Austral Entomology

Austral Entomology (2021) **60**, 276–284

Review

Review of the biosystematics and bio-ecology of the groundnut/soya bean leaf miner species (Lepidoptera: Gelechiidae)

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Abstract *Aproaerema modicella* (Deventer), *Aproaerema simplexella* (Walker) and *Stomopteryx subsecivella* (Zeller, 1852) (Lepidoptera: Gelechiidae) are micro moth (Micro-Lepidoptera) pests of groundnut and soya bean that have been described as different species on different continents. Recent DNA analyses of these species suggest that they are conspecific. Here, a review with emphasis on the genetics, biology, ecology and known host plant preferences of this apparent species is given. We argue, through the genetic/DNA data and analyses, that the three species should be grouped as a single species. The review ends by highlighting the areas that need further research to confirm our hypothesis.

Key words *Aproaerema modicella*, *Aproaerema simplexella*, conspecific, *Stomopteryx subsecivella*.

INTRODUCTION

Aproaerema modicella (Deventer, 1904) in Asia (Mohamad 1981), *Aproaerema simplexella* (Walker 1864) in Australia (Common 1990; Bailey 2007) and *Stomopteryx subsecivella* (Zeller 1852) in Africa (Mohamad 1981) (Lepidoptera: Gelechiidae) have historically been treated as separate species on the separate continents. Their larvae are leaf miners that are major pests of groundnut (*Arachis hypogaea* L.) and soya bean (*Glycine max* (L.) Merr.) (Rawat & Singh 1979; Shanower *et al*. 1993a; Buthelezi *et al*. 2013; Namara 2015; Ibanda *et al*. 2018; Namara *et al*. 2019). They also impact minor crops such as pigeon pea (*Cajanus cajan*) (Shanower *et al*. 1993a; Buthelezi *et al*. 2013), *Lablab purpureus* (Shanower *et al*. 1993a), and lucerne (*Medicago sativa*) (Sandhu 1978; Shanower *et al*. 1993a; Du Plessis 2003; Buthelezi *et al*. 2013). The species have different, but overlapping host plant ranges. In this review, they are collectively referred to as the groundnut–soybean leaf miner (GSLM). However, recent research, which included molecular (MtDNA CO1) and ecological studies on these species (Buthelezi *et al*. 2012, 2013, 2016, 2017) provides evidence that these species are very closely related and can be classed as conspecific. This hypothesis is further supported with evidence collected from published materials in the public domain which include research reports, international newsletters, books, journal articles, museums and dissertations (see reference list). Lepidoptera specialists Dr Klaus Sattler of British Museum (Natural History) in London and Dr Martin Kruger of Ditsong Museum in South Africa were also consulted regarding the updated taxonomic study of these species.

BIOSYSTEMATICS OF THE GSLM

The Asian GSLM (*Aproaerema modicella* Deventer, 1904)

There are several synonyms applied to *Aproaerema modicella* in the literature. These include *Anacampsis nerteria* (Meyrick) (Fletcher 1914, 1917, 1920), *Stomopteryx nerteria* (Meyrick 1906) (Anon 1941; Cherian & Basheer 1942), *S. subsecivella* (Zeller 1852) (Abdul Kareem *et al*. 1972–73; Litsinger *et al*. 1978) and *Bilobata subsecivella* (Zeller 1852) (Feakin 1973; Anon 1977; Dean 1978). A specimen of the moth from Java (Indonesia) was originally described by Van Deventer in 1904 who gave it the name *Xystophora modicella* (Van Deventer 1904). Meyrick (1906) first described groundnut leaf miner (GLM) in India as *Anacampsis nerteria*. This name was also used by Maxwell-Lefroy and Howlett (1909) and by Maxwell-Lefroy (1923). *Anacampsis nerteria* was subsequently synonymised with *Gelechia (Brachmia) subsecivella* (Meyrick 1925). In 1980, *A. modicella* (Deventer) was proposed as the scientific name for the Indian-Indonesian GLM, with the synonyms *X. modicella*, *Anacampsis nerteria* and *S. subsecivella* (Mohammad 1981). The prevalence of *A. modicella* has been reported in several countries in this region, including India, Bangladesh, Cambodia, China, Indonesia, Java, Malaysia, Myanmar, Nepal, Tasmania, Orissa, Pakistan, Philippines, Sri Lanka, Thailand and Vietnam

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 doi: 10.1111/aen.12528

(CAB International 2014). It has however also been reported in Africa, from Uganda, DRC, Malawi, Mozambique, Kenya, South Africa (CAB International 2014) Egypt (Daily Monitor 2010) and the Indian Ocean islands of Madagascar, Reunion and Mauritius (M. Bippus, 2019, unpublished data).

In India, *A. modicella* is a serious pest of groundnut (Fletcher 1914, 1917; Anon 1941; Cherian and Basheer 1942; Channabasavanna 1951, 1954, 1957; Usman & Puttarudraiah 1955; Kapoor *et al*. 1975; Mohammad 1981; Lakshminarayana *et al*. 2018), soya bean (Rai *et al*. 1973; Rawat & Singh 1979) and lucerne (Sandhu 1978).

The Australasian soya bean leaf miner (*Aproaerema simplexella* Walker, 1864)

Aproaerema simplexella, commonly known as the soya bean moth is thought to be native to Australia, and is generally regarded as a minor pest of soya bean (Common 1990; Bailey 2007). The Australian soya bean leaf miner was first described as *A. simplexella* (*Gelechia Simplexella*) by Walker in 1864 (Walker 1864). Synonyms of *A. simplexella* (*G. simplexella*) are *Stomopteryx simplexella* (Walker) (Bailey 2007), *Aproaerema simplicella* (Meyrick 1904). In 1904, Meyrick made an unjustified emendation of *G. simplexella* (Walker) to *Anacampsis simplicella* (Lepidoptera: Gelechiidae) (Meyrick 1906). In Australia, the moth is prevalent in Western Australia, the Northern Territory, Queensland, New South Wales, Victoria, Tasmania, South Australia and Norfolk Islands (Herbison-Evans and Crossley 2018). In New Zealand, the soya bean leaf miner was recorded as *Stomopteryx simplicella* (Walk.), but was later re-described as a new species, *Stomopteryx columbina* (Philpott 1928), based on comparison of the genitalia (Philpott 1928). Records from the British Museum (Natural History), London, indicate that *S. columbina* is a synonym of *Bilobata subsecivella* (Zeller 1852). However, there are no other publications available that mention this synonym.

The African GSLM (*Bilobata subsecivella* Zeller, 1852)

In Africa, the GSLM was first reported as a serious pest of groundnut and soya bean in Uganda in 1998 (Page *et al*. 2000), and since then, it has been reported as a major pest for both groundnut and soya bean in Malawi (Subrahmanyam *et al*. 2000), Democratic Republic of Congo (Munyuli *et al*. 2003) and South Africa (Du Plessis 2002). When the GSLM first emerged as a new pest on the African continent in 1998 (Page *et al*. 2000), it was assumed to be an invasion of *A. modicella* from Indo-Asia (Kenis and Cugala 2006). This assumption resulted in the adoption of the name *A. modicella* for the pest. Van der Walt *et al*. (2008) examined the gonads of the female and male larvae of the GLM specimens collected in South Africa and concluded that they were similar to those reported for *A. modicella* in Asia by Shanower *et al*. (1993a), which reinforced the assumption that the pest was *A. modicella*. However, there are records of a micro moth captured from South Africa as far back as 1852 that was similar to *A. modicella*. This micro moth was first described by Zeller (1852) who named it *Gelechia* (Brachmia) *subsecivella*. This taxon has also been identified from India (Abdul Kareem *et al*. 1972–1973; Gujrati *et al*. 1973; Kapoor *et al*. 1975; Litsinger *et al*. 1978; Sandhu 1978; Kapadia *et al*. 1982) as *Stomopteryx subsecivella* (Zeller). The South African GSLM was also described as *Anacampsis nerteria* (Meyrick 1909). In 1954, Janse was the first to revise *S. subsecivella*, and his conception was that it was congeneric with *A. modicella*. He also proposed a new genus, *Biloba* Janse, for *S. subsecivella*. However, the name *Biloba* was unavailable as it was preoccupied (Mohammad 1981). In 1986, *Bilobata* Vári was established as an objective replacement name for the junior homonym *Biloba* (Vári 1986).

CONFIRMATION OF THE RELATEDNESS OF THE GROUNDNUT/SOYA BEAN LEAF MINER FROM ASIA, AFRICA AND AUSTRALASIA

In an effort to confirm the identity of the South African GSLM, Buthelezi *et al*. (2012) sequenced the mitochondrial DNA COI (mtDNA COI) gene of specimens collected from six widely separated sites in South Africa and compared them with international sequences in the Barcode of Life Data System (BOLD). All of the specimens matched 100% with *A. simplexella* (the Australasian soya bean moth) in the Barcode of Life Data System (BOLD). This caused more confusion, as there was no record of *A. simplexella* previously recorded from Africa, and it was not known to be a groundnut pest anywhere in the world. Subsequently, five different gene regions of mitochondrial and nuclear DNA (COI, COII, cytb, 28S and EF-1 ALPHA) of larval specimens from South Africa, India and Mozambique, and adult specimens from Australia caught in Brisbane through traps that utilised pheromone synthesised for *A. modicella* were compared (Buthelezi 2015; Buthelezi *et al*. 2016). In addition, mtDNA COI gene regions were compared to *A. simplexella* sequences in the BOLD and NCBI gene banks. In phylogenetic trees (COI, COII, cytb, EF-1 ALPHA), sequences of specimens from India, South Africa, Mozambique and one Australian specimen (*Aproaerema simplexella* PS1) from the BOLD gene bank grouped together to form one cluster, whereas all sequences of specimens collected from Brisbane in Australia grouped separately from others (Buthelezi 2015). However, in the phylogenetic tree for 28S region, all sequences grouped together to form one cluster irrespective of the locality from which they were obtained (Buthelezi 2015). It was therefore concluded that the GSLM in Asia and Africa and the soya bean moth in Australia were conspecific, but the Australian population was much more diverse genetically than the other two populations (Buthelezi 2015; Buthelezi *et al*. 2016). This conclusion was supported by the fact that moths from South Africa, India and Australia were all similarly attracted to the synthesised pheromone for *A. modicella* (Buthelezi *et al*. 2016). Previous research furthermore pointed towards this conclusion in that GSLM male genitalia of the population in Africa was shown to be similar to that of the population in Asia (Van der Walt *et al*. 2008).

Thus, according to the opinions of the lepidopteran expert Dr Sattler (K. Sattler, in litt unpublished data) and based on the DNA analyses and the morphological features described for the GSLM (Bailey 2007; Van der Walt *et al*. 2008; Buthelezi *et al*. 2012, 2016; Ranga Rao & Rameshwar Rao 2013) of the separate species from Africa, India and Australia, it is proposed that they be referred to as a single species, classified as follows:

- *Bilobata* Vári 1986.
- *Biloba* Janse 1954, nom. Praeocc.
- *Bilobata subsecivella* (Zeller 1852).
- *Gelechia* (Brachmia) *subsecivella* Zeller 1852.
- *Gelechia simplexella* Walker 1864, syn. Nov.
- *Xystophora modicella* Deventer, 1904, syn. rev. (synonymised with *G*. (B.) *subsecivella* by Meyrick 1925, p. 111, but subsequently recalled from synonymy).
- *Anacampsis simplicella* Meyrick 1904 (an unjustified emendation of *G. simplexella* Walker).
- *Anacampsis nerteria* Meyrick 1906 (synonymised with *G*. (B.) *subsecivella* by Meyrick 1925, p. 111).

On this basis, Buthelezi (2015) proposed and used *Bilobata subsecivella* (Zeller 1852) as the name for the South African population she studied, and this name should be used for the combined three GSLM species identified from Africa, the Indian subcontinent and Australasia.

MORPHOLOGICAL SIMILARITIES OF GROUNDNUT/SOYA BEAN LEAF MINER POPULATIONS FROM AFRICA, INDIA AND AUSTRALIA

The three continental populations of *B. subsecivella* (*A. modicella*, *A. simplexella* and *S. subsecivella*) display similar adult morphological characteristics. The adult moth of *A. modicella* is 6-mm grey mottled moth, with a full wing span of up to 18 mm with a transverse white band across the fore wing (Shanower *et al*. 1993a; Bailey 2007; Ranga Rao & Rameshwar Rao 2013). A similar description has been provided for the soybean moth *A. simplexella* (Common 1990; Bailey 2007) and South African GSLM *S. subcesivella* (Buthelezi *et al*. 2012). The latter authors noted that the adult moths are light grey when newly emerged from the pupae. As they age, they turn dark grey or brownish and mottled, with dark brown forewings and pale brown hind wings covered with whitish scales towards the lower part. The South African moth is about 4- to 5-mm long (Buthelezi *et al*. 2012).

The eggs of all species are small shiny white and oval shaped often laid singly on leaf veins (Shanower *et al*. 1993a; Bailey 2007; Buthelezi *et al*. 2012; Ranga Rao and Rameshwar Rao 2013; GRDC 2016; Herbison-Evans and Crossley 2018). The larval colour varies from green to grey-green with a black head (Shanower *et al*. 1993a; Bailey 2007; Buthelezi *et al*. 2012; GRDC 2016; Herbison-Evans and Crossley 2018). When fully grown and close to pupation, larvae become cream coloured (Buthelezi *et al*. 2012). The pupae form inside folded over leaflets. In India, pupae of GSLM rarely exceed 8 mm in length (Shanower *et al*. 1993a). Buthelezi *et al*. (2012) noted that the pupae of the GSLM in South African are light brown when newly formed, but later become dark brown, and as is the case with the GSLM in India and Australia, each pupate is enclosed in a thin silken cocoon inside the folded leaflets. There is no information available on the description of the pupae of the Australian population.

BIO-ECOLOGY OF THE GSLM

Information on the biology and ecology of the soya bean moth in Australia is scanty, but what has been gleaned from the literature (Bailey 2007) closely reflects that described for *A. modicella*. The biology for GSLM in Africa has been provided by Buthelezi *et al*. (2013) and is also similar to that described for the Asian GSLM (Shanower *et al*. 1993a). Hence, the biology provided in this review is inclusive of GSLM populations in Asian, African and Australasian.

Adult female leaf miners lay eggs directly on the undersides of groundnut leaflets, stems and petioles (Shanower *et al*. 1993a; Kenis & Cugala 2006; Ranga Rao & Rameshwar Rao 2013). The number of eggs range from 87 to 473 (Cherian and Basheer 1942; Gujrati *et al*. 1973). Under field conditions, eggs generally hatch in 3–4 days, but at lower temperatures may require 6–8 days (Kapadia *et al*. 1982; Shanower *et al*. 1993a). The development to adulthood may take from 15 to 28 days in warm conditions (Cherian & Basheer 1942) and from 37 to 80 days in cool and cold weather, respectively (Sandhu 1978). Larval development to the pupal stage of the Asian population requires approximately 325 degree-days above a threshold temperature of 11.3°C (Shanower 1989). Different numbers of larval instars of the Asian population have been reported in the literature, ranging from three (Kapadia *et al*. 1982), four (Gujrati *et al*. 1973), five (Amin 1987; Shanower 1989; Ranga Rao and Rameshwar Rao 2013) and six (Islam *et al*. 1983). The first instar of the Asian population has an average length of 0.56 mm, at pupation, they rarely exceed 8 mm in length (Ranga Rao & Rameshwar Rao 2013). The larva of the Australian population only reach 7 mm (Bailey 2007).

Pupation in the Asian population, which occurs in the webbed leaflets (Kenis & Cugala 2006; Ranga Rao & Rameshwar Rao 2013), requires 72 degree-days (Shanower 1989). At ambient temperature, pupation can be completed in 3 to 10 days (Cherian and Basheer 1942; Sandhu 1978). Adults eventually emerge from the pupa and the cycle repeats. In India, number of annual generations of GSLM per crop is highly variable and has been reported to range from two to seven (Wheatley *et al*. 1989; Shanower *et al*. 1993a; Kenis and Cugala 2006) whereas in South Africa, Buthelezi *et al*. (2017) reported that there were two peaks (generations) per season with a generation cycle of between 28 and 30 days. There is no information available for the Australian population on the temperature requirement for the development to adulthood as well as the number of generations per season.

FACTORS THAT AFFECT THE INCIDENCE OF THE GSLM

The Asian, Australasian and African GSLM populations are adapted to wide ranges of agro-ecological areas that differ widely in climates. In Africa, the distribution range covers areas that are very diverse in climate from the temperate region in north eastern coastal areas of South Africa (Buthelezi *et al*. 2013, 2017) northwards to the Nile Delta in Egypt (Daily Monitor 2010) and Islands on the eastern part of Africa inclusive of Madagascar, and Mauritius (M. Bippus, in litt unpublished data). In Australasia, the range includes all Australian states (Bailey 2007; CAB International 2014), New Zealand (CAB International 2014), Tasmania (CAB International 2014) and probably islands surrounding them. Similarly, the range of the GSLM in Asia covered diverse climates across the span of India, Pakistan and Vietnam (CAB International 2014). However, despite the diverse ranges, the outbreaks of the GSLM in India, Africa and Australia are highly sporadic (Shanower *et al*. 1993a; Kenis and Cugala 2006; Bailey 2007; Van der Walt 2007; Du Plessis 2011; Buthelezi *et al*. 2017), with substantial fluctuations in populations between locations, seasons and years (Logiswaran and Mohanasundaram 1986; Van der Walt 2007; Buthelezi *et al*. 2017). In Australia, severe soya bean moth outbreaks are said to occur generally once every 20 years (Bailey 2007).

The level of infestation of GSLM is largely dependent on environmental conditions (Amin 1987), with rainfall, humidity and temperature being the most important modulating climatic factors (Amin and Reddy 1983; Ranga Rao *et al*. 1997; Gadgil *et al*. 1999; Narahari Rao *et al*. 2000; AICRPAM 2001; Buthelezi *et al*. 2017; Naresh *et al*. 2017). It is generally accepted that the conditions most favourable for the growth of the Asian population are long dry spells in association with high temperature and low humidity (Amin and Reddy 1983; Ranga Rao *et al*. 1997; Gadgil *et al*. 1999; Narahari Rao *et al*. 2000; AICRPAM 2001; Naresh *et al*. 2017). Heavy rainfall reduces this populations (Amin 1987). Similarly, Buthelezi *et al*. (2017) observed that high moth catches in pheromone traps coincided with low rainfall periods, whereas low moth catches coincided with the rainy periods in the South African populations. However, simulation of rainfall with overhead irrigation by Wheatley *et al*. (1989) was ineffective in lowering Asian population densities. A rain free period of 21 days or more has been associated with severe infestation in India (Gadgil *et al*. 1999; Narahari Rao *et al*. 2000). It has also been observed in India that infestations of their populations were severe when the groundnut crop suffered from moisture stress (Ranga Rao *et al*. 1997). Thus, it might be expected that GSLM infestations may be lower in wetter compared with drier seasons. Studies in Uganda have reported that that the infestation of soya bean by the African population of GSLM was lower in places with high temperature and humidity (Ibanda *et al*. 2018). Thus, it appears that high humidity might be the most important factor that discourages GSLM infestation. Generally, infestations of GSLM are favoured by hot, dry weather, with crops under severe moisture stress most at risk (Amin and Reddy 1983; Bailey 2007; GRDC 2016; Buthelezi *et al*. 2017).

Temperature influences egg production and the survival of the pest in its immature stages, especially the larval stage (Shanower *et al*. 1993b). Eggs production has been reported to be lower at 15°C than at 30°C for Asian population (Shanower *et al*. 1993b) also, hatching is slower at 15°C than at higher temperatures, and larval mortality approaches 100% at 15°C (Shanower *et al*. 1993b).

HOST PLANT PREFERENCES AND TIMING OF INFESTATIONS

The only known common host plant for the Asian, Australasian and African GSLM populations is soya bean. The African and Indian GSLM attack groundnut but the Australasian soya bean moth is not known to attack groundnut; although the crop is grown in that country, soya bean is its only crop host in Australia (Common 1990; Bailey 2007; GRCD 2016; Herbison-Evans and Crossley 2018). The additional hosts mentioned in the literature for the soya bean moth in Australia is *Cullen tenax* (synon: *Psoralea tenax*) (Bailey 2007), *Psoralea patens* and *Trifolium* L. (clover) (Common 1990). Listings of host plants (Table 1) by Shanower *et al*. (1993a), Van der Walt (2007) and Buthelezi *et al*. (2013) show that the Asian and African GSLM populations share a number of these. However, the entire host range of host plants on the Asian continent is made up of legumes (14), with exception of *Boreria hispida* (of Rubiaceae family). The host plants of the African population identified in South Africa include 10 legumes, two Malvaceae, two Convolvulaceae, one in each, Asteraceae, Lamiaceae, Pedaliaceae, Tiliaceae and Capparaceae (Table 1).

Groundnut and soya bean are the main crop hosts of the GSLM populations in India and South Africa with soya bean being the most preferred host (Shanower *et al*. 1993a; Buthelezi *et al*. 2013; Ranga Rao and Rameshwar Rao 2013). Although soya bean is grown in Mozambique, Malawi and DRC, GSLM is not reported to be a serious pest of soya bean in these countries while groundnut is reported as the main host (Subrahmanyam *et al*. 2000; Munyuli *et al*. 2003; Cugala *et al*. 2010). However, in experiments in which groundnut and soya bean have been grown side by side, it has been observed that soya bean is the most preferred host in India (Birajdar *et al*. 2015) and South Africa (Buthelezi *et al*. 2013). Soya bean is also the most important host in Uganda (Namara 2015; Ibanda *et al*. 2018) and Kenya (Kinyanjui *et al*. 2018). Mild attack on lucerne and pigeon pea has been observed in India (Shanower *et al*. 1993a) and South Africa (Buthelezi *et al*. 2013). Although lablab bean and *Psoralea corylifolia* L. recorded by Shanower *et al*. (1993a) as host plants for the GSLM in India are present in South Africa, the GSLM in South Africa has no interest in eating them (Buthelezi *et al*. 2013). Geographical differences in host plant species preferences have also been noted within South Africa. For example, Van der Walt (2007) observed that plants of *Crotalaria vasculosa* Wall. ex Benth. (Fabaceae), *Corchorus tridens* L. (Tiliaceae), and *Cleome monophylla* L. (Capparaceae) in Tshiombo irrigation scheme (22°15′25.24″ S;

Table 1 Host plants for groundnut/soya bean leaf miner populations obtained from various literature sources across its geographic range

Host plants family	Host plants for *A. modicella* (Shanower et al. 1993a)	Host plants for *S. subsecivella* (Van der Walt 2007)	Host plants for *S. subsecivella* (Buthelezi et al. 2013)
Legume	*A. hypogea* (L.) (groundnut)	*A. hypogea* (L.) (groundnut)	*A. hypogea* (L.) (groundnut)
	G. max (Merril), (L.) (soya bean)	*G. max* (Merril), (L.) (soya bean)	*G. max* (Merril), (L.) (soya bean)
	Vigna radiata (L.) Willzeek (=*Phaseolus aureus*) (mung bean)	*Medicago sativa* (L.) (lucerne)	*Cajanus cajan* (L.) Millsp. (pigeon pea)
	Cajanus cajan (L.) Millsp. (pigeon pea)	*Hibiscus* sp., *Senna obtusifotia* (L.) Irwin &. Bamaby	*Medicago sativa* (L.) (lucerne)
	Medicago sativa L. (lucerne)	*S. occidenialis* (L.) Link (L.)	*I. hirsuta* (Linn.) (L.)
	Psolarea corylifolia (L.) (babchi)	*Indigofera astragalina* (DC.) (L.)	*Desmodium tortuosum* (Sw.) DC. (L.)
	Indigofera hirsuta (L.) (hairy indigo)	*Crotalaria vasculosa* Wall, ex Benth.) (L.)	*G. wightii* L. Merr. (L.) (wild soya bean)
	Vigna umbellata (Thunb) Ohwi and Ohashi (= *Phaseolus calcaratus*) (rice bean) (L.)		
	Glycine soja Sieb. & Zucc. (wild soya bean) (L.)		
	Trifolium alexandeium (L.) (berseem clover)		
	Teramnus labialis (L.) Spreng (blue wiss)		
	Lablab purpureus (L.) (lablab bean)		
	Rhynchosia minima DC. (jumby bean) (L)		
Rubiaceae	*Boreria hispida* (shaggy button weed)		
Convolvulaceae		*Ipomoea sinensis* (Desr.) Choisy subsp. blepharosepala (Hochst. ex A. Rich) Verde ex A. Meeuse) (Convolvulaceae)	*Ipomoea sinensis* (Desr.) Choisy subsp. blepharosepala Hochst. ex A. Rich. (Convolvulaceae) Ipomoea wightii (Wall) Choisy (Convolvulaceae)
Malvaceae			*Malvastrum coromandelianum subsp. coromandelianum* (L.) (Garcke) (Malvaceae) *Pavonia burchellii* (DC.) (Dyer) (Malvaceae)
Asteraceae			*Acanthospermum hispidum* DC. (Asteraceae)
Lamiaceae			*Ocinum canum (Sims)* (Lamiaceae) (African basil)
Capparaceae		*Cleome monophylla* L. (Capparaceae)	
Pedaliaceae		*Sesamum alaium Thonn* (Pedaliaceae)	
Tiliaceae		*Corchonis tridens* L. (Tiliaceae)	

29°50′20.31″ E) were attacked by the GSLM. These plant species are abundant in Bhekabantu (27°01′12.38″ S; 32°19′ 18.29″ E) in South Africa, but no infestation was observed on any of the plants growing adjacent to a heavily infested groundnut crops in this location (Buthelezi *et al*. 2013). Thus, the host plant range of the GSLM also appears to vary with locality in South Africa.

In South Africa, infestation of the host plant species was found to vary with the time of the year. In a seasonal monitoring study in South Africa, Buthelezi *et al*. (2013, 2017) observed that infestation of all hosts plants, including the perennial crops pigeon pea and lucerne, occurs only in the summer months. Even groundnut, which is traditionally grown in the mild winter and spring months (June to October) in the northern coastal region of KwaZulu Natal in South African, remains free of the leaf miner until December, despite male moths being detected throughout the winter and spring months (Buthelezi *et al*. 2017). Also, pigeon pea and lucerne were barely attacked, with very low infestations occurring only between March and April (Buthelezi *et al*. 2013, 2017). These observations indicate that planting date could be considered as one of the control strategies to be adopted for reducing crop losses from the African GSLM population. The plant developmental stage also appears to be of importance in the infestation of groundnut. In South Africa, it was noted that larval infestations on the groundnut crop occurred some 5–6 weeks after crop emergence, which coincides with the flowering and pegging stage of the crop (Buthelezi *et al*. 2017). This may suggest the presence of volatile compounds produced by groundnut during flowering that attract GSLM to the crop.

OVERWINTERING

Groundnut–soya bean leaf miner occurs in diverse climates. In some places like Brits in South Africa and Brisbane in Australia, winter temperatures are very cold unlike in Hyderabad in India where temperatures are warmer and they grow crops throughout the year. Therefore, it might be suggested that the pest overwinters in places which experience severe cold temperatures in winter. However, it is currently not known how GSLM overwinters and bridges the summer season temperature. Studies done in South Africa by Buthelezi *et al*. (2017) indicate that in localities with mild winters, the male moths are active throughout the year, albeit in very small numbers (two to five moths caught per trap per 2 weeks) in the winter months. However, despite some adult activity in the winter months, the larval stage of the pest was not found on any of its hosts. In localities experiencing frosts in winter, there was no male moth flight activity in winter, but it re-commenced in early spring after the frost has stopped to occur. As the temperature improves, adult flight activity increases dramatically even in the absence of host plants. Deductions from these observations therefore indicate that GSLM population in South Africa somehow diapauses during off-season/winter periods or overwinters as pupae (June to September).

CROP DAMAGE SYMPTOMS

Crop damage symptoms of GSLM are shown in Figure 1. Damage symptoms on groundnut crops in Africa (Kenis & Cugala 2006; Buthelezi *et al*. 2012) and India (Shanower *et al*. 1993a; Ranga Rao & Rameshwar Rao 2013) mirror each other. Similarly, damage symptoms on soya bean described for the leaf miner in Africa (Namara 2015), India (Ranga Rao & Rameshwar Rao 2013) and Australia (Common 1990; Bailey 2007) are similar. In groundnut, the first instar larvae feed within the epidermis on leaf mesophyll, creating winding mines between the upper and lower epidermis. The mines extend outwards from an initial serpentine shape and enlarge to become blotch like as the larvae grow (Shanower *et al*. 1993a). Later, when the larvae become too large to occupy the mines, they emerge onto the leaf surface and either fold over a single leaf and hold it down with silk, or web together two or more leaflets, and thereafter live and feed in the shelter they have constructed until they pupate (Shanower *et al*. 1993a; Kenis and Cugala 2006). Similar crop damage symptoms were observed on soya bean in Australia (Common 1990; Bailey 2007) and Africa (Namara 2015). Infestations of GSLM are usually detected by the presence of small brown blotches on (or in) the leaves and the webbing of leaflets

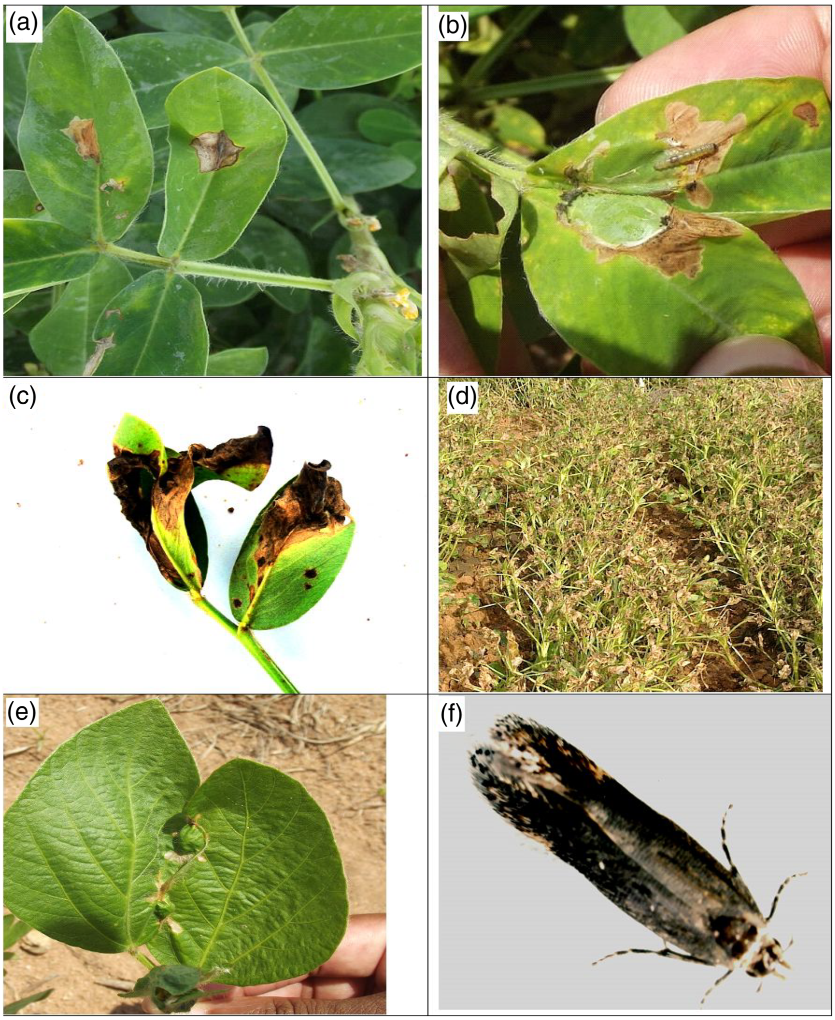

Fig. 1. Pictogram showing (1) symptoms of groundnut/soya bean leaf miner infestation in groundnut; early season leaf symptoms (a, b), late season symptoms, usually, inside the necrotic tissue are found pupae or non-feeding larvae (c) and crop defoliation (d), (2) groundnut/soya bean leaf miner symptoms on soya bean (e), exposed larva from between two attached groundnut leaves (b) and the groundnut/soya bean moth (f); the necrotic bubble/blotches in the middle of leaflets is shown in (a), the folding and webbing of leaflet is shown in (b, e) and the extensive necrosis of leaflets is shown in (c).

(Wightman & Ranga Rao 1993; Kenis & Cugala 2006; Lavanya 2009; Buthelezi *et al*. 2012; GRCD 2016; Ranga Rao & Rameshwar Rao 2013; Namara 2015; Herbison-Evans & Crossley 2018). The mined leaves become distorted within a few days. Three or four mines per groundnut leaflet can cause so much distortion that an infested leaf exposes as little as 30% of its potential photosynthetic area to the sun, which further affects the growth and yield of the crop (Kenis & Cugala 2006). The damaged leaves eventually become brownish, rolled and desiccated, resulting in early defoliation that aggravates yield losses (Kenis & Cugala 2006; Ranga Rao & Rameshwar Rao 2013).

Damage symptoms vary with time of season and growth stage of the crop (Buthelezi *et al*. 2012). Early in the growth season, the mines are relatively small, and the larvae produce small necrotic areas, mostly in the middle of the leaflets, or a slight folding at the end of a leaflet. Leaf folding and webbing may be less visible compared with the mid and late season symptoms. In late growth stages of the groundnut crop, the affected leaves are severely necrotic and distorted (Fig. 1). In severely affected plants, almost all leaflets are affected/infested (Buthelezi *et al*. 2013).

ECONOMIC THRESHOLD LEVELS

The economic threshold levels for GSLM differ between regions both locally and internationally and with the growth/development stage of the crop. In India, threshold level is reported to be two larvae per plant (Ghewande & Nandagopal 1997). In Uganda, control action against the pest is initiated when the infestation levels reach 5 and 10 larvae per plant at 30 and 50 days, respectively, after crop emergence (Epieru 2004). In southern Mozambique, infestation levels that cause economic damage range from 29 to 38 larvae per plant (Kenis & Cugala 2006). In South Africa, the threshold has been set at between 2 and 10 larvae per plant (Van der Walt *et al*. 2009). However, the critical plant growth stages at which these infestation levels reach the economic threshold levels have not been specified for Mozambique or South Africa. In Australia, where the leaf miner is regarded as a minor pest of soya bean, the threshold level is based on tolerable defoliation, which is 33–40% pre flowering and 15–20% during early pod filling (Bailey 2007).

RECOMMENDATIONS FOR FUTURE WORK

Recommendations for future research to facilitate the biosystematics of GSLM worldwide include the following:

1. Morphological and DNA analyses
   Even though intensive DNA analyses revealed that GSLM occurring in Africa, Asia and Australia, are very closely related, it is crucial to undertake morphological studies, including male genitalia dissections and descriptions, to confirm the taxonomic status of these populations. To complement the morphological studies, molecular and phylogenetic studies should include more samples from different worldwide geographical populations of GSLM to confirm the genetic relatedness of these populations.
2. Investigation on the off season survival strategies
   The off-season survival tactics of the different populations of GSLM is still vague, as there is no information on how it's populations carry over from one season to another in the different geographical regions where it occurs. Getting to understand how the leaf miner bridges the summer seasons under the various agro-climatic regions will assist in developing effective control strategies against GSLM.
3. Understanding the genetic basis for the non-virulence of the Australian populations on groundnut
   Although the GSLM is a serious pest for groundnut on the Asian and African continent, the Australian leaf miner population is not known to infest groundnut. It is thus assumed that the trait of discriminating host plants is under genetic control. Hence, solving the riddle why the Australian leaf miner population does not infest groundnut may provide biotechnological strategies for dealing with groundnut leaf miner infestations in Africa and India.

CONCLUSION

This review provided an insight on the identity as well as the bio-ecology of the three GSLM species, *A. modicella* from the Asian subcontinent, *A. simplexella* from Australasia and *S. subsecivella* from Africa, now regarded as populations of *B. subsecivella*. Various synonyms applied to this species are also provided. Information from the literature indicated that these species shared similarities in terms of host plants. Although there is overlap, different hosts are preferred in different regions. Morphology descriptions, crop damage symptoms as well as environmental conditions favouring the occurrence of these species are similar. Molecular studies (DNA analyses) indicated that these species are very closely related and are the major factors used to group these populations into one species. One of the main issues needing urgent attention is the revision of the general taxonomy of these populations, as correct identification of insect pests is crucial when developing control strategies against them.

ACKNOWLEDGEMENTS

Authors acknowledge Dr Klaus Sattler of the National History Museum, London, and Dr Martin Kruger of Ditsong Museum in South Africa for their valuable inputs regarding the taxonomy of the groundnut/soya bean leaf miner, Maik Bippus for his input on groundnut/soya bean leaf miner occurrence in Madagascar and Inqaba Biotech Industries for DNA sequencing.

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Accepted for publication 28 January 2021.