

Chrysomya chloropyga (Wiedemann, 1818) and *C. putoria* (Wiedemann, 1830) (Diptera: Calliphoridae) are two different species

K. Rognes^{1*} & H.E.H. Paterson^{2†}

¹Faculty of Arts and Education, University of Stavanger, N-4036 Stavanger, Norway

²School of Integrative Biology, University of Queensland, Brisbane, Queensland 4072, Australia

The blowflies *Chrysomya chloropyga* (Wiedemann, 1818) and *Chrysomya putoria* (Wiedemann, 1830) (Diptera: Calliphoridae) of veterinary and medical importance are taxonomically revised and formally reestablished as two different species. Characters in the adult morphology by which they can be distinguished, including characters in the genitalia, are described. The form with a darkened anterior margin of the wing, 'f. *taeniata* Bigot' sensu Zumpt 1956, is treated as a variant of *C. putoria*. In order to preserve stability of nomenclature, lectotypes are designated for both nominal species, fixing their identity in accordance with current usage. *Somomyia cuprinitens* Rondani, 1873, and *Somomyia taeniata* Bigot, 1877, (= *C. chloropyga* 'f. *taeniata* Bigot' of Zumpt) are considered new synonyms of *C. putoria*.

Key words: Blowflies, taxonomy, forensics, medical entomology, veterinary entomology, Afrotropical Region, Neotropical Region, *Chrysomya*, *C. putoria*, *C. chloropyga*, *C. taeniata*.

INTRODUCTION

For a long time there has been confusion about the taxonomic status of two Afrotropical species of *Chrysomya* Robineau-Desvoidy, 1830, of medical and veterinary importance, namely *C. chloropyga* (Wiedemann, 1818) and *C. putoria* (Wiedemann, 1830), the latter having established itself also in the New World since 1975. The confusion stems from the opinion held by F. Zumpt, the leading authority on Afrotropical Calliphoridae for many years, who repeatedly (Zumpt 1956, 1962, 1965, 1972), though with varying emphasis, stated that the two nominal species first named and described by Wiedemann, and subsequently regarded as good species by e.g. Malloch (1925) and Curran (1928), were one and the same species, which should carry the senior name *C. chloropyga*. This opinion found its way into two widely used reference works (Pont 1980; Dear 1985).

Paterson (1967, 1977) maintained that two good species were involved, and listed a number of features by which they could be distinguished, many referring to the male genitalia.

Zumpt's argument rested on a single assumption only, namely that the male genitalia of the two nominal species were identical. He published drawings of these structures, believing they underpinned his opinion. The external features known to him to distinguish the two species were

dismissed as the result of individual or other variation, and the species were in the end treated as 'phenotypes' of a single species (Zumpt 1972). He was well aware that their geographical distribution in Africa showed great overlap and thus could not reflect subspecific status.

In this assumption he found support in van Emden (1953), who was the first to state explicitly that the two species 'have identical male genitalia'. However, van Emden drew another conclusion from this, in effect relying on the external features to maintain a separate status for the two species, notwithstanding the alleged 'identical genitalia'.

The confusion has lasted up to the present day. Some authors have chosen to use both binomina – *Chrysomya chloropyga* and *Chrysomya putoria* – in print, implying an interpretation that two different species are involved (e.g. Boyes & Shewell 1975; Ullerich 1976; Baumgartner & Greenberg 1984; Erzinçioğlu 1987; Laurence 1988; Parise-Maltempi & Avancini 2001; Wells *et al.* 2004). Even Zumpt (1965) did so, but in his case only for 'practical reasons' (p. 93) since he did not believe they were separate species.

Other authors, even if many of them certainly believed two true species were involved, usually adopted a nomenclature that did not challenge Zumpt's (1972) taxonomic judgements. For instance, Guimarães *et al.* (1978: 57) were 'regarding *putoria* as a synonym of *chloropyga* for practical

*To whom correspondence should be addressed.

E-mail: knut@rognos.no

†E-mail: h.paterson@mailbox.uq.edu.au

reasons'. Baumgartner & Greenberg (1984), though regarding it as a distinct species, and using the binomen '*C. putoria*' in place for '*Chrysomya chloropyga* form *putoria*' (the terminology introduced by Zumpt 1956), explicitly did so 'for brevity'. Greenberg & Szyska (1984) adopted the trinomen '*Chrysomya chloropyga putoria*'. Baumgartner & Greenberg (1985) used both the trinomen '*Chrysomya chloropyga putoria*' (p. 569, Table 2, p. 580) and the binomen '*C. putoria*' in the same paper (passim). Erzinçlioğlu (1987) described features by which their third instar larvae could be distinguished, but nevertheless treated them as separate species and retained the two names explicitly only '[f]or practical purposes' (p. 122). González Mora & Peris (1988: 125), when discussing the occurrence of '*Chrysomya chloropyga*' from the Canary Islands (material of which they did not see themselves), followed Zumpt: 'Nosotros consideramos que se trata de 'formas' distintas de una sola especies'. Wells & Kurahashi (1996) considered '*C. chloropyga* (= *C. putoria*)'. Wells, Byrd & Tantawi (1999) did the same. Wells & Sperling (2001) also 'chose to be taxonomically conservative' in denoting the New World species as '*C. chloropyga* because Dear did not distinguish between the two species in his monograph'. Mariluis (2002) did the same in his recent key to common adult blowflies of South America.

Until recently, *Chrysomya chloropyga* was listed in the GenBank (NCBI –National Center for Biotechnology Information) with the following synonyms: '*Chrysomya chloropyga putoria*' and '*Chrysomya putoria*', with the single taxon identifier No. 142978, again in acceptance of the view that only one species is involved [printout dated April 25, 2003].

This situation has changed (2 October 2003) and the two species now have their own taxon-identifiers [Taxonomy ID: 142978 = *Chrysomya chloropyga*, Taxonomy ID: 235600 = *Chrysomya putoria*] (NCBI 2003), possibly in anticipation of the appearance of the present taxonomic revision, which many colleagues have known was forthcoming.

In the present paper we argue that the assumption of identical male genitalia is fundamentally wrong. We describe in detail the adult features, including genitalia, by which the two species *C. chloropyga* and *C. putoria* can be distinguished, describe the female ovipositor for both species, not done before, and formally reestablish *C. putoria* as a separate species. Hopefully this will lay the matter to rest. Even though the problem whether

different species may have identical genitalia is an interesting one, it does not arise in this case.

It should be noted that there is a third 'species' involved in this problem. It was treated by Zumpt (1956: 182, 189, 190) under the name '*Chrysomya chloropyga* f. *taeniata* (Bigot)' (with several synonyms). It was distinguished by him by an infuscated fore margin of the wing. Later he included it, as he did with the two others, among '*Chrysomya chloropyga* (Wiedemann) and its phenotypes' (Zumpt 1972). In the Afrotropical Catalogue (Pont 1980) it was subsequently listed among the synonyms of *C. chloropyga*. We suggest below that the 'f. *taeniata* (Bigot)' is nothing but a true *C. putoria* with a darkened wing margin, and have transferred *Somomyia taeniata* Bigot, 1877 syn. n. into the synonymy of *C. putoria*.

MATERIAL AND METHODS

The study is based on 364 adult specimens from the following museums and collections, including 38 genital slides (15 of *C. chloropyga*, 23 of *C. putoria*, all from NMSA): Natural History Museum, London, U.K. (BMNH), private collection of Knut Rognes, Stavanger, Norway (KR), Natal Museum, Pietermaritzburg, South Africa (NMSA), Naturhistorisches Museum, Vienna, Austria (NMW), Zoological Museum, University of Copenhagen, Copenhagen, Denmark (ZMC), Museum of Zoology, Lund University, Lund, Sweden (ZML), and the Zoological Museum, Moscow, Lomonosov State University, Moscow, Russia (ZMUM).

Methods for the preparation of genitalia and the drawings follow Rognes (2002).

Measurements for frons width/head width ratios were made with an ocular micrometer with 120 divisions.

In numerous cases the genital slides from NMSA (males only) contained information on locality and date, but were not accompanied by the corresponding dissected adult specimen. In all these cases the species was easily established by examination of the aedeagus and other genital parts under the coverglass. In the lists below records of this type are indicated by 'Zumpt slide only'. 'Dissected by Zumpt, slide no. 26' implies that one of us (K.R.) has examined the actual slide and the adult specimen. 'Dissected by K.R.' implies that K.R. has performed the dissection.

In the lists of material examined, countries and provinces are listed alphabetically.

It is obviously the same specimen as the one reported upon by Villeneuve (1914: 436): 'Une ♀ avec l'étiquette: «*M. chloropyga* mihi. Prom. B. spei. Hesse.» Espèce bien caractérisée par le dessin du thorax.'

It is in good condition, except that both fore legs are missing (left fore coxa is in place), and some parts of the face and antenna and anterior ventral part of the thorax have been eaten away. The distal part of the abdomen is wrinkled, testifying to the immaturity of the specimen. It fits the original description very well, and shows the characteristic pattern on the front part of the dorsum (well described by Wiedemann). The two last visible segments of the abdomen are bright green, contrasting dramatically with the colour of the preceding segments.

In view of the facts that (1) all species described by Wiedemann in the 1818 paper, according to his own statements in the introduction (p. 40), were collected by 'Herr Pastor Hesse', that (2) the label carries Hesse's name and that the only place where this name is mentioned at all any time is in the same introduction to the 1818 paper (cf. Pont 1995: 145), that (3) the locality is correct, and that (4) the specimen fits the original description, the specimen is most probably a syntype. To preserve the current use of the species group name *chloropyga* for the present species one of us (K.R.) has therefore labelled and we hereby designate this female as the lectotype of *Musca chloropyga* Wiedemann, 1818.

The frons/head width ratio is $43/120 = 0.358$, there are two orbital seta on the right side, one on the left side, and the vestiture on middle part of fronto-orbital plates moderately dense.

Zimsen (1954: 24) listed two specimens (citing Wiedemann 1830: 'In Westermann's und meiner Sammlung') under the entry '316': '*Musca chloropyga* (Ausz. Zw. Ins. II p. 400.28)' as 'type specimens described by C.R. Wiedemann from collections belonging to the Zoological Museum of Copenhagen' (1954: 5). These specimens have been examined. They are both females. One of the females has the following labels:

(1) (small square whitish yellow card) '♀' (printed); (2) (whitish-yellow card) 'Mus/Westerm [ann].' (printed); (3) (large whitish yellow card) '*M. chloropyga*/Wied./Cape of Good Hope/May 1817' (elaborate, beautiful handwriting in ink by Wiedemann (?));

The second female has only a single label, similar

to label (2).

These specimens cannot be syntypes as Zimsen maintains. They were collected by Westermann (*teste* the 'Mus Westerm.' labels) and not Hesse. Westermann returned from the Cape to Copenhagen in 1818 (Pont 1995: 137), and entrusted Wiedemann with the identification of the Diptera he had collected. Obviously they were subsequently included in Wiedemann's monograph on exotic Diptera (Wiedemann 1830: 400), which explains the 'In Westermann's collection' statement in the latter work (p. 401).

Thompson & Pont (1993: 60), probably following Zimsen, report under *chloropyga*: 'TA ZMC'. This translates to 'Type, status unknown or typical specimen(s); Adult specimen; Universitetets Zoologiske Museum, Copenhagen'. The status of these specimens has therefore now been resolved as not being types at all. One of us (K.R.) has added labels to this effect on the pins.

Material examined (63♂, 50♀). CAMEROON, 29 miles North N'Gaoundéré, 1230 m, 1♂ 30 September 1966 (E.S. Ross & K. Lorenzen) (dissected by Zumpt, slide no. 47) (NMSA). DEMOCRATIC REPUBLIC OF CONGO [ZAIRE], Mt Kamatembe, 2♂ January 1935 (both Zumpt slides only, one labelled 'terminalia no. 8') (NMSA). ETHIOPIA, Addis-Abeba, 6♂ 3♀ May–June 1989 (S. Mazin) (2♂ dissected by K.R.; 1♀ dissected by K.R., spermathecae in glycerol in vial on pin, ST1-5 and ovipositor on slide G. pr. 395) (ZMUM); KENYA, Njoro, Montello Farm, 1♀ 14 January 1973 (I. Bampton) (NMSA); Limuru, 50 km NW Nairobi, 2500 m, 1♀ 1–20 March 1990 (Tungland) (dissected by K.R.; spermathecae in glycerol in vial on pin, ST1-5 and ovipositor on slide G. pr. 394) (KR). LESOTHO, Mamathes 1♀ 16 May 1948, 1♂ 18 November 1949, 1♂ 2 July 1950 (dissected by K.R., 'H') (all C. Jacot Guillarmot); Mokhotlong, 1♀ 6 April 1951 (Swedish South Africa Expedition) (all ZML); ST HELENA, Centre, S. Stitch's Ridge, 1600 ft, 1♂ 22 November 1965 (Zumpt slide only, 'slide 62') (NMSA); 'Coffee Grove, Sandy Bay distr.', 1♀ 15 August 1959 (C.R. Wallace) (BMNH); Varneys, 1♀ 23 May 1963, 1♀ 20 August 1963 (both A. Loveridge) (both BMNH). SOUTH AFRICA, ?Province: ?locality (unlabelled) 2♂; 'Schoefield Tropo Nat', 1♂ November 1911, [apparently bred, together with 143 others, from larvae found in] 'Dirty Fleece of live sheep' (? leg.) (all NMSA). *Eastern Cape Province*: Blinkwater 8 km N Fort Beaufort, 750 m, 1♂ 21 October 1994 (R. Danielsson) (ZML);

Graaff-Reinet, 2♀ September 2001 (1♀ dissected by K.R.; spermathecae in glycerol in vial on pin, ST1-5 and ovipositor on slide G. pr. 398) (KR); Grahamstown, 1♀ 25 May 1967 (J.G.H. Londt) (NMSA); Grahamstown 11♂ August 2001 (N. Lunt) (1♂ dissected by K.R.) (KR); Tsitsikamma National Park, Stormsriver Pass, 1♂ 19 October 1994 (R. Danielsson) (ZML); Willowmore, 11♀ August 1912, 1♀ November 1922 (all Dr Brauns) (all NMSA); Gauteng: Johannesburg, 1♂ (Zumpt slide only), 1♂ November 1948 (Zumpt slide only), 1♀ 28 November 1948 (Zumpt), 1♂ 25 December 1948 (Zumpt), 1♂ 1♀ 17 April 1949 (Zumpt) (male dissected by Zumpt, 'Terminalia II'), 1♂ 4 August 1949 (Zumpt), 2♂ October 1950 (Zumpt slides only), 1♂ 1–15 October 1950 (Zumpt slide only), 2♂ January 1971 (Zumpt); KwaZulu-Natal: Cathedral Peak area, 1♂ 6–18 December 1977 (J.G.H. Londt) (NMSA); Drakensberg, Giants Castle Res., 5800 feet, 6♀ 18–23 September 1963 (B. & P. Stuckenberg), 3♂ 1 November 1972 (M. Irwin) (all NMSA); Drumna-dochit Farm, 1♂ 1♀ January 2001 (K. Smith) (KR); Durban, 1♂ 1 November 1906 (G.F. Leigh) (NMSA); Karkloof Range near Mt Alida, Geekie's Farm, 1500 m, 1♀ 19 November 1963 (B. & P. Stuckenberg) (NMSA); 'Karoo at junction of/Calvinia Sutherland Rds/Nr Inverdoorn Ceres', 3♂ 1♀ 2–3 October 1959 (B. & P. Stuckenberg) (NMSA); Maritzburg, 1♀ 28 September 1904 (Cl. Fuller) (NMSA); Oliv. Hock Tass [Tagg?], 1♂ (Zumpt slide only) (NMSA); Pietermaritzburg, 2♂ 4 July 2001 (M.H. Villet) (1♂ dissected by K.R.) (KR); Richmond, 1♀ 22 November 1973 (F. Zumpt) (NMSA); Royal NMSA National Park, Tugela Valley, 2♀ 3 April 1951 (Swedish South Africa Expedition) (1♀ dissected by K.R.; spermathecae in glycerol in vial on pin, ST1–5 and ovipositor on slide G. pr. 401) (ZML); Mpumalanga: Delmas, 1♂ (Zumpt slide only, 'terminalia no. 8'); Machadodorp, 1♂ February 1969 (Zumpt); Nelspruit, 1♂ 1♀ 17 April 1974 (E.A. Nesbitt) (all NMSA); Northern Cape Province: Riet[fontein?], 1♀ 6 September 1904 (?leg.) (NMSA); Western Cape Province: Cape of Good Hope, 1♀ [1818?] (Hesse) (LECTOTYPE) (NMW); 2♀ May 1817 (Westermann) (ZMC); De Hoop Nature Reserve, 1♀ 19 October 1994 (R. Danielsson) (ZML); Hout Bay, Skoorsteenkop, Cape Peninsula, 1♀ 22 January 1951 (Swedish South Africa Expedition) (ZML); Malgas, 40 m, 1♂ 11 October 1994 (R. Danielsson) (dissected by K.R., 'G') (ZML); Montagu Pass George [?], 1♀ [no date] (Dr Brauns) (NMSA); Pakhuis Mountains, 2 miles

NNE Pakhuis Farm, 1800 feet, 1♀ 14 September 1972 (M.E. & B.J. Irwin) (NMSA); Stellenbosch, 1♀ November 1925, 1♀ October 1925, 1♂ November 1925 (all Dr H. Brauns) (all NMSA); Wellington Distr., Bainskloof, 2000 feet, 1♀ 4–5 October 1959 (B. & P. Stuckenberg) (NMSA); Witsands Dunes, Cape Peninsula, 1♂ 1♀ 25–26 September 1959 (B.P. Stuckenberg) (NMSA). TANZANIA, Kikori, 1♂ (Zumpt slide only); Mufindi, 1♀ October 1938 (Zumpt), 1♂ October 1938 (Zumpt slide only), 1♂ October 1939 (Zumpt slide only, 'terminalia no. 1'); Sinyanga, 1♂ (Zumpt slide only) (all NMSA). ZIMBABWE: Bulawayo, 1♂ 3 August 1923 (R. Stevenson) (NMSA); Bulawayo, 1♂ 17 August 1924 (R.H.R. Stevenson) (NMSA).

***Chrysomya putoria* (Wiedemann, 1830) stat.**

rev., Figs 2, 4, 6, 8, 10, 12, 14, 16, 18, 20

Musca putoria Wiedemann, 1830: 403.

Somomyia cuprinitens Rondani, 1873: 285. **Syn.n.**

[teste notes by Adrian C. Pont on holotype ♂ in the Genoa museum]

Somomyia taeniata Bigot, 1877: 36. **Syn.n.**

Further synonyms in Zumpt (1956) under '*f. putoria* (Wiedemann)' (p. 188) and '*f. taeniata* (Bigot)' p. 189.

Remarks on type material

Musca putoria was described from '♀. – Aus Sierra Leona. In meiner Sammlung', thus at least one specimen. One female specimen in NMW has been examined.

Labels: (1) small (about 2 × 2 mm) square pink piece of paper without text; (2) (red) 'Type' (black print); (3) (white) '*putoria*/Wied[emann]/Sierra Leona (black ink handwriting; Wiedemann's?); (4) (white) '*putoria*' (black ink handwriting)/'Coll. Winthem.' (black print); (5) (blue) '*Compsomyia* (*Pycnosoma*)/eod.nom.' (black ink handwriting).

It is obviously the same specimen as the one reported upon by Villeneuve (1914: 440): 'Au dernier moment, je découvre, dans la collection du Kais.-Königl. Naturh. Hofmuseum de Vienne, le type de *Musca putoria* Wied. C'est une ♀ indiquée de « Sierra Leona»...'

It is in fair condition with glue added around the pin both above and below the specimen to compensate for considerable destruction of the thorax around the pin. Both fore legs are present but the left fore tarsus lacks the distal four segments. Both mid legs are present but both lack all tarsal segments. Only the left hind leg is present

and it has lost all tarsal segments. The head and abdomen are in good condition. Otherwise the specimen fits the description perfectly.

There is no evidence in the original work that more than one specimen was included in the type series, and only one specimen is present in NMW. On the other hand, there is no evidence in the original publication nor from outside sources that only a single specimen was involved. The single known specimen is therefore considered to be a syntype. To preserve the current use of the species group name *putoria* for the present species one of us (K.R.) has therefore labelled, and we hereby designate this female syntype as the lectotype of *Musca putoria* Wiedemann, 1830.

The frons/head width ratio is $36/120 = 0.300$, there are two orbital setae on right side, one on left side, and the vestiture on middle part of fronto-orbital plates normal.

Thompson & Pont (1993: 112) reported under *putoria*: 'T A NMW'. This translates to 'Type, status unknown or typical specimen(s); Adult specimen; Naturhistorisches Museum, Vienna'. This is the same specimen as the one designated as lectotype above.

Material examined (129♂, 122♀) (specimens marked with an asterisk have been identified by Zumpt as 'f. *taeniata* Bigot').

Afrotropical Region

BOTSWANA, Martin's Drift, 1♀ February 1953 (?leg.) (NMSA); Ngamiland, Gomare, 1♂ 5 July 1949 (Zumpt slide only) (NMSA); Snake Island, 2♂ 3♀ January 2001 (N. Lunt) (1♀ dissected by K.R.; spermathecae in glycerol in vial on pin, ST1-5 and ovipositor on slide G. pr. 397) (KR). CAMEROON, Yaoundé, Centre Agron., 710 m, 1♂ 8 November 1966 (E.S. Ross & K. Lorenzen) (dissected by Zumpt, slide no. 26) [extremely slightly darkened fore margin of wing]; Yaoundé, 1♂ (Zumpt slide only); *Yaoundé, 3♀ ?date (Rageau); *Bombe (Mungofluhs) 1♂ 21 October 1935 (F. Zumpt) (dissected by Zumpt, slide no. 24); *2 miles NW Mbouda, nr. Bamenda, 1♂ 9 October 1966 (E.S. Ross & K. Lorenzen) (dissected by Zumpt, slide no. 58) (all NMSA). DEMOCRATIC REPUBLIC OF CONGO [ZAIRE], Bulu, Nele, 1♂ (Zumpt slide only); Kivu, 1♂ 14 October 1934 (Zumpt slide only, 'terminalia no. 76'); Lac Kivu, 1♂ (Zumpt slide only, 'terminalia no. 9'), 1♂ February 1934 (Zumpt slide only, 'terminalia no. 38'); Lac Mokoto, 1♂ (Zumpt slide only, 'terminalia no. 10'), 1♂ 23 September

1935 (Zumpt slide only, 'terminalia no. 5'), 1♂ 23 September 1935 (Zumpt slide only, 'terminalia no. 11'); Lubumbashi [= Elisabethville], 1♀ 19 May 1920 (M. Bequert), 1♂ 1♀ April 1925 (Ch. Seydel), 1♂ 1 March 1928 (M. Bequert); Luilu (Kambai), 1♀ December 1925 (Ch. Seydel); Ngoma (Zumpt slide only); Rumangabo, 1♂ April 1946 (Zumpt slide only, 'terminalia no. 77'); Rutshuru, 1♂ April 1934 (Zumpt slide only); Rwindi, 1♂ November 1934 (Zumpt slide only, 'terminalia no. 6'); Tshibinda, 1♀ December 1927 (Ch. Seydel) (all NMSA); Uvira, 1♀ 1939 (J. Aspenlind) (ZML). GAMBIA, Abuko Nature Reserve, 1♂ 11 February 1977 (Cederholm, Danielsson, Larsson, Mireström, Norling, Samuelsson); Abuko Nature Reserve at Bamboo Pool, 1♂ 11 March 1977 (Cederholm, Danielsson, Larsson, Mireström, Norling, Samuelsson); Bakau at Tropic Bungalow, 4♂ 2♀ 16–18 November 1977 (Cederholm, Danielsson, Hammarstedt, Hedquist, Samuelsson), 1♀ 21–24 November 1977 (Cederholm, Danielsson, Hammarstedt, Hedquist, Samuelsson); Bakau Botanical Garden, 2♂ 21 November 1977 (1♂ dissected by K.R.) (Cederholm, Danielsson, Hammarstedt, Hedquist, Samuelsson); Bakau at Tropic Bungalow, on dead dolphin on the beach, 15♀ 16 November 1977 (Cederholm, Danielsson, Hammarstedt, Hedquist, Samuelsson); Kotu Stream about 3 km SW Bakau, 1♀ 23 February 1977 (Cederholm, Danielsson, Larsson, Mireström, Norling, Samuelsson), 1♀ 22–23 November 1977 (Cederholm, Danielsson, Hammarstedt, Hedquist, Samuelsson); Outside Abuko Nature Reserve at Waterworks, 1♂ 26 February 1977 (Cederholm, Danielsson, Larsson, Mireström, Norling, Samuelsson); 1 km ESE Georgetown at river Gambia, 1♀ 15 November 1977 (Cederholm, Danielsson, Hammarstedt, Hedquist, Samuelsson) (all ZML). GHANA, Ashanti Region, Kumasi, Agyase, 6♂ 4♀ 17 June 1965 (I.K.B. Acheampong) (2♂ dissected by K.R.) [all with slightly darkened fore margin of wing] (ZML); *Forest locality at 5°23'N and 2°28'W, 2♂ 2♀ July 1968 (L.R. Cole) (NMSA). KENYA, Limuru, 50 km NW Nairobi, 2500 m, 20♂ 28♀ 1–20 March 1990 (Tungland) (3♂ dissected by KR, specimens 'A', 'B', 'F'; 1♀ dissected by K.R., spermathecae in glycerol in vial on pin, ST1-5 and ovipositor on slide G. pr. 334) (KR); Nairobi, Nairobi Museum, 1♂ 1♀ 28 May 2001 (M.H. Villet) (KR); Nairobi (Zumpt slide only, labelled 'f. *taeniata*', ♂ terminalia no. 15) (NMSA); Njoro, Montello Farm, 5♀ 14 January 1973 (I. Bampton) (NMSA). MADAGASCAR, Aloatra,

District Ambatondrazaka, Station Agric., 1♂ 24 December 1957 (B. Stuckenberg) (dissected by Zumpt, slide no. 32); Nosy Bé [=Nossi Be], Lokobe, 6 m, 1♂ 1♀ 9–23 November 1957 (B. Stuckenberg); Fenerive, coastal forest, 1♂ 1♀ December 1955 (B. Stuckenberg); Tsimbazaza, 1♂ 16 September 1947 (G.B.); Tsimbazaza/Tananarivo, 1♀ (?leg.) (all NMSA). MAURITIUS, On grapefruit ('Pamplemousse'), 1♂ 1♀ 26 April 1963 (Paterson) (NMSA); MOZAMBIQUE, Tete-Angonia, Vila Coutinho, 1♀ 19 March 1974 (T. Dias); Niassa, Vila Cabral, 1♀ 18 March 1974 (T. Dias) (both NMSA). RÉUNION, Bretagne, 1♀ 18 July 1951 (J.R. Williams) (BMNH). SENEGAL, 1.5 km NE Djibélor *ca* 6.5 km SW Ziguinchor, 10♂ 1♀ 8 March 1977 (Cederholm, Danielsson, Larsson, Mireström, Norling, Samuelsson) (1♂ dissected by K.R.) (ZML). SEYCHELLES, Mahe, Beau Vallon, 1♂ 1♀ 20 February 1965 (Tams & Nye); Plateau la Passe, Silhouette 1♂ 1♀ July 1965 (R.A.A. Blackman) [the male has an outer vertical seta on each side, and the wing is very slightly infuscated along fore margin], Sans Souci, 1♀ 2 February 1906 (P.R. Dupont), 1♂ 20 February 1906 (P.R. Dupont) (dried genital capsule with visible aedeagus glued to tip of card); ?locality, 1♀ 16–17 July 1974 (I.H. Haines) (all BMNH). SIERRA LEONE, ?locality 'Sierra Leona' (lectotype NMW); Freetown, Cape Sierra Hotel area, 1♂ 18 November 1993, 1♂ 1♀ 19 November 1993, 2♀ 23 November 1993; Freetown, Fourah Bay College, 1♂ 24 November 1993 (dissected by KR) (all L. Cederholm, R. Danielsson, R. Hall) (all ZML). SOUTH AFRICA, ?Province: Dan Village, Buloi Farm, 2♀ 11 January 1984 (K. Hargreaves); ?Province, Petanenge, Ngobeni Farm, 1♀ 27 January 1984 (K. Hargreaves); ?Province, Petanenge, Rakgorwana, 1♀ 16 February 1984 (K. Hargreaves) (all NMSA); *Eastern Cape Province*: Paterson (sand dunes), 300 m, 1♂ 15 March 1972 (M.E. & B.J. Irwin leg.) (NMSA); *Gauteng*: Johannesburg, 1♂ (Zumpt slide only), 2♂ 28 November 1948, 1♂ 3 December 1948, 1♂ 6 March 1949, 1♂ 20 March 1949, 3♂ 7♀ 17 April 1949 (1♂ with genitalia on card; 1♂ with genitalia in glass vial) (all Zumpt); Onderstepoort, 1♂ November 1941 (Zumpt slide only) (all NMSA); *KwaZulu-Natal*: 10 miles N of Jozini (dry forest), 800 feet, 1♂ 28 November 1971 (M.E. & B.J. Irwin) (NMSA); Drumnadochit Farm, 1♂ January 2001 (K. Smith leg) (dissected by KR, specimen 'D') (KR); Duku-duku Forest, 4 miles W of St Lucia, 880 m, 1♀ 26 November 1971 (M.E. & B.J. Irwin); Ngome Forest between Vryheid and Nongoma, 1♂ 11–12 April

1960 (B. & P. Stuckenberg); Nobanda School, Sweetwaters, 1♂ 1♀ March 1993, 1♀ April 1993 (all R. Burgess) (all with puparium in vial; reared from larvae taken from latrines); Richmond, 880 m, 1♀ 29 November 1991 (A.E. Whittington); St Lucia, 1♂ 26 July 1962 (Zumpt?); Umfolozi Game Park, 1♂ 21 July 1973 (M.E. Irwin) (all NMSA). SWAZILAND, Malkerus, 2♀ 31 December 1967 (Zumpt) (NMSA). TANZANIA, Amani, 1♀ (Paterson); Kondo, 1♂ June 1927 (Zumpt slide only); *Rivuma, Liparamba b[ei]. Nindi, 2♂ 22 January 1937 (F. Zimmer); Shinyanga, 1♂ November 1938 (Zumpt slide only); Songea, 1♂ December 1935 (Zumpt slide only) (all NMSA). UGANDA, *Ankole, Kichwamba 1♂ 23–29 April 1968 (P.J. Spangler) (NMSA). ZAMBIA, Kitwe, 1♂ 3♀ 12 December 2001 (N. Mkize) (KR); Ndola, 1♀ June–July 1949 (?leg) (NMSA).

Neotropical Region

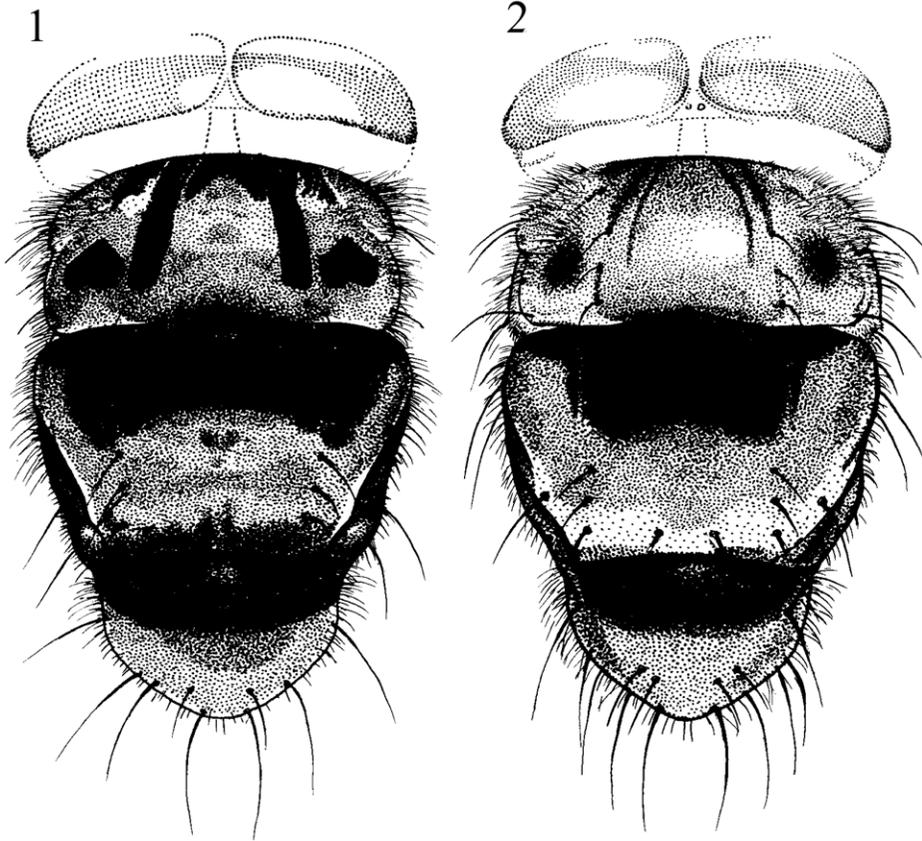
BRAZIL, Campinas – SP, 1♂ ('2781') 1♀ ('2874') February 1979 (A.X. Linhares) (KR). COLOMBIA, Leticia, 1♂ 1♀ 7 August 1978 (G. Wilder) (female dissected by K.R. spermathecae in glycerol in vial on pin, ST1-5 and ovipositor on slide G. pr. 400) (KR). PANAMA, El Maranon, 1♂ 2 June 1994 (?leg.) (dissected by K.R.) (KR). PERU, Junin Province, Lab. strain F1 reared in San Ramon, 1000 m, [P1 from Puerto Bermudes, Pasco Province 200 m 26/28 June 1980, UICC No. 90-1] 16♂ 15♀ ecdosed 7 September 1980 (B. Greenberg) (2♂ dissected by K.R., specimens 'C', 'E'; 1♀ dissected by K.R., no slide prepared; 1♀ dissected by K.R., spermathecae in glycerol in vial on pin, ST1-5 and ovipositor on slide G. pr. 399); Junin Province, San Ramon, 1000 m, eusynanthropic, 1♂ 20 June 1980 (fish bait) (dissected by K.R.) (D. Baumgartner & B. Greenberg); Pasco province, Puerto Bermudes, 200 m, eusynanthropic, 2♂ 28 June 1980 (fish bait) (D. Baumgartner & B. Greenberg) (all KR).

Diagnostic features

Head

Female frons vestiture (Figs 3–4)

The female fronto-orbital plate is very dark in its upper half and clothed with black vestiture. A number of orbital setae (named proclinate orbital setae by Rognes 1991: figs 1–3, but directed outwards in both *chloropyga* and *putoria*) are usually present in front of the prevertical seta (named latero-clinate orbital seta by Rognes 1991: figs 1–3).



Figs 1–2. Head and thorax, dorsal view. 1, *Chrysomya chloropyga*; 2, *C. putoria*.

In *chloropyga* the ground vestiture is rather long, dense and erect, and there is usually one rather inconspicuous orbital seta on each side (rarely 0 or 2) (Fig. 3). In *putoria* the ground vestiture is more sparse, shorter and decumbent, and the usual number of orbital setae is 2 on each side (sometimes 1 or 3, often asymmetrically developed) (Fig. 4). These setae are stronger than those in *chloropyga*.

Both van Emden (1959: 189, figs 3–4, reproduced here) and Paterson (1967: 116) noted these distinguishing features. van Emden described 'the black hairs on the upper half of the parafacialia being dense, erect and longer in *chloropyga*'. He also wrote that the orbital setae in *chloropyga* were reduced in number so that 'as a rule only one is present' and 'very inconspicuous'. Paterson elaborated upon the second point: 'In *putoria* females there are 2–3 relatively strong orbitals, whereas in *chloropyga* females there is rarely more than 1.'

Female frons width at vertex

The female frons is slightly broader in *chloropyga* than in *putoria*. The ratio of the frons width at vertex/head width in *chloropyga* has a range of 0.32–0.37 (mean = 0.34, $n = 15$), whereas this ratio in *putoria* has a range of 0.27–0.33 (mean = 0.29, $n = 31$). Surprisingly, there is very little overlap.

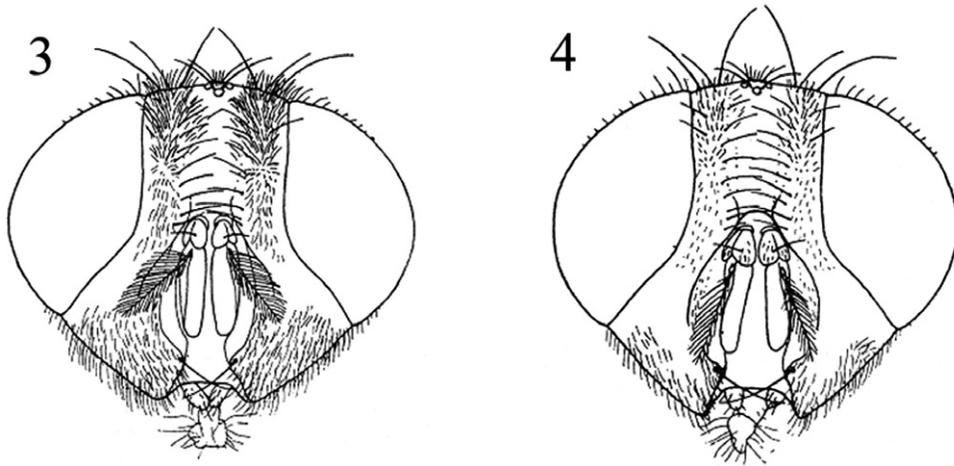
Thorax

Pattern of presutural part of dorsum (Figs 1–2)

The following descriptions apply when the thorax is viewed from behind at a rather low angle, and with light falling on to the mesonotum anterolaterally and obliquely from above both from the left- and the right-hand side. Emphasis is placed on the pattern of white dusting.

Immediately in front of the suture there is present in both *chloropyga* and *putoria* a rather thick transverse band of white dusting across the whole mesonotum.

In *chloropyga* there is present in addition to this



Figs 3–4. Head, anterior view, female. **3,** *Chrysomya chloropyga* (Deelfontein, South Africa) (width of head 3.4 mm); **4,** *C. putoria* (Maun, Botswana) (width of head 2.6 mm). (After van Emden 1959, with permission.)

band a rather broad and strongly white-dusted vitta that extends very far forwards along the midline, almost to the front end of the mesonotum where it ends in a blunt point. Its lateral edge is situated well inside of the imaginary line through the bases of the dorsocentral setae.

In *putoria* a similarly situated but rather more thinly white-dusted vitta does not proceed more than halfway toward the front end of the mesonotum, sometimes even not that far, and in some specimens is lacking altogether. When present it does not end anteriorly in a point, but is more truncated. It is broader than in *chloropyga*, reaching laterally to the row of dorsocentral setae. Often its front end is difficult to discern. Sometimes, as shown in Fig. 2, the vitta stands out less clearly against the area around it when this is relatively light.

On each side of this white-dusted vitta there is present in *chloropyga* a dark pattern shaped as the letter 'L', composed of a dark vitta and a large lateral transverse hind spot, the latter somewhat enlarged in its lateralmost part. The transverse parts of the two 'L's are delimited posteriorly by the transverse band of white dusting that forms the continuous white-dusted band across the mesonotum just in front of the suture. The transverse part of each 'L' is delimited anteriorly by strongly white-dusted areas. The longitudinal part of the 'L' separates these white-dusted areas from the median white-dusted broad vitta along the midline. The *prs dc* seta in *chloropyga* is situated at the hind edge of the 'L' just at the posterior end

of an imaginary line drawn backwards along the lateral edge of the longitudinal part of the 'L'.

In *putoria* no such L-shaped pattern is present, although smaller lateral dark spots are present in addition to a pair of dark thin lines inside of them.

The pattern in *chloropyga* was described accurately by Wiedemann (1818, 1830), and e.g. Malloch (1925). Curran (1928: 369, in key) described it as the presence in front of the suture of a 'roughly L-shaped dull black spot on either side'. Paterson (1967: 114) gave an elaborate analysis of it in both species, including its mode of inheritance, with emphasis on the dark parts of the pattern.

The illustration of *chloropyga* (Fig. 1) shows a thin pale line between the transverse and longitudinal sections of the 'L'. This is only visible under certain angles of view and direction of lighting.

Pattern on postsutural part of dorsum

In *chloropyga* there is a broad, dark and rather well-defined area behind the suture across the anterior half of the postsutural part of the dorsum. It has three backwardly directed and rather well-delimited projections. The two lateral ones end a little in front of the midpoint of an imaginary line drawn between the hindmost dorsocentral seta and the hindmost (and only) intra-alar seta. The middle projection ends a little in front of the only (and hindmost) pair of postsutural acrostichal setae. Behind the dark area the dorsum is strongly dusted with white.

In *putoria* this pattern is less distinct with obscurely defined projections, and the area

behind it is much less conspicuously dusted.

Length of ground vestiture on dorsum

The clothing hairs of the mesonotum in the male *chloropyga* are very long, soft and dense as compared with *putoria*, as already noted by Paterson (1967: 116). This also applies to females.

Number and strength of dorsocentral setae

In *C. chloropyga* the *prs dc* setae are difficult to make out against the high and rather dense ground vestiture, and are hardly longer than the ground hairs. One can almost always find a single *prs dc* seta just behind the transverse part of the 'L' in line with the lateral edge of the longitudinal part of the 'L'. Occasionally there is an additional one farther forwards, often asymmetrically developed.

In *chloropyga* there are usually also three *post dc* (occasionally only the two hindmost *post dc*, or the full number of four *post dc* is present, the latter pattern resembling that in *putoria*). The anteriormost one of these is very weak and situated at the middle of the postsutural part of the mesonotum, thus far behind the position of the anteriormost *post dc* seta in *putoria*. The setae are weaker than in *putoria*.

C. putoria has 2–3 *prs dc* and 4–5 *post dc* setae in both sexes, all of them strong and conspicuous, standing out clearly against, and about twice as long, as the ground vestiture. The middle *prs dc* seta (when their number is 3), is often weaker than the two others. The first *post dc* is usually smaller than the others and situated somewhat isolated from the other 3–4 *post dc* setae, but well in front of the middle of the postsutural part of the mesonotum.

Both Curran (1928: 369) and Paterson (1967: 116) noted differences between the species in the number of dorsocentral setae. Curran gave a number of 'one anterior dorsocentral' seta in *chloropyga*, whereas *putoria* was keyed out as having 'two or three' such setae. Paterson gave the corresponding numbers as 1–2 *prs dc* and 2–3 *post dc* (*chloropyga*) and 2–3 *prs dc* and 4–5 *post dc* (*putoria*). He also remarked that these setae were much stronger in *putoria* than in *chloropyga*.

Abdomen

T4 and T5 colour

The most striking difference between the two species is the colour of the last two visible abdomi-

nal tergites T4 and T5. Whereas T1–2, T3, T4 and T5 in *putoria* and T1–2, and T3 in *chloropyga* are of 'normal' blowfly type bluish-green metallic colour, T4 and T5 in *chloropyga* are bright brassy green and contrast very strikingly with the colour of the preceding tergites. Hence the name (*chloro* = green; *pyga* = tail).

T3

In *chloropyga* the T3 in both the male and the female has a dark transverse marginal band about one-third as long as tergite laterally, broadening (i.e. lengthening) medially to about halfway and continuing forwards along midline as broad dark conspicuous vitta. The area in front of the dark transverse band is strongly dusted white. In *putoria* the T3 band in both male and female is about a quarter [Zumpt's material: almost a third] as long as the tergite both laterally and medially, in rare cases a very narrow vitta is reaching the front edge of the tergite, sometimes only indicated as a forwardly directed point, but usually not indicated at all. There is weak or no dusting at all in front of the marginal band.

T4

In *chloropyga* the marginal dark band of the abdominal tergite T4 is narrow, one-fifth to one-sixth of the tergite length. In *putoria* the band is broader, about a quarter of the tergite length.

Male T4 ground vestiture

In males of both *chloropyga* and *putoria*, the vestiture on the dorsal part of T4 is erect, in contrast to the condition in the females. In *chloropyga* the vestiture is definitely longer and denser than in *putoria*.

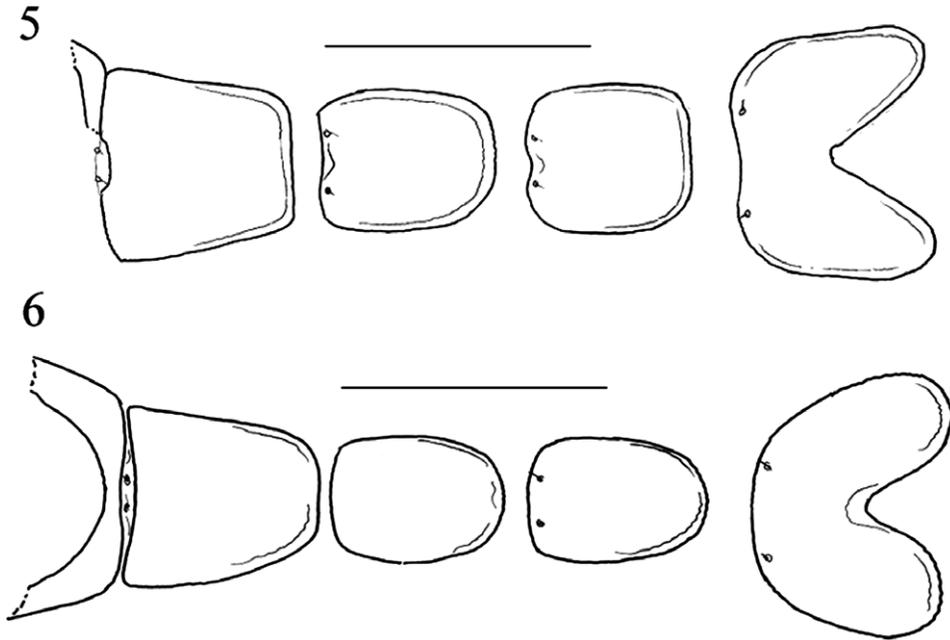
Male ST5 (Figs 5–6)

The ST5 in *chloropyga* is broader proximally than in *putoria*. This is also evident in the figures provided by Paterson (1967: 117, fig. 3-3e (*chloropyga*), fig. 3-3f (*putoria*)).

Male genitalia

Cerci (Figs 7–10)

The differences in the cerci are most readily appreciated in the profile view of the undisturbed (as opposed to flattened) epandrium, cerci and surstyli complex (Figs 7–8). Important landmarks are indicated by small, labelled arrows in the



Figs 5–6. ST1–5, male. **5**, *Chrysomya chloropyga* (Addis Abeba, Ethiopia, v.–vi.1989, S. Mazin leg., ZMUM); **6**, *C. putoria* (Limuru, Kenya, KR – specimen ‘F’). Scale bars = 1 mm.

figures. In *chloropyga* (Fig. 7) the horizontal part of the cerci (distance a–b) is about as long as the oblique hind part bordering the anal membrane (distance b–c). In *putoria* (Fig. 8) the horizontal part (distance a–b) is much shorter than the oblique part (distance b–c).

This feature is also evident in Paterson’s figures (Paterson 1967: 117, fig. 3-3 a (*chloropyga*) and fig. 3-3b (*putoria*)).

A second distinguishing feature of the cerci concerns the oblique line proceeding backwards and downwards from the tip of the cerci. In *chloropyga* (Fig. 7) this line is bent, and proceeds at first backwards, paralleling for a distance the dorsal surface, then it bends downwards in its ventralmost half. In *putoria* this line is straight, proceeding directly downwards and backwards in an angle of about 45 degrees with the dorsal edge in profile view. In its course it parallels the hind edge of the cerci (line between points pointed at by the arrows b and c). This feature is evident in Séguy’s figures (Séguy 1928; compare his fig. 26 (*chloropyga*) with his fig. 32 (*putoria*)).

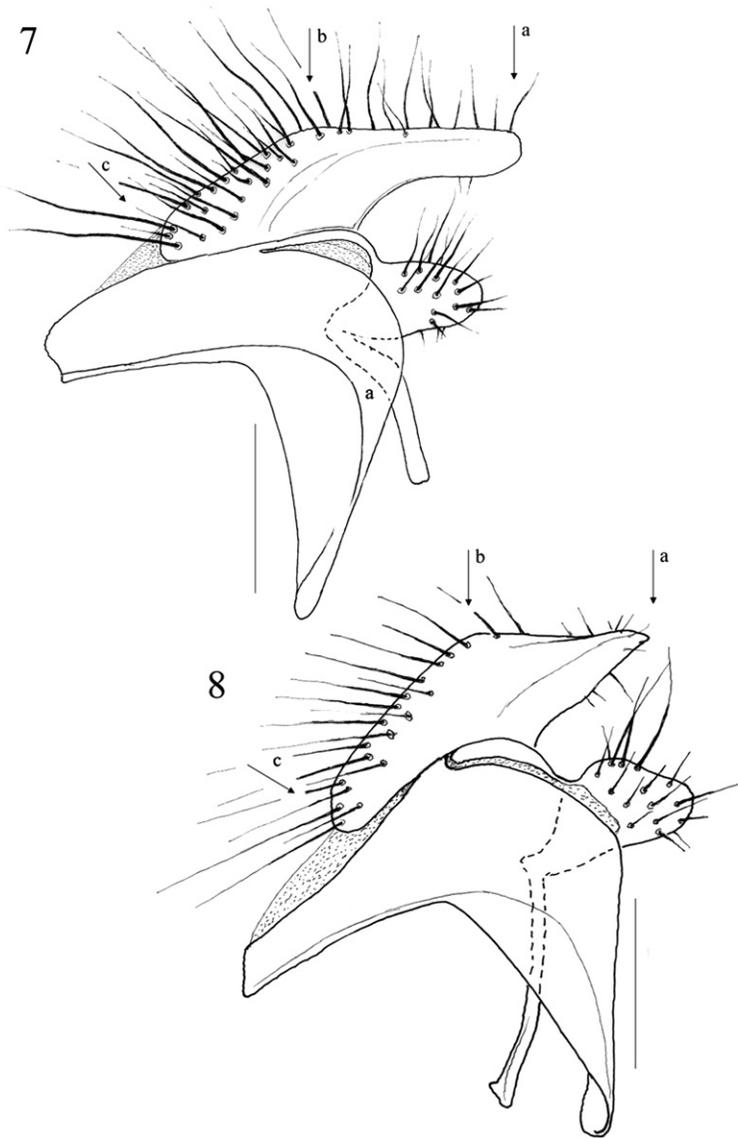
Surstyli, basal part (Figs 9–10)

The posterior part of the surstylus projects backwards as a small strap of sclerotization that

wedges itself in between the epandrium and the lateral part of the cercus. In *chloropyga* it is relatively short and broadly triangular, whereas in *putoria* it is longer and resembles a narrow almost parallel-sided band. Interestingly, these differences are also evident in the figures which Zumpt (1972) offered to argue the ‘great similarity of the hypopygia of these forms’. In his figs 1 and 4 (both ‘f. *typica*’ from Johannesburg) the hind part of the surstylus is similar to the one shown in Fig. 9 in the present paper, and in his figs 2 (‘f. *putoria*’ from Johannesburg) and 3 (‘f. *taeniata*’ from Nairobi) the corresponding part of the surstylus is long and band-shaped with almost parallel sides, just as shown in Fig. 10 of the present paper.

Aedeagus, dorsal view (Figs 11–12)

Length of flaps (‘harpes’ in Paterson’s terminology). In *chloropyga* the length of flaps, as defined by distance from base of paraphallic process to tip of flap (distance c–e), is greater than the distance from base of distiphallus to base of paraphallic process (distance a–c). In *putoria* the length of the flap (c–e) is clearly shorter than the a–c distance. The different sizes of the flaps were pointed out by Paterson (1967: 118, figs 3–4c, 3–4d (both *chloropyga*) and 3–4a, 3–4b (both *putoria*)). Interestingly,

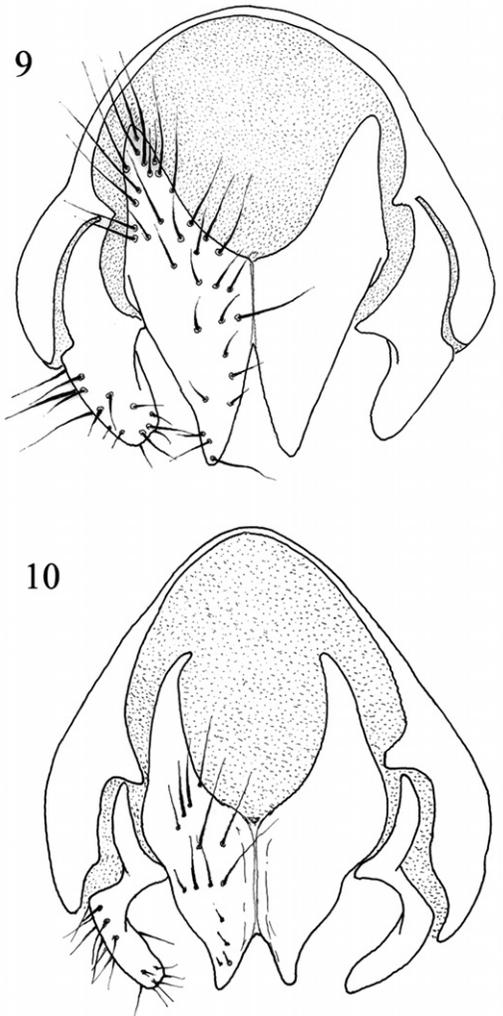


Figs 7–8. Epandrium, cerci, surstyli and bacilliform sclerite, profile view (arrows, see text). **7.** *Chrysomya chloropyga* (Addis Abeba, Ethiopia, v.–vi.1989, S. Mazin leg., ZMUM); **8.** *C. putoria* (Limuru, Kenya, KR – specimen 'F'). Scale bars = 0.2 mm.

this difference is also evident in the figures which Zumpt (1972) offered to argue the 'great similarity of the hypopygia of these forms'. In his figs 1–3, the point corresponding to point 'c' in Figs 11–12 is easy to establish. It is found just where the outer border of the solid black area joins the outer edge of the stippled area in the middle of the aedeagus. In his fig. 1 ('f. *typica*' from Johannesburg) this point is closer to the base of the

distiphallus (which corresponds to a long flap), whereas in his figs 2 ('f. *putoria*' from Johannesburg) and 3 ('f. *taeniata*' from Nairobi) the point is much closer to the tip of the flap (corresponding to short flaps).

Position of flaps. In *chloropyga* the flaps are orientated more vertically and in dorsal view the dorsalmost edge is visible in the middle of the rest of the flap seen as a background immediately



Figs 9–10. Epandrium, cerci, surstyli and bacilliform sclerite, dorsal view. **9**, *Chrysomya chloropyga* (Addis Abeba, Ethiopia, v.–vi.1989, S. Mazin leg., ZMUM); **10**, *C. putoria* (Limuru, Kenya, KR – specimen 'F'). Scale bars = 0.2 mm.

below it. The middle part is somewhat angular so that the distalmost parts proceed more or less parallel with the longitudinal axis of the distiphallus or even converge towards it at their apices (Fig. 11). In *putoria* the flaps are inclining obliquely inwards, forwards and downwards, so that the dorsalmost edge is the one that is seen closest to the midline and closest to the acrophallus (Fig. 12). Furthermore, the flaps are not angled in the middle so that the distalmost parts proceed obliquely outward more or less evenly from the

longitudinal axis of the distiphallus.

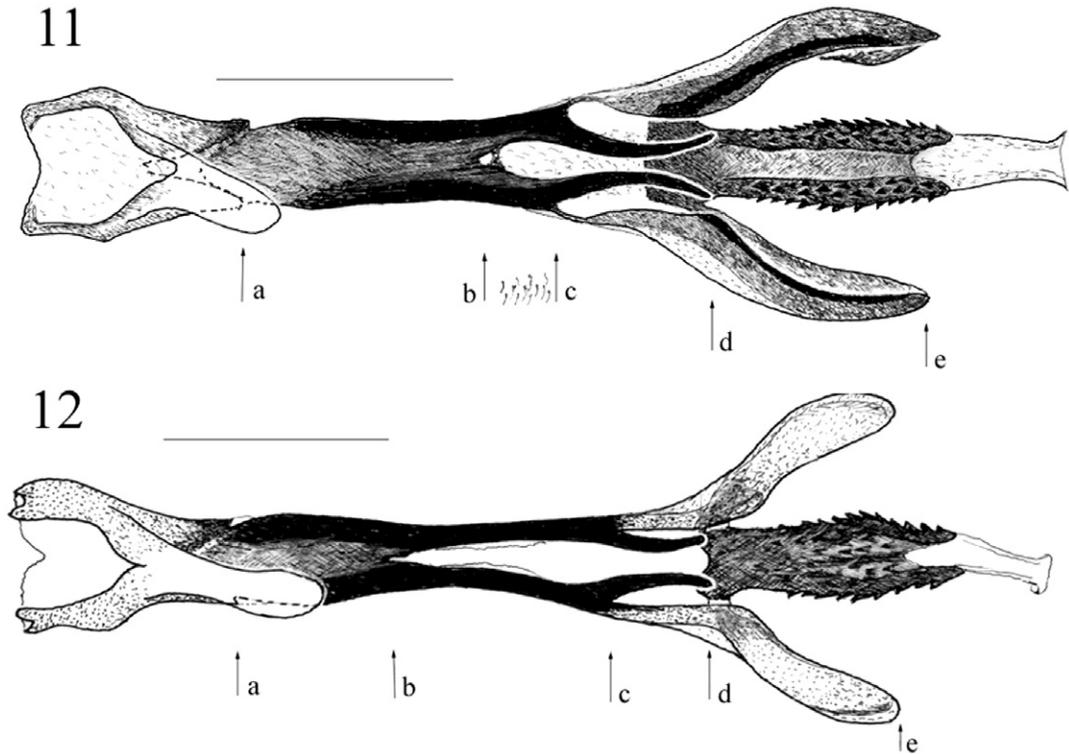
Depth of 'bay' of unsclerotized cuticle mid-dorsally and proximal to bases of paraphallic processes. In general the bay in *chloropyga* is very shallow (distance b–c) and much shorter than the part of the mid-dorsal wall of the distiphallus that is completely sclerotized (distance a–b). In *putoria* the bay is very long (distance b–c), much longer than the well-sclerotized part of the mid-dorsal wall (distance a–b). Sometimes the bay is very narrow, but never closed as in *chloropyga*. The short bay in *chloropyga* and the long bay in *putoria* are also evident in the figures given by Zumpt (1972) in spite of his intention to demonstrate the 'great similarity of the hypopygia' (cf. above). The shallow bay is also evident in the figure of the *chloropyga* aedeagus in dorsal view made by Prins (1979: 43, fig. 2C).

Length of paraphallic processes. In *chloropyga* the paraphallic processes, as defined by the distance c–d, are at least as long as the bay (b–c). They also overlap considerably the base of the sclerotized part of the acrophallus below it. In *putoria* the paraphallic processes are relatively short both compared to the whole length of the aedeagus, as well as to the length of the bay (b–c). They neither overlap the base of the strong sclerotizations at the base of the acrophallus to the same extent as in *chloropyga*. The same are also evident in the figures given by Zumpt (1972) in spite of his intention to demonstrate the 'great similarity of the hypopygia' (cf. above).

The same facts relating to the morphology of the aedeagus in dorsal view are evident in all examined Zumpt slides with a quality that permits a decision.

Aedeagus, lateral view (Figs 13–14)

Shape of flaps. The flaps in *chloropyga* are much larger than in *putoria*, and differently shaped. In *chloropyga* they are more or less oval, the dorsal edge straight or slight concave (concavity upwards), and the ventral edge well rounded. Also, the area of attachment of the flaps to the distiphallus is about half as high as the maximum height of the flaps. In *putoria* the flaps are elongate and more or less rectangular. The upper edge is slightly rounded, with convexity upwards, and the ventral edge hollowed out from below so that the concavity is facing downwards. The area of attachment to the distiphallus is about as high or only slightly less high than the flaps themselves. The different



Figs 11–12. Aedeagus, dorsal view (arrows, see text). **11,** *Chrysomya chloropyga* (Addis Abeba, Ethiopia, v.–vi. 1989, S. Mazin leg., ZMUM); **12,** *C. putoria* (Wiedemann) (Limuru, Kenya, KR – specimen 'F'). Scale bars = 0.2 mm.

shapes of the flaps were clearly demonstrated by Paterson (1967: 118, figs 3–4c, 3–4d (both *chloropyga*) and 3–4a, 3–4b (both *putoria*)).

Length of ventral plates. In *chloropyga* the ventral plates are relatively short compared to those in *putoria* (compare distance f–g with distance g–h in both species).

Vestiture on mid-ventral surface. The usual condition (in four of six males dissected by K.R., and in 14 of the 15 Zumpt slides examined) is for *chloropyga* to have a dense cover of very small hairs over the entire ventral surface of the distiphallus from the apex of the basiphallus to the basis of the acrophallus, thus also covering the unsclerotized membrane proximally and distally, whereas the usual condition for *putoria* is to lack such hairs altogether.

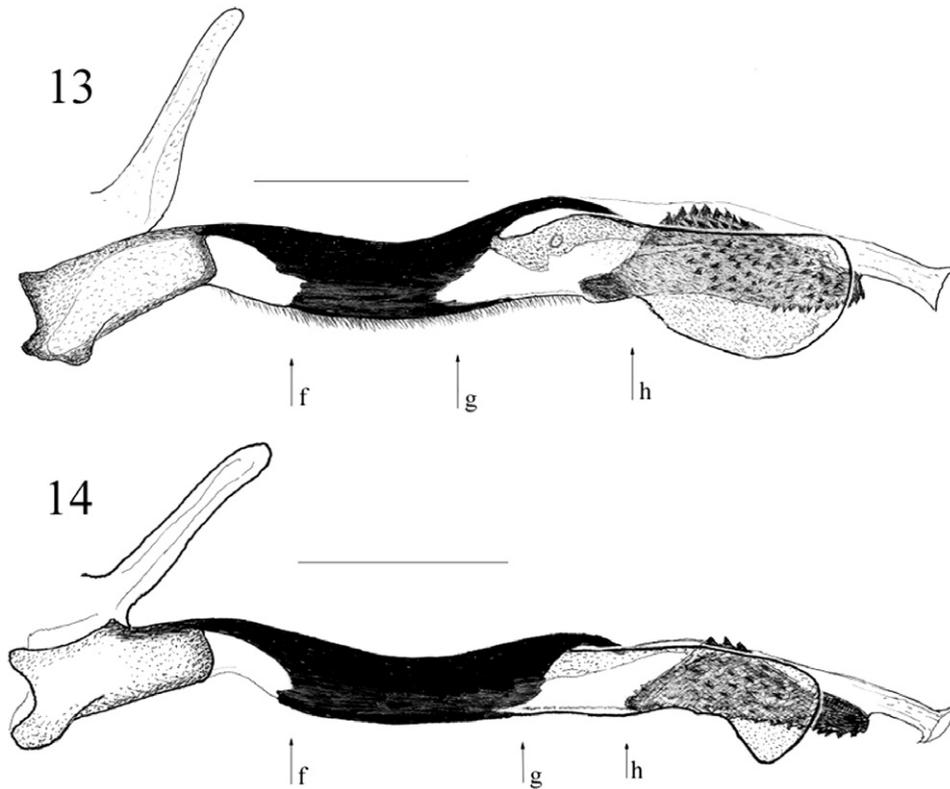
However, there are exceptions to this description. In a male *chloropyga* (labelled 'G') from Malgas, Western Cape Province (ZML), very few (7–8) hairs were present and only mid-ventrally in the area below the ventral plates, not on the unsclerotized membrane in front and behind. In

a male from Mamathes (Lesotho) (labelled 'H') (ZML) the conditions are opposite: hairs are present mid-ventrally on the unsclerotized membranes but not in the area just below the ventral plates.

Among the 15 Zumpt slides of *chloropyga* (NMSA) the hairs were present and easily inspected in 14 slides, in the last slide hairs were possibly present below the ventral plate, but this could not be confirmed because of the bad quality of the slide (hairs were absent from ventral membrane in front of basiphallus).

We have not seen *chloropyga* where these hairs are altogether absent.

In *putoria* there were three exceptions among the 13 specimens dissected by K.R. In a male (labelled 'B') from Limuru, Kenya (same locality as the one figured) (KR) there were some small hairs present mid-ventrally in two different areas: 3–5 very tiny hairs on the unsclerotized membrane distal to the area just below the ventral plate and about 13 small hairs in proximal half of the area below the ventral plates. In a male from Drumnadochit



Figs 13–14. Aedeagus, profile view (arrows, see text). **13**, *Chrysomya chloropyga* (Addis Abeba, Ethiopia, v.–vi. 1989, S. Mazin leg., ZMUM); **14**, *C. putoria* (Limuru, Kenya, KR – specimen 'F'). Scale bars = 0.2 mm.

Farm, KwaZulu-Natal, South Africa (labelled 'D') (KR), a dense covering of hairs is present in the hind half of the mid-ventral area that is usually covered completely with hairs in *chloropyga*. The third exception was found in a specimen from Peru (among the reared series from Junin, specimen 'C') (KR) where a few hairs were visible mid-ventrally in the hind third of the area just below the ventral plate. In all the cases the aedeagi were typical of *putoria* in other characteristics.

Among the 23 Zumpt slides of *putoria* genitalia (NMSA) there were some small hairs on the ventral membrane at the proximal end of the distiphallus in three of twenty-three slides: in a specimen from South Africa (Gauteng, Onderstepoort), and in two from the Democratic Republic of Congo (Bulo/Nele; hairs somewhat more widely distributed in the specimen from Rumangabo).

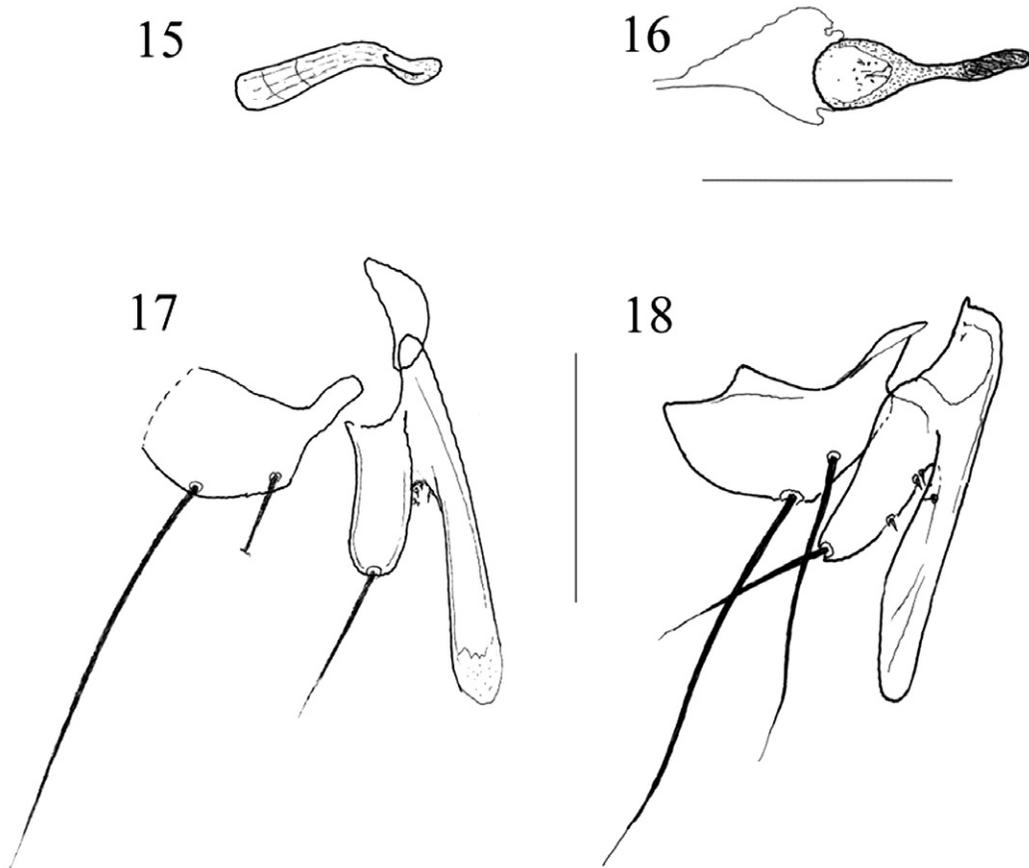
Surprisingly, the dense vestiture along the midline of the ventral surface of the distiphallus of

chloropyga has been overlooked by all previous authors (Séguy 1928; Paterson 1967; Prins 1979; Zumpt 1956, 1965, 1972) except Patton & Cushing (1934: 129, Fig. 4). Their figure shows the small hairs very clearly.

Female genitalia

Ovipositor (Figs 19–20) and spermathecae

We have found no constant differences between the species in the structure of the ovipositor. In both species the shape of the sclerites, the distribution and shape of the microtrichiae are very similar. However, in the particular specimen of *C. chloropyga* illustrated (Fig. 19) the ovipositor differs from those of other specimens dissected of this species (G. pr. 394, Kenya; G. pr. 395, Ethiopia; G. pr. 401, South Africa) in having more elongate tergites and sternites, especially those on segments 6 and 7. Neither have we found any differences in ovipositor structure between specimens from the Afrotropical and Neotropical



Figs 15–18. 15, 16, Ejaculatory sclerite; 17, 18, Pre- and postgonites; 15, 17, *Chrysomya chloropyga* (Addis Abeba, Ethiopia, v.–vi.1989, S. Mazin leg., ZMUM); 16, 18, *C. putoria* (Limuru, Kenya, KR – specimen ‘F’). Scale bars = 0.2 mm.

Regions. Notable in both species is the lack of microtrichiae on the hypoproct, a feature shared with *C. albiceps* (Wiedemann) and *C. marginalis* (Wiedemann) and to my knowledge not known outside the genus *Chrysomya* (cf. Rognes 2002: 12). Both species have spermathecae of the oval type, i.e. being a little longer than broad.

Breeding habits

Chrysomya chloropyga is a typical carcass breeder (Paterson 1977), also causing myiasis in sheep and cattle. It has also been reported in cases of human myiasis (Cuthbertson 1938; Zumpt 1965; Paterson 1977). *Chrysomya putoria* is ‘a major domestic pest in much of tropical Africa because of its habit of breeding in pit latrines. This habit has never been found in *chloropyga* populations’ (Paterson 1977). It is not ‘dependent on living or dead animal tissues’,

but is occupying a niche similar to that of *C. megacephala*, in breeding ‘around houses in pit latrines and septic tanks, and in animal manure’, only ‘occasionally in carcasses’ and is abundant on waste tips and breeds near houses in the Afrotropical Region (Laurence 1988). *C. putoria* also breeds in poultry dung in South Africa (sources in Baumgartner & Greenberg 1985). In Africa, *C. putoria* comes to ‘a wide variety of baits, including garbage, meat, carrion, fish, decaying fruit, human feces, and, rarely, horse and pig feces’. In Peru, *C. putoria* were attracted to fish and liver, [but only once] visited human feces. This contrasts with observations in Brazil where *C. putoria* represented 12.3 % of total blow flies attracted to human feces’ (Baumgartner & Greenberg (1984, 1985). *C. putoria* is eusynanthropic in Peru (Baumgartner & Greenberg 1985).

19

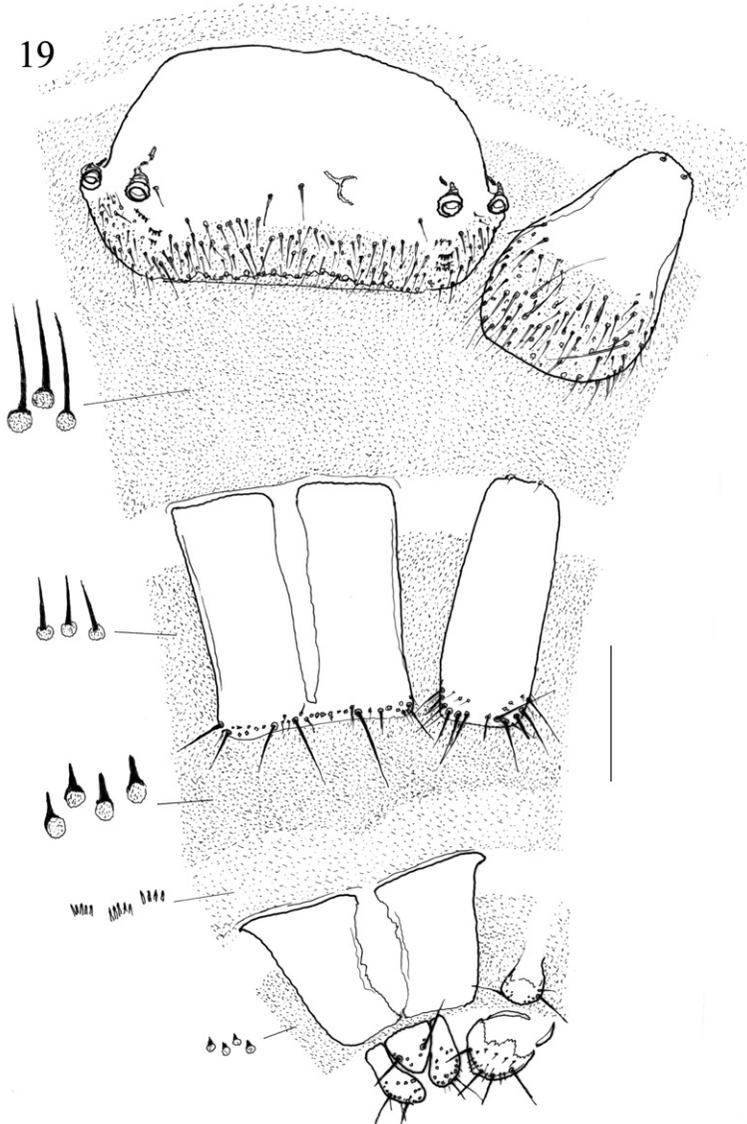


Fig. 19. Ovipositor (G. pr. 398). *Chrysomya chloropyga* (Graaff-Reinet, Eastern Cape, South Africa, September 2001, C. Simon leg., KR). Insets: shape of microtrichiae in indicated regions, enlarged. Note: a number of pale marginal setae on T6 and ST6 were lost during preparation of slide. Scale bar = 0.5 mm.

'Intermediate specimens' of Zumpt

Zumpt (1956: 189) described *chloropyga* (as the 'typical form') as being 'mainly dark blue'. On the next page he described *putoria* as '[A] green form mostly listed as a distinct species'. After stating that the genitalia of *putoria* 'were identical with those of *chloropyga* s. str.' he said he had 'also seen specimens which are transitional with respect to colouring'. Paterson (1967: 118) examined with

great care the features of a male from Amani (Tanzania) identified by Zumpt as 'intermediate between *chloropyga* and *putoria*'. Paterson concluded that it was an ordinary *putoria*, but rather more bluish than usual. One of us (K.R.) has been able to examine a female from the same locality and labelled by Zumpt as 'F. typ → *putoria*', thus evidently considered by him to be intermediate between these forms. It is also a *putoria* with a more

20

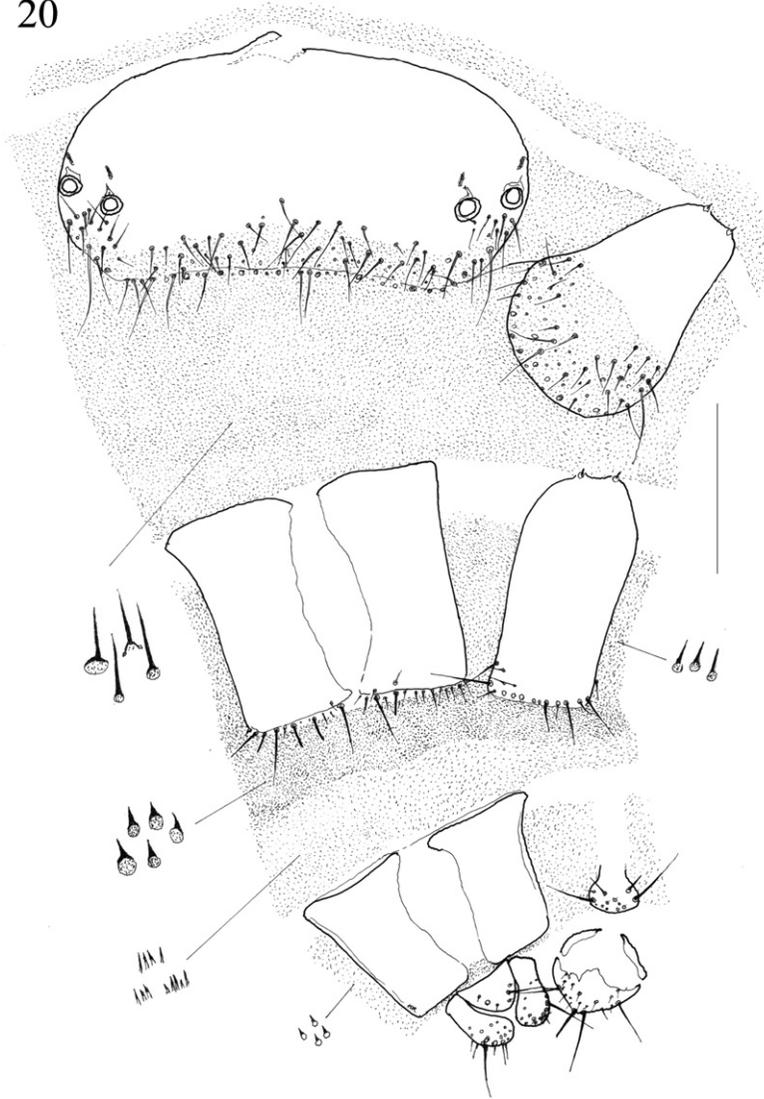


Fig. 20. Ovipositor (G. pr. 397). *Chrysomya putoria* (Snake Island, Botswana, January 2001, N. Lunt leg., KR). Insets: shape of microtrichiae in indicated regions, enlarged. Note: a number of pale marginal setae on T6 and ST6 were lost during preparation of slide. Scale bar = 0.5 mm.

bluish colour than usual, lacking, as expected, the usual pattern of the presutural part of the thorax of *chloropyga*. Particularly noteworthy is the short forward extension of the medial white-dusted vitta, which does not reach more than halfway towards the front end of the thorax, exactly as in most *putoria* specimens, and very different from the *chloropyga* pattern. As to the bluish colour, in our experience this is a common feature among green metallic blowflies (e.g. of *Lucilia* species), most

likely due to some factor related to the age of the specimen. It should serve as a warning that several authors in the past (e.g. Robineau-Desvoidy) have described the same species over and over again on the basis of slight differences in the hue of the metallic colour varying between bright green and blue. The Amani specimen seen by KR most likely derives from a laboratory stock started 18 April 1961 from larvae collected in a pit latrine (Paterson 1967: 124) and not wild-caught specimens.

Distribution

The distribution below is based on specimens examined for this paper and Paterson (1967).

Chrysomya chloropyga

From South Africa northwest to Cameroon and Fernando Po, in the northeast to the highlands in Ethiopia. Also St Helena.

Palaeartic Region

The occurrence of *Chrysomya chloropyga* on the Canary Islands, reported by Hanski (1977) and Baez *et al.* (1981) could not be confirmed. Neither Baez nor Hanski could retrieve any of the specimens on which their records were based (both pers. comm.) so we were unable to decide which species they had before them. We believe it most likely that their reports in fact concern *C. putoria* in view of the recent immigration of this species into the Neotropical Region.

Afrotropical Region

Botswana [Bechuanaland], Cameroon, Democratic Republic of Congo [Zaire], Equatorial Guinea (Macias Nguema) [Fernando Po], Ethiopia, Kenya, Lesotho, Namibia [South West Africa], St Helena, South Africa, Tanzania, Zambia, Zimbabwe.

Chrysomya putoria

All over Africa south of the Sahara, including West Africa. Northwest to Senegal and Gambia, northeast to Sudan, Eritrea and Ethiopia, south to South Africa. Neotropical Region. Probably also on the Canary Islands (not confirmed) in the Palaeartic Region.

Afrotropical Region

Botswana [Bechuanaland], Cameroon, Democratic Republic of Congo [Zaire], Eritrea, Ethiopia, Gambia, Ghana, Kenya, Liberia, Madagascar, Mauritius, Mozambique, Nigeria, Réunion, Senegal, Seychelles, Sierra Leone, South Africa, Sudan, Swaziland, Tanzania, Uganda (f. *taeniata*), Zambia, Zimbabwe.

Neotropical Region

Brazil, Colombia, Panama, Peru.

On 'forma *taeniata* (Bigot)' sensu Zumpt 1956

We have found specimens that fit this 'form' in three collections (NMSA, ZML, BMNH).

Zumpt's collection (NMSA)

In the part of Zumpt's collection one of us (K.R.) has recently studied, there were seven males and five females carrying undated labels in Zumpt's handwriting identifying them as belonging to the 'f. *taeniata* (Bigot)' of Zumpt (1956), i.e. having a darkened fore margin to the wing. The specimens differ from ordinary *putoria* in none of features discussed above. Neither have we been able to spot any differences in the genitalia from *putoria* on the basis of the well preserved genitalia slides no. 15 (Kenya), and nos. 24 and 58 (both Cameroon) in Zumpt's collection. All of this material has been included among the material of *putoria* listed above, though marked with an asterisk (*).

The darkening varies considerably among these specimens. Three females from Yaoundé, Cameroon (leg. Rageau), have a distinctly darkened fore margin (the darkest among the *taeniata* specimens). The darkening, which is brown, affects all the cells immediately behind the costa and in front of R_{2+3} , including the base of the wing such that both basal cells are darkened (inside of the *bm-cu* and *CuA₂* cross-veins) and also a part of the cell which is proximal to the *r-m* crossvein, namely the part that lies basad of the node at the base of the vein R_{4+5} . The area just behind the stem vein is almost hyaline in contrast. The darkening also extends behind almost the whole of the R_{2+3} vein so that an area two to three times the width of that vein is darkened, the darkening reaching out to the tip of that vein. The remainder of the wing is hyaline, and the boundary between the dark and hyaline parts is very distinct.

Two females from Ghana (L.R. Cole leg.) are similar but the darkening is slightly less pronounced.

In the male from Uganda (Spangler leg.) the outer half of the cell between R_1 and R_{2+3} is almost hyaline so that the margin is dark only to the tip of R_1 .

Two males from Tanzania are very much less darkened along the costa, only pale brownish, but similar to the female from Yaoundé regarding the extent of the darkening.

Two males from Cameroon (Bombe and a locality 2 mi NW Mbouda; slides 24 and 58, respectively) are also rather pale along the fore margin of wing, although the darkening is not in doubt.

Two males from Ghana are almost as dark as the Yaoundé females, but with almost hyaline spots

here and there.

A male from Yaoundé (Cameroon) (Ross and Lorenzen leg.) (dissected by Zumpt, slide 26) have been identified by Zumpt in 1972 (according to labels both on slide and specimen) as belonging to the '*Chrysomya chloropyga* Wd.'. The fore margin of the wing is very inconspicuously but definitely darkened. It is not sure that this has been noted by Zumpt, and this may be the reason that he did not label it '*f. taeniata*'. Whatever the case, at this date Zumpt had decided to lump all forms into the category named *chloropyga*, and may not have bothered to identify it as the particular form '*taeniata*'.

Collection in the Museum of Zoology, Lund (ZML)

In the Lund collection examined there is one male from Sierra Leone (Freetown, Fourah Bay college, 24 November 1993) which has a very faint darkening along the forewing margin, the hind border of which is lying a little behind the vein R_{2+3} and reaching as far outwards as that vein. Similarly, a female from the same area (Sierra Leone, Freetown Cape Sierra Hotel area, 19 November 1993) has the same feature, even more pronounced. In the three other specimens from Sierra Leone the wings are hyaline (a fourth has immature wings).

Six males and four females from Ghana (Ashanti Region, Kyase, 17 June 1965) have a slight darkening along the fore margin of the wing. It usually reaches the tip of R_{2+3} , in a few specimens the darkening does not reach beyond the tip of R_1 .

In all other specimens of *putoria* the wings are hyaline except for these areas: (1) the area behind the costa from wing base to a little beyond humeral crossvein, (2) a small spot distal to the tip of Sc , and (3) an area encompassing the inner third of the cell inside of the *r-m* crossvein, and the cell inside *bm-cu* crossvein.

Zumpt (1956: 190) also found that the '*taeniata*' form was 'very often mixed with typical *putoria* in the same population.'

Collection in the Natural History Museum, London (BMNH)

A male from Seychelles (Plateau la Passe) has a slightly infuscated fore margin to the wing reaching the tip of R_{2+3} . A female carrying an identical label (thus possibly captured at the same time) has no such darkening. The male also has an

outer vertical seta on each side, a very unusual feature.

Conclusion

We maintain, as far as we know at present, that the darkening only occurs in specimens from a belt across the central tropical part of Africa: Sierra Leone, Ghana, Cameroon, Democratic Republic of Congo [material of '*taeniata*' reported by Zumpt 1956], Uganda, Tanzania, Seychelles. Zumpt's conclusion is similar.

Because of the varying development of the darkening (including its absence) among specimens from some of these countries (Democratic Republic of Congo, Sierra Leone, Seychelles, Tanzania) the feature may have no taxonomic value. We prefer at present to emphasize the characters shared with ordinary *C. putoria* rather than the variable wing infuscation and consider all the specimens belonging to the taxon *C. putoria*.

Interrelationship of *C. chloropyga* and *C. putoria*

Wells *et al.* (2004) recently suggested that *C. putoria* evolved very recently from *C. chloropyga*. They based this on a study of mitochondrial DNA (mtDNA) sequence data from a 593-bp region of the gene for cytochrome oxidase subunit one (COI). A maximum parsimony analysis 'indicated paraphyletic *C. chloropyga* mtDNA with *C. putoria* nested therein.' Of the five haplotypes found, none were unique to *C. putoria*.

This conclusion may find support from some morphological features also. Several chrysomyines, e.g. *Phormia regina*, *Chrysomya cabrerari* Kurahashi & Salazar, *C. chani* Kurahashi, *C. greenbergi* Wells & Kurahashi, *C. megacephala* (Fabricius), *C. pacifica* Kurahashi, *C. phaonis* (Séguy), *C. pinguis* (Walker) (Thomas 1951; Kurahashi & Salazar 1977; Kurahashi 1979, 1991; Wells & Kurahashi 1996) have an aedeagus covered with small hairs along the ventral surface, like those present in *C. chloropyga*. This may be a primitive feature within the genus, and the lack of the hairs in the aedeagus of *C. putoria* (and others) apomorphic.

However, the pattern of the presutural part of the thorax suggests that the *chloropyga* pattern is derived from the pattern in *putoria* and therefore that the latter is the primitive species. The *putoria* pattern is present also in *chloropyga* but in the latter it is underlying the *chloropyga* pattern. This is discussed in more detail by Paterson (1967). We

suggest a resolution of the matter must await a reliable cladistic analysis of the whole genus based on a much higher number of features.

ACKNOWLEDGEMENTS

We would like to thank the following colleagues and friends for loan or gift of material, provision of reprints and manuscripts, and help in numerous other ways: M. Baez (Universidad de La Laguna, Tenerife, Spain), D. Barraclough and C. Conway (Natal Museum, Pietermaritzburg, South Africa), R. Contreras-Liechtenberg (Naturhistorisches Museum, Vienna, Austria), R. Danielsson (Zoological Museum, Lund, Sweden), B. Greenberg

(University of Illinois at Chicago, Chicago, U.S.A.), I. Hanski (Zoological Museum, Helsinki, Finland), R. Meier and L. Wilhelmson (Zoological Museum, Copenhagen, Denmark), A.L. Ozerov (Moscow Lomonosov State University, Moscow, Russia), W. Reeves (Clemson University, Clemson, South Carolina, U.S.A.), R. Tungland (Stavanger, Norway), N. Lunt and M. Villet (Rhodes University, Grahamstown, South Africa), J. Wells (West Virginia University, West Virginia, U.S.A.) and N. Wyatt (Natural History Museum, London, United Kingdom). Special thanks go to J. Marsden, Linnaean Society, London, for permission to reproduce Figs 3 and 4, and to the University of Stavanger for covering publication costs.

REFERENCES

- BAEZ, M., ORTEGA, G. & KURAHASHI, H. 1981. Immigration of the Oriental latrine fly, *Chrysomya megacephala* (Fabricius) and the Afrotropical filth fly, *Ch. chloropyga* (Wiedemann), into the Canary Islands (Diptera, Calliphoridae). *Kontyû, Tokyo* **49**: 712–714.
- BAUMGARTNER, D.L. & GREENBERG, B. 1984. The genus *Chrysomya* (Diptera: Calliphoridae) in the New World. *Journal of Medical Entomology* **21**: 105–113.
- BAUMGARTNER, D.L. & GREENBERG, B. 1985. Distribution and medical ecology of the blow flies (Diptera: Calliphoridae) of Peru. *Annals of the Entomological Society of America* **78**: 565–587.
- BIGOT, J.M.F. 1877. Diptères nouveaux ou peu connus. 7^e partie. IX. Genre *Somomyia* (Rondani) *Lucilia* (Rob.-Desv.) *Calliphora*, *Phormia*, *Chrysomyia* (id.). *Annales de la Société Entomologique de France* (5) **7**: 35–48.
- BOYES, J.W. & SHEWELL, G.E. 1975. Cytotaxonomy of Calliphoridae. *Genetica* **45**: 435–488.
- CURRAN, C.H. 1928. Diptera of the American Museum Congo Expedition. Part II. – Asilidae, Conopidae, Pyrgotidae, Micropezidae, Chloropidae, Drosophilidae, Lonchaeidae, Sapromyzidae, Muscidae, Calliphoridae, and Tachinidae. *Bulletin of the American Museum of Natural History* **57**: 327–399.
- CUTHBERTSON, A. 1938. The breeding habits and economic significance of some common muscoidean flies (Diptera) in Southern Rhodesia. *Proceedings of the Rhodesia Scientific Association* **38**: 53–57.
- DEAR, J.P. 1985. A revision of the New World *Chrysomyini* (Diptera: Calliphoridae). *Revista Brasileira de Zoologia* **3**: 109–169.
- EMDEN, F. VAN 1953. The male genitalia of Diptera and their taxonomic value. *Transactions of the Ninth International Congress of Entomology* **2**: 22–25.
- EMDEN, F. VAN 1959. Journey to High Simen (Northern Ethiopia), 1952–53: Diptera, Calyptrata. *Journal of the Linnaean Society of London, Zoology*, **44**: 186–195.
- ERZINÇLIOĞLU, Y.Z. 1987. The larvae of some blowflies of medical and veterinary importance. *Medical and Veterinary Entomology* **1**: 121–125.
- GONZÁLEZ MORA, D. & PERIS, S.V. 1988. Los Calliphoridae de España; 1: Rhiniinae y Chrysomyinae (Diptera). *Eos: Revista Española de Entomología* **64**: 91–139.
- GREENBERG, B. & SZYSKA, M.S. 1984. Immature stages and biology of fifteen species of Peruvian Calliphoridae (Diptera). *Annals of the Entomological Society of America* **77**: 488–517.
- GUIMARÃES, J.H., PRADO, A.P. DO, & LINHARES, A.X. 1978. Three newly introduced blowfly species in southern Brazil (Diptera, Calliphoridae). *Revista Brasileira de Entomologia* **22**: 53–60.
- HANSKI, I. 1977. Biogeography and ecology of carrion flies in the Canary Islands. *Suomen hyönteistieteellinen aikakauskirja* **43**: 101–107.
- KURAHASHI, H. 1979. A new species of *Chrysomya* from Singapore, with notes on *C. defixa* (Diptera: Calliphoridae). *Journal of Medical Entomology* **16**: 286–290.
- KURAHASHI, H. 1987. The blow flies of New Guinea, Bismarck Archipelago and Bougainville Island (Diptera: Calliphoridae). *Occasional Publications by the Entomological Society of Japan* No. 1, 1–99.
- KURAHASHI, H. 1991. Blow flies from Samoa with description of a new species of *Chrysomya* (Diptera, Calliphoridae). *Japanese Journal of Entomology* **59**: 627–636.
- KURAHASHI, H. 2002. Key to the calliphorid adults of forensic importance in the Oriental Region. In: Greenberg, B. & Kunich, J.C. *Entomology and the Law. Flies as Forensic Indicators*. 127–138. Cambridge University Press, Cambridge.
- KURAHASHI, H., BENJAPHONG, N. & OMAR, B. 1997. Blow flies (Insecta: Diptera: Calliphoridae) of Malaysia and Singapore. *The Raffles Bulletin of Zoology, Supplement* No. 5.
- KURAHASHI, H. & SALAZAR, N.P. 1977. A new species of *Chrysomya* (Diptera: Calliphoridae) from the Philippines. *Kalikasan. Philippines Journal of Biology* **6**: 251–256.
- LAURENCE, B.R. 1988. The tropical African latrine blowfly, *Chrysomya putoria* (Wiedemann). *Medical and Veterinary Entomology* **2**: 285–291.

- MALLOCH, J.R. 1925. Exotic Muscaridae (Diptera). – XVI. *Annals and Magazine of Natural History* (9)16: 81–100.
- MARILUIS, J.C. 2002. Key to common adult blowflies of South America. In: Greenberg, B. & Kunich, J.C. 2002. *Entomology and the Law. Flies as Forensic Indicators*. 94–100. Cambridge University Press, Cambridge.
- NCBI [National Center for Biotechnology Information] 2003. <http://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi>; <http://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=142978>; <http://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?id=235600>
- PARISE-MALTEMPI, P.P. & AVANCINI, R.M.P. 2001. C-banding and FISH in chromosomes of the blow flies *Chrysomya megacephala* and *Chrysomya putoria* (Diptera, Calliphoridae). *Memorias do Instituto Oswaldo Cruz* 96(3): 371–377.
- PATERSON, H. 1967. Evolutionary and population genetical studies of certain Diptera. Ph.D. thesis, University of the Witwatersrand, Johannesburg.
- PATERSON, H. 1977. The status of *Chrysomya chloropyga* and *Chrysomya putoria* (Diptera, Calliphoridae). *Proceedings of the 2nd National Entomological Congress, Pretoria*, 13–16 September 1977. 5–6. Entomological Society of Southern Africa, Pretoria.
- PATTON, W.S. & CUSHING, E.C. 1934. Studies on the higher Diptera of medical and veterinary importance. A revision of the genera of the subfamily Calliphorinae based on a comparative study of the male and female terminalia. The genus *Chrysomya* Robineau-Desvoidy (*sens. lat.*). *Annals of Tropical Medicine and Parasitology* 28: 123–130.
- PONT, A.C. 1980. 90. Family Calliphoridae. In: Crosskey, R.W. (Ed.), *Catalogue of the Diptera of the Afrotropical Region*. 779–800. British Museum (Natural History), London.
- PONT, A.C. 1995. The Dipterist C.R.W. Wiedemann (1770–1840). His life, work and collections. *Stenstrupia* 21: 125–154.
- PRINS, A.J. 1979. Discovery of the Oriental latrine fly *Chrysomya megacephala* (Fabricius) along the south-western coast of South Africa. *Annals of the South African Museum* 78(5): 39–47.
- ROGNES, K. 2002. Blowflies (Diptera, Calliphoridae) of Israel and adjacent areas, including a new species from Tunisia. *Insect Systematics & Evolution, Supplement* 59.
- RONDANI, C. 1873. Muscaria exotica Musei Civici Januensis. Fragmentum I. Species aliquae in Abyssinia (Regione Bogos) lectae a Doct. O. Beccari et March. O. Antinori, anno 1870–71. *Annali del Museo Civico di Storia Naturale di Genova* 4: 282–300.
- SÉGUY, E. 1928. Études sur les mouches parasites et les formes voisines. II. I.–Contributions à la connaissance des Chrysomyiini typiques. *Encyclopédie entomologique Série B. II. Diptera. Pars IV*, 101–116. Paul Lechevalier, Paris.
- THOMAS, H.T. 1951. Some species of the blow-fly genera *Chrysomyia* R.-D., *Lucilia* R.-D., *Hemipyrellia* Tnsd. and *Calliphora* R.-D. from South-Eastern Szechuan, China. *Proceedings of the Zoological Society of London* 121: 147–200.
- THOMPSON, F.C. & PONT, A.C. 1993. Systematic database of *Musca* names (Diptera). *Theses zoologicae* 20: iv 1–219.
- ULLERICH, F.-H. 1976. Chromosomenverhältnisse, konstitutives Heterochromatin und Geschlechtsbestimmung bei einigen Arten der Gattung *Chrysomya* (Calliphoridae, Diptera). *Chromosoma* 58: 113–136.
- VILLENEUVE, J. 1914. Étude sur quelques types de myodaires supérieurs. *Revue Zoologique Africaine, Bruxelles* 3: 429–441.
- WELLS, J.D., BYRD, J.H. & TANTAWI, T.I. 1999. Key to third-instar Chrysomyinae (Diptera: Calliphoridae) from carrion in the continental United States. *Journal of Medical Entomology* 36: 638–641.
- WELLS, J.D. & KURAHASHI, H. 1996. A new species of *Chrysomya* (Diptera: Calliphoridae) from Sulawesi, Indonesia, with a key to the Oriental, Australasian and Oceanian species. *Medical Entomology and Zoology* 47: 131–138.
- WELLS, J.D., LUNT, N. & VILLET, M.H. 2004. Recent African derivation of *Chrysomya putoria* from *C. chloropyga* and mitochondrial DNA paraphyly of cytochrome oxidase subunit one in blowflies of forensic importance. *Medical and Veterinary Entomology* 18: 445–448.
- WELLS, J.D. & SPERLING, F. 2001. DNA-based identification of forensically important Chrysomyinae (Diptera: Calliphoridae). *Forensic Science International* 120: 110–115.
- WIEDEMANN, C.R.W. 1818. Neue Insecten vom Vorgebirge der guten Hoffnung. *Zoologisches Magazin (Kiel)* 1(2): 40–48.
- WIEDEMANN, C.R.W. 1830. *Aussereuropäische zwei-flügelige Insekten. Als Fortsetzung des Meigenschen Werkes* 2, Schulz, Hamm.
- ZIMSEN, E. 1954. The insect types of C.R.W. Wiedemann in the Zoological Museum in Copenhagen. *Spolia Zoologica Musei Hauniensis* 14: 1–43.
- ZUMPT, F. 1956. Calliphoridae (Diptera Cyclorrhapha) Part I: Calliphorini and Chrysomyiini. *Exploration du Parc National Albert Mission G. F. de Witte (1933–1935)*. Fascicule 87, 1–201.
- ZUMPT, F. 1962. The Calliphoridae of the Madagascar Region (Diptera). Part I. Calliphorinae. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 73: 41–100.
- ZUMPT, F. 1965. *Myiasis in Man and Animals in the Old World. A Textbook for Physicians, Veterinarians and zoologists*. Butterworths, London.
- ZUMPT, F. 1972. Notes on Diptera (Sarcophagidae, Calliphorinae) from the Ethiopian geographical region. *Zeitschrift für Angewandte Zoologie* 59: 439–445.