Observations on larval tunneling by the enigmatic South African Keurboom Moth *Leto venus* (Cramer, 1780) (Lepidoptera: Hepialidae)

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Abstract: Details of tunneling and feeding by larvae of *Leto venus* are described and illustrated for the first time. Larval tunnels were examined from a section of lower trunk of the host plant *Virgilia oroboides ferruginea* from the Garden Route Botanical Gardens. Tunnels were 255-324 mm in length and of irregular cross sectional shape and located in the outer cortex and phloem, sometimes intersecting bark. Emergent pupae protrude from the host, sometimes from a 'cocoon' of silk and debris that also forms a tubular extension beyond the bark surface. The location of tunnels and their short length relative to the size of the larva and duration of larval development suggests that larvae are not primarily wood consumers, but utilize a replenished food supply, perhaps grazing phloem resulting in a sustained release of nutrient rich sap. The tunneling and feeding mode of *L. venus* provides new insights into possible modes of evolutionary transition between general tissue feeding found in many root feeders and callus feeding that occurs in other stem boring Hepialidae.

Key words: Garden Route Botanical Gardens, Hepialidae, Keurboom, larva, Lepidoptera, *Leto venus,* stem boring, South Africa, *Virgilia oroboides*

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INTRODUCTION

Ghost moths (Hepialidae) are found in most of the habitable regions of the world with notable exceptions being the Caribbean, central West Africa (including most of the Congo Basin) and Madagascar. African ghost moths are represented by *Neohepialiscus algeriensis* (de Joannis, 1903) [not in References] in the coastal regions of North Africa, and five genera to the south and east of the Congo basin (Grehan & Mielke, 2018). Of these, *Antihepialus* (four species), *Eudalaca* (36 species), and *Gorgopis* (30 species) have subterranean larval stages that feed on roots or ground vegetation (Grehan, 1989). There is no information on the genus *Metahepialus* (two species) although it is also likely to be subterranean. The remaining genus, represented by the Keurboom moth *Leto venus* (Cramer, 1780), is a stem borer. This larval habit has been known for nearly 80 years (Janse, 1939) but over that time there has been very little published about the details of larval feeding. This may seem quite surprising as the adult moth is such a large and visually stunning insect (Fig. 1).

The Keurboom Moth is endemic to the southern Cape Region of South Africa between Worcester and Witelsbos

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**Figure 1** - Keurboom moth, *Leto venus*. Bergville, South Africa. February 13, 2016.

(Fig. 2). Moths emerge from about 18h45 during the late summer (February) and autumn (April) (Duke & Taylor, 1964). There are at least three host plant species that are all in the family Fabaceae – the Honeybush (Heuningbos) *Cyclopia subternata*, and the Keurboom trees *Virgilia divaricata*, and *V. oroboides* (Grehan *et al.*, 2018). *Virgilia* trees are important pioneer species in forest succession and are often found on forest margins (Coetsee & Wigley, 2013; Machingambi, 2013). *Cyclopia* species

Figure 2 – Distribution records for *Leto venus*. Modified from Grehan *et al*. (2018).

are long-lived perennial shrubs in fire-prone fynbos vegetation of the Cape Region (Schutte, 1997; McGregor, 2017).

The earliest published notes on the biology of *Leto venus* were by Janse (1939, 1942) who knew only that the larva lived under the bark of an unnamed host tree and that one local family was keeping details of the life history secret in order to restrict the market and keep up the price for selling the moth. Details were later made available to Janse (1945) who reported that *Virgilia oroboides* is the host plant (then the only known host), eggs are laid in the earth around the stem or roots, larval tunneling occurred at the base of the tree with the top of the tunnel usually reaching about 60 cm (two feet) above ground, larvae eject "sawdust" from an opening at the top of the tunnel (Fig. 3) and at pupation this opening is filled with a cap of "gummy sawdust" and the upper tunnel is filled with fine silk threads (Figs 3 & 4). At adult emergence pupae were reported protruding from the stem in February and March (Figs 5–7).
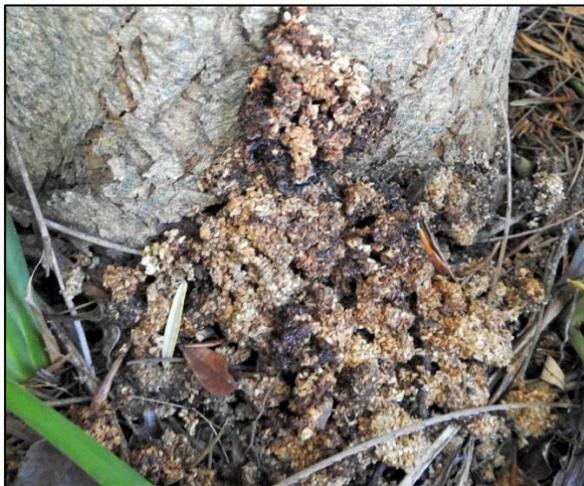
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Figure 3 – Frass ejection from tunnels of *Leto venus*, showing exudates seeping from tunnel opening. Garden Route Botanical Gardens (GRBG), 16 April 2018.

Not until nearly two decades later were further observations published, both in the same year. Duke & Taylor (1964) reported moths emerging from a Keurboom stump between 6.45 and 10.15 pm during February and March, and reported a heavy larval infestation at Longridge farm near Plettenberg Bay, where nearly all the larger trees were occupied and many trees were infested by more than one larva.

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Figure 4 – Frass ejected from base of tree. GRBG, 17 April 2018.

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Figure 5 – Pupal stage of *Leto venus*, showing pupal exuviae with minimal silk/frass tubing. GRBG, 23 July 2018.

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Figure 6 – *Leto venus* pupal exuvium protruding from silk/frass tube. GRBG, 25 Mar 2018.

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Figure 7 – *Leto venus* frass/silk lining forming a pupal 'cocoon' in the upper tunnel. Lower end of the tube to the left.

More extensive notes were made by Geertsema (1964) for infestations of *Virgilia* trees at Farleigh and Groenkop Forest Reserve, where an estimated one third of trees were damaged. Larval development was thought to last up to three years, and he observed courtship, where females seek out males followed by copulation lasting about one hour. Eggs were reported to be dropped over the ground between or near Keurboom roots where they matured over a 1–2 week period. Larval tunnels were found near the pith and extended up from the point of entry and reached a diameter of about 14 mm. At pupation larvae hollowed out a pupal chamber up to 1 m above ground and constructed a tubular extension of silk and frass projecting beyond the trunk surface for several centimeters. The only subsequent observation on larval biology was by Scoble (1981) who also noted high densities of larval activity in some Keurboom trees and reported one tree with over 20 protruding pupal cases.

This paucity of information on larval tunneling and feeding for one of South Africa's most prominent and unique moths came to the attention of one of the authors (CDR), who made some close observations on infestations of Keurboom trees at the Garden Route Botanical Gardens (GRBG) in George (http://www.botanicalgarden.org.za/). As a result of these observations it was apparent that an examination of tunnel structure and distribution was desirable in order to better characterise the biology of *L. venus* in comparison with other Hepialidae. We report here some preliminary observations from this study of larval infestation in *Virgilia oroboides*.

MATERIALS AND METHODS

In addition to casual observations of larval activity externally visible on keurboom trees (*Virgilia oroboides ferruginea* B.-E. van Wyk) in and near the Garden Route Botanical Gardens, a small tree (height 3.5-4 m, basal diameter about 120 mm) was selected for removal and internal examination to assess the extent and form of larval tunneling (Fig. 8). The tree was located near the boundary of the GRBG (https://www.inaturalist.org/observations/13505590 - last accessed 29 June 2018), growing among some border vegetation between the park boundary and adjacent housing in the city of George. This site is about 0.10 km from forest extending as a spur from George Peak of the nearby Outeniqua Mountains. The tree was

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Figure 8 – Excavation of the host tree.

removed, with permission from the GRBG, and the basal 40 cm section of the trunk and roots was separated (Fig. 9) and subjected to a magnetic resonance imaging (MRI) scan. Guided by the scan, cross sections were then cut through the stem to confirm scan interpretation. A longitudinal section was also made to characterise the full extent of tunnel development.

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Figure 9 – Excavated base of host tree to be examined.

RESULTS

The tunnels were all within the lower 40 cm of the stem (Figs 10 & 11) and did not penetrate into the roots. The MRI scan (Fig. 12) revealed the presence of five tunnels, all located between the outer cortex and the bark, with some sections penetrating through the bark at or near the top end of tunnels (Fig. 12). Subsequent sectioning of the

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Figure 12 – Cross section of *Leto venus* host plant trunk MRI section showing position of tunnels.

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Figure 13 – Cross section of *Leto venus* host plant at region of maximum tunnel damage. Tunnels all partially or completely filled with frass, tunnels outlined with white dashes.

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Figure 10 – Dissection of *Leto venus* host plant – basal section intact showing signs of bark damage from tunnels within.
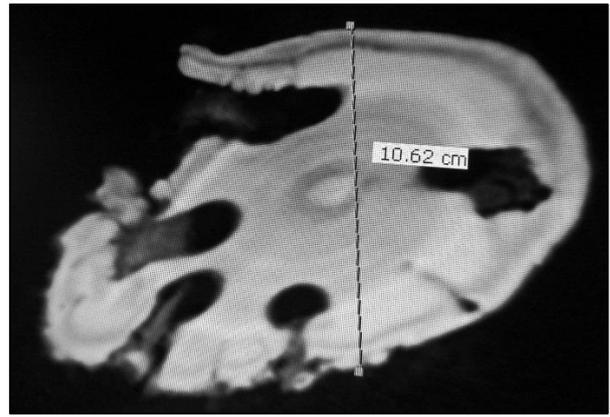

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Figure 11 - *Leto venus* host plant section of trunk with entire length of one tunnel exposed. Pupal exit at the top.

stem confirmed this distribution and revealed extensive frass in the tunnels (Fig. 13). The maximum total tunnel lengths did not exceed 40cm and they showed only a very slight decrease in diameter towards the lower end. The tunnels all ended between one and 4-5cm above the root zone, the average distance being two centimeters.

The base of all tunnels was filled with frass, which has a different texture to finer grained "sawdust" higher up. No exit or entry holes were seen near the base of the tunnels. The only opening in each tunnel was about

20cm above ground level where frass was ejected and from which the pupae emerges. Frass was found to fill about half the tunnel length and sometimes the entire tunnel was filled. Frass sometimes filled the entire width of the tunnel or only one side of the tunnel. There were also large amounts of frass towards the bark side where major bark damage had occurred. This frass partially blocked what appeared to almost be gashes in the stem. Tunnel length averaged 287 mm in length (255, 268, 278, 310, 324 mm).

The shape of the tunnels in cross-section varied from almost circular to a range of ovoid extensions, sometimes broad, sometimes flattened (Figs 12–15). In various parts of the tunnel tissue excavation extended into the bark or immediately subtending tissue (phloem), and in some cases the bark was removed entirely or had died, resulting in lateral regrowth on either side (Fig. 15).

DISCUSSION

Observations by Geertsema (1964) stated that larvae tunnel into the 'pith', presumably meaning the central

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Figure 14 – *Leto venus* host plant tunnel centered on region adjacent to bark with local extension (ex) into cortex.

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Figure 15 – *Leto venus* host plant tunnel damage to adjacent bark with lateral regrowth.

region of the stem. But in our sample, along with other external observations made by one of us (CDR), leads us to infer that tunnels are usually excavated in the outer cortex and phloem. Geertsema (1964) also stated that the full grown larva descends and moves just under the bark of the tree, but it is our impression that the mature larva moves to the top of the tunnel, where it pupates. Based on the extent of bark damage and the presence of lateral regrowth we would agree with earlier inferences for larval development to last more than one year. Geertsema (1964) also refers to entry of the host plant after egg eclosion, but there is currently no independent corroboration of his observations. If early development in *L. venus* follows the pattern of other stem borers (Grehan, 1989) the first and early instars may be expected to have an initial detrital feeding stage of development among plant detritus on the ground. Future work on early instar development and sampling of new tunnels following adult emergence will be necessary to elucidate which form of early larval development is applicable to *L. venus*.

Most genera and species of Hepialidae have subterranean larvae that feed on roots or ground foliage, while a smaller number of genera have a larval habit characterised by feeding that is limited to grazing wound tissue (callus) around the tunnel entrance under a web of silk and wood particles. This pattern of feeding is recorded for the genera *Aenetus* (Asia-Australia), *Endoclita* (Asia), *Zelotypia* (Australia), *Phassus* and *Schausiana* (Mexico-Central America), and *Trichophassus* and allied genera (Mexico-South America) (Grehan, 1989). In these genera the tunnels are initiated above ground and the tunnel is permanently open to the surface of the host other than the web covering over the entrance, and tunnel construction is usually limited in extent even for species with multi-year development. A third pattern of stem feeding is recorded for *Phymatopus californicus* in *Lupinus arboreus* Sims (Fabaceae), a fast-growing shrub that grows in dense monospecific stands in coastal grasslands (Maron, 2001). Larvae usually tunnel in the base of the stem and tap-root, feeding on live woody tissues but sometimes in dead stems. Tunnels have one or two openings to the surface that are plugged with a mixture of frass, wood shavings and silk. Masses of this material are ejected from the tunnel (Fig. 16). Larvae appear to feed exclusively on cortical tissues (Fig. 17). Some tunnels are almost the same length as the body, possibly suggesting that larvae construct new tunnels, since wandering late instar larvae have been occasionally observed (Wagner, 1985; Maron 1998, 2001).

D. Strong

Figure 16 – Damage to *Lupinus arboreus* in California by larvae of *Phymatopus californicus* – external view of damaged bark and larval frass ejection at trunk base.

D. Strong

Figure 17 – Damage to *Lupinus arboreus* in California by larvae of *Phymatopus californicus* – exposed larvae and tunnels.

Tunnel features of *L. venus* shared in common with callus feeding Hepialidae include above ground initiation, a short tunnel relative to the size of the larva and duration of development, and tunneling into the stem rather than roots (some callus feeding species sometimes extend their tunnels into the upper roots). Contrasting features involve the absence of callus feeding and the upward expansion of the tunnel, and the packing of tunnels with frass in *L. venus*. While the food substrate of callus feeders is made obvious by the restricted location of feeding and by callus growth, the food substrate of *L. venus* is less certain. The short tunnel length suggests that the larva is not primarily xylophytic and consuming cortical tissue, as in Coleoptera, such as cerambycid beetles where tunnels are extended as the wood is consumed. The close proximity of the tunnels to the bark, and especially with portions of the tunnel extending to the bark and phloem region, may suggest that the larvae feed on the nutrient rich phloem, but without producing a callus regrowth or feeding on adjacent areas of regrowth that can sometimes be observed on the lateral edges of the tunnel.

The consumption of woody tissues in root feeding Hepialidae is variable. In Australia, species of *Abantiades* that feed on the roots of *Eucalyptus* trees consume callus tissue (Simonsen, 2018). In this respect they have the same feeding mode as callus feeding stem borers. In North America larvae of *Korscheltellus gracilis* consume tissues immediately below the bark but they do not extend tunnels into the cortex, and when feeding on young seedlings they consume only the thin bark and phloem (Wagner *et al.*, 1991). Descriptions of feeding on woody roots in other Hepialidae is too sparse to characterise fully. Larvae of *Korscheltellus fusconebulosa* may consume entire roots and sometimes bore tunnels within the roots of beech trees (Fagaceae) and blueberry shrubs (Ericaceae) (Gößwein, 2014). Larval feeding by *L. venus* may represent an 'intermediate' mode of feeding in the evolution of callus feeding stem borers, where the larva is a specialist stem feeder (in constrast

to the combined stem and root boring of *Phymatopus*) that has a grazing mode of food consumption (that may include fluid feeding from damaged phloem) but without generating a callus that is grazed.

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