

Eye morphology and colour preferences in a semi-field test of the pine pest, *Sirex noctilio* (Hymenoptera: Siricidae)

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The woodwasp, *Sirex noctilio*, is a global pest of pines. Although it is known to be attracted to light and possess sexually dimorphic body colouration, the visual ecology of *S. noctilio* is poorly understood. Photoreceptor sensitivity of the compound eyes in *S. noctilio* is not sexually dimorphic. These previous results suggest that colour tracking of one sex by the other might not be an important input for mate searching. This study aimed to expand our knowledge of the visual system of *S. noctilio* by means of i) morphological description of the compound eyes and ocelli; and ii) semi-field behavioural tests of the colour preference of newly emerged wasps. Eye and ocellus morphological features were investigated in 21 males and 21 females. Measurement of male and female median ocellus diameter, compound eye surface area, number of ommatidia and facet diameter varied from 0.22 to 0.40 mm, 0.589 to 2.277 mm², 1820 to 4207 and 1.88×10^{-2} to 2.82×10^{-2} mm, respectively. In addition, all traits significantly correlated with body size. Male and female wasps emerged from infested host material in a flight cage with five traps, each reflecting a different colour. Analysis of trap captures did not identify any colour preference, but an effect of trap location was observed with traps in the north-eastern position capturing more woodwasps, suggesting that other factors, e.g., global landmarks or other non-colour visual cues might guide initial flight behaviour of *S. noctilio*.

INTRODUCTION

The woodwasp, *Sirex noctilio* (Hymenoptera: Siricidae), is a global pest of pines. It is native to Eurasia and has been accidentally introduced in the southern hemisphere (Miller & Clark 1935; Gilbert & Miller 1952; Rebuffo et al. 1990; Tribe 1995) and recently in North America (Hoebeke et al. 2005) and China (Li et al. 2015). Females use their ovipositor to drill a hole in the bark of pine trees and lay eggs, with a phytotoxic mucus and the symbiotic fungus, *Amylostereum areolatum* (Talbot 1977). The combination of these three elements can result in tree mortality when multiple attacks occur (Coutts 1969; Bordeaux & Dean 2012). Control programmes based on silvicultural practices, surveillance with baited traps, and biological control sometimes provide unsatisfactory results and losses still occur (Hurley et al. 2007, 2015; Dodds & de Groot 2012; Slippers et al. 2012; Dodds et al. 2014).

Adults of *S. noctilio* are diurnal, do not feed, and only live for a few days (Neumann & Minko 1981). During this short time, there is strong selective pressure on the adults to find mates and oviposition sites. In insects, sexual dimorphism in olfactory and/or visual traits (e.g. pheromones, body shape and colouration) are commonly associated with mate location and attraction. A putative male pheromone released from the sexually dimorphic hind legs has been identified in *S. noctilio* (Cooperband et al. 2012; Guignard et al. 2020). However, the addition of the synthetic male pheromone to traps baited with a commercial pine kairomone did not increase the number of insects captured in the field (Hurley et al. 2015).

The biology of *S. noctilio* suggests that colour vision could play an important role in reproduction, and thus, knowledge of the stimuli involved could be exploited to increase trapping efficiency. Various species of Symphyta show colour preferences in choice experiments, where yellow traps are generally more attractive than other colours (reviewed in Guignard et al. 2022a, see also Anderbrant et al. 1989, Barker et al. 1997, Holuša & Drápela 2006, Taniwaki 2013, Song et al. 2015, Véték et al. 2016). Male and female *S. noctilio* are sexually dimorphic, females are all black whereas males are black with an orange abdomen. Before mating, males form leks in the forest canopy, and these leks may be an attractive visual stimulus to females. For example, simulated leks in a field experiment increased the number of females captured when no host volatiles were present (Allison et al. 2019). A vertical flight distribution experiment in Patagonia demonstrated that males flew higher than females, but when males are present females flew higher than when males were not present (Martínez et al. 2014). Flight experiments in a large wind-tunnel demonstrated that traps baited with ultraviolet (UV) lights capture significantly more *S. noctilio* than traps without UV lights or baited only with a commercial pine kairomone (Sarvary et al. 2015). However, to date no studies have tested for colour preferences in *S. noctilio*.

Recently, it was speculated that colour vision might be less developed in *S. noctilio* than in other hymenopterans (Guignard et al. 2021). The ability to discriminate between colours depends on the

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DATES

Received: 9 March 2022

Accepted: 26 July 2022

KEYWORDS

monitoring
surveillance
Symphyta
visual ecology

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number of photoreceptor types in the compound eyes, differing in their spectral sensitivity. In hymenopterans, like in most other insects, spectral sensitivity is mainly determined by the opsins expressed in each photoreceptor. Three common groups of opsins exist in insects: long, short and UV opsins, named after the wavelengths of light for which they have maximum sensitivity (Briscoe & Chittka 2001; Feuda et al. 2016; van der Kooi et al. 2021). The vast majority of Apocrita have been shown to express one copy of the long, short and UV opsin in their compound eyes coding for green, blue and UV wavelength-sensitive photoreceptors, respectively (Peitsch et al. 1992; van der Kooi et al. 2021; Guignard et al. 2022b). In contrast to most Apocrita, the short opsin is missing in the genome of *S. noctilio*, and the corresponding blue wavelength-sensitive photoreceptor was not found in electroretinogram experiments (Guignard et al. 2021). This suggests that *S. noctilio* might be less sensitive to different colours than most Hymenoptera, indicating that colour vision may have a limited role in the ecology of this insect.

The goal of the study was to provide detailed information on the visual system and visual ecology of *S. noctilio*. Specifically, we aimed to i) characterise morphological traits of the compound eyes and ocelli and ii) test whether trap colour had an effect on *S. noctilio* captures in an outdoor cage experiment.

MATERIALS and METHODS

Insects

The collection and rearing protocol of the *S. noctilio* wasps used in this experiment are identical to those described in Guignard et al. (2020). In brief, in September 2018 pine logs naturally infested with *S. noctilio* were collected from Knysna, South Africa. Logs were transported to and stored in an insectarium at 20 °C with ambient relative humidity and a photoperiod of 12 hours from late October until the following January. Wasps used for morphological measurement were caught after eclosion, and individually stored in a refrigerator at 12 °C.

Morphological measurements

Morphological measurements of the compound eyes and ocelli were made on a total of 21 males and 21 females. The intertegular span (ITS) was used as a proxy of body size (Cane 1987; Streinzer & Spaethe 2014). Four morphological variables were measured for all individuals: diameter of the median ocellus (mm), eye surface area (mm²), number of ommatidia and facet diameter (mm); as described in Streinzer and Spaethe (2014). In brief, ITS and ocelli were measured from digital photographs, taken with a stereomicroscope (Leica EZ4D with integrated camera, Leica Microsystems, Wetzlar, Germany). Ommatidia number, facet lens diameter and eye surface area were measured from eye replicas made of nail polish (Forrest 1962; Streinzer & Spaethe 2014). Ommatidia numbers were determined by manually marking all facets of digital photographs of the eye replica in Fiji (Schindelin et al. 2012), which were taken by a Canon 6D Mark II (Canon, Tokyo, Japan) attached to a Leitz Orthoplan (Leica Microsystems). To measure facet lens diameter, we measured a row of ten ommatidia in all three axes in the centre of the compound eye and calculated the mean facet lens diameter (Streinzer & Spaethe 2014). Eye surface area was determined by tracing the outline of the eye replica in Fiji.

Behavioural tests

Ten black panel traps were painted with one of 5 different colours (i.e., two of each colour). Traps were first painted with two layers of undercoat and then with two layers of the test colour (black: RAL 9005, blue: RAL 5015, red: RAL 3020, yellow: RAL 1018, green: RAL 6037; Figure 2A) on the entire trap and bucket. A second set of similarly painted 5 panel traps were

used for reflectance measurements. All measurements were performed following standard protocols (e.g. Chittka & Kevan 2005). We used a JAZ spectrometer unit equipped with a pulsed Xenon light source (Ocean Optics, Dunedin, FL, U.S.A). The spectrometer was calibrated against a white standard (WS-1-SL, Ocean Optics).

Fourteen infested logs from George (South Africa) were stacked by alternating parallel pairs oriented perpendicular to each other to make a square log deck pile 1.6 m high, in two different walk-in-cages 20 m apart. In each cage, five panel traps, one of each colour, were placed at a distance of 1.6 m from the centre of the log pile with the bottom of the collecting cup 60 cm above the ground. The first trap was placed directly south of the log pile (= 180°) and the rest of the traps were placed every 72 degrees clockwise. In both cages, trap colours were randomly placed and then moved daily so that each colour was placed at each position for an equal amount of time. Traps were checked daily, the collection cups emptied and the number of *S. noctilio* were recorded for 7 weeks. Due to low emergence numbers, insects caught in the two cages were pooled together for statistical analyses.

Statistical analyses

The ITS between male and female was compared using a Welch *t*-test. Linear regression analyses of the relationship between ITS and the four morphological variables measured for both sexes were computed after verification of normality for each variable ($\alpha = 0.05$). All models were validated after graphical verification of the normality of residuals and homoscedasticity. The percentage of insects captured per week was not normally distributed and a Kruskal-Wallis test ($\alpha = 0.05$) was used to determine if there were position or treatment effects followed by a pairwise Wilcoxon test (Holm correction) post hoc analysis. All statistical analyses were performed in Rstudio (v 1.1.383).

RESULTS

Morphological measurements

The ITS was significantly smaller in males (minimum = 1.57 mm, maximum = 3.80 mm, average = 2.60 ± 0.55 mm) than females (minimum = 1.84 mm, maximum = 4.29 mm, average = 3.19 ± 0.64 mm) (p -value = 0.0053, $t = 2.96$, $df = 37.98$). The median ocelli diameter, compound eye surface area, number and diameter of ommatidia were all positively correlated with the ITS (Figure 1 and Table 1). Inclusion of sex alone or together with the ITS in the model did not significantly improve the fit for each of the four variables tested (Table 1). Thus, no differences between males and females of similar ITS (size) were detected for the four morphological variables measured.

The median ocellus diameter was 0.28 ± 0.04 mm (min = 0.22 mm, max = 0.36 mm) for males and 0.31 ± 0.05 mm (min = 0.23 mm, max = 0.40 mm) for females. The compound eye surface area was 1.25 ± 0.40 mm² (min = 0.59 mm², max = 2.28 mm²) for males and 1.67 ± 0.52 mm² (min = 0.67 mm², max = 2.66 mm²) for females. The number of ommatidia was estimated to be 2607 ± 466 (min = 1820, max = 3987) for males and 3188 ± 560 (min = 2126, max = 4207) for females. The estimated ommatidia diameter was $2.28 \times 10^{-2} \pm 2.29 \times 10^{-3}$ mm (min = 1.91×10^{-2} mm, max = 2.82×10^{-2} mm) for males and $2.29 \times 10^{-2} \pm 2.17 \times 10^{-3}$ mm (min = 1.88×10^{-2} mm, max = 2.78×10^{-2} mm) for females.

Trapping experiment

A total of 51 woodwasps were captured (28 males and 23 females) during the 7 weeks. No significant differences were observed between captures in traps of the 5 colours (Figure 2B) ($H(4) = 2.62$, $p = 0.623$). However, there was a position effect with trap

Table 1. Linear regression analyses of the four dependant variables tested (ocellus diameter, compound eye surface area, number of ommatidia and ommatidia diameter) from males ($n = 21$) and females ($n = 21$). Males and females were pooled to calculate the mean \pm SD. Asterisk indicate a p -value < 0.05 of the Student t -test

Dependent variable	Average (mean \pm SD)	Independent variable	Estimate	Standard Error	p -value (Student t -test)	Significance
Ocellus diameter (mm)	0.294 \pm 0.047	Intercept	0.103414	0.028536	0.00081	*
		ITS	0.063346	0.008646	6.6×10^{-9}	*
		Sex	0.037834	0.037596	0.32032	
		ITS \times sex	-0.011583	0.012429	0.35696	
Compound eye surface area (mm ²)	1.46 \pm 0.5	Intercept	-0.84801	0.14838	1.4×10^{-6}	*
		ITS	0.78793	0.04566	$<2 \times 10^{-16}$	*
		Sex	0.33820	0.20379	0.105	
		ITS \times sex	-0.10865	0.06972	0.127	
Number of ommatidia	2897.9 \pm 588	Intercept	532.25	202.07	0.0121	*
		ITS	832.51	62.18	5.78×10^{-16}	*
		Sex	34.66	277.52	0.9013	
		ITS \times sex	-46.49	94.94	0.6272	
Diameter of ommatidia (mm)	0.0234 \pm 0.00228	Intercept	0.01463	0.001656	9.61×10^{-11}	*
		ITS	0.002921	0.0005097	1.33×10^{-6}	*
		Sex	0.0008008	0.002275	0.727	
		ITS \times sex	-0.00007688	0.0007782	0.922	

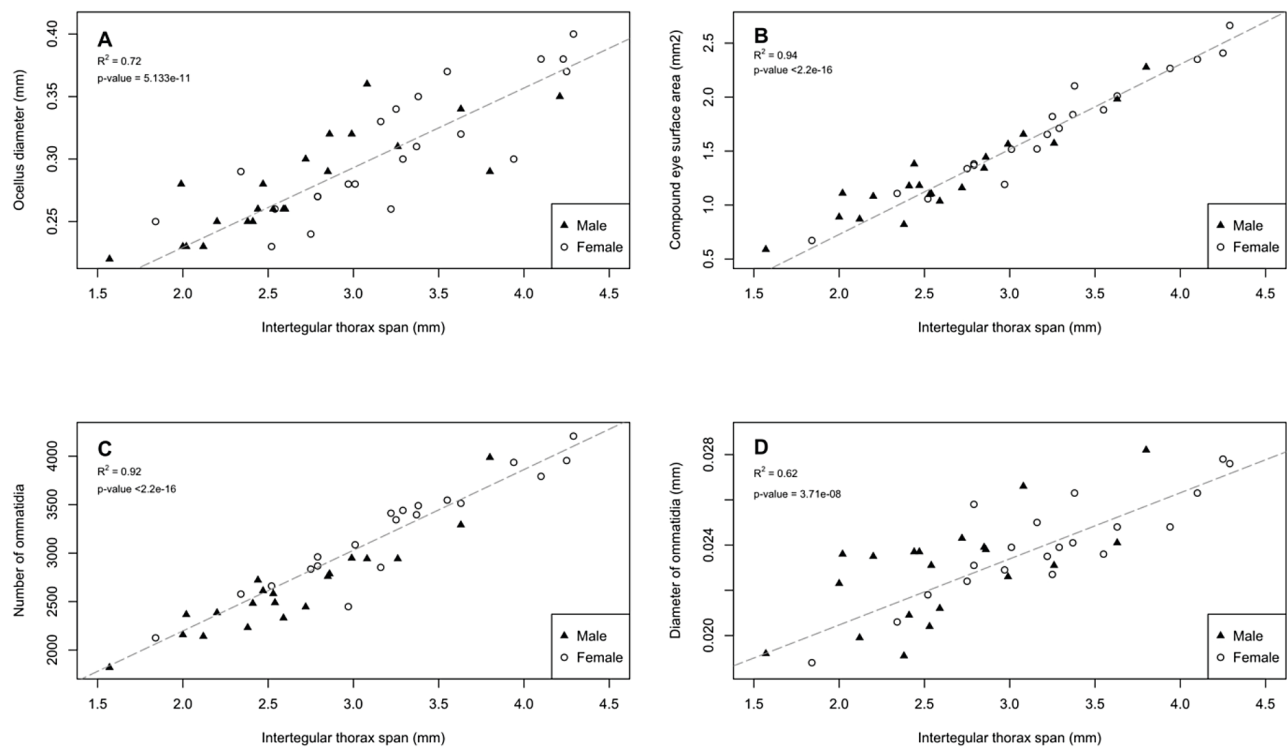


Figure 1. Intergular thorax span (ITS) plotted against the ocellus diameter (A), compound eye surface area (B), number of ommatidia (C) and the diameter of ommatidia (D) for 21 male (triangles) and 21 females (circles). All variables were positively correlated with the ITS but no difference between males and females were found (Table 1). Linear regression results (Multiple R^2 and p -value of F -statistic) were combined for males and females and lines were added for each variable tested

position four (36 degrees, northeast) capturing significantly more woodwasps than the other locations (Figure 2C) (52% \pm 12%, $H(4) = 16.59$, $p = 0.023$).

DISCUSSION

This study added new information on *S. noctilio* eye morphology and colour preferences. The results show no sexual dimorphism in the visual system but a positive correlation between insect size and eye morphology was observed. No preference for any of the colours tested was observed; however, relatively few

wasps emerged from the logs due to a low level of infestation. Traps placed at the north-east position of the cage captured more individuals than all other positions independent of trap colour. We conclude that immediately post-emergence positive phototaxis has a stronger impact on *S. noctilio* orientation behaviour than any potential colour preferences.

The compound eyes and ocelli of *S. noctilio* possess typical features of a diurnal visual system and their morphology are comparable to typical diurnal bees of similar size (Jander & Jander 2002; Kelber & Somanathan 2019). Our study showed

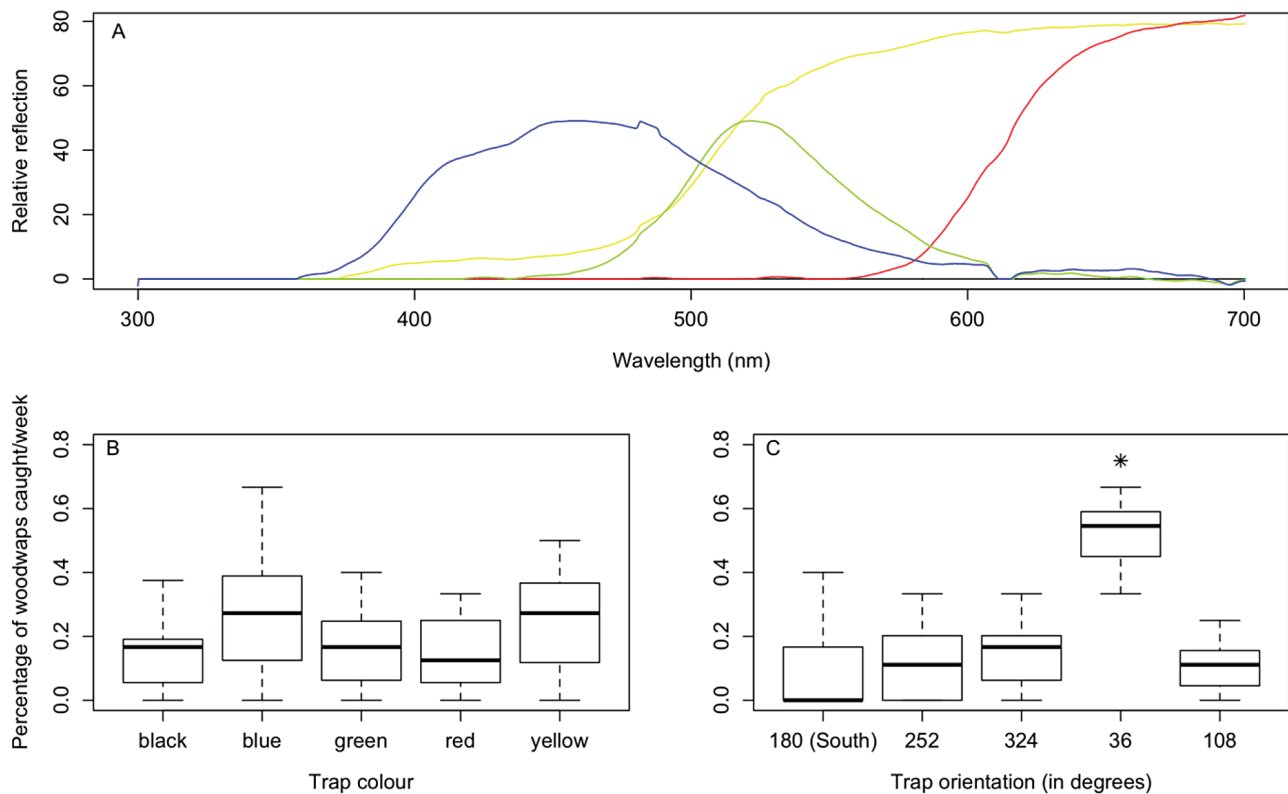


Figure 2. Relative reflectance (%) of panel traps painted with different colours used in the behavioural tests (A) and box-and-whisker plots of the proportion of total captures ($n = 51$) of *S. noctilio* caught per week in traps painted different colours (B) and placed at different positions (C). No effect of trap colour, but a significant effect of trap position was observed (for statistics see text)

that the ocelli diameter, the compound eye surface area, and ommatidia number and diameter were positively correlated with body size in *S. noctilio*. Ommatidia number and eye surface area can double between small and large *S. noctilio*. Similar research on other hymenopterans demonstrated that larger individuals have bigger eyes and possess better visual discrimination (e.g. image resolution, low-light sensitivity) than smaller individuals (Spaethe & Chittka 2003; Kapustjanskij et al. 2007; Kelber et al. 2011). In *S. noctilio*, body length within sex can vary from 9.3 to 34.9 mm for males and 10.0 to 44.0 mm for females (Ryan & Hurley 2012). In addition to putatively better visual acuity, larger females in *S. noctilio* were shown to perform longer and faster flights than smaller females (Bruzzone et al. 2009; Gaudon et al. 2016). The increased eye size and ommatidia number and flight capability of larger *S. noctilio*, likely increase their chances to find mates and suitable oviposition sites but empirical support does not currently exist. Such variation in eye morphology is not common in insects of the same sex or cast making *S. noctilio* an interesting model to study how eye size affects visual acuity in insects.

There are no differences between male and female *S. noctilio* eye morphology, opsin expression or spectral sensitivity (Guignard et al. 2021). Differences in eye morphology between sexes have been observed when the use of visual stimuli differs between males and females (Wehrhahn 1979; Meyer-Rochow & Reid 1994; Hornstein et al. 2000; Lau & Meyer-Rochow 2006; Straw et al. 2006; Meyer-Rochow & Lau 2008; Streinzer & Spaethe 2014; Brand et al. 2018). Similarly, differences in spectral sensitivity between males and females have been observed in species where one sex uses visual signals to attract the other sex (Arikawa et al. 2005; Sison-Mangus et al. 2006; Lau et al. 2007; Ogawa et al. 2013). Although previous studies have observed behavioural responses to visual stimuli (Martínez et al. 2014; Sarvary et al. 2015; Allison et al. 2019), our data suggest that colour vision may play a minor role in mate location and recognition in *S. noctilio* compared to achromatic cues or other non-visual stimuli.

The behavioural experiment found no evidence of any colour preference in newly emerged wasps. However, a significant position effect was observed in the circular trapping arrays with approximately five-times more individuals captured in traps placed on the north-east side of the array (e.g., 36°). Similar results were found when males and females were analysed separately, but were poorly supported due to the low number of insects, and thus further experiments are needed. A possible explanation for this pattern could be higher morning activity. *Sirex noctilio* is known to have strong positive phototaxis (Morgan & Stewart 1966; Sarvary et al. 2015; Hurley et al. 2015). These results suggest that the position of the sun in the morning might be attractive to newly emerged *S. noctilio* and could explain why more insects were captured on the north-eastern side of the cage. These results agree with earlier reports that *S. noctilio* concentrate on the eastern side of emergence cages, are most active in the morning, and that mating occurs in the morning (Dolezal 1967). However, other factors (e.g., prevailing wind direction) may explain the observed position effect.

In summary, *Sirex noctilio* possesses typical apposition eyes and no sexual dimorphism in eye morphology. In contrast to what has been observed in most Symphyta, no colour preferences were recorded. However, it is unclear why the north-eastern position captured significantly more individuals, but this might be due to positive phototaxis to the morning sun. Thus, the morphology, physiology and behaviour of *S. noctilio* do not indicate a strong role of colour vision in the biology of *S. noctilio*. Further studies on the use of achromatic cues such as brightness contrast or light intensity should be conducted to better understand the visual ecology of *S. noctilio*.

ACKNOWLEDGEMENTS

We thank the Entomological Society of Southern Africa (ESSA) for the travel grant to QG to visit JS at the University of Wurzburg where the morphological measurements were done. We thank Amanda Adlam for her review of an early

draft of the manuscript. This research was funded by the United States Department of Agriculture-Forest Service Forest Health Protection (USDA-FS FHP), Natural Resources of Canada (NRCAN), the Tree Protection Cooperative Programme (TPCP) and the DSI NRF Centre of Excellence in Plant Health Biotechnology (CPHB) in South Africa. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

AUTHORS' CONTRIBUTIONS

QG did the conceptualisation, method, data curation, formal analyses, visualisation, wrote the original draft and reviewed and edited the manuscript; JS did the conceptualisation, supervision of NN, methodology, reviewed and edited the manuscript; BS did conceptualisation, funding acquisition, supervision of QG, reviewed and edited the manuscript; NN did the data methodology and data curation of the eyes morphology, reviewed and edited the manuscript; JA did conceptualisation, funding acquisition, supervision of QG, reviewed and edited the manuscript.

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