



Geometric morphometrics of wing venation to differentiates new species of *Scaura* Schwarz populations (Hymenoptera: Apidae: Meliponini)

Morfometria geométrica da venação alar para diferenciar populações de uma nova espécie de *Scaura* Schwarz (Hymenoptera: Apidae: Meliponini)

D. S. Nogueira^{1,2*}; J. S. G. Teixeira³; T. Mahlmann²; M. L. Oliveira²; D. W. Roubik⁴

¹Instituto Federal de Educação, Ciência e Tecnologia do Amazonas, Campus São Gabriel da Cachoeira, 69750-000 São Gabriel da Cachoeira -AM, Brasil

²Laboratório de Hymenoptera, Instituto Nacional de Pesquisas da Amazônia, 69067-375, Manaus - AM, Brasil

³Instituto Tecnológico Vale – Desenvolvimento Sustentável, 35400-000, Belém - PA, Brasil

⁴Smithsonian Tropical Research Institute, 0843-03092, Balboa, Panamá

dsnogueira@ifam.edu.br

(Recebido em 27 de setembro de 2018; aceito em 13 de dezembro de 2018)

Scaura Schwarz, 1938 is a small Neotropical genus of stingless bees widely distributed in Brazil. The new species of *Scaura* is a widespread species, and its wide distribution may suggest that it is a species complex. In order to differentiate populations that could compose cryptic species, we studied the wing venation variation using geometric morphometrics in 56 workers, 23 of these from remaining of Atlantic Forest in Ceará state and 33 from the Amazon region. Bees from Atlantic Forest differed of the bees from Amazon region, corresponding to 38.05% of total variation (principal components analysis), 100% of canonical variation and 52.93% of canonical variation between localities, with significant difference between populations in discriminant function analysis ($p < 0.001$). The results suggest that the Atlantic Forest bees may be a new species. However, it is necessary more detailed morphological studies, and/or a molecular analysis to confirm this possibility.

Keywords: Stingless bee, bee population, forewing.

Scaura Schwarz é um gênero Neotropical de “abelhas sem ferrão” amplamente distribuído no Brasil. Considerando que a espécie nova desse gênero é a mais amplamente distribuída, sua ampla distribuição e algumas diferenças morfológicas sugerem que se trate de um complexo de espécies. Para diferenciar populações que poderiam compor espécies crípticas, nós estudamos a variação da venação alar utilizando morfometria geométrica em 56 operárias. 23 oriundas de remanescentes de Mata Atlântica no Estado do Ceará e 33 da região Amazônica de ninhos diferentes. As abelhas da Mata Atlântica diferiram das amazônicas com 38,05% de variação (análise de componentes principais), 100% (análise de variação canônica) e 52,93% de variação entre localidades amostradas (variação canônica), com diferença significativa entre populações na análise da função discriminante ($p < 0,001$). Esses resultados sugerem que as abelhas da Mata Atlântica possam formar uma espécie nova, entretanto, é necessário que estudos morfológicos mais detalhados e/ou uma análise molecular para confirmar essa possibilidade.

Palavras-Chave: Abelha sem ferrão, população de abelha, asa anterior.

1. INTRODUCTION

Bees are an important group of organisms, especially by effecting pollination in tropical forests [1] and also augmenting crop production [2, 3, 4, 5, 6, 7, 8].

There are about 20,500 species of bees [9], but with estimates that the total number of species could be 50% higher [10]. In Meliponini, or stingless bees, 551 species are documented [11]. Various digital tools have been developed in order to assist in the identification of species, such as the identification based on wing venation patterns [12, 13, 14, 15, 16].

The genus *Scaura* Schwarz, 1938, is generally composed of small and dark bees, with unusual and extended hind basitarsus. The basitarsus is as wide as or wider than the hind tibia, and is used to scrape pollen from the surfaces of leaves and petals, after other bees visited flowers and spill

pollen onto leaves and petals [17]. The genal area of *Scaura* is narrower than compound eye in side view and the malar space shorter than the diameter of the flagellum [18]. *Scaura* has four recognized species, with three recorded in Brazil [*S. longula* (Lepeletier, 1836), *S. latitarsis* (Friese, 1900) and *S. atlantica* Melo, 2004] while the distribution of the genus is broadly Neotropical, from Mexico to southern Brazil. Recently Nogueira et al. (2017) [19] synonymized *S. tenuis* (Ducke, 1916) under *S. latitarsis* (Friese, 1900), leaving a new species to be described (Figure 1).

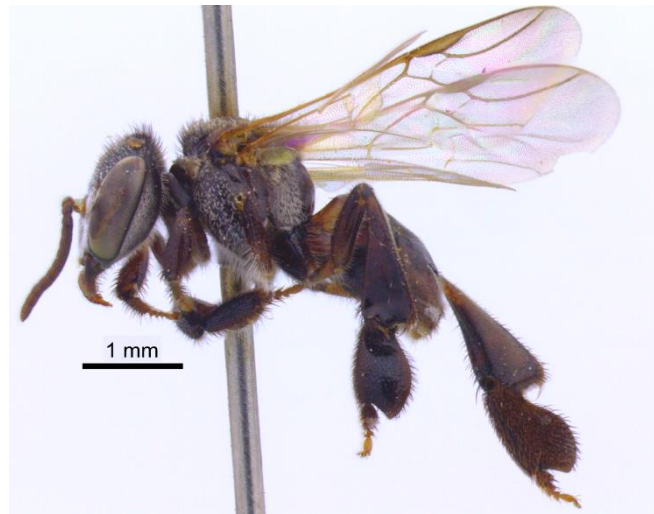


Figure 1: Lateral view of worker of *Scaura Schwarz* new species.

Their nests are built in wood cavities or active arboreal termites, which afford thermal stability and some defense, and because they are dependent on nesting in termites, it has not yet been possible to create rationally for the use of their products by man [20, 21, 22, 23].

The wide distribution of new species of *Scaura* from the state of Tachira in Venezuela to the State of Paraná, in Brazil, and its occurrence to different environments demand more thorough distribution studies, as well as investigation of biology and potential cryptic species. Melo e Costa (2001) [24] mention that this species is actually a complex of species, by morphological differences, as observed by authors of this study, such as length and abundance of plumose hairs on the mesepisternum.

The aim of this study was to determine whether variation of wing venation between population from the Brazilian Atlantic Forest and Amazon Forest, and among populations of the latter, suggest two potentially unrecognized species.

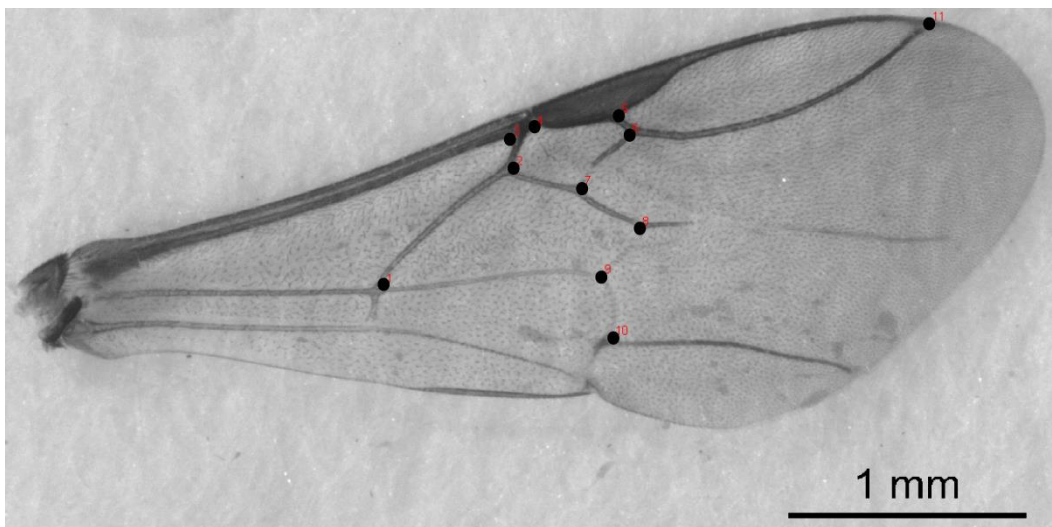
2. MATERIAL AND METHODS

The specimens studied here were from UFC (Universidade Federal do Ceará) and INPA (Instituto Nacional de Pesquisas da Amazônia) dry collections. A total of 56 workers were obtained from different nests in several localities. Each right wing was mounted on a slide, glued on label and pinned with the specimen. Twenty-three of the specimens were collected in Atlantic Rain Forest remaining in Meruoca (11 from two different nests) and Ubajara (12 collected on flowers) in mountainous areas, both in the state of Ceará. The remaining 33 specimens were collected with Malaise traps in the Brazilian Amazon region: Acre (1), Amazonas (14), Pará (2), Rondônia (7) and Roraima (9).

Table 1: Amount of workers used and their respective localities and biomes.

State	Locality	Amount specimens	Biome
Acre (AC)	Rio Branco	1	Amazon Forest
Amazonas (AM)	Itacoatiara	14	
Pará (PA)	Trombetas River	2	
Rondônia (RO)	Vilhena	1	
Rondônia (RO)	Campo Novo	6	
Roraima (RR)	Jufari River	7	
Roraima (RR)	Uraricoera River	2	
Ceará (CE)	Meruoca	11	Atlantic Forest
Ceará (CE)	Ubajara	12	
TOTAL		56	

We prepared photomicrographs using a Leica M205C stereomicroscope coupled with a Leica DFC295 camera and a Leica Application Suite V4.1 software. Interactive Measurements and Montage were used tpsUtil software version 1.64 [25] to generate a TPS file and then tpsDig version 2.22 [26] to assign 11 landmarks [27] to each photo (Figure 2). The intersections were aligned using Procrustes [28] and the relative and partial deformations and centroid size were obtained by tpsRelw software version 1.46 [29]. For Principal Component Analysis (PCA), Discrimination Function Analysis (DFA) and Canonical Variates Analysis (CVA) we used MorphoJ software version 1.6 [30], with which the values of the Mahalanobis and Procrustes distances were obtained. Those results generated a morphological proximity dendrogram by the Neighbor-Joining method with Mega software version 5.5 [31]. To relate the geographical distances of the locations with the morphometric Mahalanobis distances, we used a Mantel test with UPGMA software, version 1.3 [32].

Figure 1: Landmarks used on each forewing of *Scaura Schwarz* new species in the tpsDig software.

3. RESULTS

The Principal Component Analysis showed that the populations of the Atlantic Forest formed a separate group from populations of the Amazon, with 38.05%, 17.61% and 11.64%, respectively, of wing shape variation in the first three axis of principal component. The Canonical Analysis of Variance showed 100% variation in the first axis (biomes) (Figure 3) and 63.53%, 16.18% and 10.35%, respectively, in the first three axis (localities) (Figure 4). The Discriminant Function

Analysis significantly separated populations between biomes ($p < 0.001$). The similarity dendrogram generated from the wing shape united the populations of the NW Amazonian area (RR, AM, AC) and separated them from those of the SE Amazon (PA, RO) and Atlantic forest (CE) (Figures 5, 6). A Mantel test showed that the morphological variation between different populations is correlated at 42% of the geographical distance between them ($r = 0,42$; $p = 0,03$). The dendrogram joining the localities by states (permutations = 1.000, $r = 0.82$, Figure 7) showed that all states are related, with PA and CE being more related. The PA+CE+RO group was conserved in both dendrograms.

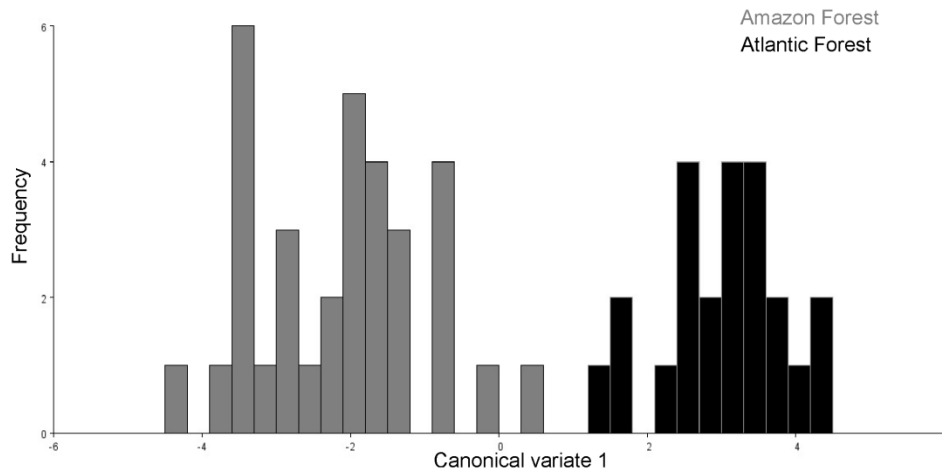


Figure 3: Canonical Variation Analysis (CVA), with 100% of variation, classification criterion: Biome.

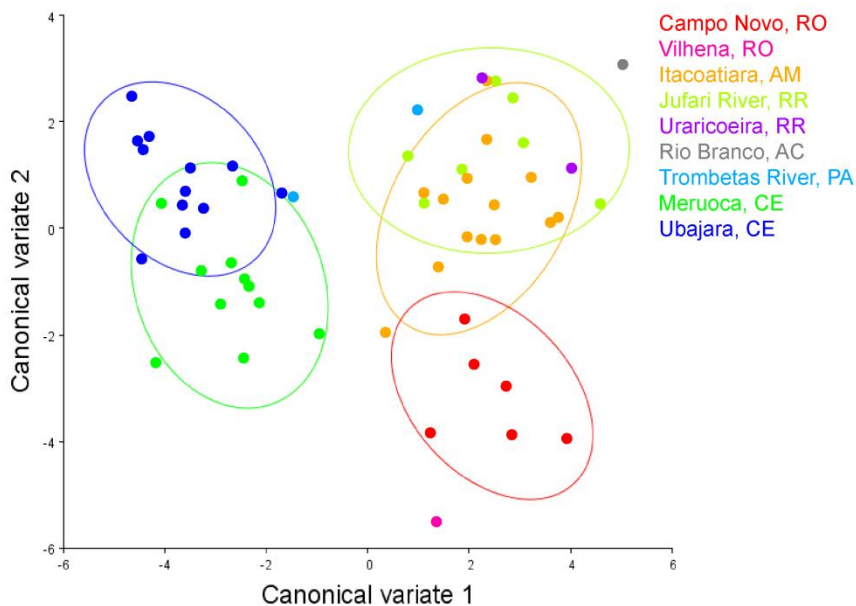


Figure 4: Canonical Variation Analysis (CVA), with 52.93% of variation in the first axis for population of new species of *Scaura Schwarz*, classification criterion: Localities.

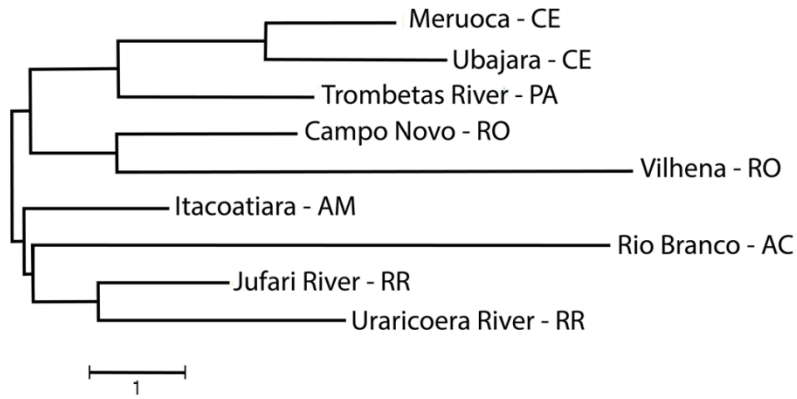


Figure 5: Dendrogram of morphological proximity showing the proximity on the wing shape of different localities in Brazil.

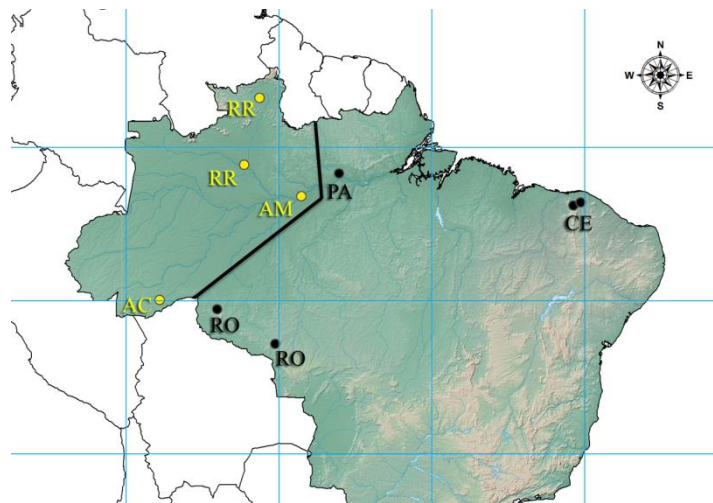


Figure 6: Location of the two groups separated by the correlation between the Mahalanobis distance and geographic distance of new species of *Scaura Schwarz*. In yellow are the places to the northwest Amazon. In black are the locations south Amazonian and east of Brazil.

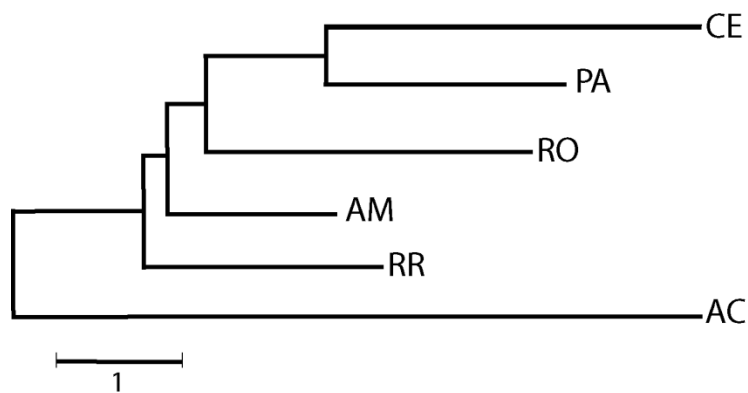


Figure 7: Dendrogram of morphological proximity showing the proximity on the wing shape of different states (permutations=1000; $r=0.82$).

4. DISCUSSION

The technique of geometric morphometrics applied to forewings venation indicate two distinct populations belonging two Neotropical biomes. Aytekin et al. (2007) [33] studying the genus *Bombus* (Hymenoptera: Apidae), [34] considering the genus *Eubazus* (Hymenoptera: Braconidae), Francisco et al. (2008) [35] in analysis of two populations of *Plebeia remota* (Holmberg) and Castañeda et al. (2015) [36] with populations of the *Anastrepha oblique* (Macquart) (Diptera: Tephritidae), distinguish cryptic populations with the same technique.

The detected separation of *Scaura* into two populations suggests that bees of the Atlantic Forest might be distinct species. The shape of the wing, as a diagnostic measure, can allow taxonomic separation of specimens. Their wing variation may be related to the time of separation or a geographical barrier between the populations, but it may include aspects, yet unstudied, of flight distance and swarming behavior of the species, among other things.

The contrasting environments of the Amazon and Atlantic Forest, should also favor increased morphological distance, because the two collection sites (Ubajara and Meruoca, Ceará) have similarity in relation to variables such as temperature, rainfall, altitude, vegetation cover and are surrounded by environments with sharp differences in those variables.

The general similarity between Amazonian and Atlantic populations may be due to previous union. Andrade-Lima (1982) [37] suggests that the origin of the vegetation in these areas of Atlantic Forest of higher elevation in NE Brazil, is associated with variations in climate that occurred during the Pleistocene (2 million - 10,000 years), which allowed the contact of the Atlantic with Amazon Forest, and subsequent separation after the interglacial periods. These events led the Atlantic Forest pieces in places with favorable microclimate, as in Ubajara and Meruoca studied here, now home of endemic species to these forest pieces within the savanna areas, observed with the bird *Picumnus limae* Sneathlage (Picidae), for example, which occurs in high areas in Ceará [38].

The morphological distance pattern of wing venation of populations of bees from Atlantic Forest in relation to the Amazonian populations was enough to separate into groups with 38.05% of variation in the first axis of the principal components analysis and 100% in canonical analysis for the two biomes. The difference may have been influenced by the Caatinga and Cerrado biomes as a barrier separating the first two biomes. These results indicate that the populations of the higher elevation pieces in Ceará may be a distinct species.

The correlation between morphological distances and geographic distance indicated by the Mantel test shows that part of the morphological differentiation observed ($r = 0.42$) may be explained by geographical isolation from biomes, which may be related to the flight distance, behavior in swarming and reproduction, and gene flow.

In the localities of the Amazon rainforest, which have large rivers as barriers, the variation between divided populations may increase over time [39]. This variability of populations was revealed in the canonical analysis by localities (52.93%, as Figure 4) in this region. This may indicate that even within the Amazon biome, there may be more than one species, as found among birds and primates that are separated by river barriers [40, 41].

The dendrogram suggests that the bees of Ceará and collected in the Rio Trombetas (Pará) form a group with the highest similarity. This Ceará+Pará group has clear similarity with bees of Rondônia. The population (Acre+Roraima) is more similar to the Amazon population. These findings suggest that there may be a variation in the shape of the wing along the Brazilian Amazonian northwest or in the opposite direction (Figure 6). The dendrogram joining the localities by states (Figure 7) did not show the division by divergence groups as in figures 5 and 6. The group CE+PA+RO was conserved, unlike the RR+AM+AC group, which remained related to the other states. With a larger sample size and scope of the Amazon rainforest and Neotropical localities or states, we may see new combinations, or be able to falsify hypotheses.

The flight distance in stingless bees is generally short compared to *Apis mellifera* L., and is mainly related to worker body size [42]. Larger bees such as *Trigona fulviventris* Guérin, *Cephalotrigona capitata* (Smith), *Melipona quadrifasciata* Lepeletier, and *Melipona compressipes* Smith can travel distances between 1500 to 2500 meters [43, 44]. Smaller bees like *Nannotrigona testaceicornis* (Lepeletier, 1836), *Tetragonisca angustula* (Latreille, 1811), *Plebeia poecilochroa* Moure and Camargo, 1993 and *Scaura* new species, fly 600 to 950 m from their nests

[42, 45]. The shorter flight distance is also related to the choice of a new location for nesting during swarming, which should be well within the particular flight radius of the species.

Another factor that influences the dispersal of new species of *Scaura* is the amount of living arboreal termites available in the environment, because the species use them as the substrate for building their nests. If the vegetation structure is compromised, restricting the spatial distribution of termites [46], it may affect the bee populations structure and contribute to the slow process of morphological differentiation.

5. CONCLUSION

The geometric morphometric technique as a tool for separating populations of new species of *Scaura* proved to be effective. Amazon rainforest bees were measurably distinctive at a high level from populations of the Atlantic Forest. The populations of each are further separable by the same techniques. However, more detailed biological studies, morphological studies, and molecular analyses are needed to appreciate whether the populations can be considered different species.

6. ACKNOWLEDGEMENTS

We thank to Invertebrate Collection of Instituto Nacional de Pesquisas da Amazônia (INPA) and Bee Collection of Universidade Federal do Ceará (UFC) for the loan of specimens for study and the team of Laboratório de Mamíferos Aquáticos (LMA/INPA) by the help with the technique of geometric morphometry, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for financial support.

7. BIBLIOGRAPHIC REFERENCES

1. Wille A. Biology of stingless bees. *Annu Rev Entomol.* 1983;28:123-147.
2. Alves JE, Freitas BM. Comportamento de pastejo e eficiência de polinização de cinco espécies de abelhas em flores de goiabeira (*Psidium guajava* L.). *Rev Ciênc Agron.* 2006;37:216-220.
3. Magalhães CB, Freitas BM. Introducing nests of the oil-collecting bee *Centris analis* (Hymenoptera: Apidae: Centridini) for pollination of acerola (*Malpighia emarginata*) increases yield. *Apidologie.* 2012;42:234-239.
4. Milfont MO, Rocha EEM, Lima AON, Freitas BM. Higher soybean production using honeybee and wild pollinators, a sustainable alternative to pesticides and autopolination. *Environm Chemistry Letters.* 2013;11:335-341.
5. Freitas BM, Pacheco Filho AJS, Andrade PB, Lemos CQ, Rocha EEM, Pereira NO, Bezerra ADM, Nogueira DS, Alencar RL, Rocha RF, Mendonça, KS. Forest remnants enhance wild pollinator visits to cashew flowers and mitigate pollination deficit in NE Brazil. *J Pollination Ecol.* 2014;12:22-30.
6. Cavalcante MC, Oliveira FF, Maués MM, Freitas BM. Pollination requirements and the foraging behavior of potential pollinators of cultivated Brazil nut (*Bertholletia excelsa* Bonpl.) trees in Central Amazon Rainforest. *Psyche.* 2012:1-9.
7. Kevan PG, Eisikowitch D. The effects of insect pollination on canola (*Brassica napus* L. cv. O.A.C. Triton) seed germination. *Euphytica.* 1990;45:39-41.
8. Rizzardo RAG, Milfont MO, Silva SEM, Freitas BM. *Apis mellifera* pollination improves agronomic productivity of anemophilous castor bean (*Ricinus communis*). *An Acad Bras Ciênc.* 2012;84:1137-1145.
9. ITIS. Interagency Taxonomic Information System. ITIS. [internet]. Available from: <<http://www.catalogueoflife.org/annual-checklist/2010/details/database/id/67>>. 2010. [Access: 15.01.2016].
10. Michener CD. *The Bees of the World*, 2nd Ed. Johns Hopkins University Press; Baltimore; 2007. 953 p.
11. Rasmussen C, Gonzalez VH. Stingless bees now and in the future. In: Vit P, Roubik DW, editors. *Stingless Bees Process Honey and Pollen in Cerumen Pots: vi–ix*. Venezuela, Merida, Facultad de Farmacia y Bioanálisis, Universidad de Los Andes; 2013. 170 p.
12. Francoy TM, Imperatriz-Fonseca VL. A morfometria geométrica de asas e a identificação automática de espécies de abelhas. *Oecologia Australis.* 2010;14:317-321.
13. Oliveira FF, Francoy TM, Mahlmann T, Kleinert AMP, Canhos DAL. O Impedimento Taxonômico no Brasil e o Desenvolvimento de Ferramentas Auxiliares para Identificação de Espécies, p. 273–300. In: Imperatriz-Fonseca VL, Canhos OAL, Alves DA, Saraiva AM, editors. *Polinizadores no Brasil -*

- contribuição e perspectivas para a biodiversidade, uso sustentável, conservação e serviços ambientais, São Paulo, EDUSP; 2012. 488 p.
14. Francoy TM, Wittmann D, Drauschke M, Müller S, Steinhage V, Bezerra-Laure MAF, De Jong D, Gonçalves LS. Identification of Africanized honey bees through wing morphometrics: two fast and efficient procedures. *Apidologie*. 2008;39:488-494.
 15. Francoy TM, Gassi ML, Imperatriz-Fonseca VL, May-Itzá WJ, Quezada-Euán JJG. Geometric morphometrics of the wing as tool for assigning genetic lineages and geographic origin to *Melipona beecheii* (Hymenoptera: Meliponini). *Apidologie*. 2011;42:499-507.
 16. Meulemeester T, Michez D, Aytakin AM, Danforth BN. Taxonomic affinity of halictid bee fossils (Hymenoptera: Anthophila) based on geometric morphometrics analyses of wing shape. *J Syst Paleontol*. 2012;10(4):755-764.
 17. Laroca S, Lauer S. Adaptação comportamental de *Scaura latitarsis* para a coleta de pólen (Hymenoptera, Apoidea). *Acta Biológica Paranaense*. 1973;2:147-152.
 18. Silveira FA, Melo GAR, Almeida EAB. Abelhas Brasileiras: Sistemática e Identificação. Belo Horizonte, MG; 2002. 253 p.
 19. Nogueira DS, Oliveira FF, Oliveira ML. The real taxonomic identity of *Trigona latitarsis* Friese, 1900, with notes on type specimens (Hymenoptera, Apidae). *Zookeys*. 2017 Nov;713:113-130, doi:<https://doi.org/10.3897/zookeys.713.11653>
 20. Schwarz HF. Stingless bees (Meliponidae) of the Western Hemisphere. *Bull Am Mus Nat Hist*. 1948;90:1-546.
 21. Wille A, Michener CD. The Nest Architecture of stingless Bees with special reference to those of Costa Rica (Hymenoptera, Apidae). *Rev Biol Trop*. 1973;219:1-278.
 22. Camargo JMF. Ninhos e biologia de algumas espécies de Meliponídeos (Hymenoptera, Apidae) da região de Porto Velho, Território de Rondônia, Brasil. *Rev Biol Trop*. 1970;16:207-239.
 23. Camargo JMF. Notas sobre hábitos de nidificação de *Scaura (Scaura) latitarsis* (Friese) (Hymenoptera, Apidae, Meliponinae). *Bol Mus Para Emilio Goeldi Ser Zool*. 1984;1:89-95.
 24. Melo GAR, Costa MA. A new stingless bee species of the genus *Scaura* (Hymenoptera, Apidae) from the Brazilian Atlantic forest, with notes on *S. latitarsis* (Friese). *Zootaxa*. 2004;544:1-10.
 25. Rohlf FJ. tpsRelw, relative warps analysis. Computer program. Version 1.46. Department of Ecology and Evolution, State University of New York at Stony Brook, New York. [internet]. Available in: <<http://life.bio.sunysb.edu/morph/>>. 2015. Access: 17.X.2015.
 26. Rohlf FJ. tpsDig. Computer program. Version 2.22. Department of Ecology and Evolution, State University of New York at Stony Brook, New York. [internet]. Available in: <<http://life.bio.sunysb.edu/morph/>>. 2015. Access: 17.X.2015.
 27. Rohlf FJ, Marcus LF. "A Revolution in Morphometrics". *Trends Ecol Evol*. 1993;8:129-132.
 28. Bookstein FL. Morphometric tools for landmark data. Cambridge University Press; New York; 1991. 435 p.
 29. Rohlf FJ. tpsUtil, Computer program. Version 1.64. Department of Ecology and Evolution, State University of New York at Stony Brook, New York. [internet]. Available in: <<http://life.bio.sunysb.edu/morph/>>. 2015. Access: 17.X.2015.
 30. Klingenberg CP. MorphoJ: an integrated software package for geometric morphometrics. Computer Program. Version 1.06. Molecular Ecology Resources, advance online [internet]. 2015. Available in: <http://www.flywings.org.uk/MorphoJ_page.htm>. Access: 17.X.2015.
 31. Tamura K, Peterson O, Peterson N, Stecher G, Nei M, Kumar S. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol Biol Evol*. 2011;28:2731-2739.
 32. Miller MP. Tools for population genetic analyses (TFPGA) 1.3: A Windows program for the analysis of allozyme and molecular population genetic data. Computer software distributed by author. 1997.
 33. Aytakin AM, Terzo M, Rasmont P, Çagatay N. Landmark based geometric morphometric analysis of wing shape in *Sibiricobombus* Vogt (Hymenoptera: Apidae: *Bombus* Latreille). *Ann Soc Entomol Fr*. 2007;43:95-102.
 34. Villemant C, Simbolotti G, Kenis M. Discrimination of *Eubazus* (Hymenoptera, Braconidae) sibling species using geometric morphometrics analysis of wing venation. *Syst Entomol*. 2007;32:625-634.
 35. Francisco FO, Nunes-Silva P, Francoy TM, Wittmann D, Imperatriz-Fonseca VL, Arias MC, Morgan ED. Morphometrical, biochemical and molecular tools for assessing biodiversity. An example in *Plebeia remota* (Holmberg, 1903) (Apidae, Meliponini). *Insectes Soc*. 2008;55:231-237.
 36. Castañeda MR, Selivon D, Hernandez-Ortiz V, Soto A, Canal NA. Morphometric divergence in populations of *Anasrrepha obliqua* (Diptera, Tephritidae) from Colombia and some Neotropical locations. *Zookeys*. 2015;540:61-51, doi: <https://doi.org/10.3897/zookeys.540.6013>. Andrade-Lima D.

- Present day forest refuges in Northeastern Brazil, p. 245-251. In: Prance GT, editor. *Biological Diversification in the Tropics*. University Press; Columbia; New York; 1982, 714 p.
37. Burn H. Picidae IV, p. 422-452. In: Del Hoyo J, Elliott A, Sargatal J, editors. *Handbook of the Birds of the World*. Lynx Edicions, Barcelona; 2002, 613 p.
 38. Ribas CC, Aleixo A, Nogueira ACR, Miyaki CY, Cracraft J. A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. *Proc R Soc B*. 2012;279:681-689.
 39. Boubli JP, Ribas C, Alfaro JW, Alfaro ME, Silva MNF, Pinho GM, Farias IP. Spatial and temporal patterns of diversification on the Amazon: A test of the riverine hypothesis for all diurnal primates of Rio Negro and Rio Branco in Brazil. *Mol Phylogenetics Evol*. 2015;82:400-412.
 40. Moore RP, Robinson WD, Lovette IJ, Robinson TR. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecol Lett*. 2008;11:960-968.
 41. Araújo ED, Costa M, Chaud-Netto J, Fowler HG. Body size and flight distance in stingless bees (Hymenoptera: Meliponini): inference of flight range and possible ecological implications. *Braz J Biol*. 2004;64:563-568.
 42. Roubik DW, Aluja M. Flight ranges of *Melipona* and *Trigona* in tropical forest. *J. Kans. Entomol Soc*. 1983;56:217-222.
 43. Kerr WE. *Biologia, manejo e genética de Melipona compressipes fasciculata* Smith (Hymenoptera, Apidae) [PhD Dissertation]. Universidade Federal do Maranhão, São Luiz, MA; 1987. 141 p.
 44. Van Nieuwstadt MGL, Iraheta CER. Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie*. 1996;27:219-228.
 45. Schowalter TO, Hargrove WW, Crossley Jr OA. Herbivory in forested ecosystems. *Annu Rev Entomol*. 1986;31:177-196.