

AFROTROPICAL *CULICOIDES*:  
BIOSYSTEMATICS OF THE IMICOLA GROUP,  
SUBGENUS *AVARITIA*  
(DIPTERA: CERATOPOGONIDAE)

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dedicated to

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## SUMMARY

Bloodsucking flies of the genus *Culicoides* Latreille, 1809 came to world prominence in 1944 when Du Toit's research at Onderstepoort revealed that *C. imicola* Kieffer, 1913 transmitted the orbiviruses of bluetongue (BT) and African horsesickness (AHS); *C. imicola* is not only the most effective vector of these viruses in the Old World but it is also the most widespread species. To date, some 50 viruses have been isolated from species of the genus worldwide, and also certain filarial and protozoal parasites.

*Culicoides* are found almost anywhere on earth; there are ± 1 300 described species in 27 subgenera. One of these subgenera, *Avaritia* Fox, 1955 was erected for the distinctive Holarctic *Obsoletus* group. The taxonomy of *Avaritia* is complex as it comprises at least 10 species groups; 75 % of the 70 known world species are found in the Afrotropical and Oriental Regions. The Imicola group is the most important; its biosystematics form the subject of this thesis.

Fiedler (1951) recorded 22 species of *Culicoides* from South Africa. During this study, 112 species were collected; 23 belong to the subgenus *Avaritia*. While half are new to Science only the true congeners of *C. imicola*, constituting the Imicola group, are treated here. Due to confusion in the literature, the Imicola and Orientalis groups are redefined and distinguished, and nine Old World species are assigned to the firstnamed group (Chapter 11). The five presently recognized African species, i.e. *C. imicola*, *C. pseudopallidipennis* Clastrier, 1958, *C. bolitinos* Meiswinkel, 1989, *C. miombo* Meiswinkel, 1991 and *C. loxodontis* Meiswinkel, 1992, are redescribed (Chapters 2, 4–6), and two new species, *C. tuttifrutti* sp. nov. and *C. kwagga* sp. nov. described (Chapters 6, 7). The remaining two species, *C. brevitarsis* Kieffer, 1917 and *C. nudipalpis* Delfinado, 1961, occur outside Africa and are briefly compared with, and distinguished from, their respective sister species *C. bolitinos* (Chapter 2) and *C. imicola* (Chapter 3).

In Europe, the immature stages of three *Avaritia* species were first shown to inhabit animal dung (Kettle & Lawson 1952); later, in Australia, the abundant *C. brevitarsis* of the Imicola group was also reared from cattle dung. Coprophily in *Culicoides* occurs on all continents but is exclusive to some 10 species. These coprophiles are scattered amongst six of the 10 groups in *Avaritia*; four of them belong in the

## Imicola group.

A bloodsucking insect developing in the dung of an animal is but a few wingbeats away from biting that animal; the transmission of viruses may form part of this association. Despite African diseases affecting domesticated livestock being harboured by indigenous game animals, no research has been done on *Culicoides* associated with wild herbivores in Africa. This thesis, to a modest extent, examines this association (Chapter 8). Emphasis is placed on unravelling the life-cycles of three species inhabiting the dung of the elephant, both species of rhinoceros, the buffalo, the blue wildebeest and the plains zebra (Chapters 2, 5 and 7); two of these have expanded their resource range and adapted to the dung of domesticates i.e. cattle and horses. This has obvious implications for disease transmission.

The study included a two-year survey of the *Culicoides* of the eastern Transvaal lowveld, the African horsesickness ‘hotspot’ of South Africa. Not only was the *Culicoides* fauna of a wilderness area (the Kruger National Park) compared with that found on adjoining farms, but the prevalence and abundance patterns of six species of the Imicola group were also investigated. This study reveals that Man can drive species to local extinction or cause a species to become widespread and superabundant (Chapter 9). In Chapter 10 the first *imicola*-free zone found in Africa is described. This has positive benefits as regards quarantining against AHS, and the holding of gymkhana events both local and international.

Collection methods involving light-trapping, truck-trapping and rearing from dung are briefly described. To improve observation and measurement of bodyparts, to obtain data of statistical value, and to facilitate greater accuracy during illustration, emphasis is placed on the study of long series of both sexes of a species, and on upgrading methods traditionally used in slide-mounting. Weaknesses in the descriptive format currently in use for world *Culicoides* are also addressed, and some new character states are employed (Chapter 1).

Finally, a key is provided for both sexes of the nine known species of the Imicola group (Chapter 12).

## ABSTRACT

A biosystematic study of seven Afrotropical and two Oriental species of the Imicola species-group was undertaken; this group of *Culicoides* of the subgenus *Avaritia* includes *C. imicola* the most important vector of the viruses of bluetongue (BT) and African horsesickness (AHS) known in the Old World.

Five African species are redescribed i.e. *C. imicola*, *C. pseudopallidipennis*, *C. bolitinos*, *C. miombo* and *C. loxodontis*. Two new species are described, and the extralimital *C. brevitarsis* and *C. nudipalpis* are discussed where relevant. These nine species comprise the Imicola group, one of 10 groups constituting the subgenus worldwide. Due to confusion in the literature, the Imicola group is redefined and distinguished from the Orientalis group (also redefined); 21 species of approximately 70 world species of *Avaritia* are reassigned to either of the two groups. A key to all nine known species of the Imicola group is given; shortcomings in the taxonomy of the Orientalis group are discussed.

The adult morphology of both sexes of the nine Imicola group species was studied; this revealed deficiencies in the descriptive format currently used in taxonomic studies of world *Culicoides*. Accordingly, greater detail has been introduced into descriptions and includes the use of new character states. Methods for mounting *Culicoides* on glass slides are also improved to ensure more accurate observation and measurement of diagnostic taxonomic features; furthermore, the descriptions are based on long series of each sex. Illustrations were made from specimens mounted symmetrically, and no feature omitted from any bodypart illustrated.

Certain aspects of the life-cycle of most species were investigated but especially those of *C. bolitinos*, *C. loxodontis* and *C. kwagga*. The immatures of these develop exclusively in the dung of the elephant, the buffalo, the blue wildebeest, both species of rhinoceros and Burchell's zebra. Two of these species, *C. bolitinos* and *C. kwagga*, have broadened their resource range as they can invade and mature in the dung of cattle and horses. This has obvious implications for the transmission of viruses, especially where indigenous herbivores are run with domesticated livestock.

In an intensive two-year survey a comparison was made between the *Culicoides* fauna of a natural area,

the Kruger National Park (KNP), and that found in areas changed by Man, namely livestock farms adjoining the KNP. This part of the eastern Transvaal lowveld is a main focus of AHS in South Africa. Light-trapping, rearing from dung, and pootering off live hosts, revealed that some species of the Imicola group are exclusively associated with certain herbivores; these include the elephant and the zebra which are suspected or proven reservoir hosts for AHS. The results thus throw further light on the epidemiology of this disease, and also show that Man plays a decisive role in determining the numbers, and distribution, of particular Imicola group species under certain conditions. In the case of *C. imicola*, the commonest and most widespread of all species, this range expansion, or establishment of foci, is due to man's maintenance of domesticated livestock in confined species, and especially where these are kept on irrigated pastures. However, the serendipitous discovery of a large *imicola*-free zone in South Africa indicates that edaphic conditions likely play an even more important role than Man and climate in determining the prevalence and abundance of *C. imicola*. This area is the sandy dune field west of Port Elizabeth and holds promise as a natural quarantine zone for the import and export of livestock.

## OPSOMMING

'n Biosistematisse ondersoek van sewe Afrotropiese en twee Orientale spesies van die Imicola groep is gedoen; by hierdie groep *Culicoides* van die subgenus *Avaritia* word *C. imicola* wat as die mees belangrikste vektor van bloutong-(BT) en perdesiekte (AHS) virus in die Ou Wêreld beskou word, ingesluit.

Vyf Afrika spesies, nl. *C. imicola*, *C. pseudopallidipennis*, *C. bolitinos*, *C. miombo* en *C. loxodontis*, is herbeskryf. Twee nuwe spesies is beskryf asook die suid-oos Asiese spesies *C. brevitarsis* en *C. nudipalpis* word bespreek waarvan toepassing. Hierdie nege spesies vorm die Imicola groep, een van die 10 groepe waaruit die subgenus *Avaritia* wêreldwyd bestaan. As gevolg van verwarring in die literatuur is die Imicola groep hergedefinieer en geskei van die Orientalis groep (ook hergedefinieer); 21 spesies van ongeveer 70 wêreld spesies van *Avaritia* is hingedeel in die twee groepe. 'n Sleutel vir al nege wêreld spesies van die Imicola groep, asook 'n verspreidingskaart vir elke spesie, word gegee. Tekortkominge in die taksonomie van die Orientalis groep word ook bespreek.

Die volwasse morfologie van beide geslagte van die nege Imicola groep spesies is bestudeer; dit het gebreke in die formaat wat tans vir die taksonomiese beskrywing van wêreld *Culicoides* gebruik word aan die lig gebring. Gevolglik is daar meer data in die beskrywings, wat nuwe karakterkenmerke insluit. Die metode van die montering van *Culicoides* op glasplaatjies is ook verbeter om meer akkurate ondersoek en meting van die diagnostiese kenmerke te verseker; verder, is beskrywings gebaseer op lang reeks van elke geslag. Illustrasies is gemaak van voorbeeld wat simmetries gemonter is en geen kenmerk is uitgelaat van enige geïllustreerde liggaamsdeel.

Aspekte van die lewensiklus van die meeste van die spesies, veral *C. bolitinos*, *C. loxodontis* en *C. kwagga* is ondersoek. Die onvolwassenes van hierdie spesies ontwikkel slegs in die mis van olifante, buffels, wildebeeste, renosters en zebras. Twee van die spesies, *C. bolitinos* en *C. kwagga*, het hulle broeimediums van voorkeur vergroot en kan eiers lê en tot volwassenheid ontwikkel in die mis van beeste en perde. Dit het vanselfsprekende gevolge vir virusoordrag tussen inheemse herbivore en vee, veral in gebiede waar die twee groepe saamloop.

In 'n intensieve twee-jaar studie, is 'n vergelyking gemaak tussen die *Culicoides* fauna soos aangetref in 'n ongerepte deel van Afrika, die Kruger Nasionale Park (KNP), en in gebiede aangrensend aan die KNP wat deur die mens in veephase omskep is. Die deel van die Oos Transvaalse laeveld is bekend as 'n perdesiekte "hotspot" in Suid-Afrika. Ligvalvangste, uitbroei van *Culicoides* uit mis en versameling vanaf lewendige gashere het aangedui dat sekere spesies van die Imicola groep eksklusief met sekere herbivore geassosieer is; hierby ingesluit is die olifant en zebra wat onderskeidelik verdagte en bevestigde gashere van AHS is. Die resultate dra by tot die verklaring van die epidemiologie van hierdie siekte en wys ook dat die mens 'n beslissende rol speel in die vasstelling van die getalle sowel as die verspreiding van spesifieke spesies van die Imicola groep. In die geval van *C. imicola*, die mees algemeenste en wydverspreidste spesie, is die uitbreiding, of daarstelling van fokuspunte, te wyte aan die mens se instandhouding van vaste bloedbanke op besproeide weiding. Die toevallige ontdekking van 'n groot *imicola*-vry sone elders in Suid-Afrika dui daarop dat grondtipe moontlik 'n bepalende rol kan speel in die aanwesigheid en volopheid van *C. imicola*. Hierdie "skoon" area is die sandduine-veld wes van Port Elizabeth en lyk belowend as 'n natuurlike kwarantyn gebied vir die invoer en uitvoer van lewende hawe.