Outline and landmark based geometric morphometric analysis in describing sexual dimorphism in wings of the white stem borer (*Schirpophaga innotata* Walker)

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Abstract. Many studies about wing morphology have been conducted in the field of entomology that aims to clarify the relationship in closely related taxa and to identify different population within and between species. However, less has been reported that exploit wing shape morphology to discriminate female and male population within species. Differences in wing morphology between sexes of the same species of insects often reflect disparity in flight performance and flight range which might be of considerable significance in the monitoring and control of pest species. This study was conducted to determine differences in flight morphology between sexes of the white stem borer (*Schirpophaga innota* Walker) by looking at variation in the shapes of the entire wing and its compartments using the method of geometric morphometrics. The results showed considerable variation in the forewings and hindwings between female and male specimen as shown in relative warp analysis. Discriminant function analysis and MANOVA also showed statistically significant wing shape variation between sexes demonstrating the presence of sexual dimorphism within the species of white stem borers.

Key Words: Sexual dimorphism, *Schirpophaga innotata*, geometric morphometric analysis, principal component analysis, relative warp analysis, discriminant function analysis.

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Introduction

Sexual dimorphism is one of the most interesting sources of phenotypic variation among organisms and have become an increasingly important area of study in evolutionary biology (Benitez et al 2011). It is defined as the variation in morphology between individuals of different sexes that belongs to the same species. Sexual dimorphism had captured the interest of entomologists since normally the differences between sexes among insects are unremarkable or the individuals are very small; thus finding discrimination in morphological characters will permit easy identification of sexes. Information concerning sexual dimorphism is crucial for understanding the ecology, behavior, and life history of a species. Wing shape morphology using geometric morphometrics has been extensively studied in the field of entomology to clarify the relationship between closely related taxa and helps in identifying population within and between species of insects. However, studies about sexual shape dimorphism in wing morphology have been less accounted. A relatively recent method in quantifying biological form is the introduction of geometric morphometrics (GM). There are two methods in describing the form of an organism through geometric morphometric; first, by landmark based analysis that uses a set of landmarks to describe the object or specimen; second, by outline based analysis which extract the margin around the specimen. GM analyzes biological form in such a way that will preserve the physical integrity of the form (Richtsmeier et al 2002). It allows better comparison of the shapes of different organisms and would no longer rely on word descriptions that usually encounter problem of being interpreted differently by scientists (Adams et al 2004).

One group of insect that is worthy to be investigated for wing shape variation is the rice stem borer which is considered to be the most

serious insect pests of rice in the Asia. By quantifying morphological variation, it could provide an easier identification in the relationship between morphology and ecology and hence, could make more informed deduction on organism's evolution (Adams 1999). Among different species of rice stem borer that exist in the Philippines, the white stem borer Walker is the most widespread species and was conceived to be studied using geometric morphometrics analysis. Differences in wing morphology between sexes of the same species of insects often reflect disparity in flight performance and flight range which might be of considerable significance in the monitoring and control of pest species. Wing sexual dimorphism was already been recorded in one species of rice stem borer, the striped stem borer Chilo suppressalis (Zahiri et al 2006), using landmarks based analysis. In this present study, an additional approach was made in establishing sexual dimorphism in rice stem borer. Both landmark and outline based analysis were employed and compared for which method is better in describing variation in the wing morphology between female and male white stem borers.

Materials and Methods

The adult stem borers were collected in the field using a light trap method. Sampling time was done during night time to attract more number of moths. The light source was placed in a white sheet to increase its luminosity. The collected samples were then processed and mounted. The fore- and hind wings of the adult stem borer were first removed from the body of the insects with the used of scalpel, dissecting needles and forceps. After which, the wings were placed properly between the two clean glass slides. Each corner of the slide was then fastened with an invisible tape to prevent the slides from moving. Each slide was labelled properly which includes the specimen number, sex and the place where it was collected. Lastly, the wings (both fore- and hind wings) were scanned under 1200 resolutions to get a clear image of the wings. These images were then used for the succeeding procedure. Analysis in the fore- and hind wing shape was done separately while analysis in the wings of the male and female was performed together to established sexual dimorphism within the species of stem borers. A total of 100 closely connected points were made along the outline of the forewing and hindwing (Figures 1a,b) in order to capture the general shape of the wings using a digitizing program tpsDig version 2.12 (Rohlf 2008a). Then, the tps curve was converted into landmark points (XY coordinates) that would serve as raw data for outline analysis. The tpsDig was also used to collect the x, y coordinates of each landmarks within the wing structure. As shown in figure 1, fifteen and ten landmarks were chosen in the forewings and hindwings (Figures1c,d) respectively for their capacity to define the major elements of shape and for their reliability as homologous structure (Zahiri et al 2006). A Generalized Procrustes analysis (GPA) was performed to superimpose the landmark configurations using least-squares estimates for translation and rotation parameters (Adams et al 2004). GPA is an important procedure because it eliminates any variation due to differences in translation, orientation, and size, and would superimpose the objects in a common coordinate system (Rohlf 1999; Slice 2001).



Figure 1. Digitized image of the wings showing the outline points in forewing (a) and hindwing (b) and the location of landmarks points in forewing (c): 1-beginning of R2, 2-beginning of R3, 3-beginning of R5, 4-beginning of M1, 5-beginning of M2, 6-beginning of M3, 7-beginning of CuA1, 8-beginning of CuA2, 9-junction of R3 and R4, 10-termination of R5, 11-termination of M1, 12-termination of M2, 13-termination of M3, 14-termination of CuA1, 15-termination of CuA2; and hindwing (d): 1-beginning of ScR3, 2-junction of ScR1 and ScR2, 3-junction of M1 and M2, 4-beginning of CuA1, 5-beginning of CuA2, 6-termination of R3, 7-termination of M1, 8-termination of M2, 9-termination CuA1, 10-termination of CuA2.

Thin-plate spline deformation grids were produced to visualize the wing shape differences between male and female rice stem borers. The coordinates of superimposed configurations in all aligned specimens was used for the thin-plate spline relative warp analysis (Bookstein 1991) in order to analyze and display the direction of shape differences among species. Relative warp analysis was employed in this study to determine and compare the shape of the forewings and hindwings between female and male population of stem borer based on the outline of the wings. The thin-plate spline technique (Bookstein 1991) consists of fitting an interpolating function to the landmark coordinates of each specimen against the reference configuration so that all homologous landmarks coincide. The projection of the superimposed specimens onto the principal warps produces the partial-warp scores, which describe their deviations from the reference configuration and that can be used as variables in subsequent multivariate statistical analyses (Rohlf 1999, 2004). The relative warps analysis and computation of partial-warp scores were done using tpsRelw program, version 1.46 (Rohlf 2008b). The relative warp scores were subjected to MANOVA and F and T test (two samples) using PAST software version 1.91 (Hammer *et al* 2001) to determine whether the shape of the forewings and hindwings differ significantly between female and male population. When MANOVA showed significant results, the analysis would proceed to Hotelling's pairwise comparisons (post-hoc) test. A cross validation test using discriminant function analysis was used for confirming or rejecting the hypothesis that two populations are morphologically distinct by classifying each specimen into one of the two groups (female or male) based on the outline of the wings. Variations between populations are considered statistically significant if the percentage of correctly classified specimen is greater than 75%.

Results and Discussion

Outline based Geometric Morphometric Analysis

The relative warp analysis (RWA) in the forewings and hindwings of white stem borer demonstrated variations in the outline of the wings. In the forewings, the 3 significant relative warps jointly accounted for 83.98% and 82.83% of the variation in the shape of left and right forewings respectively. While in the hindwings, the 3 significant relative warps collectively accounted for 87.69% and 88.28% of the variation in the shape of left and right forewings respectively. The CVA scatter plot in Figure 2 shows the distribution of female and male white stem borer population based on the outline analysis of its forewings and hindwings. Multivariate analysis of variance (MANOVA) on relative warp scores showed significant variation in the forewings and hindwings between female and male population as shown in Table 1. Moreover, Table 2 shows the specific shape variable in the forewing and hindwing as explained by each of the significant relative warp.

F and T test was performed in each of the significant relative warps to compare the variance and mean shape of the forewings and hindwings between female and male population. The results, as shown in table 3, revealed significant difference (p<0.05) in the shape of the forewings and hindwings as defined by each of the significant relative warps, although there are few relative warps that showed non-significant difference. The results also suggest the presence of localized shape variation in the outline of the wings between female and male *S. innotata*. Table 4 shows the discriminant score table where the percentage of correctly classified values and the reclassification data are given. It can be seen from the results that the male and female sexes of *S. innotata* are correctly classified.

Landmark based Geometric Morphometric Analysis

The CVA scatter plot in Figure 4 shows the distribution of female and male white stem borer population based on the landmark analysis its forewings and hindwings. Moreover, MANOVA test on relative warp scores showed significant variation in the forewings and hindwings between female and male population as shown in Table 5. The results of relative warp analysis in the left and right forewings both showed 6 significant relative warps which defined the wing shape variation in the forewings between female and male population. Meanwhile, the left and right hindwings both yield 5 significant relative warps. Tables 6,7 and Figures 5,6 describe the variation in the forewings and hindwings between female and male sexes respectively based on the location of landmark points within the wing's structure.

Table 8 show the results of the F and T test for the landmark based analysis on wing shape. The information yielded the same result as that of outline based analysis. Though some of the relative warps gives a non-significant p value (p>0.05), majority revealed significant differences (p<0.05) in the shape of the forewings and hindwings between sexes. Thus, indicating the presence of localized shape variation based on the homologous landmarks within the wing structure between female and male population of white stem borers. Table 9 shows the results of the discriminant analysis indicating that the male and feale sexes were correctly classified.

Table 1. Results of MANOVA test for significant variation in the shape of the forewings and hindwings between female and male populations of white stem borer based on outline analysis

		Wilk's Lambda	df1	df2	F	p(same)
Forewings	Left	0.00087	100	19	39.860	0.00124
	Right	0.06154	100	19	2.898	0.00517
Hindwings	Left	0.02755	60	9	5.294	0.00543
	Right	0.04559	60	9	3.140	0.03415

Table 2. Variation in the landmark's position within the forewings and hindwings between female and male population as defined by each of the significant relative warps

	Forew	ing	Hindwing		
	Left	Right	Left	Right	
RW1	Female and male differ in the shape of the wing's apex. The shape of the female's apex is pointed compared to the male which is rounded.	Female and male differ in the shape of the wing's apex. The shape of the female's apex is pointed compared to the male which is rounded.	Female and male differ in the shape of the apex. Females have more pointed and tilted apex compared to that of males	Female and male differ in the shape of the apex. Females have more pointed and tilted . apex compared to that of males.	
RW2	Female and male differ in the over- all span of the wings. Females have broader wings compared to males which have slender wings.	Female and male differ in the over-all span of the wings. Females have broader wings compared to males which have slender wings.	Female and male differ in the over-all span of the wings. Females have broader wings while males have slender wings.	Female and male differ in the over-all span of the wings. Females have broader wings while males have slender wings.	
RW3	Female and male differ in the shape of the wing's basal region. The basal region in males is curved compared to females which are slightly pointed.	Female and male differ in the shape of the wing's basal region. The basal region in males is curved compared to females which are slightly pointed.	Female and male differ in the shape of the wing's basal region. The male's basal region is more curved with more prominent anal fold compared to the females.	Female and male differ in the shape of the wing's basal region. The male's basal region is more curved with more prominent anal fold compared to the females.	



Figure 2. CVA scatter plot showing the distribution of male and female populations based on the outline analysis of the shape of its forewings (A=left, B=right) and hindwings (C=left, D=right) obtained from outline Legend: Red=Female, Blue=Male.

Table 3. F and T test for each of the significant relative warp obtained from the outline based analysis of forewings and hindwings of the pooled female and male population

	RW	F value	p (value)	T value	p (value)
Left Forewing	1	2.6387	2.7073x10 ⁻⁴	3.7207	3.0572x10 ⁻⁴
	2	1.0081	0.97542	-1.6239	0.10706
	3	1.2463	0.40022	-7.8408	2.2155x10 ⁻¹²
Right Forewing	1	1.1022	0.70987	3.193	1.8055x10 ⁻³
	2	1.3381	0.26617	0.95931	0.33936
	3	1.4304	0.17211	7.4897	1.375x10 ⁻¹¹
Left Hindwing	1	1.3439	0.25912	2.6457	9.264x10 ⁻³
	2	1.4107	0.18924	7.425	1.9187x10 ⁻¹¹
	3	1.1095	0.69109	4.9599	2.3915x10-6
Right Hindwing	1	1.0262	0.92122	1.2006	0.23229
	2	1.3336	0.27177	4.9481	2.514x10 ⁻⁶
	3	1.0866	0.75067	3.6386	4.080x10 ⁻⁴

Table 4. Reclassification of white stem borer (Schirpophaga innotata Walker) into female or male based on the outline analysis of the wings

		Female	Male	Total
Left Forewings	Female	35	0	35
	Male	0	35	35
	% Correctly Classified			100%
Right Forewings	Female	34	1	35
	Male	0	35	35
	% Correctly Classified			99.17%
Left Hindwings	Female	35	0	35
	Male	0	35	35
	% Correctly Classified			100%
Right Hindwings	Female	33	2	35
	Male	1	34	35
	% Correctly Classified			95.71%

Table 5. Results of MANOVA test for significant variation in the shape of the forewings and hindwings between female and male populations of white stem borer based on landmark analysis

		Wilk's Lambda	df1	df2	F	p(same)
Formings	Left	0.2533	26	43	4.877	2.422E ⁻⁰⁶
rorewings	Right	0.2769	26	43	4.319	1.154E ⁻⁰⁵
Hinduringa	Left	0.2704	16	53	8.939	5.156E ⁻¹⁰
ninuwings	Right	0.2164	16	53	11.99	2.270E ⁻¹²

In can be seen from the results obtained from the outline and landmark based analysis of the wings that variation existed in the shape of the forewings and hindwings between the female and male sexes. The overall outline of the wings and the landmarks located within the structure of the wings can both serve as criteria for determining wing sexual dimorphism. In this study, the outline based analysis of the wing's variation allows better discrimination between female and male species of white stem borer compared to the landmark based analysis.

Significant wing shape variation has been observed between male and female in *Drosophila melanogaster* Meigen (Kunkel & Bettencourt 2001), in *Chilo suppressalis* Walker (Zahiri *et al* 2006) and in *Synneuria* sp. (Benitez *et al* 2011). A number of hypotheses have been proposed to explain sexual dimorphism in insects. One of the most commonly used is the hypotheses indicating the connection between sexual selection versus natural selection and environmental variation (Anderson 1994;

Moller & Zamora-Munoz 1997). It is frequently argued that individual variation in shape may be strongly dependent on environmental conditions (Tatsuta *et al* 2004). Most of the morphological variations in moth and butterflies are due to the effects associated with the environment, whether phenotypic responses (plasticity) or particularly those which act during ontogenetic development (Mutanen *et al* 2007). The environment of the living organisms, with rather few exceptions, is spatially and temporarily diverse resulting in a continuous movement of organisms to colonise empty habitat and to offset the inevitable local extinctions. In the study of sexual dimorphism in *Chilo suppressalis* Walker (Zahiri *et al* 2006), environmental factors (geographic condition and host type) were considered in asserting that the phenotypes of an individual is the result of the interaction between in genotype and environment. The results showed that the most geographically distant population are also the most morphologically varied.



Figure 3. Summary of outline based geometric morphometric analysis showing the consensus morphology (uppermost pannels) and the variation in the shape of forewings and hindwings between female and male population of white stem borer (*Schirpophaga innotata* Walker) explained by each of the significant relative warps.



Figure 5. Summary of landmark based geometric morphometric analysis showing the consensus morphology (uppermost pannels) and the variation in the shape of forewings between female and male population of white stem borer (*Schirpophaga innotata* Walker) explained by each of the significant relative warps. Legend: F = female; M = male.



Figure 4. CVA scatter plot showing the distribution of male and female populations based on the landmark analysis of the shape of its forewings (A=left, B=right) and hindwings (C=left, D=right) obtained from outline Legend: Red=Female, Blue=Male.

Table 6. Variation in the landmark's position within the left and right forewings between female and male population as defined by each of the significant relative warps

		Left Forewing		Right Forewing
RW1	Variation in R2(1) and R3(2)	The distance between the landmark point at the beginning of R2 and R3 RW1 is farther in females than in males.	Variation in R5(10) and M1(11)	In females, the landmark point at the end of R5 and M1 is located in the same alignment while in males; the termination of R5 is located above the termination of M1 (shifted towards the apex of the wings).
RW2	Variation in R2(1) and CuA2(8)	In males, the beginning of R2 is located inferior to the beginning of CuA2 (shifted towards the base of the wings) while in females; the RW2 beginning of R2 is superior to the beginning of CuA2 (shifted towards the wing's apex).	Variation in R2(1) and R3(2)	The distance between the landmark point at the beginning of R2 and R3 is farther in females than in males.
RW3	Variation in R3,R4(9) and CuA2(15).	In females, the distance between the landmark point at the junction of R3 and R4 and the termination of CuA2 is farther compared to that of males.	Variation in R3(2) and R3,R4(9)	The distance between the beginning of R2 and the junction of R3 and R4 is farther in males compared to the females.
RW4	Variation in M2(5) and R3,R4(9).	The distance between the landmark point at the beginning of M2 and the junction of R3 and R4 and is farther in males than in females.	Variation in R5(3) and M1(4)	In males, the landmark point at the beginning of R5 is located slightly below the beginning of M1 (shifted towards the base of the wings) while in females, it is located slightly higher (shifted towards the apex of the wings).
RW5	Variation in M2(5) and M3(6)	In males, the beginning of M2 is located superior to the beginning of M3 (shifted towards the apex of the wings) while in females; M2 is inferior to the position of M3 (shifted towards the base of the wings).	Variation in R2(1) and CuA2(8)	In males, the beginning of R2 is inferior to the beginning of CuA2 (shifted towards the base of the wings) while in females, it is located superiorly to CuA2 (shifted towards the apex of the wings).
RW6	Variation in R3(3) and R3,R4(9)	The distance between the beginning of R3 and the junction of R3 and R4 is farther in females compared to that of males.	Variation in M1(4) and M2(5)	In females, the location of landmark points at the beginning of M1 and M2 are located in the same alignment while in males, the beginning of M1 is inferior to M2 (shifted towards the base of the wings).

Table 7. Variation in the landmark's position within the left and right hindwings between female and male population as defined by each of the significant relative warps

Left H	lindwing	J	Right	Hindwing	
RW1	Variation in ScR3(1) and CuA2(5)	The distance between the landmark point at the beginning of ScR3 and CuA2 is I farther in males than in females.	RW1	Variation in ScR3(1) and CuA2(5)	The distance between the landmark point at the beginning of ScR3 and CuA2 is farther in males than in females.
RW2	Variation in ScR3(1) and ScR1,ScR2(2)	The distance between the beginning of ScR3 and the junction of ScR1 and ScR2 is farther in males compared to that of females.	RW2	Variation in ScR3(1) and ScR1,ScR2(2)	The distance between the beginning of ScR3 and the junction of ScR1 and ScR2 is farther in males compared to the females.
RW3	Variation in CuA1(4) and CuA2(5)	In females, the distance between the landmark point at the beginning of CuA1 and CuA2 is farther compared to that the males.	RW3	Variation in M1,M2(3) and CuA1(4)	The distance between the junction of M1 and M2 and the beginning of CuA1 is farther in males compared to that of females.
RW4	Variation in M1,M2(3) and CuA1(4)	The distance between the junction of M1 and M2 and the beginning of CuA1 is 1 farther in females compared to males.	RW4	Variation in CuA1(4) and CuA2(5)	The distance between the landmark point at the beginning of CuA1 and CuA2 is farther in females than in males.
RW5	Variation in ScR1,ScR2(2) and ScR3(6)	The distance between the landmark at the junction of ScR1 and ScR2 and the beginning of R3 is farther in males than in females.	RW5	Variation in ScR1,ScR2(2) and ScR3(6)	The distance between the junction of ScR1 and ScR2 and the beginning of ScR3 is farther in males than in females.

Table 8. F and T test for each of the significant relative warp obtained from the landmark based analysis of forewings and hindwings of the pooled female and male population

	RW	F value	p (value)	T value	p (value)
Left Forewing	1.2415	0.53167	4.4771	2.9642x10-5	2.9642x10 ⁻⁵
	1.352	0.38361	3.7615	3.5396x10 ⁻⁴	3.5396x10 ⁻⁴
	1.3772	0.35547	-2.1297	3.6815x10 ⁻²	3.6815x10 ⁻²
	1.3693	0.36397	1.2193	0.22694	0.227
	1.3133	0.43089	-2.2508	2.7635x10 ⁻²	2.7635x10 ⁻²
	1.4403	0.29234	0.39988	0.6905	0.691
Right Forewing	25.827	6.7382x10 ⁻¹⁶	1.4449	0.15307	0.153
	1.4369	0.29545	1.9005	6.1612x10 ⁻²	6.1612x10 ⁻²
	2.4469	1.0813x10 ⁻²	-2.3247	2.5079x10-2	2.5079x10 ⁻²
	2.9917	1.9507x10 ⁻³	2.2623	2.688x10 ⁻²	2.688x10 ⁻²
	1.3133	0.75668	-1.7523	0.96516	0.965
	1.4403	0.79146	-1.4271	0.15812	0.158
Left Hindwing	1.8087	8.8592x10 ⁻²	4.097x10 ⁻²	0.98574	0.986
	1.9714	5.1646x10 ⁻²	5.701x10 ⁻²	0.9547	0.955
	1.2276	0.55315	-4.9955	4.3471x10 ⁻⁶	4.3471x10 ⁻⁶
	2.0492	3.9891x10 ⁻²	-3.6568	4.9897x10 ⁻⁴	4.9897x10 ⁻⁴
	1.4338	0.29834	2.2578	2.717x10 ⁻²	2.717x10 ⁻²
Right Hindwing	1.0309	0.9298	-0.83571	0.40624	0.406
	1.7665	0.10185	1.6809	9.7375x10 ⁻²	9.7375x10 ⁻²
	1.3625	0.37163	-2.0491	4.4314x10 ⁻²	4.4314x10 ⁻²
	3.1048	1.3858x10 ⁻³	4.0024	1.5744x10 ⁻⁴	1.5744x10 ⁻⁴
	2.1951	2.4622x10 ⁻²	-3.0839	2.9513x10 ⁻³	2.9513x10 ⁻³

Table 9. Reclassification of white stem borer (Schirpophaga innotata Walker) into female or male based on the landmark analysis of the wings

		Female	Male	Total
Left Forewings	Female	34	1	35
	Male	2	33	35
	% Correctly Classified			94.29%
Right Forewings	Female	35	0	35
	Male	1	34	35
	% Correctly Classified			96.71%
Left Hindwings	Female	34	1	35
	Male	2	33	35
	% Correctly Classified			95.71%
Right Hindwings	Female	34	1	35
	Male	1	34	35
	% Correctly Classified			97.14%

Another proposed factor that relates to sexual dimorphism in insects is the variation in the functions performed between sexes. McLachlan (1986) believes that the wing shape sexual dimorphism in *Chironomus imicola* Kieffer (Dip.: Chironomidae) is due to different roles of adult female and male individuals. In insects, flight is the most likely considered selective pressures influencing the evolution of sexual shape dimorphism in the wing. Since characteristic flight behaviour in females is to search for a host plants for oviposition sites and in males for the nuptial flight, territoriality and search mating opportunities, flight requirements and optimal wing shapes may differ between sexes. Therefore, the selection would act on wing shape to optimize flight characteristics (DeVries *et al* 2010). Also, such difference has been reported for a midge, where different flight behaviour in males and females is associated with sexual shape dimorphism in the wings. As cited by Mozaffarian *et al* (2007) from Gilchrist *et al* (2000), there is a constant gender related shape differences of wing shape among populations of *D. melanogaster* and suggested that the gender differences represent a developmental restriction on wing shape.

Conclusion

Following a series of geometric morphometric analysis made in the forewings and hindwings of white stem borer (*Schirpophaga innotata*



Figure 6. Summary of landmark based geometric morphometric analysis showing the consensus morphology (uppermost pannels) and the variation in the shape of hindwings between female and male population of white stem borer (*Schirpophaga innotata* Walker) explained by each of the significant relative warps. Legend: F = female; M = male.

Walker), it was found out that there exist a variation in the wing shape between the male and female individuals based on both outline and landmarks position on the wings. Thus, suggesting the presence of wing shape sexual dimorphism within the species of white stem borers. Both outline and landmark analysis showed that variation in the shape of forewings was more evident between female and male sexes. In contrast with the methods used for determining sexual dimorphism, outline based geometric morphometric analysis on the wing shape was observed to be a better means of discriminating female and male individuals of white stem borers. Nonetheless, this study demonstrates the effectiveness of both geometric morphometric methods in describing morphological variation in the organism.

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