

A comparison of the eye anatomy of tropical stingless bees



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Abstract

Vision is the most important tool for flying insects to control their flight behaviour. It is especially important for tropical stingless bees living in a cluttered environment, for example the rainforest, where there vegetation is dense making it difficult to navigate through. Stingless bees possess apposition compound eyes, and there is still only a little information about how volume of different regions within the eye might affect the visual acuity. In this study the morphological and anatomical difference of six species of tropical stingless bees were compared. Morphological and anatomical variations correlate with behavioural differences and result from natural selection pressure. This study investigated if evolution has selected for different traits and morphological differences to better adapt to the needs of the tropical stingless bees. The results showed that there are some variations between the different species. We found that *Melipona Bicolor* is a species with a large volume of lenses and photoreceptors indicating that they might be adapted in to having eyes that are capable of sensitive vision with good resolution.

1. Introduction

Among all senses vision is the most important tool for flying insects to control their flight behaviour. It is especially important for them to have a good vision because insects are flying long distances at high speeds, sometimes in cluttered environments. They also have to be able to perform a lot of different tasks, for example identifying predators, distinguish flowers based on shape and colour and navigate back to their nests using environmental cues (Michener, 2007).

For all these tasks they use visual information detected by their two compound eyes. Like many insects, bees have apposition compound eyes; they consist of a large number of small units called ommatidium. The ommatidium contains a lens, a crystalline cone and a cluster of photoreceptors. The function of the lens, or the facets, is to collect the light in to the crystalline cones the aperture through which light is focused. Finally the light reaches the photoreceptors, rhabdomeres, and the information is passed through to the brain. Each ommatidium supplies one 'pixel' of information to the apposition eyes, the pixels are later reconstructed in the brain in to one image (Land and Nilsson, 2012).

Bees can achieve a very controlled flight despite their small size and limiting brain regions (Lars Chittka and Niven, 2009). This is partially due to being very adapted to specific tasks. For example in the rainforest it is very important to be able to have a good flight control because there is a lot of vegetation that bees have to navigate through. In the rainforest of South America the stingless bees are the most common species of bees and a very important pollinator (Michener, 2007). Stingless bees or Meliponines are a tribe group of bees comprising about 500 species and can be found in most tropical or subtropical regions of the world (Michener, 2007).

However, little is known about if there is a need for better vision in bees living in a cluttered environment, for example in the rainforest. To begin investigating this, we tried to determine if there is a variation in the eye anatomy of different species of stingless bees, living within the rainforest. Has evolution selected for different traits and morphological differences to better adapt to their specific needs? Or are the apposition eyes invariant among the bees? The comparison will include six different species of stingless bees collected from South America.

Previous studies have shown that there is a relationship between facet diameter and vision (Land and Nilsson, 2012 ; Pearl et al. 2016). Although previous studies have failed to show if the volume of the lens, the crystalline cones and the photoreceptors has an effect on vision and how the width of these areas might affect the vision. However, in this study we tried to determine if there is any change in volume or width of the different regions within the eyes, comparing the species and analysing what kind of affect that can give.

2. Material and methods

2.1 Specimen preparation

Six species of stingless bees were chosen for this study, *Melipona Bicolor*, *Trigona Spinipes*, *Melipona Quadrifasciata*, *Tetragonisca Angustula*, *Tetragona Clavipes* and *Plebeia Remota*. The comparison was made with two specimens of each species, and all of the specimens were female worker bees.

Stingless bees were collected from Sao Paulo Brazil and Barro Colorado Island Panama, prepared by the vision group at Lund University, Sweden. The specimens were prepared on site by dissecting them and preserving the heads. The heads were later fixated in a phosphate buffer solution (0.2 M) with 2% glutaraldehyde and 3% parapharmaldehyde for two hours, to preserve the biological tissue. Before secondary fixation they were washed in the buffer once more and then fixated with 2% OsO₄ for one hour, to increase the contrast for x-ray tomography. Afterwards the specimens were dehydrated in a graded alcohol series ranging from 70% to 100% for 10 minutes in each step, and later moved to acetone. Lastly they were embedded in liquid epoxy resin, and the outside excessive resin was removed.

Synchrotron X-ray microtomography experiments were used at beamline I13-2 (Rau et al. 2011) in Diamond Light Source located in Oxfordshire, United Kingdom. The radiographic projections obtain by the X-ray microtomography were reconstructed in to 3D volumes using DAWN v1.7 (Basham et al. 2015). The original resolution of the scans was 1.6 microns in each dimension.

2.2 Measurements

The 3D images collected by the X-ray microtomography were cropped in a software called Drishti to only show the eye and thereafter transferred to a software called Amira. In Amira the apposition eye structures; the lens, the cones and the photoreceptors were manually labelled and selected in to different colours in all images (fig. 1). Figure 2 shows the whole eye when it is fully segmented; the colours represent different regions of the eye. The total volume and the volume of the different areas of the eye were computed by Amira and noted. Taking the volume of the different regions and dividing them by the total volume of each species normalized the values. This was done to compare the species.

In order to take measurements in the lateral plane of the eye the total length of the eye was measured (fig. 3). To able to view the eye from a 2D perspective instead of a 3D perspective a 2D oblique slice was inserted. This was done to take measurements in the lateral plane of the eye. The oblique slice was inserted in the same place as the total length of the eye, to be consistently placing the slice at the same position on all of the different eyes. Lastly the measurements were taken in 90° angel from the total eye length. This was done at five different places, at 5, 25, 50, 75 and 95% of the total eye length (fig. 3). Corresponding to the 5, 25 and 50% values in the ventral and the dorsal plane of the eye.

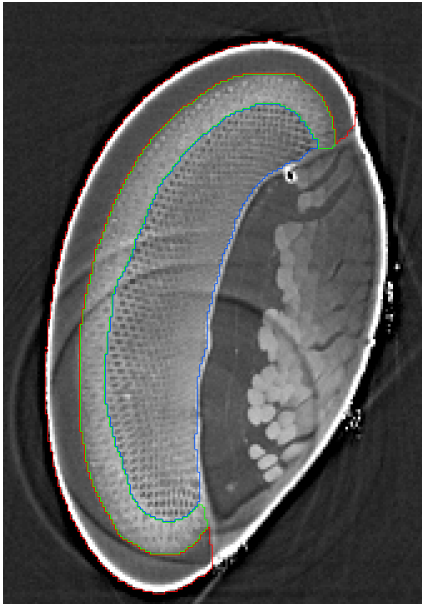


Figure 1. A picture of the eye in Amira with lens, crystalline cones and photoreceptors singled out for notice. The lens in red, the crystalline cones in green and the photoreceptors in blue.

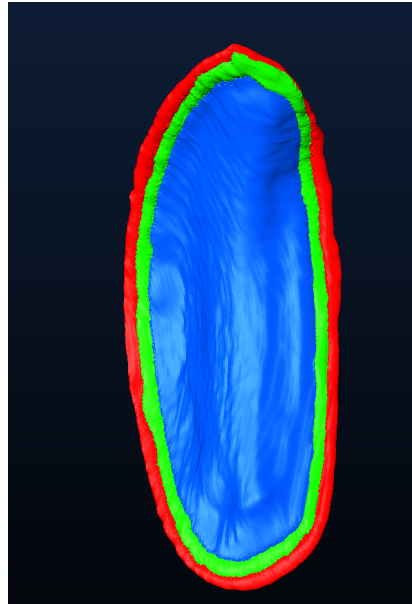


Figure 2. An example of what it looks like when the eye is fully segmented. The lens in red, the crystalline cones in green and the photoreceptors in blue.

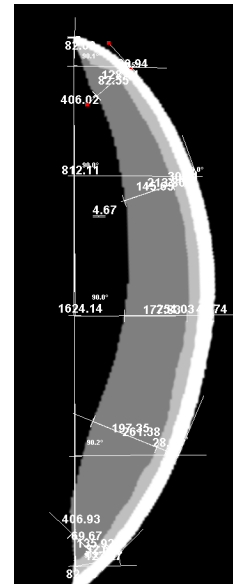


Figure 3. Measurements taken in a cross section in the lateral plane of the eye. The lens is white, the crystalline cones are light grey and the photoreceptors are dark grey.

3. Results

3.1 Measurements of volume

Six species of tropical stingless bees were compared to each other to investigate if there are morphological variations between them. The volume of lens, cones and photoreceptors were compared to each other with normalized values. Comparison of the volume of the different areas within the eye shows that some of the species, *M. bicolor*, *T. spinipes* and *M. quadrifasciata*, has more lens volume compared to crystalline cones volume. And the other species, *T. clavipes* and *P. remota*, has more crystalline cone volume than lens volume. For *T. angustula* this varies within the species; one of the specimens has more lens volume and the other has more crystalline cone volume (fig. 4).

The species with the largest volume of photoreceptors are *M. bicolor* with 56.5 and 54.6%. The species with the smallest volume of photoreceptors are *T. angustula* and *M. quadrifasciata* with volumes ranging from 48.6% to 43.9%. The species that differ the most from the other ones is *M. bicolor*, a species with a large volume of photoreceptors and lens but a low volume of crystalline cones (fig. 4).

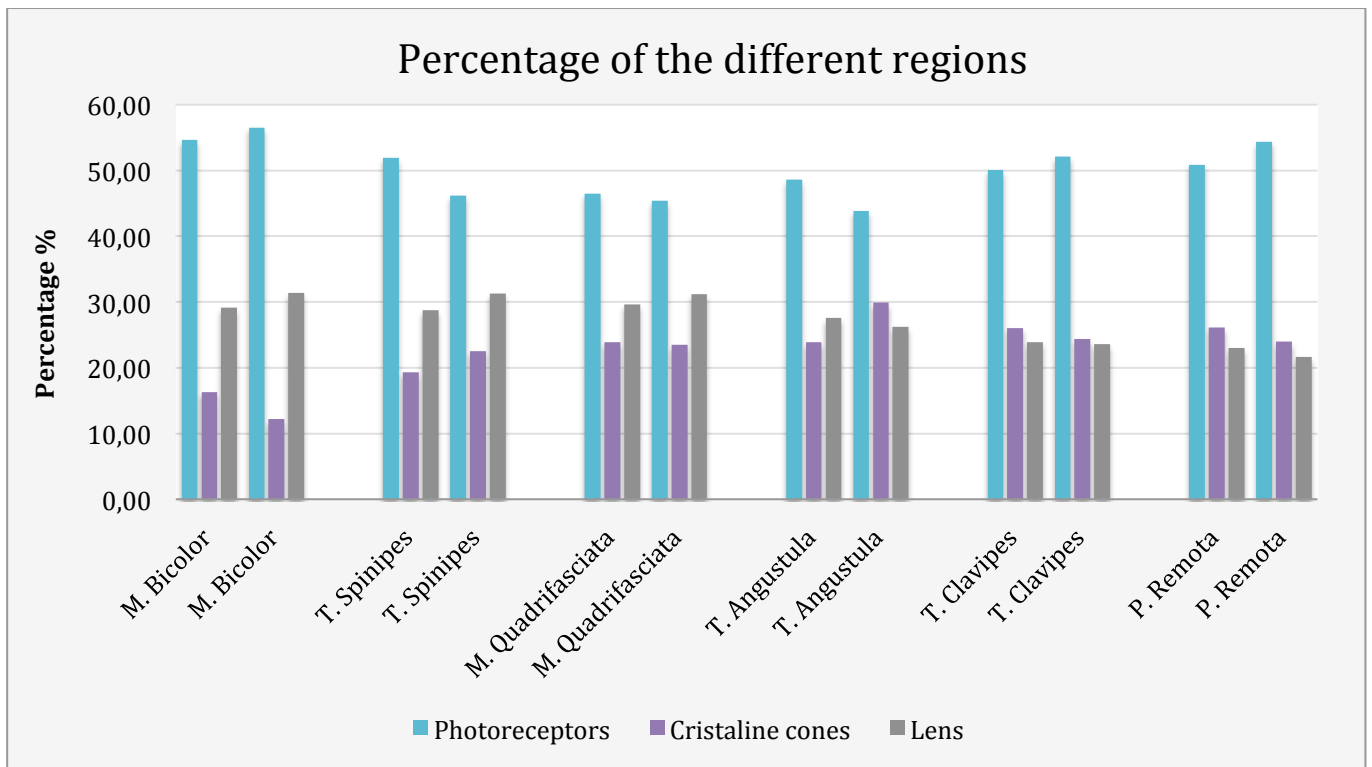


Figure 4. Normalized values of the volume (in percentage) of the photoreceptors, crystalline cones and lens. The X-axis shows the different species.

3.2 Measurements of the length

There is a relatively linear relationship between the total eye length and the photoreceptors width in the 50% measurements of the eyes, R^2 is equal to 0.75 (fig. 5). As the length of the eyes increases so to does the photoreceptors width where as the lens and the crystalline cone width are only increasing slightly with eye size.

The measurements of the total eye length show that *M. bicolor* has the largest width of the eye at all the measurements in both the dorsal and ventral plane of the eye length. Both *M. bicolor* and *M. quadrifasciata* have considerably larger measurements at the width of the eye and thereby differing a lot from the other four species investigated in this study (Fig. 6).

The 50% measurements of the total eye size in the lens width is generally the widest part of the eye, all of the species except for *T. spinipes* have the widest part at 50% of the eye size. *T. spinipes* has the widest part in the 25% ventral side of the eye. The results also showed that *M. bicolor* and *M. quadrifasciata* have a substantial width of the lens compared to the other species (fig. 7).

The measurements of the crystalline cones vary a lot between the species. *T. clavipes* has the largest width of the crystalline cones. One of the specimens of *M. bicolor* has a very wide measurement at the 5% dorsal value of the crystalline cones. *T. spinipes* has a very wide measurement at the 50% value of crystalline cones (fig. 8).

In the middle of photoreceptors, at the 50% measurement, there is generally a wider measurement, shown in most species. Although *M. bicolor* and *M. quadrifasciata* have a substantially larger width of the photoreceptors along the whole eye. *T. spinipes* has wide photoreceptors at the ventral 75% measurement (fig. 9).

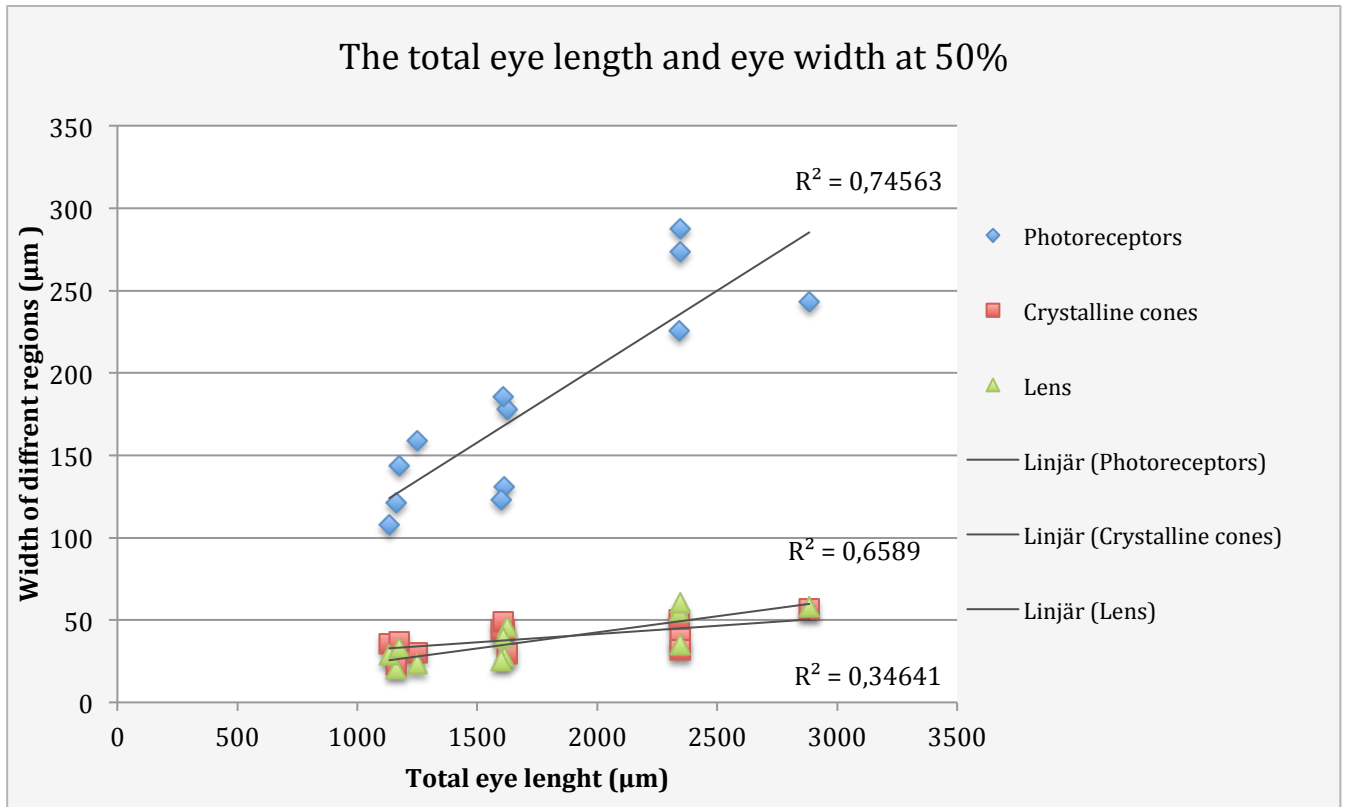


Figure 5. A linear relationship between the total eye length and the width of the different regions of the eye taken at 50% of the total eye length. In the regression line for the photoreceptors $R^2 = 0.75$, the crystalline cones $R^2 = 0.66$ and the lens $R^2 = 0.35$

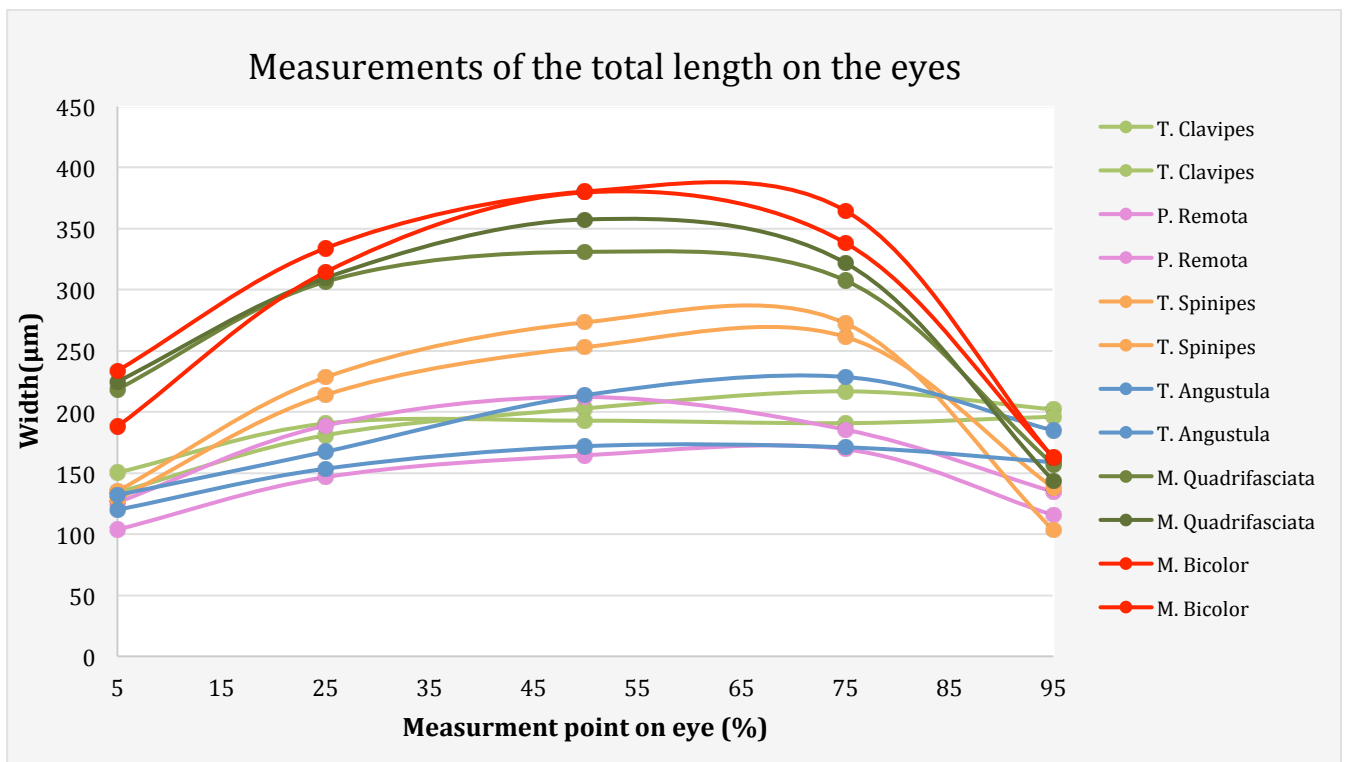


Figure 6. Measurements were taken in the lateral plane of the eye to measure the total width at five sites: 5, 25, 50, 75 and 95% from the ventral to the dorsal side of the eye. The values to the right show the ventral side part of the eye.

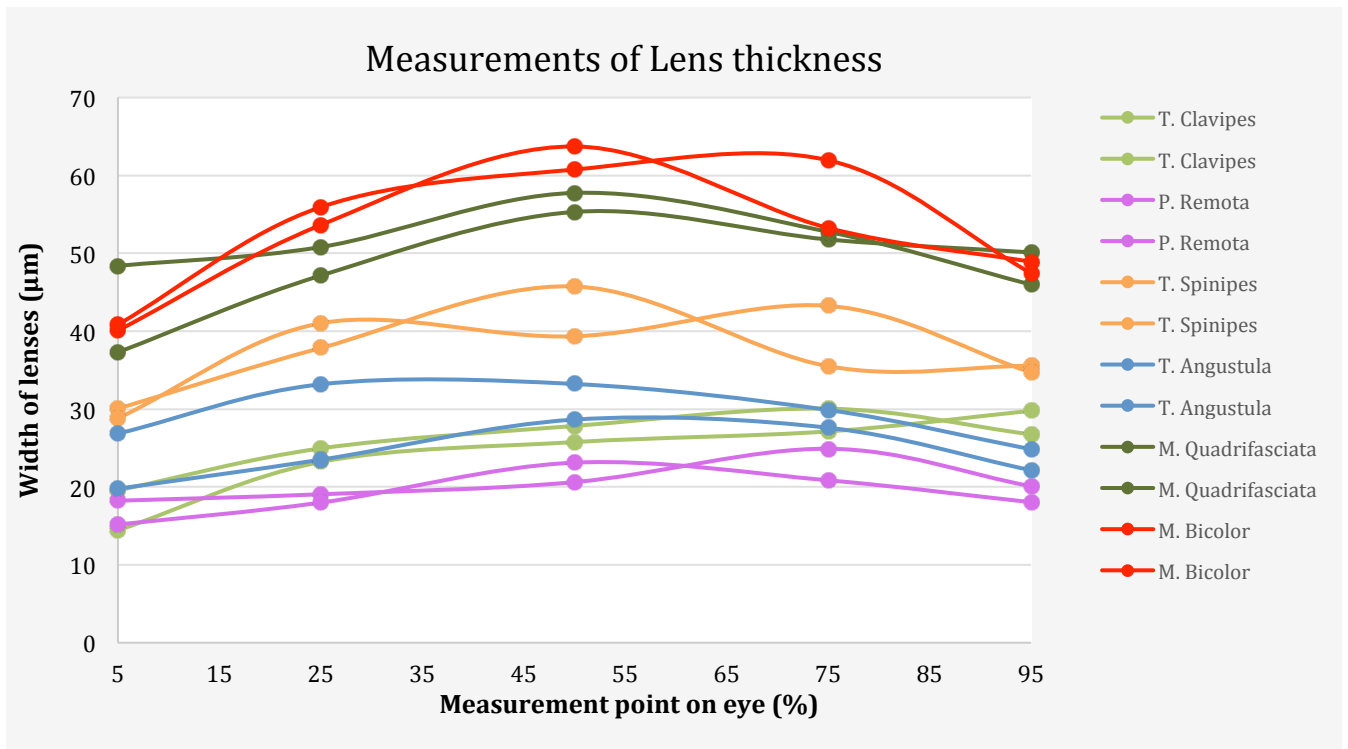


Figure 7. Measurements were taken in the lateral plane of the eye to measure the width of the lens at five sites: 5, 25, 50, 75 and 95% from the ventral to the dorsal side of the eye. The values to the right show the ventral side part of the eye.

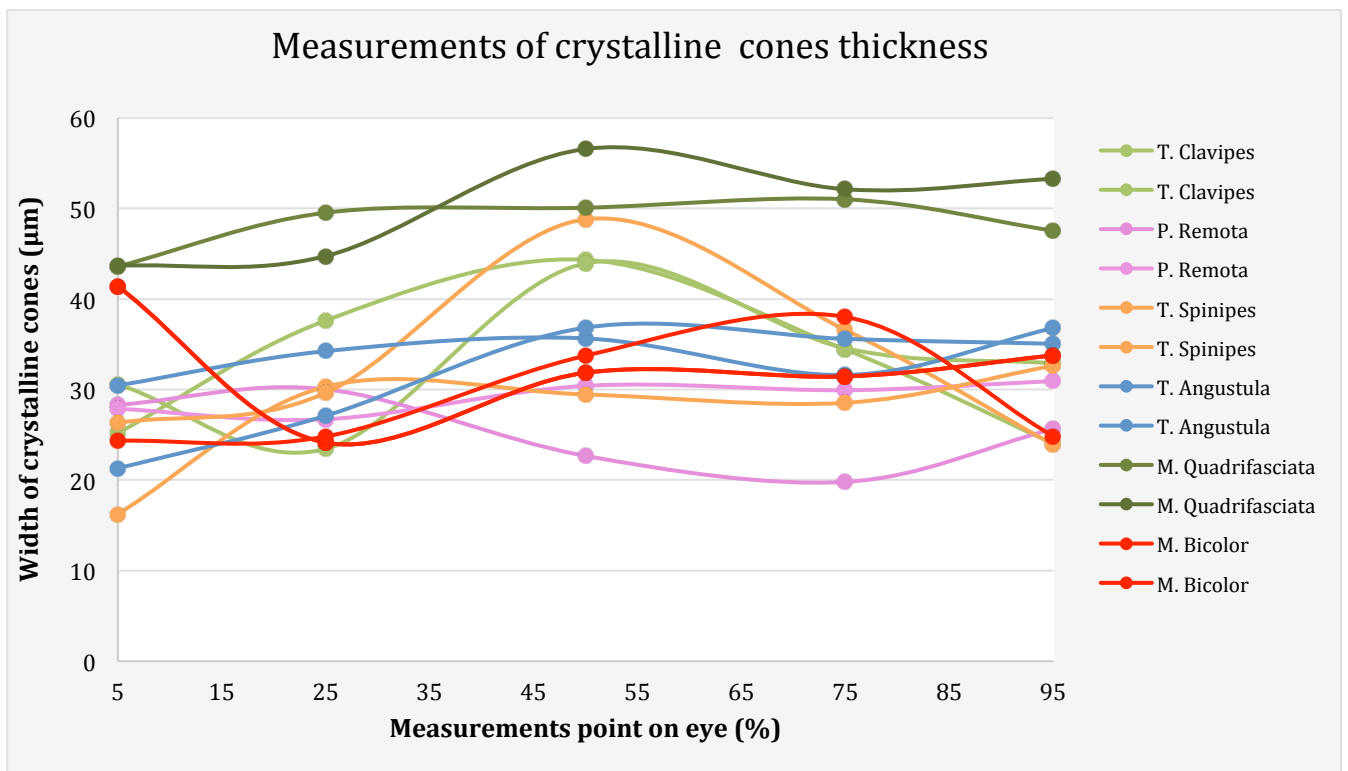


Figure 8. Measurements were taken in the lateral plane of the eye to measure the width of the crystalline cones at five sites: 5, 25, 50, 75 and 95% from the ventral to the dorsal side of the eye. The values to the right show the ventral side part of the eye.

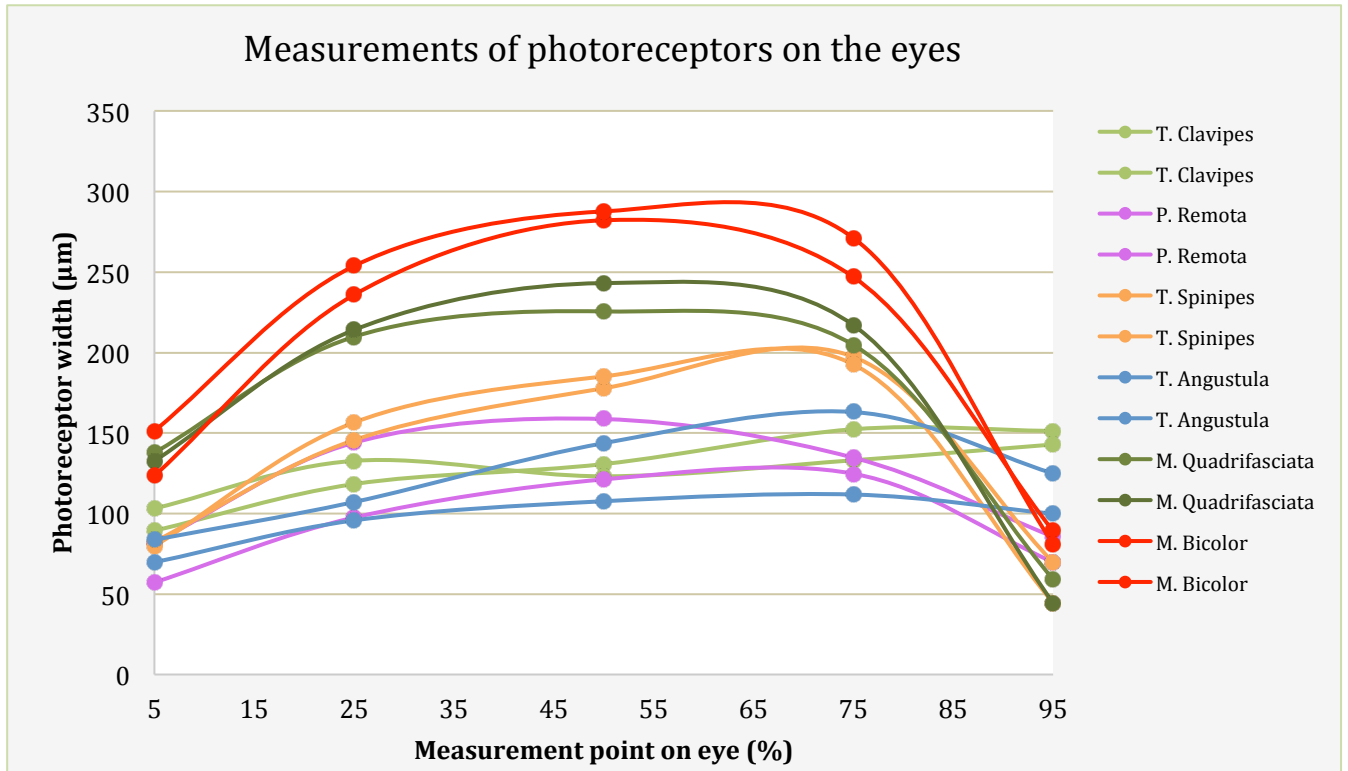


Figure 9. Measurements were taken in the lateral plane of the eye to measure the width of the photoreceptors at five sites: 5, 25, 50, 75 and 95% from the ventral to the dorsal side of the eye. The values to the right show the ventral side part of the eye.

4. Discussion

This study set out to determine the morphological differences of the eyes of tropical stingless bees and its impact on the quality of their vision. Morphological and anatomical variations correlate with behaviour, and result from different natural selections pressures. The factors determining the quality of an eye are resolution and sensitivity. The sensitivity of the apposition eye is to a certain degree determined by the diameter of the lens as well as the acceptance angles and volume of the photoreceptors. As these regions of the eye increase in size, so does the sensitivity of the eye. The resolution of the eye is determined by the diameter of the lens, how close their optical axis is together and the size of the lens. A larger diameter and a bigger lens give a greater resolution (Land, 1997 ; Land and Nilsson, 2012).

A linear relationship was found between the total eye length and the photoreceptors at 50% of the eye width in all of the investigated species. However the lens and the crystalline cones are only increasing slightly with eye size (fig. 5). This indicates that generally when the eyes increase the most important parameter is the photoreceptors. Indicating that larger eyes are adapted to absorbing more light.

Structural and environmental features affect the performance of any eye. Among the former wider photoreceptors let more light in to the eyes (Land, 1997; Land and Nilsson, 2012). *M. bicolor* and *M. quadrifasciata* have wide photoreceptors (fig. 9) indicating that their eyes are capable of capturing a lot of light. A trait that can be very important in the rainforest where the light conditions varies a lot due to a lot of vegetation hampering the flight conditions. An environmental feature that is affecting the eyes is the amount of light available to the receptors. At low light conditions there is not a lot of photons available for the receptors making it difficult to provide a statistically reliable signal (Land, 1997 ; Warrant et al. 2004).

As mentioned in the results section there is variation in the volumes of the different areas when comparing the species. Some of the species, *M. bicolor*, *T. spinipes* and *M. quadrifasciata*, has more lens than crystalline cones (fig 1). When looking at the Lensmaker's equation (ekv. 1) a large volume of crystalline cones indicates that the focal length increases. This is due to the fact that the crystalline cones are responsible for the length of the focal point (f). The Land sensitivity equation (ekv. 2) explains that as the focal length decreases the sensitivity of the eye increases (Land F. and Nilsson 2012). Indicating that *M. bicolor*, *T. spinipes* and *M. quadrifasciata* have a short focal length and a high sensitivity.

Ekvation 1. The Lensmaker's equation:

$$P = \frac{1}{f} = (n - 1) \left[\frac{1}{R_1} - \frac{1}{R_2} + \frac{(n - 1)d}{n \cdot R_1 \cdot R_2} \right]$$

P is the power of the lens

f is the focal length of the lens

n is the refractive index of the lens material

R_1 is the radius of curvature of the lens surface closest to the light source

R_2 is the radius of curvature of the lens surface farthest from the light source, and

d is the thickness of the lens (the distance along the lens axis between the two surface vertices).

Ekvation 2. Land Sensitivity equation:

$$S = \left(\frac{\pi}{4}\right)^2 \cdot A^2 \cdot \frac{\left(\frac{d}{f}\right)^2 \cdot (k \cdot l)}{2.3 + k \cdot l}$$

S is the optical sensitivity of an eye

A is the diameter of the eye's aperture

d is the diameter of the photoreceptors

f is the focal length

k is the absorption coefficient of the photoreceptor

l is the photoreceptor length.

M. bicolor is a species with a large volume of photoreceptors and lens, as well as a low volume of crystalline cones (fig 4). This indicates that the eyes have the capability to capture a lot of light, they have a high sensitivity and also a good resolution. (Land and Nilsson 2012 ; Snyder, 1977). *M. bicolor* also has a long total eye length. A bigger eye and larger lens volume is likely to have more facets giving the eye a higher resolution. Taking this in to account *M. bicolor* seems to be selected for high visual acuity. A specialization that could be due to the fact that *M. bicolor* forages for food in the first few hours of the morning, this trend is similar to that of the species *M. quadrifasciata* (Hilário, 2000). This indicates that the species are adapted for lower light conditions as this has previously been shown in nocturnal insects that are adapted in to having 4–5 times wider photoreceptor diameter than found in diurnal bees (Greiner et al. 2004).

Both *M. bicolor* and *M. quadrifasciata* have a wide lens and wide photoreceptors (fig. 7 and fig. 9) correlating with the volume of these areas (fig. 4) again indicating that they are adapted to lower light conditions (Land and Nilsson, 2012).

Larger eyes capture more light but are consequently more metabolically expensive (Barlow, 1952). This again points to the evolutionary advantage for *M. bicolor* and *M. quadrifasciata* to have a good visual acuity (fig. 6). Another reason the eyes of *M. bicolor* might be adapted for high visual acuity is that they nests close to the soil, next to the roots or the trunks of trees (Hilário and Imperatriz-Fonseca, 2009). Having to fly a lot close to the ground might require better visual acuity.

The results showed that some of the species had a larger volume of lens while others had a larger volume of crystalline cones (fig 4). A larger volume of lens indicates that the eyes have a greater resolution because a larger volume of lens will presumably contain more individual lenses (Spaethe and Chittka 2003). Whilst wider crystalline cones gives the eyes a longer focal point (ekv. 1). Indicating that some of the species has evolved in to having a greater resolution while others have evolved in to having a longer focal point.

T. spinipes is one of the most generalistic species of stingless bees when it comes to plant interactions, diet and presents colonies with a great number of individuals. Moreover they are distributed in a large geographical area. Independence of nests and the huge numbers of workers may determine the degree of dispersion over the countryside and their generalist interacting behaviour (Kleinert and Giannini, 2012). This however does not explain the fact that the specimens in this study has a wide total eye length and wide photoreceptors at the 75% ventral measurement (fig. 6 and fig. 9), indicating that they might be adapted to capture more light in the ventral part of the eyes.

The absence of any complications ensured a good quality of the results in this study. However, when looking at the 95% width on the ventral side of the photoreceptors (fig. 9) the values are decreasing quickly. This could be due to some of the width of the photoreceptors did not get measured accurately when doing the measurements. This is because a measurement that only withholds 5% from the ventral side is not a high enough

value on the ventral part of the eye. For future studies a measurement criteria that better represents the length of the photoreceptors would be a good objective.

An on going trend that has been observed in this study is that within all of the species the ventral side portion of the eye is thicker. All of the regions, total length of the eye, the lens and the photoreceptors gets thicker at the ventral side portion (fig. 6-9). The reason for this is unknown and could be something to investigate in future studies.

5. Conclusion

This study found a linear relationship between the total eye length and the photoreceptors at 50% of the eye width. The lens and the crystalline cones are only increasing slightly in width. This points to that generally when the eyes increase in size, so does the photoreceptors (fig. 5). Indicating that the width of the photoreceptors is very important for the total eye length, which indicates that larger eyes are adapted to capturing more light.

Another finding is the adaptations in the visual system of *M. bicolor*. This is due to their large volume of photoreceptors and lens (fig. 4), giving their eyes a very good resolution and sensitivity. This could be a specialization to the fact that they mostly forage for food during the early hours of the day.

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Appendix

	Volym total (µm)	Volym photo (µm)	Volym cones (µm)	Volyme lense (µm)
T. clavipes (60167)	139595128	69839504	36376500	33379124
T. clavipes (60166)	131888224	68662736	32183744	31041744
P. remota (60164)	48939492	24890746	12781498	11267248
P. remota (60206)	63367127	34462752	15175750	13728625
T. spinipes (60203)	143290230	74443864	27675246	41171120
T. spinipes (60163)	139123108	64208744	31355496	43558868
T. augustula (60204)	56233992	24667622	16808872	14757498
T. audustula (60205)	68930869	33476872	16472749	18981248
M. quadrifaceta (60208)	334998744	155779744	79967752	99251248
M. quadrifaceta (602089)	319961120	145104624	74992496	99864000
M. bicolor (60160)	351405625	191981750	57181625	102242250
M. bicolor (60161)	378995861,8	214143861,9	46036747,19	118815252,7

Raw data, the total volumes of the different regions

	Normalised volume (photo)	Normalised volume (cones)	Normalised volume (lens)
T. Clavipes (60167)	50,03	26,06	23,91
T. Clavipes (60166)	52,06	24,40	23,54
P. Remota (60164)	50,86	26,12	23,02
P. remota (60206)	54,39	23,94893175	21,67
T. Spinipes (60203)	51,95	19,31	28,73
T. Spinipes (60163)	46,15	22,54	31,31
T. Augustulata (60205)	48,57	23,90	27,54
T. Augustulata (60204)	43,87	29,89	26,24
M. Quadrifaceta (60208)	46,50	23,87	29,63
M. Quadrifaceta (602089)	45,35	23,44	31,21
M. Bicolor (60160)	54,63	16,27	29,10
M. Bicolor (60161)	56,50	12,14703162	31,3500132

Raw data, normalised values of the different regions

	Total vertical length (µm)	Total 5 % top	Photoreceptors 5% top	Cones 5% top	Lense 5 % top	Total 25 % top	Photo 25 % top	Cones 25 % top	Lense 25 % top
T. clavipes (60167)	1612,97	134,08	89,35	25,17	19,56	180,89	118,33	37,61	24,95
T. clavipes (60166)	1600,8	150,35	103,04	32,89	14,42	190,51	132,75	34,55	23,21
P. remota (60164)	1162,73	103,7	57,2	28,27	18,23	146,6	97,52	30,02	19,06
P. remota (60206)	1247,6	125,93	81,89	27,87	15,17	188,75	144,05	26,71	17,99
T. spinipes (60203)	1625,38	128,44	82,55	16,25	30,04	213,8	145,65	30,31	37,84

T. spinipes (60163)	1608,72	134,98	79,88	26,32	28,78	228,23	156,59	29,62	41,02
T. augustula (60204)	1133,25	119,79	69,59	30,45	19,75	153,5	95,77	34,23	23,5
T. audustula (60205)	1176,7	131,83	83,71	21,28	26,84	167,45	107,17	27,1	33,18
M. quadrifaceta (60208)	2340,89	218,61	137,73	43,59	37,29	306,51	209,85	49,52	47,14
M. quadrifaceta (60209)	2883,84	224,83	132,75	43,67	48,41	309,64	214,11	44,73	50,8
M. bicolor (60160)	2323,8	187,79	123,42	24,32	40,05	314,35	235,91	24,81	53,63
M. bicolor (60161)	2347,73	233,67	151,44	41,39	40,84	333,89	253,82	24,14	55,93

Raw data, the measurements taken in the dorsal part of the eye.

T. clavipes (60167)	Total 50 %	Photoreceptor 50%	Cones 50%	Lens 50 %	Total 25 % bot	Photoreceptors 25% bot	Cones 25% bot	Lens 25 % bot	Total 5 % bot	Photo 5 % bot	Cones 5 % bot	Lense 5 % bot
T. clavipes (60166)	202,9	130,75	44,32	27,83	216,83	152,38	34,4	30,05	202,12	151,34	24,03	26,75
P. remota (60164)	192,83	123,15	43,92	25,76	190,8	133,11	30,56	27,13	196,04	142,91	23,45	29,78
P. remota (60206)	164,52	121,23	22,67	20,62	169,44	124,74	19,8	24,9	115,52	69,79	25,64	20,09
T. spinipes (60203)	212,24	158,72	30,4	23,12	185,47	134,7	29,92	20,85	134,63	85,66	30,93	18,04
T. spinipes (60163)	253,02	177,83	29,45	45,74	261,38	197,35	28,53	35,5	137,85	69,67	32,62	35,56
T. augustula (60204)	273,33	185,2	48,79	39,34	272,45	192,63	36,57	43,25	103,09	44,5	23,9	34,69
T. audustula (60205)	171,95	107,66	35,64	28,65	171,04	111,82	31,6	27,6	158,81	99,89	36,78	22,14
M. quadrifaceta (60208)	213,77	143,72	36,83	33,22	228,55	163,08	35,59	29,88	184,78	124,9	35,05	24,83
M. quadrifaceta (60209)	330,96	225,58	50,07	55,31	307,52	204,75	51	51,77	156,8	59,16	47,53	50,11
M. Bicolor (60160)	357,47	243,16	56,56	57,75	321,86	217	52,11	52,75	143,69	44,46	53,26	45,97
M. bicolor (60161)	379,64	282,2	33,73	63,71	338,22	246,96	38,01	53,25	162,87	89,13	24,84	48,9
M. bicolor (60161)	380,33	287,73	31,85	60,75	364,56	271,18	31,44	61,94	162,11	80,91	33,76	47,44

Raw data, the measurements taken in the ventral part of the eye. The 25 and 5 % bot corresponds to the ventral 75 and 95 % measurements