https://doi.org/10.17576/serangga-2023-2803-02

MORPHOLOGICAL VARIATIONS OF PROCOXAE AND METACOXAE *Hypothenemus hampei* FERRARI, 1867 (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE) ON THREE SPECIES OF COFFEE BERRIES IN SUMATRA, INDONESIA

Aida Fitriani Sitompul, Dahelmi & Dewi Imelda Roesma*
Department of Biology,
Faculty of Mathematics and Natural Sciences,
Universitas Andalas,
Limau Manis, Kec. Pauh,
Kota Padang, 25175,
Sumatera Barat, Indonesia
*Corresponding author: *dewiroesma@sci.unand.ac.id*

Received: 19 May 2023; Accepted: 28 August 2023

ABSTRACT

The Coffee Berry Borer (*Hypothenemus hampei* Ferarri, 1867) is a serious pest of coffee and has a wide distribution worldwide, including in Sumatra, Indonesia. During our investigation on the coffee plantations of Sumatra, we found that *H. hampei* infested three different species of coffee (*Coffea arabica*, *C. cenophora*, and *C. liberica*). This study aimed to describe the morphological variations of *H. hampei* that infested the three coffee species. The morphological variations recorded in *H. hampei* infested on the three species of coffee were: the number of denticles on the fore legs (procoxae) and hind legs (metacoxae). The result showed that the number of denticles on procoxae and metacoxae, respectively: are six and four (in *C. arabica*), seven and four (in *C. cenophora*), and seven and three (in *C. liberica*). The highest result of the hardness and thickness test of coffee was in *C. liberica* (236,81 N/Cm2; 2.33 mm).

Keywords: Coffee Berry Borer, morphology, procoxoae, metacoxae, coffee.

ABSTRAK

Penebuk Biji Kopi (*Hypothenemus hampei* Ferarri, 1867) merupakan perosak kopi yang serius dan mempunyai taburan yang meluas di dunia, termasuk Sumatera, Indonesia. Semasa kajian di ladang kopi di Sumatera, kami mendapati *H. hampei* telah menginfestasi tiga spesies kopi (*Coffea arabica*, *C. cenophora*, and *C. liberica*). Kajian ini bermatlamatkan untuk memperihalkan variasi *H. hampei* yang menginfestasi tiga spesies kopi tersebut. Variasi morfologi *H. hampei* telah direkodkan ke atas tiga spesies kopi merujuk ciri ini; bilangan dentikal ada kaki hadapan (prekoksa) dan kaki belakang (metakoksa). Bilangan dentikal pada prekoksa dan metakoksa masing-masing, enam dan empat (pada *C. arabica*), tujuh dan empat (pada *C. cenophora*) dan tujuh dan tiga (pada *C. liberica*). Hasil kekerasan dan ketebalan tertinggi adalah pada *C. liberica* (236.81 N/Cm2; 2.33 mm). Walaubagaimanapun, variasi

morfologi prekoksa dan metakoksa pada tiga spesies kopi tidak berkorelasi dengan faktor kekerasan dan ketebalan biji kopi.

Katakunci: Penebuk Biji Kopi, morfologi, prekoksa, metakoksa, kop**i.**

INTRODUCTION

The Coffee Berry Borer, *Hypothenemus hampei* Ferrari, 1867 (Coleoptera: Curculionidae: Scolytinae), is a small bark beetle endemic to Africa and nowadays present in most coffee-producing countries (Vega et al. 2015). *Hypothenemus hampei* is a well-known seed-feeding bark beetle and one of the serious pests of coffee (Damon 2000; Vega et al. 2009). This species is widely distributed worldwide, especially in every coffee-producing region (Vega et al. 2009), including new records from China (Sun et al. 2020). Economically the most important *Coffea* species are one of the most important global commodities, with over 10 million hectares planted in 80 countries in tropical and subtropical regions (Aristiza´bal et al. 2015; Escobar et al. 2019; FAOSTAT 2015). This species causes serious economic losses affecting worldwide more than 20 million rural households (Vega et al. 2003). Qualitative and quantitative losses through larval feeding and oviposition gallery construction by the females (Damon 2000; Decazy et al. 1989).

The ability of *H. hampei* to attack coffee berries is strongly influenced by environmental conditions such as temperature, humidity, altitude, cultivation methods, and plant varieties (Matiello et al. 2002; Sera et al. 2010). The optimum temperature for *H. hampei* beetle development is 20–33ºC. At temperatures ≤15ºC or ≥35ºC, female beetles are frequently fail to broach the coffee cherries. Although able to brood, *H. hampei* cannot lay eggs (Jaramillo et al. 2009; Mathieu et al. 2001; Silva et al. 2014). The humidity optimum for *H. hampei* development ranges from 90%–95% (Sera et al. 2010). In Indonesia, the *H. hampei* was reported for the first time attacking Liberika coffee on Lampegan plantations, West Java, in 1909 due to the entry of coffee from Uganda. The pest then spreads to coffee production centers (Susilo 2008). Efforts to control *H. hampei* continue, the application of *B. bassiana* isolates can reduce attacks and cause *H. hampei* death and reduce damage to coffee fruit (Apriyanto et al. 2016).

This cryptic life history of Coffee Berry Borer inside the coffee berry makes the pest extremely difficult to control (Brun et al. 1995). The multiple cryptic species were reported in the name *H. hampei* by Gauthier (2010). However, the *H. hampei* complex is extremely difficult to identify by its external features due to its limited morphological diversity and poorly defined characters (Wood 1982).

The morphological characters of *H. hampei* analyzed were the eye, antennae, setae on the elytra, mandible, pronotum, wings, legs (procoxae, mesocoxae, metacoxae), and the number of protibial denticles (Bright & Torres 2006; Gomez et al. 2018; Johnson et al. 2022; Vega et al. 2014). During our investigation on the coffee plantations of Sumatra, we found that *H. hampei* infested three different species of coffee (*Coffea arabica, C. cenophora*, and *C. liberica*). This research was conducted on three coffee types in Indonesia: *Coffea arabica* L., *C. canephora* Pierre ex A. Froehner, and *C. liberica* var. *liberica*. In the present study, the objectives were to determine the morphological variation of *H. hampei* on three species of coffee in Sumatra and to investigate the correlation between the morphological variation in *H. hampei* with the thickness and hardiness of the coffee berries.

MATERIALS AND METHODS

Insect Sampling

The study was conducted from June to November 2022. The samples of *H. hampei* were collected using an exploratory survey method from Arabica, Robusta, and Liberica coffee plantations in the following locations of Aceh Province: Bener Meriah district, Pintu Rime Gayo, Alur Cicin (Arabica coffee plantation, N 04˚53'38.8" E 096˚44'25.8"); North Aceh District, Negeri Antara, Alue Dua (Robusta coffee plantation, N 05˚ 00'07.0" E 096˚57'01.8"); Pidie District, Tangse, Blang Malo (Liberica coffee plantation, N 05˚05'29.9" E 095˚54'06.6"). The specimens examined in this study were female *H. hampei* with a total of nine individuals. Each sample is made of several parts of specimen preparations such as procoxae, metacoxae, antennae, mandibles and wings.

Species Identification

The specimen was examined at the Invertebrate Taxonomy Laboratory, Biology Department, Faculty of Mathematics and Natural Sciences, Andalas University, Padang, and the Ecology Laboratory, Biology Department, Faculty of Mathematics and Natural Sciences, Universitas Negeri Padang. Species determination of *H. hampei* was made by referring to the original description by Ferrari (1867) and key to species level by c and images of the type material provided by the Database of the Bark and Ambrosia Beetles (Atkinson. 2022). Images were taken by a Canon EOS KissX5 digital camera attached to a Nikon SMZ1270 stereomicroscope.

Measurement of Thickness and Hardiness of Coffee Berry

In this study, we also examined the hardness and thickness of the three types of arabica, robusta and liberica. The analysis was carried out at the Central Instrument Laboratory of the Faculty of Agricultural Technology, Andalas University. The tool used to test the hardness of coffee fruit is Texture Analyzer CT3. The workings of this Teture Analyzer are by pressing or pulling the fruit sample, through a probe that is in accordance with the desired application. The unit used to express the hardness value is N/cm2. The tool used for the fruit thickness test is a vernier caliper. The unit used to express the thickness value is mm.

Photograph of Specimens

Multi-focused montage images were produced using Helicon Focus Pro. (Helicon Soft Ltd., http://www.heliconsoft.com/) from a series of source images taken by a Canon EOS KissX5 digital camera attached to a Nikon SMZ1270 stereomicroscope. To get a focused image, it is necessary to take pictures of each specimen generally five to ten times. Artifacts/ghosts and unnecessary parts (unfocused appendages, insect pins, etc.) surrounding or covering target objects were erased and cleaned up using the retouching function of Helicon Focus Pro. The color balance, contrast, and sharpness were adjusted using Adobe Photoshop CS6.

Statistical Analysis

The Spearman-rho correlation is used to test the hypothesis of the relationship between the two variables (species of coffee, procoxae, metacoxae, and exocarp) and to see the strength and weaknesses of the relationship and the direction of the relationship between two variables that are at least on an ordinal scale (de Winter et al. 2016). The Spearman-rho correlation coefficient equation is stated as follows:

$$rho = 1 - \frac{6 \sum d^2}{n(n^2 - 1)}$$

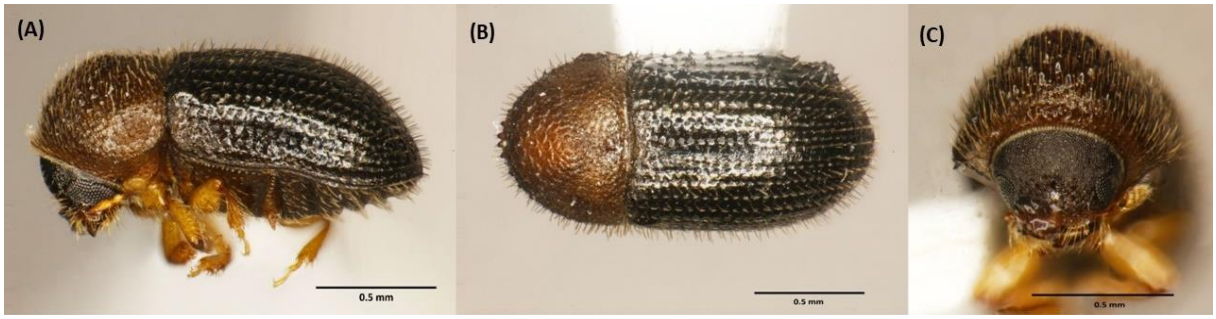
Information:
Rho: Spearman Rank Correlation Coefficient
d2: Rank squared
n: Number of data (sample)

Determining the level of correlation strength of the calculated variables.
Category:
0.00 -0.25: very low relationship
0.26 -0.50: enough relationship
0.51 -0.75: strong relationship
0.76 - 0.99: very strong relationship
1.00: perfect relationship

RESULTS

The Coffee Berry Borer was collected from three species of coffee plants (*C. arabica*, *C. cenophora*, *C. liberica*) and confirmed as *H. hampei* Ferarri, 1867 based on morphological observation and fit with the identification key provided by Bright & Torres (2006); Vega et al. (2014). *Hypothenemus hampei* is distinguished from other species of the genus *Hypothenemus* by the following characteristics: frons broad, indistinct frontal groove, or no groove at all; usually with four marginal asperities; mixed type of setae on pronotum, with some slightly flattened; pronotum in dorsal view, slightly more narrowly rounded; elytral declivity more broadly rounded, without a distinct transition from the elytral disc; elytral declivity in lateral view, more than half of the length of the elytra; elytral disc takes up more than half of the length; interstrial bristles prominent and in almost perfectly uniseriate rows; interstrial bristles long, narrow, and slightly flattened; the tip of each bristle square, narrow than the rest of its length; bristles on the elytral disc longer than those on the declivity (Johnson et al. 2022).

The morphological appearance of *H. hampei* from three species of coffee plants is generally similar, including the antennae, mandible, and wings (Figure 1 & 3). However, in our careful examination of the specimens, we found the following morphological variations among the populations from three species of coffee plants: the number of denticles on the fore legs (procoxae) and hind legs (metacoxae) (Figure 2).



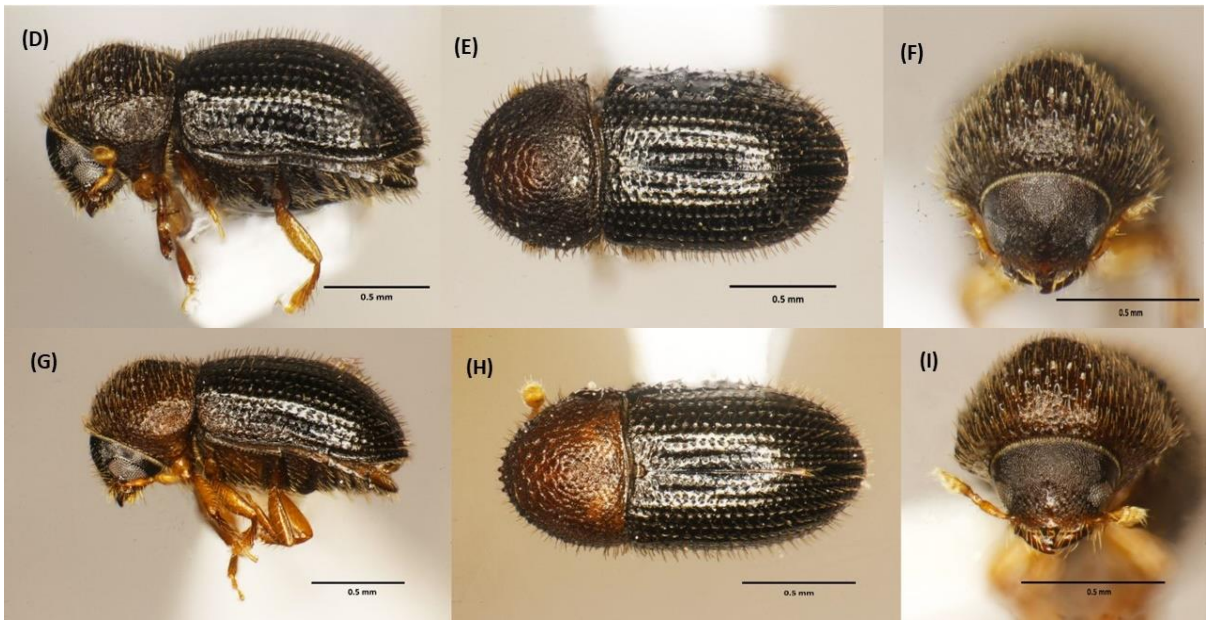
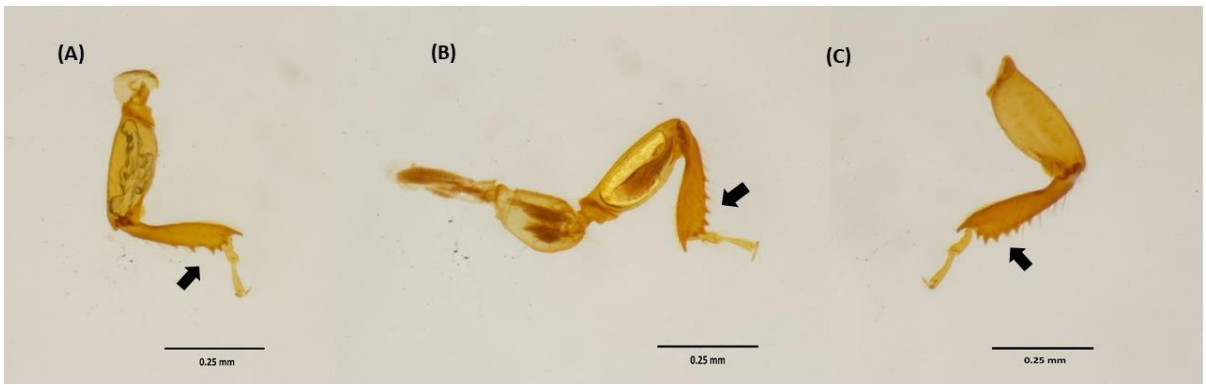


Figure 1. The Coffee Berry Borer, *Hypothenemus hampei*: A−C, collected in *Coffea arabica*; D−F, collected in *C. chenopora;* G−I, collected in *C. liberica*. A, D, G, habitus in lateral view; B, E, H, habitus in dorsal view; C, F, I, habitus in frontal view

The number of denticles on procoxae and metacoxae is six and four in *C. arabica* (A), Seven and four in *C. cenophora*, and seven and three in *C. liberica* (B). The characteristics of the legs can be a rich source of taxonomic and phylogenetic characteristics in the genus *Hypothenemus*, such as the protibiae. The Coffee Berry Borer and strong mandibles resistant to abrasion are needed to construct galleries within the coffee seed, where the females oviposit, and to feed on the seed. Andersen (2010) discovered heavy metal elements (Zn) in insect mandibles, which offer hardness and abrasion resistance to the incisors, or the cutting edge of the mandible.

Antenna identification in this study followed the description of Vega et al. (2014) and Johnson et al. (2022). The antennae have three to five funicular segments. The antennal club has sutures marked with setae and a partial septum, visible as a dark line.



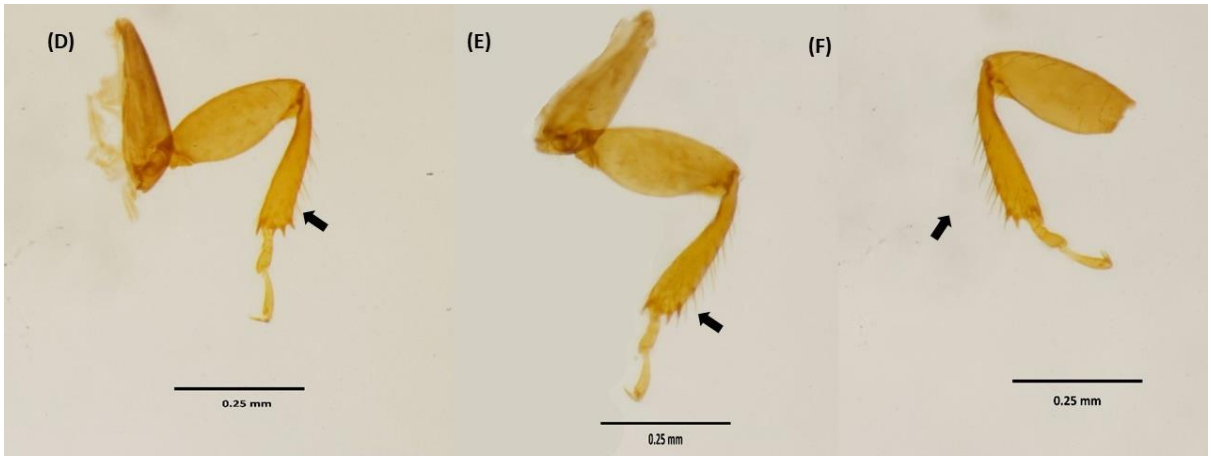


Figure 2. The legs of *Hypothenemus hampei*: A, B, C Procoxoae; D,E,F. Metacoxae; A, D, collected in *Coffea arabica*: B, E, collected in *C. cenophora*; C, F, collected in *C. liberica* (black arrows indicated the variation in numbers of denticles)

Although there are no antennae, mandibula, and wing differences of this species in the three coffee varieties closest to Sumatra, further studies regarding the mandibular cuticular elements are needed because each coffee type has different fruit characteristics.

Figure 3. The *Hypothenemus hampei*: A, antenna; B, left mandible; C, hindwing

In the present study, the hardness and thickness of the fruits from three coffee species also was analyzed. The fruits were reanalyzed based on the level of their maturity and colors: Red (R) for ripe fruit, Yellow (Y) for half-ripe fruit, and Green (G) for unripe fruit. The coffee weevil, *H. hampei*, is commonly found in all three types of fruit maturity. However, the hardness and thickness of the three types of coffee maturity are different (Table 1). *Hypothenemus hampei* feeds on and reproduces in the endosperm of the seed of the coffee berry, burrowing through the exocarp, mesocarp, and endocarp (Sponagel 1994).

Table 1. The average of the hardness and thickness test of fruits of *C. arabica, C. cenophora, C. liberica* based on color red, yellow, and green

Sample	Hardness (N/cm^2)	Thickness (mm)
C. arabica (red)	111.51	1.41
C. arabica ((yellow)	49.97	1.17
C. arabica (green)	125.85	1.38
C. cenophora (red)	93.03	2.05
C. cenophora (yellow)	54.04	1.44
C. cenophora (green)	121.81	1.69
C. liberica (red)	156.07	2.09
C. liberica (yellow)	236.81	2.33
C. liberica (green)	221.1	2.13

The *Coffea liberica* is the highest result of hardness and thickness among the three species of coffee fruits (236,81 N/cm^2; 2.33 mm), while the lowest is *C. arabica* with (49.97 N/cm^2; 1.17 mm (Table 1). Therefore, we assumed that the morphological variations found in the *Hypotnemus hampei* were related to the hardness and thickness of the coffee berries. Suffers more damage due to its continuous production of flowers and the constant availability of berries in various stages of development throughout the year.

Based on Spearman's rho test, a correlation coefficient of 0.707* is obtained. This score means that the number of denticles in procoxae strongly correlates with the type of coffee. The Star sign (*) means that the correlation is significant at a significant number of 0.01. The correlation coefficient number is positive, so the relationship between the two variables is unidirectional; thus, increasing the effect of the number of procoxae denticles on the type of coffee. The output above is known for its significance or Sig. (2-tailed) 0.03<0.05 means a significant relationship between the variable number of procoxae denticles and the type of coffee.

Table 2. Correlation of coffee fruit exocarp hardness against procoxae and metacoxae *H. hampei*

Correlation			Coffee Species	Procoxae Number	Metacoxae Number	Exocarp Hardness
Spearman's rho	Coffee species	Correlation Coefficient	1	.707*	0.612	0.41
		Sig. (2-tailed)	.	0.033	0.08	0.273
		N	9	9	9	9
	Procoxae number	Correlation Coefficient	.707*	1	0	0.369
		Sig. (2-tailed)	0.033	.	1	0.329
		N	9	9	9	9
	Metacoxae number	Correlation Coefficient	0.612	0	1	0.274
		Sig. (2-tailed)	0.08	1	.	0.476
		N	9	9	9	9
	Exocarp hardness	Correlation Coefficient	0.41	0.369	0.274	1

Sig. (2-tailed)	0.273	0.329	0.476	.
N	9	9	9	9

DISCUSSION

Hypothenemus hampei is widely considered to be the most devastating pest of coffee and spread all over the world. The West Indies recorded from Jamaica and Puerto Rico also from throughout the coffee-producing regions of Africa, Asia, Indonesia, Central America, and South America (Vega et al. 2002). This species has also been analyzed morphologically and molecularly by Gauthier (2010) based on specimens found in various locations worldwide, but the analysis conducted does not include specimens scattered from Sumatra Island. In the present study, we recorded the *Hypothenemus hampei* in Sumatera. Uniquely, the species which is collected from Sumatra have morphological variations. Therefore, the morphological variations of this species should be important characteristics to support the delimitation of multiple cryptic species proposed.

The front of *H. hampei* may have a broad, indistinct frontal groove or no groove. There are usually four marginal asperities. The setae on the pronotum are mixed, with some slightly flattened. The shape of the pronotum, viewed from above, is slightly more narrowly rounded (i.e., more triangular) than the similar *Hypothenemus* species. The elytral declivity of *H. hampei* is much more broadly rounded than in similar species, without a distinct transition from the elytral disc. When viewed laterally, the declivity takes up more than half of the length of the elytra, whereas, in similar species, the elytral disc takes up more than half of the length. As with most *Hypothenemus*, the interstrial bristles are prominent in almost perfectly uniseriate rows. The shape of the interstrial bristles, however, is distinctive and differentiates the coffee berry borer from most other *Hypothenemus* species. The bristles are long, narrow, and slightly flattened. The tip of each bristle is square and not much wider than the rest of its length. The bristles on the elytral disc are shorter than those on the slope. Males are smaller with reduced eyes (Vega et al. 2014).

The legs, particularly the hind tibia, are useful for distinguishing *Hypothenemus* from other genera. *Hypothenemus* have very few denticles (spine-like structures) on the tibia. Denticles are only found at the apex (furthest from the body) in *Hypothenemus.* The shape is also narrow and straight. Many other genera have denticles that are over one-third or more of the length of the tibia or flattened with a semicircular margin. This study also supported, that there are variations in the number of denticles in procoxae and metacoxae in the three types of coffee in Sumatra. In the study by Johnson et al. (2022) antenna is an important character in *H. hampei*. The shape of the antenna is characterized by the presence of a septum and partial suture with three sutures and a dark-striped septum.

The previous study has visualized and identified the mandibles of *H. hampei* (Metcalf et al. 1962; Vega et al. 2017). The mandibles of females were characterized by three denticles. However, we found no difference in the mandible for this species in three different species of coffee in Sumatra. In previous research by Metcalf et al. (1962), the shape of the mandible and maxilla transverse from side to side. Several cuticular elements were detected in the mandible, including Al, C, Ca, Cl, Mg, Na, O, P, and Zn. Zinc, a heavy metal, is only detectable in the incisors and can provide abrasion resistance. *Hypothenemus hampei* contains Zn in the mandible (Vega et al. 2017). The incisors in *H. hampei* contain the Zn required to reduce

abrasion, or it is an evolutionary relic of what may have been a previous life history involving drilling into the bark, as was done by *Hypothenemus* species (Vega et al. 2015).

The berries of *C. cenophora* take longer to mature than those of *C. arabica*, tend to be infested at an earlier stage of development, and are easier to penetrate, having a thinner and softer exocarp and endocarp. The berries take longer to mature than those of *C. arabica*, tend to be infested at an earlier stage of development, and are easier to penetrate, having a thinner and softer exocarp and endocarp. The higher temperatures and humidity of the lower altitudes where robusta coffee is grown also favor the pest (Klein-Koch et al. 1988). Damage caused by the coffee berry borer commences after adult females bore a hole in the coffee berry and lay their eggs in galleries built in the endosperm, followed by larval feeding within the galleries. Consequences of infestation include the abscision of berries, loss in seed weight, and loss in quality (Duque O. 2000; Duque Orrego et al. 2002; Duque O. & Baker 2003).

Based on the results of the hardness and fruit thickness test of the three coffees. The results obtained with yellow arabica coffee showed a minimum hardness of 49.97 N/cm2 and a thickness of 1.17 mm. The yellow liberika coffee showed a maximum hardness of 236.81 N/cm2 and a thickness of 2.33 mm. The values is following the endosperm of fruit infested with *H. hampei* in arabica coffee which showed total damage compared to liberica coffee.

CONCLUSION

There was a difference in morphological variations among the populations from three species of coffee plants: the number of denticles on the fore legs (procoxae) and hind legs (metacoxae). There was no correlation between the coffee hardness and thickness test with the number of denticles in the procoxae and metacoxae legs of *H. hampei.* The results of this study reveal the diversity of morphological variation of *H. hampei* on coffee plants in Sumatra. This information is the basis for determining the handling of *H. hampei* by stakeholders and other researchers.

ACKNOWLEDGEMENTS

We thank the Ministry of Education, Culture, Research and Technology Directorate General of Higher Education, Research, and Technology (190/E5/PG.02.00.PT/2022) which has provided research grants. We thank the Department of Biology, FMIPA, Andalas University. We also thank Rijal Satria, Ph.D for his support in conducting in Universitas Negeri Padang.

AUTHORS DECLARATIONS

Conflict of Interest
All authors declare that they have no conflicts of interest to influence the findings reported in thispaper.

Ethics Declarations
Ethics declarations are not applicable for this research.

Data Availability Statement
This manuscript has no associated data.

Authors' Contributions

Aida Fitriani Sitompul performed all experiments, and data analysis, and wrote the manuscript. Dewi Imelda Roesma guided the research process, analyzed the data, revised the manuscript, and improved the final manuscript. Dahelmi guided the research process and guided in writing the manuscript.

REFERENCES

Andersen, S.O. 2010. Insect cuticular sclerotization: A review. *Insect Biochemistry and Molecular Biology* 40(3): 166–178.

Apriyanto, D., Nadrawati, Bustamam, H. & Zarkani, A. 2021. Effect Of *Beauveria bassiana* against coffee bean borer, *Hyphothenemus hampei* (Ferrari) in small scale field trials. *Serangga* 26(3): 69-88.

Atkinson, T.H. 2022. Bark Beetles And Ambrosia Beetles Of The America. Biodiversity Center, University of Texas at Austin. https://www.barkbeetles.info/amer_links.php. [viewed 10 May 2022].

Bright, D.E. & Torres, J.A. 2006. Studies on West Indian Scolytidae (Coleoptera) 4. A review of the Scolytidae of Puerto Rico, U.S.A. with descriptions of one new genus, fourteen new species, and notes on new synonymy (Coleoptera: Scolytidae). *Koleopterologische Rundschau* 76: 389–428.

Brun, L.O., Stuart, J., Gaudichon, V., Aronstein, K. & Ffrench-Constant, R.H. 1995. Functional haplodiploidy: A mechanism for the spread of insecticide resistance in an important international insect pest. *Proceedings of the National Academy of Sciences* 92: 9861–9865.

Damon, A. 2000. A review of the biology and control of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bulletin of Entomological Research* 90: 453–465.

Decazy, B., Ochoa, H., Lotode, R. 1989. Indices de distribution spatiale et methode dechantillonnage des populations du scolyte des drupes du cafeier, *Hypothenemus hampei* Ferr. *Café, Cacao, Thé* 33: 27–41.

de Winter, J. C. F., Gosling, S. D., & Potter, J. 2016. Comparing the Pearson and Spearman correlation coefficients across distributions and sample sizes: A tutorial using simulations and empirical data. *Psychological Methods* 21: 273–290.

Duque, O.H., & Baker, P.S. 2003. *Devouring Profit. The Socio-Economics of Coffee Berry Borer IPM*. Cenicafé: The Commodities Press.

Duque-Orrego, H., Ma´rquez, Q.A. & Herna´ndez, S.M. 2002. Estudios de caso sobre costos de manejo integrado de la broca del cafe´ en el Departamento de Risaralda. *Cenicafe´* 53: 106–118.

Duque, O.H. 2000. *Economics of coffee berry borer (Hypothenemus hampei) in Colombia. In: Workshop, Coffee Berry Borer: New Approaches to Integrated Pest Management*. Starkville: Mississippi State University Publishers.

Escobar, R.S., Grassa, I., Armbrechtc, I. & Tscharntkea, T. 2019. Biological control of the coffee berry borer: Main natural enemies, control success, and landscape influence. *Biological Control* 136: 103992.

FAOSTAT. 2015. Food and Agriculture Organization of the United Nations, Statistics Division. http://faostat.fao.org/ [21 April 2023].

Ferrari, J.A.G. 1867. *Die Forst- und Baumzuchtscha¨dlichen Borkenka¨fer (Tomicides Lac.) aus der Familie der Holzverderber (Scolytides Lac.), mit besonderer Beru¨cksichtigung vorzu¨glich der europa¨ischen Formen, und der Sammlung des k. k. zoologischen Kabinetes in Wien*. Vienna: Carl Gerold's Sohn Press.

Gauthier, N. 2010. Multiple cryptic genetic units in Hypothenemus hampei (Coleoptera: Scolytinae): evidence from microsatellite and mitochondrial DNA sequence data. *Biological Journal of the Linnean Society* 101(1): 113-129.

Gomez, D.F., James, K. & Steininger, M.S. 2018. Species delineation within the *Euwallacea fornicatus* (Coleoptera: Curculionidae) complex revealed by morphometric and phylogenetic analyses. *Insect Systematics and Diversity* 6: 1–11.

Jaramillo, J., Chabi-Olaye, A., Borgemeister, C., Kamonjo, C., Poehling, H. & Vega, F.E. 2009. Where to sample? Ecological implications of sampling strata in determining abundance and impact of natural enemies of the coffee berry borer, *Hyphotenemus hampei*. *Biological Control* 49: 245–253.

Johnson, A., LeMay, G., & Hulcr, J. 2022. Identification of Coffee Berry Borer from Similar Bark Beetles in Southeast Asia and Oceania: *EDIS* 17: 1-7.

Klein-Koch, C., Espinoza, O., Tandazo, A., Cisneros, P. & Delgado, D. 1988. Factores naturales de regulacio´n y control biolo´gico de la broca del cafe´ (*Hypothenemus hampei* Ferr.). *Sanidad Vegetal (Ecuador)* 3: 5–30.

Metcalf, C.L., Flint, W.P. & Metcalf, R.L. 1962. *Destructive and useful insects: Their habits and control.* 4th Edition. New York: McGraw-Hill Book Company, Inc.

Mathieu, F., Gaudichon, V., Brun, L.O. & Frérot, B. 2001. Effect of physiological status on olfactory and visual responses of female *Hypothenemus hampei* during host plant colonization. *Physiological Entomology*26: 189– 193.

Matiello, J.B., Santinato, R. & Garcia, A.W.R. 2002. *Cultura de café no Brasil - novo manualde recomendações*. Rio de Janeiro: Procafe Foundation.

Sera, G.H., Sera, T., Shiguer Ito, D., Ribeiro Filho, C., Villacorta, A., Seidi Kanayama, F. 2010. Coffee berry borer resistance in coffee genotypes. *Brazilian Archives of Biology and Technology* 53: 261–268.

Silva, W.D., Costa, C.M. & Bento, J.M.S. 2014. How old are colonizing *Hypothenemus hampei* (Ferrari) females when they leave the native coffee fruit? *Journal of Insect Behaviour* 27: 729–735.

Sponagel, K.W. 1994. La broca del cafe´ *Hypothenemus hampei* en plantaciones de cafe´robusta en la amazonı´a ecuatoriana. Ph.D. Thesis. (Traducida del alema´n por Wilma Miranda-Sponagel), Universidad de Giessen, Alemania.

Susilo, A.W. 2008. Ketahanan tanaman kopi (*Coffea* spp.) terhadap hama penggerek buah kopi *Hypothenemus hampei* Ferr. *Review Penelitian Kopi dan Kakao* 24(1): 1–14.

Sun, S., Zheng, W. & Aiqin, L. 2020. First record of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae) on Hainan Island, China. *Journal The Coleopterists Bulletin University of Florida* 74(4): 710-713.

Vega, F.E., Benavides, P., Stuart, J. & O'Neill, S. 2002. Wolbachia infection in the coffee berry borer (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 95: 374-378.

Vega, F.E., Rosenquist, E. & Collins, W. 2003. Global project needed to tackle coffee crisis. *Nature* 435: 343.

Vega, F.E., Infante, F., Castillo, A. & Jaramillo, J. 2009. The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae): A short review, with recent findings and future research directions. *Terrestrial Arthropod Reviews* 2(2): 129.

Vega, F.E., Simpkins, A., Bauchan, G., Infante, F., Kramer, M. & Land, M.F. 2014. On the eyes of male coffee berry borers as rudimentary organs. *PLoS One* 9 (1): e85860.

Vega, F.E., Infante, F. & Johnson, A.J. 2015. The genus *Hypothenemus* with emphasis on *H. hampei* the coffee berry borer. In Vega, F.E. & Hofstetter, W. (eds.). *Bark Beetles: Biology and Ecology of Native and Invasive Species*, pp. 427-494. San Diego: Academic Press.

Vega, F.E., Bauchan, G., Infante, F. , S. 2017. Mouthpart structure and elemental composition of the mandibles in the coffee berry borer (Coleoptera: Curculionidae: Scolytinae). *Annals of the Entomological Society of America* 110(4): 381–389.

Wood, S.L., 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs* 6: 1-1359.