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The South African keystone pollinator *Moegistorhynchus longirostris* (Wiedemann, 1819) (Diptera: Nemestrinidae): notes on biology, biogeography and proboscis length variation

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ABSTRACT

Moegistorhynchus longirostris Wiedemann, 1819 has the longest proboscis relative to body size of all known insects. It is a keystone species along the west coast of South Africa, where it pollinates, partly or exclusively, the long-tubed flowers of at least 20 species of Iridaceae, Geraniaceae and Orchidaceae. *M. longirostris* has been widely discussed in the pollination biology literature and has a suggested co-evolutionary arms race between it and the long-tubed flowers it pollinates.

A current taxonomic revision has presented new biogeographical and morphometric data. Available records suggest that the species is widely distributed along the west coast of South Africa between about 29°30'S and 34°15'S, a distance of almost 500 km. It is restricted to sandy, lowland coastal plains at less than 300 m, where it occurs in nine different vegetation types across seven bioregions and is consequently not a habitat specialist.

Proboscis length from 13 localities ranged from 32 to 83 mm, and mean proboscis length at these localities from 32 to 71 mm. There was a decline in proboscis length with increasing latitude south. Research investigating a possible allometric relationship between body size and proboscis length, and between latitude and proboscis length, is required.

KEY WORDS: Diptera, Nemestrinidae, *Moegistorhynchus longirostris*, Cape Floral Province, pollinator, long-tubed flowers, biogeography, proboscis length variation.

INTRODUCTION

Moegistorhynchus Macquart, 1840 is an endemic genus of Nemestrinidae known only from the west coast of South Africa (Western and Northern Cape Provinces), and includes four described species (Bowden 1980; Barraclough 2006), and at least two additional new species from montane areas in the southern part of its range (Barraclough 2006). By far the most frequently encountered species is *M. longirostris* (Wiedemann, 1819) (Fig. 1). This striking taxon is the best-known in the genus, and arguably is one of the most remarkable of all known South African species of Diptera. It has the longest proboscis in the Diptera, and the longest proboscis relative to body size of all known insects (Grimaldi 1999; Grimaldi & Engel 2005; Barraclough 2006). A comparable and frequently cited, long-proboscid taxon—but in the Lepidoptera—is the hawk moth *Xanthopan morgani praedicta* Rothschild & Jordan, 1903 from Madagascar (proboscis length about 25 cm), which pollinates the long-spurred Madagascan star orchid *Angraecum sesquipedale* Thou. (Nilsson 1998). This species departs dramatically from the allometric relationship between body size and proboscis length typically found in hawk moths (Agosta & Janzen 2005).

Moegistorhynchus longirostris is an important pollinator of regional endemic plants along the west coast, and this ecosystem service has attracted considerable attention from pollination biologists, and has been referred to in more than 30 publications since 1995 (e.g. Johnson & Steiner 1997; Manning & Goldblatt 1997; Grimaldi 1999;

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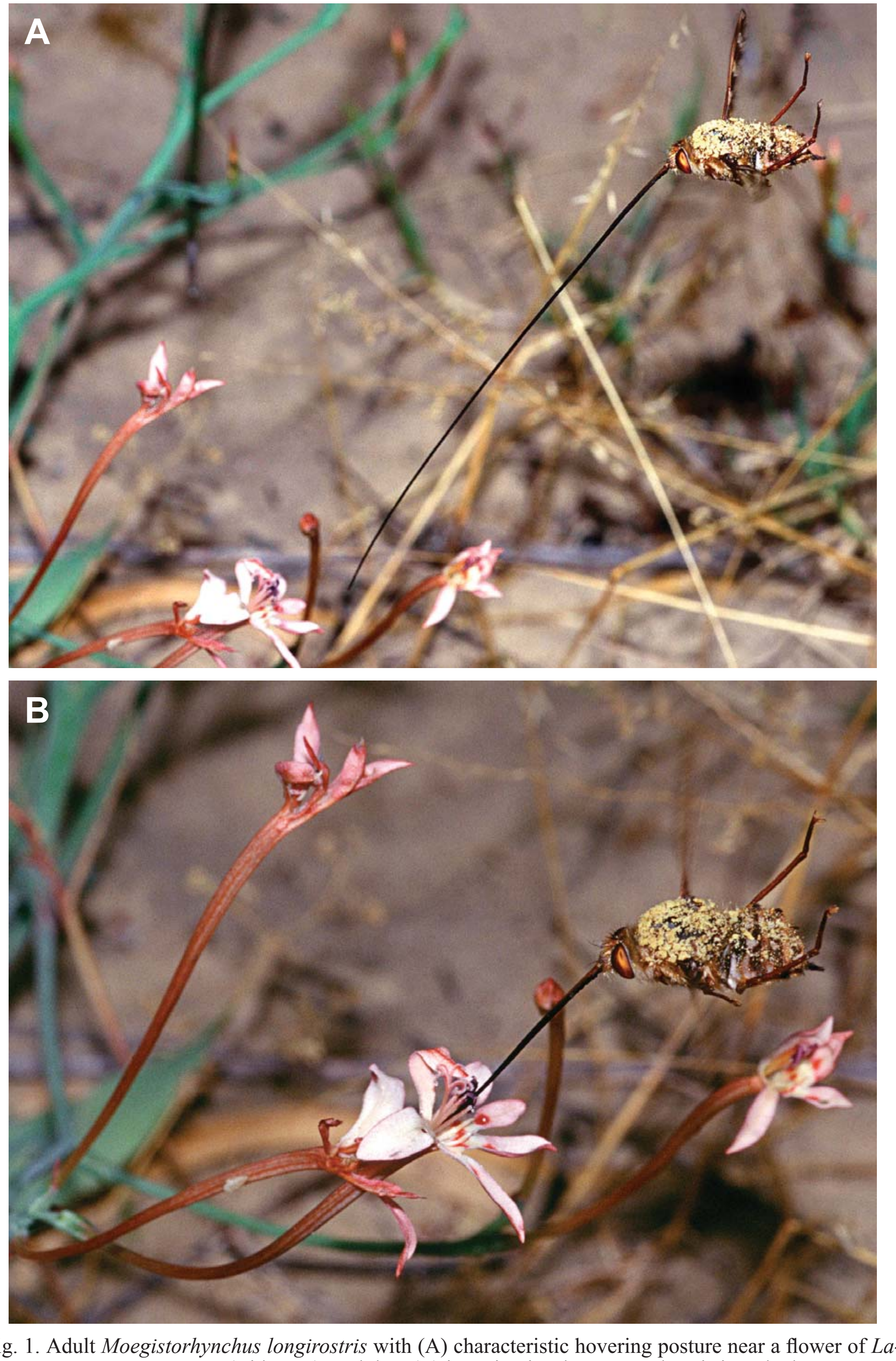

Fig. 1. Adult *Moegistorhynchus longirostris* with (A) characteristic hovering posture near a flower of *Lapeirousia anceps* (Iridaceae), and then (B) inserting its elongate proboscis into the long, narrow floral-tube. (Courtesy C. Patterson-Jones)

Goldblatt & Manning 2000; Barraclough 2006; Pauw *et al.* 2009). It is considered to be a keystone species (see Scott Mills *et al.* 1993; Payton *et al.* 2002; Davic 2003) in the habitats in which it occurs. Pollination is a critical ecosystem function, especially in the Western Cape and the Cape Floristic Province, which has more than 5500 endemic plant species, and is considered to be one of 25 global biodiversity hotspots (Myers *et al.* 2000; Brooks *et al.* 2002).

Interest in *M. longirostris* also derives in part from a suggested co-evolutionary process between it and the long-tubed flowers it pollinates. This form of interaction was described as an arms race between long-tubed flowers and pollinating insects (Nilsson 1988) – a process driving the evolution of increasing flower depth and further increases in proboscis length. Similar processes have been described for numerous other taxa (Benkman *et al.* 2003; Muchhala & Thomson 2009). Valuable and pioneering insights into reciprocal selection in the *M. longirostris* pollination system are now available, but there is no categorical confirmation that co-evolution is taking place (Pauw *et al.* 2009), and further research is warranted.

A pollination guild of at least 20 late spring or early summer-flowering species of Iridaceae, Geraniaceae and Orchidaceae centred on *M. longirostris*, is established in the literature (Johnson & Steiner 1997; Manning & Goldblatt 1997). Unusual features shared by these flowers include a very narrow floral tube (length 45 to 90 mm), and unscented flowers which are white through pink to salmon, with contrasted markings usually in red (Manning & Goldblatt 1997). Guild members use five different deposition sites for pollen on the fly, typically using different sites when two or more species co-occur (Manning & Goldblatt 1997). Supplementary information is available in Manning & Goldblatt (1997) and in Pauw *et al.* (2009).

With regard to the importance of *M. longirostris* in South African pollination biology and co-evolutionary theory, the botanical literature makes widespread commentary about variation in proboscis length and the implications thereof. However, much of the data are anecdotal and no entomological treatment exists. In fact, in the entomological literature nothing has been published on the geographical distribution of *M. longirostris*, or the marked variation in its proboscis length. In the interests of inter-disciplinary research, we profile *M. longirostris* and treat these issues in order to provide accurate, verifiable data for focused research by pollination biologists, conservationists and workers interested in co-evolutionary theory. Using museum specimens, we describe the distribution of the species, especially in relation to altitude, and the vegetation types with which it is associated. Furthermore, we present data on variation in proboscis length across the distribution range, a measure of critical importance to its ecological role as a pollinator.

MATERIAL AND METHODS

Some 116 specimens were examined from six major museum collections. Two of the South African collections include voucher specimens deposited there by pollination biologists. The identity of material was determined by examination of the two syntypes of *M. longirostris* (Zoological Museum, Copenhagen), as part of a wider taxonomic revision of *Moegistorhynchus* (Barraclough, in prep.). The most recent taxonomic treatment was published by Bequaert (1935).

Museum specimens were measured using calipers. Proboscis measurement was problematic, because in dried specimens the proboscis may be sinuous or variously curved.

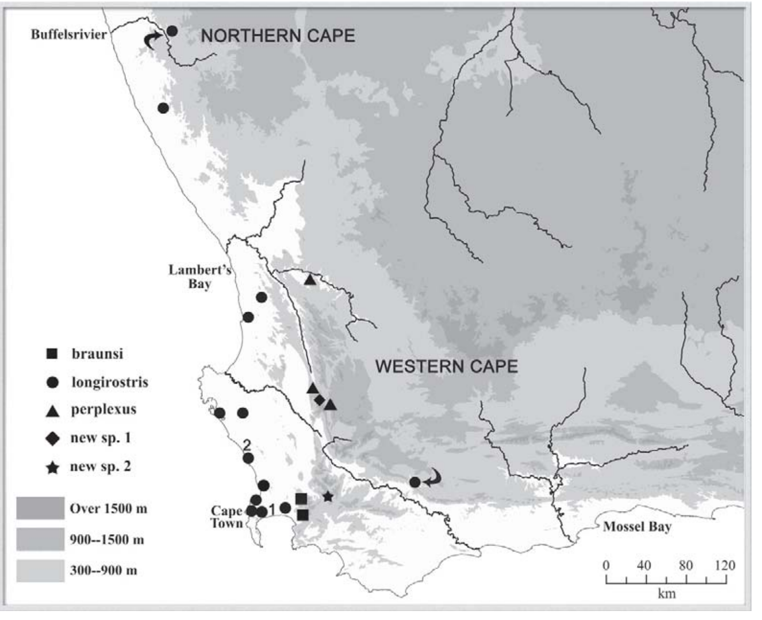

Fig. 2. Distribution of *Moegistorhynchus longirostris* along the west coast of South Africa (Northern Cape and Western Cape Provinces), showing its restriction to lowland areas below 300 m. *M. brevirostris* is distributed between 1 and 2 in the extreme southwest, north of Cape Town.

To compensate for this, such specimens were pinned beneath a glass surface. By viewing them directly from above, it was possible to trace with a fine black marker directly onto the glass above the line of curvature of the proboscis. Thereafter, a piece of thread was laid along the length of the curvature drawn on the glass, and cut to length. This length of thread was then straightened and measured with calipers.

Collection localities were assigned a vegetation type and associated data from Mucina and Rutherford (2007) using the Geoprocessing Wizard in Arcview 3.2 (ESRI, Redmond, CA, USA).

RESULTS

Although material from at least 17 different localities was seen, four localities were indeterminate and are thus not reflected in the distribution (Fig. 2). The most striking conclusion is that *M. longirostris* is a lowland species, distributed at altitudes of less than 300 m along the west coast between Cape Town and Stellenbosch in the extreme south (Western Cape), to the region of the Buffelsrivier (= Buffalo River) in Namaqualand (Northern Cape) in the north (29°30'S to 34°15'S). This is a distance of almost 500 km. The Stellenbosch area (33°55'S:18°51'E) is probably the eastern limit of the species' range. *M. longirostris* is commonly found in sandy coastal plains dominated by sand plain fynbos. Such areas consist of coastal sands and limestones (Manning & Goldblatt 1997).

M. longirostris is not limited to a particular vegetation type, with the localities occurring across nine different vegetation types (Mucina & Rutherford 2007). In addition, the species occurred across seven different bioregions (Table 1). The species is therefore not a habitat specialist.

Only the related species *M. brevirostris* (Wiedemann, 1821) is sympatric or parapatric with *M. longirostris* in lowland areas (Fig. 2), although its range appears to be limited to the coastal region in the extreme southwest. *M. brevirostris* has a much shorter proboscis (<20 mm), and is not part of the *M. longirostris* pollination guild. All other congeners (*M. braunsi* Bequaert, 1935, *M. perplexus* Bequaert, 1935 (see Manning 2004) and several undescribed species) are distributed at higher altitudes further from the coast in the Western Cape (Fig. 2), and all except *M. perplexus* are considered to have a very narrow range, or to be threatened or even extinct.

Of note is an old outlying record at Montagu in the extreme southeast (arrowed), where *M. longirostris* is recorded collected at higher altitude. Further collecting is required there to confirm this record; we believe the specimen has been mislabelled. An arrowed locality in the far north (Spektakelberg Pass) represents the probable northern limit of the range, although this material is excluded from consideration in this paper, as the material is based on females and taxonomic placement in *M. longirostris* is not definitive. A significant possibly of a record further north at Port Nolloth in the Northern Cape, also exists (Dikow, pers. comm.). We have not seen this material and the indicated proboscis length (36 to 45 mm) is closer to that of southern populations, which also suggests that the material may not be conspecific.

Proboscis length for the 13 different localities studied ranged from 32 to 83 mm. Mean length for individual localities ranged from 32 to 71 mm. There was a clinal trend, with longer proboscides in the north of the range (Table 1). The five localities in the far north have proboscides longer than 50 mm. The Silverstroomstrand and Bloubergstrand material is somewhat intermediate (42 to 55 mm), whereas the majority of specimens from the southernmost localities in the Cape Town metropolitan area have proboscides shorter than 40 mm (seven of the eight Strandfontein specimens have proboscides of 38 mm or less (mean = 36 mm)). In general, there were more males collected than females, and for the two sites with reasonable samples, this was also the case.

DISCUSSION

M. longirostris is assumed to be a parasitoid of other insects, probably Orthoptera or Coleoptera, although no data are available (Barraclough 2006). Effort needs to be devoted to discovering the insect host species, as this will facilitate further understanding of the interactions of *M. longirostris* with its host plants.

Of concern is that about half of the collection sites of *M. longirostris* occur in vegetation types that are not well protected, two sites fall into vegetation types that are critically endangered, with another five sites falling into vegetation types that are endangered (conservation status following Mucina and Rutherford (2007)). Given its keystone functioning in these vegetation types, a conservation assessment of *M. longirostris* is urgently required.

The range found in proboscis length (32 to 83 mm) differs somewhat from data published in the botanical literature. The minimum and maximum lengths are less than the 37 and 90 mm referred to by Manning and Goldblatt (1997). Elsewhere, a maximum length of 100 mm (Goldblatt & Manning 2000), a range of 60 to 100 mm (Johnson 2004), a range of 40 to 90 mm (Johnson 2010) and a range of 43 to 86 mm based on mean proboscis length (Pauw *et al.* 2009) are reported. Much of this discrepancy probably results from proboscis retraction in museum specimens and from variable

TABLE 1

Proboscis length measurements of *Moegistorhynchus longirostris* (in mm) and the distribution of the species across bioregions and vegetation types (Mucina & Rutherford 2007). Measurements of specimens are represented from north (Wallekraal) to south (Muizenberg) in the Northern Cape and Western Cape provinces of South Africa. Numbers of specimens per locality are indicated in parentheses. Vegetation type protection and conservation status follows Mucina and Rutherford (2007).

Locality	**Co-ordinates**	**Range**	**Mean**	**Bioregion**	**Protection status**	**Conservation status**
Near Wallekraal	30°24'S:17°31'E	55–61	59 (n=3)	Namaqualand Hardeveld	Poorly	Least threatened
Graafwater	32°09'S:18°36'E	59–83	68 (n=43)	Northwest Fynbos	Hardly	Endangered
Leopoldtville	32°13'S:18°29'E	52–73	64 (n=23)	Northwest Fynbos	Hardly	Endangered
West Coast Nat. Park	33°10'S:18°03'E	71	71 (n=1)	West Strandveld	Well	Vulnerable
Yzerfontein	33°10'S:18°10'E	51–64	57 (n=6)	West Strandveld	Poorly	Endangered
Silverstroomstand	33°35'S:18°20'E	42–55	49 (n=5)	West Strandveld	Well	Vulnerable
Near Blouberg-strand	33°45'S:18°26'E	43	43 (n=1)	Southwest Fynbos	Hardly	Critically endangered
Montagu	33°47'S:20°07'E	33	33 (n=1)	Southern Fynbos	Moderately	Least threatened
Near Mowbray	33°56'S:18°28'E	32–37	35 (n=2)	West Coast Renosterveld	Moderately	Critially endangered
Near Stellenbosch	34°04'S:18°43'E	32	32 (n=1)	West Strandveld	Poorly	Endangered
Strandfontein	34°05'S:18°35'E	33–43	36 (n=8)	West Strandveld	Poorly	Endangered
Muizenberg	34°07'S:18°28'E	34	34 (n=1)	Southwest Fynbos	Well	Least threatened

measuring techniques used by different researchers. Functional (extended) proboscis length, which is relevant in pollination biology studies, is likely closer to the 37 to 90 mm range previously reported (Manning & Goldblatt 1997; Anderson *et al.* 2005). There is an urgent need for standardisation of measuring techniques.

A notable pattern is that of longer proboscides in the north of the species' range and shorter forms in the far south. Theory dictates that direct co-evolutionary pressures would produce an increase in proboscis length independent of body size or latitude, to match regional changes in flower-tube length. Recent research (Anderson & Johnson 2008, 2009) has treated clinal trends relating to proboscis length and body size in the nemestrinid species *Prosoeca ganglbaueri* Lichtwardt, 1910, and suggests that flower-tube length was a significant predictor of fly proboscis length, but that altitude and body size may also influence proboscis length. Based on some initial observations, we believe that the allometric relationship between proboscis length, body size and latitude in *M. longirostris* warrants additional research with larger data sets. The results of this research would be important in terms of current studies of co-evolutionary processes using the species as a model taxon.

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