this group. Ecological work has been hampered by taxonomic confusion stemming from combining two similar-looking species groups/clades and grouping taxa based on proboscis length. With researchers able to separate *P. aethiopica* from *P. rondani* in both males and females, the complexity of this species group problem shifts to understanding the relationships of taxa within the *rondani* and *aethiopica* species groups (clades B and C, Fig. 2). This study presents the additional data required to study the evolution of a recently diverged group of pollinating flies with interesting floral-associated morphology.

The aethiopica species group

Historically, all the species mentioned in this paper, with the exception of *P. elegans*, have been at one time synonymised with *P. aethiopica*. Only two of the three geographic

forms of *P. aethiopica* discussed are clearly separate. The only consistent character, other than general geographic range, is the presence of a spot of white hairs in the centre of the hind margin of the fourth segment of the abdomen in the larger Albany form, and the presence of a white fringe along the entire hind margin of the fourth abdominal segment in the smaller, Zimbabwe form. The Natal form appears to be intermediate in the body size, in the proboscis length, and in having all states of white vestiture along the hind margin of the fourth abdominal segment. The Natal form may represent a hybrid zone between the Albany and Zimbabwe forms; however, it is important to note that where the three forms overlap at the edges of their ranges, they appear to be distinct (Figs 6, 7). These might represent zones of secondary contact following recent speciation.

P. formosa is known only from the male sex. The species is rare; I encountered none during extensive collecting, and I know of only four specimens other than the type series. The scarcity of specimens diagnosable to *P. formosa*, and the fact that the dorsolateral stripes represent the end of a spectrum of variation found within *P. aethiopica*, led Oldroyd (1957) to designate *P. formosa* as a possible synonym of *P. aethiopica*. Males are the more rarely collected sex in Tabanidae, so it is unusual to find 8 males and no females. Also, males in tabanids are often more boldly coloured. Perhaps the distinct thoracic stripes of *P. (P.) formosa* are due this general trend in sexual dimorphism. Molecular analysis of the Zimbabwe form of *P. aethiopica* and of *P. formosa* will aid in understanding the validity and relationships of the morphotypes in this group.

The rondani species group

The closely related members of the *rondani* species group have both long and short proboscis forms. *P. umbratipennis* have proboscis lengths of 20–27 mm, whereas *P. rondani* and *P. rubiginosa* have proboscis lengths ranging 7–15 mm. The evolutionary implications of this morphological variation among such closely related species have been discussed by Morita (in press *b*). *P. umbratipennis* and *P. rondani* are sympatric. Unfortunately, the mating biology of these species is unknown and patterns of gene-flow are not understood. Although, to the extent sampled, previous molecular work shows strong support for monophyly of Clade E (*P. rubiginosa* + *P. rondani* + *P. umbratipennis*, Fig. 2) there is little support for relationships between these taxa. With more exhaustive sampling (Morita, unpubl.), *P. umbratipennis* appears as a monophyletic group, arising from within a paraphyletic *P. rondani*, and the status of monophyly in *P. rubiginosa* is questionable, with only two sequenceable samples. This analysis was based on a 349 bp segment of the mitochondrial gene ND4 that was subsequently found to have multiple paralogues (data not shown). However, even if *P. rondani* is found to be paraphyletic, it does not necessarily preclude it from species status (De Queiroz 2005; see Sites & Marshall 2003, 2004 for reviews). The biogeography, ecology and paraphyletic nature of *P. rondani* with respect to *P. umbratipennis* are patterns consistent with recent, parapatric speciation (Funk *et al.* 1995*a, b*; Funk & Omland 2003). This is also supported by the inferred young age of these lineages (Fig. 2) and their current distribution. More directed molecular work on this problem is planned for future studies.

The male of the species was unknown at the time that Dias (1966) described *P. rubiginosa*. I now describe the male; all males of the *rondani* species group clearly

share distinct eye facet dimorphism. This trait is not seen in other members of *P. (Philoliche)*, and appears to be derived in the group. Interestingly, *P. elegans*, with a grey hind-margin on the scutum, is sister to the rest of the *rondani* clade, indicating that this patterning may be plesiomorphic for the clade. *P. rubiginosa* has what might be considered an intermediate state in a transition towards the absence of this grey hind-margin in *P. rondani*. This, combined with the disjunct distribution of these two taxa (Figs 8, 9), indicates that *P. elegans* may have had a wider historical distribution, and that *P. rubiginosa* and *P. rondani* may have speciated due to vicariance. Such a hypothesis implies that *P. rondani* has re-invaded the Albany region, where it overlaps with *P. elegans* and the longer proboscis form of *P. aethiopica* (Figs 6–9). This might explain the evolution of *P. umbratipennis*, which represents a second evolution of long-proboscis morphology in the Albany region of endemism (Morita 2006, in press *b*) and is coincident with a hypothesis of parapatric speciation for *P. umbratipennis* under divergent selection. The young age of these lineage divergences, and the suggestion that *P. rondani* has not yet achieved monophyly subsequent to divergence, support this. However, distinguishing between vicariant speciation followed by a range expansion, and parapatric speciation by divergent selection is extremely difficult since dispersal events occur on a much shorter time-scale than speciation (Coyne & Orr 2004).

The purpose of describing forms or morphospecies here is to identify possible incipient species and entities of potential ecological or evolutionary importance, in the absence of adequate data to delineate new species. Both the *rondani* and *aethiopica* species groups and corresponding clades are divisible into at least two geographic morphotypes that have discrete differences in proboscis length where they overlap in distribution (Figs 7, 9). The most striking example of this is *P. umbratipennis*, which has a long proboscis and is restricted in distribution to the Albany Centre of Endemism, where it overlaps with the long-proboscis *P. aethiopica* Albany form. These species exhibit convergent morphology to a similar environment or habitat—namely the available floral community (Morita 2006, in press *b*). However, for other such examples, such as the *aethiopica* species group, consistent external morphological characters other than proboscis length are lacking. Phylogenetic monophyly is not the only or even a necessary criterion for species; lineages may be genetically isolated and yet not be reciprocally monophyletic, or populations within a species may show genetic structure (i.e. monophyly) but not be reproductively isolated (De Queiroz 2005; see Sites & Marshall 2003, 2004 for reviews). Although some discrete morphological differences exist where forms overlap (Fig. 7), implying genetic isolation, the data presented here are inadequate to understand the true nature of gene flow within the *aethiopica* species group.

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REFERENCES

- ARNETT, R.H., SAMUELSON, G.A. & NISHIDA, G.M. 1993. *The insect and spider collections of the world*. Gainesville, FL: Sandhill Crane Press, Inc.
- AUSTEN, E.E. 1920. Notes on the nomenclature of certain African Tabanidae (sub-family Pangoniinae), with descriptions of a new genus and new species. *Bulletin of Entomological Research* **11** (43–45): 139–152.
- BEQUAERT, J.C. 1930. Medical and economic entomology: The African Republic of Liberia and the Belgian Congo based on the observations made and material collected during the Harvard African Expedition 1926–1927, vol. 2. *Contributions from the Institute for Tropical Biology and Medicine* **5**: 797–1001.
- BERTOLONI, G. 1861. Illustrazione dei prodotti naturali del Mozambico [Exhibit and description of new Diptera from Mozambique]. *Memorie della Accademia delle scienze dell'Istituto di Bologna. Classe di scienze fisiche* **1860–1861**: 28–29.
- 1862. Illustrazione dei prodotti naturali del Mozambico. Dissertazione intorno ad insetti ditteri. *Memorie della Accademia delle scienze dell'Istituto di Bologna* **12** (1961): 41–60.
- BIGOT, J.M.F. 1892. Descriptions de Dipteres nouveaux. Tabanidi. *Mémoires de la Société Zoologique de France* **5**: 602–691.
- BRADY, S.G., GADAU, J. & WARD, P.S. 2000. Systematics of the ant genus *Camponotus* (Hymenoptera: Formicidae): a preliminary analysis using data from the mitochondrial gene cytochrome oxidase I. In: Downton, M. & Austin, A., eds, *Hymenoptera: evolution, biodiversity and biological control*. Melbourne: CSIRO Publ., pp. 131–139.
- BRETHES, J. 1914. Notes synonymiques sur quelques insectes argentins. *Bulletin de la Société Entomologique de France* **1914**: 58–59.
- BURGER, J.F. 2002. Description of five new species of Tabanidae (Diptera) from Costa Rica and revised keys to species for the genera *Fidena* Walker, *Scione* Walker, and *Chrysops* Meigen in Costa Rica. *Proceedings of the Entomological Society of Washington* **104** (4): 928–940.
- BURGER, J.F. & CHAINEY, J.E. 2000. Revision of the Oriental and Australasian species of *Chrysops* (Diptera: Tabanidae). *Invertebrate Taxonomy* **14** (5): 607–654.
- CHAINEY, J.E. & OLDROYD, H. 1980. Family Tabanidae. In: Crosskey, R.W., ed., *Catalogue of the Diptera of the Afrotropical region*. London: British Museum (Natural History), pp. 275–306.
- COLE, F.R. 1927. A study of the terminal abdominal structures of male diptera (two-winged flies). *Proceedings of the California Academy of Sciences, Series 4* **16** (14): 397–499.
- COQUILLET, D.W. 1910. The type-species of the North American genera of Diptera. *Proceedings of the United States National Museum* **37**: 499–647.
- COYNE, J.A. & ORR, H.A. 2004. *Speciation*. Sunderland, Mass.: Sinauer Associates, Inc. Publ.
- DE QUEIROZ, K. 2005. A unified concept of species and its consequences for the future of taxonomy. *Proceedings of the California Academy of Sciences* **56** (Suppl. 1): 196–215.
- DIAS, J.A.T.S. 1955. Tabanídeos (Diptera: Tabanidae) de Moçambique colhidos pela Misso de Estudo do “Instituto de Medicina Tropical”. *Anais do Instituto de Medicina Tropical, Lisbon* **12** (1–2): 155–181.
- 1966. *Tabanídeos (Diptera–Tabanidae) de Moçambique. Contribuição para o seu conhecimento*. Lourenço Marques [= Maputo]: Universitários de Moçambique.
- ENDERLEIN, G. 1922. Ein neues Tabanidensystem. *Mitteilungen aus dem Zoologischen Museum in Berlin* **10**: 333–351.

- 1925. Studien an blutsaugenden Insekten I. Grundlagen eines neuen Systems der Tabaniden. *Mitteilungen aus dem Zoologischen Museum in Berlin* **11**: 253–409.
- FUNK, D.J., FUTUYMA, D.J., ORTI, G. & MEYER, A. 1995a. A history of host associations and evolutionary diversification for Ophraella (Coleoptera: Chrysomelidae): New evidence from mitochondrial DNA. *Evolution* **49** (5): 1008–1017.
- 1995b. Mitochondrial DNA sequences and multiple data sets: A phylogenetic study of phytophagous beetles (Chrysomelidae: Ophraella). *Molecular Biology and Evolution* **12** (4): 627–640.
- FUNK, D.J. & OMLAND, K.E. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology and Systematics* **34**: 397–423.
- GOLDBLATT, P. & MANNING, J.C. 1996. Phylogeny and speciation in *Lapeirousia* subgenus *Lapeirousia* (Iridaceae: Ixioidae). *Annals of the Missouri Botanical Garden* **83** (3): 346–361.
- 1999. The long-proboscid fly pollination system in *Gladiolus* (Iridaceae: Ixioidae). *Annals of the Missouri Botanical Garden* **86** (3): 758–774.
- 2000. The long-proboscid fly pollination system in southern Africa. *Annals of the Missouri Botanical Garden* **87** (2): 146–170.
- 2006. Radiation of pollination systems in the Iridaceae of sub-Saharan Africa. *Annals of Botany (London)* **97** (3): 317–344.
- HARDWICKE, T. 1823. VIII. Description of *Cermatia longicornis* and of three new Insects from Nepal. *Transactions of the Linnean Society of London* **14**: 131–136 + 2 pls.
- HASEGAWA, E., TINAUT, A. & RUANO, F. 2002. Molecular phylogeny of two slave-making ants: *Rossomyrmex* and *Polyergus* (Hymenoptera: Formicidae). *Annales Zoologici Fennici* **39** (3): 267.
- JOBLING, B. 1976. On the fascicle of blood-sucking Diptera. In addition a description of the maxillary glands in *Phlebotomus papatasi*, together with the musculature of the labium and pulsatory organ of both the latter species and also of some other Diptera. *Journal of Natural History* **10** (4): 457–461.
- JOHNSON, C.W. 1898. Diptera collected by Dr. A. Donaldson Smith in Somaliland, eastern Africa. *Proceedings of the Academy of Natural Sciences of Philadelphia* **50**: 157–164.
- JOHNSON, S.D. 1997. Pollination ecotypes of *Satyrium hallackii* (Orchidaceae) in South Africa. *Botanical Journal of the Linnean Society* **123** (3): 225–235.
- 2000. Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behaviour. *Biological Journal of the Linnean Society* **71** (1): 119–132.
- JOHNSON, S.D., EDWARDS, J., CARBUTT, C. & POTGIETER, C.J. 2002. Specialization for hawkmoth and long-proboscid fly pollination in *Zaluzianskya* section *Nycterinia* (Scrophulariaceae). *Botanical Journal of the Linnean Society* **138** (1): 17–27.
- JOHNSON, S.D. & MORITA, S.I. 2006. Lying to Pinocchio: floral deception in an orchid pollinated by long-proboscid flies. *Botanical Journal of the Linnean Society* **152** (3): 271–278.
- JOHNSON, S.D. & STEINER, K.E. 1995. Long-proboscid fly pollination of two orchids in the Cape Drakensberg mountains, South Africa. *Plant Systematics and Evolution* **195**: 169–175.
- 1997. Long-tongued fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchidaceae). *Evolution* **51** (1): 45–53.
- 2000. Generalization versus specialization in plant pollination systems. *Trends in Ecology & Evolution* **15** (4): 140–143.
- 2003. Specialised pollination systems in southern Africa. *South African Journal of Science* **99** (7–8): 345.
- KAPPEMEIER, K. 2000. A newly developed odour-baited “H trap” for the live collection of *Glossina brevipalpis* and *Glossina austeni* (Diptera: Glossinidae) in South Africa. *Onderstepoort Journal of Veterinary Research* **67** (1): 15–26.
- LATREILLE, P.A. 1802. *Histoire naturelle, generale et particuliere, des crustaces et des insectes. Tome troisieme.* Paris: Dufart.
- 1804. Tableau methodique des insectes. In: *Societe de Naturalistes et d'Agriculteurs, Nouveau dictionnaire d'histoire naturelle*. Tome 24 [Section 3]. Paris: Deterville, pp. 129–200.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* T. 1. Tenth edition. Holmiae [= Stockholm]: L. Salvii.
- MACKERRAS, I.M. 1954. The classification and distribution of Tabanidae (Diptera) I. General Review. *Australian Journal of Zoology* **2**: 431–454.
- MACQUART, P.J.M. 1837 [1838]. Notice sur le genre Pangoie. *Annales de la Société entomologique de France* **1** (6): 429–438.
- 1838. Dipteres exotiques nouveaux ou peu connus. [Vol. 1, Part 1]. *Mémoires de la Société (Royale) des Sciences, de l'Agriculture et des Arts à Lille* **1838** (2): 9–225, 25 pls.

- MANNING, J.C., GOLDBLATT, P. & WINTER, P.J.D. 1999. Two new species of *Gladiolus* (Iridaceae: Ixioideae) from South Africa and notes on long-proboscid fly pollination in the genus. *Bothalia* **29** (2): 217–223.
- MCALPINE, J.F. 1981. Morphology and terminology—adults. In: McAlpine, J.F. *et al.*, eds, *Manual of Nearctic Diptera*. Vol. 1. Monograph 27. Ottawa: Research Branch, Agriculture Canada, pp. 9–63.
- McKEEVER, S. & FRENCH, F.E. 1999. Comparative study of adult mouthparts of fifty-two species representing thirty genera of Tabanidae (Diptera). In: Burger, J.F., ed., *Contributions to the knowledge of Diptera. Memoirs on Entomology, International* **14**: 327–353.
- MEIGEN, J.W. 1804. Versuch einer neuen Gattungs-Eintheilung der europäischen zweiflügeligen Insekten. *Magazin für Insektenkunde* **2**: 259–281.
- MITTER, J.L. 1918. Note on the method of feeding of *Corizoneura (Pangonia) longirostris* Hardwicke, with a redescription of the mouth parts. *Indian Journal of Medical Research* **5**: 523–528.
- MORITA, S.I. 2006. The evolution of long-proboscid horse flies (Diptera: Tabanidae) in the genus *Philoliche* (Wiedemann). Unpublished Dissertation, University of California, Davis.
- In press a. A phylogeny of long-tongued horse flies (*Philoliche*, Tabanidae, Diptera) with the first cladistic review of the higher relationships within the family. *Invertebrate Systematics*.
- In press b. Multiple evolutions of both long- and short-proboscid morphology in long-tongued horse flies (Diptera: Tabanidae). *Biological Journal of the Linnean Society*.
- MOULTON, J.K. & WIEGMANN, B.M. 2004. Evolution and phylogenetic utility of CAD (rudimentary) among Mesozoic-aged Eremoneuran Diptera (Insecta). *Molecular Phylogenetics and Evolution* **31** (1): 363–378.
- OLDROYD, H. 1957. The horseflies of the Ethiopian region. Vol. III. Subfamilies Chrysopsinae, Sepsidinae and Pangoniinae, and a revised classification. London: British Museum (Natural History).
- RICARDO, G. 1900. Notes on the Pangoniinae of the family Tabanidae in the British Museum collection. *Annals & Magazine of Natural History* (7) **5**: 97–121, 167–182.
- RONDANI, C. 1864. Dipterorum species et genera aliqua exotica revisa et annotata novis nonnullis descriptis. *Archivios per la Zoologia, l'Anatomia e la Fisiologia* **3** (1): 1–99, pl. 5.
- SABROSKY, C.W. 1999. Family-group names in Diptera. *Myia* **10**: 1–360.
- SEN, S.K. 1931. Notes on the bionomics and anatomy of *Corizoneura longirostris* Hardwicke (Diptera: Family Tabanidae; subfamily Pangoniinae). *Indian Journal of Veterinary Science* **1**: 24–28.
- SITES, J.W., JR. & MARSHALL, J.C. 2003. Delimiting species: A Renaissance issue in systematic biology. *Trends in Ecology & Evolution* **18** (9): 462–470.
- 2004. Operational criteria for delimiting species. *Annual Review of Ecology and Systematics* **35**: 199–227.
- SURCOUF, J.M.R. 1921. Diptera. Family Tabanidae. *Genera insectorum* **175**: 1–182.
- TETLEY, H. 1918. The structure of the mouthparts of *Pangonia longirostris* in relation to the probable feeding-habits of the species. *Bulletin of Entomological Research* **9**: 253–267.
- THUNBERG, C. 1789. D. D. Museum Naturalium Academiae Upsaliensis. *Cujus Partem Septiman [= Part 7], Upsaliae [=Uppsala]*, pp. [ii] + 85–94.
- 1827. *Tanyglossae septendecim novae species descriptae. Nova Acta Regiae Societatis Scientiarum Upsaliensis* **9**: 63–75.
- USHER, P.J. 1965. Records and descriptions of Tabanidae from southern Africa (Diptera). *Annals of the Natal Museum* **18**: 27–87.
- 1972. A review of the South African horsefly fauna (Diptera: Tabanidae). *Annals of the Natal Museum* **21** (2): 459–507.
- VAN WYK, A.E. & SMITH, G.F. 2001. Regions of floristic endemism in southern Africa: a review with emphasis on succulents. Hartfield, South Africa: Umदाus Press.
- WALKER, F. 1850. Vol. 1. Diptera [Part I]. In: *Insecta Saundersiana: or characters of undescribed insects in the collection of William Wilson Saunders, Esq., F.R.S., F.L.S., &c.* London: Van Voorst, pp. 1–76, pls 1–2.
- WIEDEMANN, C.R.W. 1820. Diptera exotica. [Ed. 1]. Section 1. Antennis multiarticulatis. Kiliae [= Kiel].
- 1828. *Aussereuropäische zweiflügelige Insekten. Als Fortsetzung des Meigenschen Werkes. Erster Theil [1st part]*. Hamburg: Schulz.