

# From the French Artist Bouguereau to Modern Science: Why Are We Captivated by Butterfly Eyespots?

De l'artiste français Bouguereau à la science modern : pourquoi sommes-nous captivés par les ocelles des ailes de papillon ?

Md Jahir Rayhan<sup>1,2</sup> and Vazrick Nazari<sup>3</sup>

<sup>1</sup> UF/IFAS School of Natural Resources and Environment, University of Florida

<sup>2</sup> McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida- 32611, USA; [jrayhan97@gmail.com](mailto:jrayhan97@gmail.com)

<sup>3</sup> Dipartimento di Biologia, Università Degli Studi di Padova, Via U. Bassi, n. 58/B, 35131 Padova, Italy; [vazricknazari@gmail.com](mailto:vazricknazari@gmail.com)

**ABSTRACT.** The French academic painter William-Adolphe Bouguereau (1825 – 1905) used real European butterfly models with vivid eyespots to depict the wings of mythological figures such as Zephyr, Flora, Eros, and Psyche in his paintings. Here we analyze these works of art, identify the butterfly species depicted, and discuss the potential symbolic meanings behind these paintings.

**RÉSUMÉ.** Le peintre académique français William-Adolphe Bouguereau (1825-1905) a utilisé de véritables modèles de papillons européens aux ocelles vifs pour représenter les ailes de figures mythologiques telles que Zéphyr, Flore, Éros et Psyché dans ses peintures. Nous analysons ici ces œuvres d'art, identifions les espèces de papillons représentées et discutons des significations symboliques potentielles de ces peintures.

**KEYWORDS.** conservation, *Hipparchia*, metamorphosis, mythology, Nymphalidae.

**MOTS-CLÉS.** conservation, *Hipparchia*, métamorphose, mythologie, Nymphalidae.

## 1. Introduction

From the abstract and enigmatic renderings of the Paleolithic cave artists to the detailed depictions in ancient Egyptian tombs, medieval manuscripts, and in various artistic tradition throughout modern history, butterflies have endured as a timeless motif in human art and culture (Nazari 2014; Nazari & Evans 2015; van Huis 2019; Nazari 2021; Hsu 2022). In many instances, these artistic portrayals echo the natural world, faithfully reflecting real-life species and revealing a quiet dialogue between artistic imagination and biological reality (Nazari 2024; Efetov & Yena, 2025). While their presence in human art throughout history is shrouded in rich symbolism (Gagliardi 1976), one particular characteristic – i.e. the eyespots on butterfly wings – stands out as a prominent feature.

The importance attributed by artists to insect eyespots supports the hypothesis concerning the significance of this feature in attracting human attention (Aldini & Pantaleoni 2012; Mandrij & Simonini 2025). It has been shown, for example, that while Flemish artists of the 16th-18th century showed considerable artistic freedom in depicting the outlines of butterfly wings, they always painted the eyespots accurately, and even chose to slightly shift the location of these eyespots in their paintings in order to give them more prominence, a phenomenon dubbed “shifting location bias” (Simbula et al. 2024).

William-Adolphe Bouguereau (1825–1905) was a French academic painter renowned for his exceptional technical skill and highly refined renderings of mythological and biblical scenes (Vachon

1899). Although Bouguereau is widely celebrated for his meticulous paintings of the human figure—most notably women, children, and youth—characterized by soft brushwork and extraordinary attention to detail, several of his paintings depicting the famous Greek mythological figures such as Eros, Psyche, and Zephyrus reveal a notable precision in his portrayal of butterfly wings. In these works, the wings of Psyche and Zephyrus are rendered with a level of realism that closely mirrors those of living butterflies, particularly species renowned for their striking eyespot patterns. For these butterflies, the eyespots not only function as an effective antipredator adaptation, but also serve as powerful visual stimuli capable of capturing attention, eliciting aesthetic responses, and even enhancing prosocial behavior (Manesi et al. 2015). It is possible that Bouguereau was genuinely captivated by the beauty of butterfly eyespots, or perhaps he deliberately employed these intricate wing patterns to draw viewers' attention and imbue the wings in his paintings with deeper symbolic significance.

Here we examine some of Bouguereau's masterpieces, identify the butterfly species depicted in them, and explore their potential symbolic significance. We selected the paintings from Bouguereau's *Catalogue illustré des œuvres de W. Bouguereau* (1885) and Vachon's *W. Bouguereau* (1899) and subsequently obtained high-resolution images from Wikimedia Commons for analysis.

## 2. Linking ecology to mythology

One of Bouguereau's iconic paintings is *Flore et Zéphyr* (1875), an oil-on-canvas work depicting Zephyrus, the Greek god of the west wind, gently kissing the nymph Chloris, who is identified with her Roman equivalent Flora, the local goddess of vegetation and fertility (Fig. 1A). According to Roman mythology, Zephyrus abducted Flora while she tried to escape him; he later married her and granted her dominion over flowers, thereby atoning for his act of abduction (Rausch 2006). As with all wind gods in ancient Greek art, Zephyrus is depicted with wings.

The use of eyespots to draw attention to the wings of Zephyrus was a recurring motif in Western art; for example, in Giovanni Battista Tiepolo's *The Triumph of Zephyr and Flora* (1734–35), Louis II de Boulogne's *Zephyr Crowning Flora* (1702), and François Boucher's *Flora and Zephyr* (1802) (Standen 1988; Aldini & Pantaleoni 2012; Mandrij & Simonini 2025). However, Bouguereau's approach was distinctive: While earlier depictions relied on symbolic wings, Bouguereau meticulously based Zephyrus's wings on a real-world nymphalid butterfly. Upon close examination, the wings clearly resemble those of the striped grayling *Hipparchia fidia* Linnaeus, 1767 (Fig. 1B), notable among French *Hipparchia* species for its prominent eyespots. These eyespots immediately draw the viewer's gaze and create a striking visual focal point.

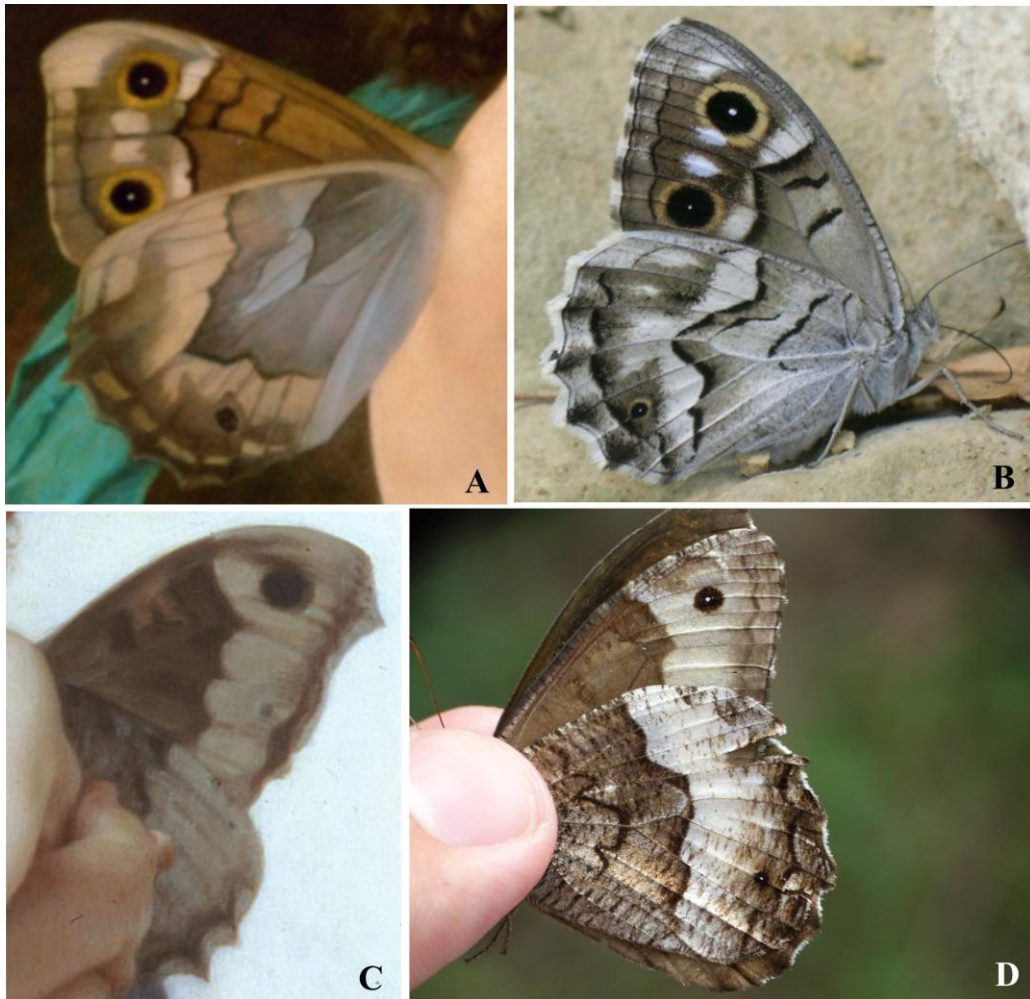
By incorporating realistic butterfly wings, Bouguereau brought the narrative of Flora and Zephyr to life. The wings not only emphasize Zephyrus's role as a winged god but also echo the natural world: the eyespots capture attention, while symbolically reinforcing the story of Flora's dominion over flowers. This interplay probably suggests a subtle ecological metaphor, highlighting the intertwined relationship between butterflies and flowers, including their mutual dependency for pollination and sustenance.

## 3. The metamorphosis through eye

Another notable painting by Bouguereau is *L'Amour et Psyché, enfants* (Cupid and Psyche, as children) (1890), an oil-on-canvas work depicting the Greek mythological figures Eros and Psyche sharing an embrace and a kiss (Fig. 1C). The subject itself, i.e. Eros (the Roman Cupid) and Psyche, was a popular theme in art at the time, centered on their dramatic love story. Psyche, though originally a mortal, was granted immortality upon her reunion with Eros.

Bouguereau broke convention once again by portraying the characters not as adults but as young children, almost infants, offering a fresh and intimate perspective on the myth, emphasizing a love that

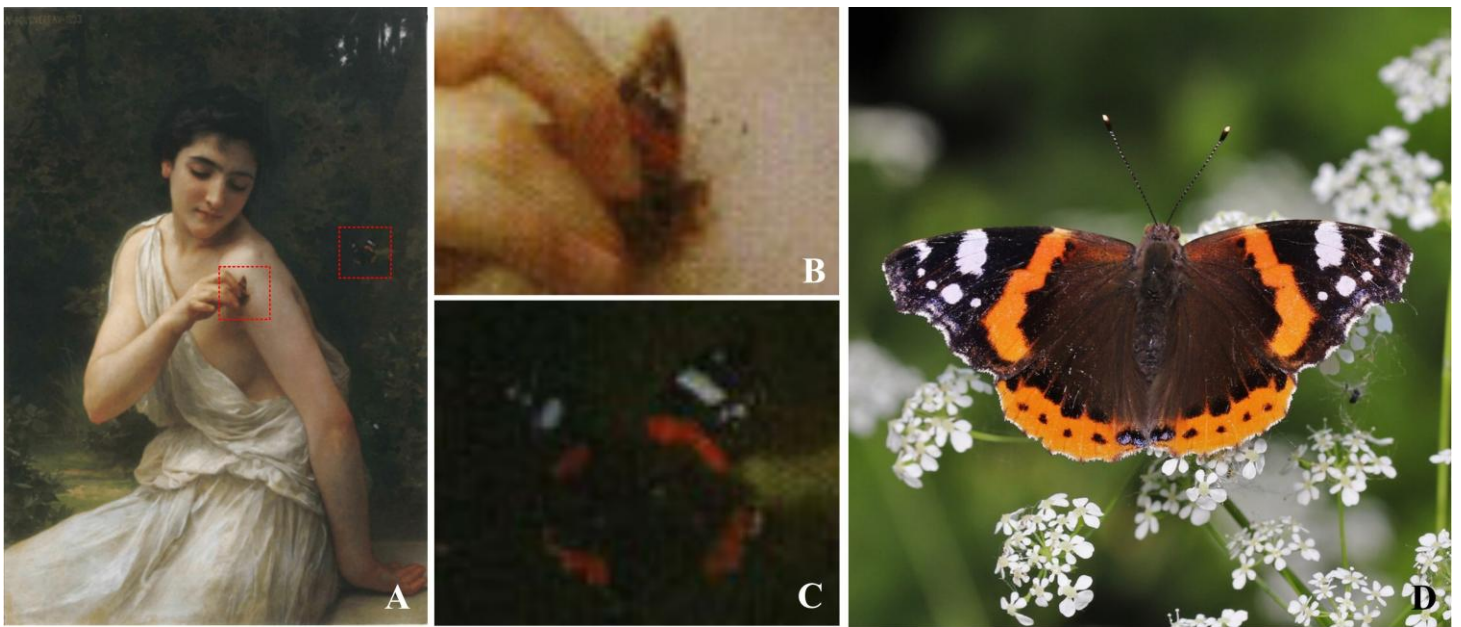
is pure and uncorrupted. True to his meticulous approach, he rendered Psyche with real butterfly wings rather than symbolic ones, reflecting the etymological origin of her name: *psychē*, the Greek word for butterfly, as noted by Aristotle (Manos-Jones 2000).



**Figure 1.** Comparison between Bouguereau's paintings and real butterflies: A, *Flore et Zéphyr*, cropped to show the wings of Zephyr; B, *Hipparchia fidia* Linnaeus, 1767 (©Franck Boue, France; from iNaturalist (<https://www.inaturalist.org/observations/218605870>), modified by the author, licensed under CC BY-NC 4.0); C, *L'Amour et Psyché, enfants*, cropped to show the wings of Psyche; D, *Hipparchia fagi* (Scopoli, 1763) from Bulgaria (© Nick Greatorex-Davies, UK).

The theme of Psyche's transformation—from mortal to immortal—was common in classical art, yet Bouguereau treated it with remarkable precision. He based Psyche's wings on the eyed nymphalid butterfly, identifiable as *Hipparchia fagi* (Scopoli, 1763) (Fig. 1D), which at the time of Bouguereau would have been known as *Satyrus hermione* Linnaeus, 1764 (e.g. see Staudinger & Wocke 1871)<sup>1</sup>. By employing these eyespots, it appears that Bouguereau first directs the viewer's gaze to Psyche and then, through the realism of the butterfly wings, animates her metamorphosis, rendering the story of her transformation vivid, engaging, and timeless. Even though some earlier artworks, such as *Psyche Receiving Cupid's First Kiss* (1798) by François Gérard, incorporated small realistic butterflies (Pieris sp.) as elements of the scene and as an allegory of Psyche's transformation, Bouguereau demonstrated his mastery by selecting distinctively eyed nymphalid butterflies to depict Psyche's wings, likely recognizing that eyespot patterns enhance aesthetic appeal by drawing human attention (Manesi et al. 2015; van Tongeren et al. 2023).

<sup>1</sup> Hermione, a Greek mythological figure, was the daughter of Helen of Troy, well known from the story of the Trojan War. However, it is unlikely that Bouguereau would have chosen this butterfly to symbolize Hermione's legacy, but rather for the eyespots on the wings of this butterflies.



**Figure 2.** Butterflies in two other paintings by William-Adolphe Bouguereau: A, *L'Amour au Papillon* (1888), showing a swallowtail (*Papilio machaon*); B, *Le Papillon* (1893) showing two red admiral butterflies (*Vanessa atalanta* Linnaeus, 1758) in red squares (C–D).

#### 4. Objects of curiosity

In two others of Bouguereau's celebrated works, namely *L'Amour au Papillon* (1888) and *Le Papillon* (1893), he depicted realistic butterflies not as wings of Psyche, but as objects of curiosity, being picked up by focal characters of the painting. While the butterfly in the former work of art can be attributed to the swallowtail (*Papilio machaon* Linnaeus, 1758) due to its hindwing eyespot, tail, and an abdominal stripe (Fig. 2A), the latter includes two realistic red admirals (*Vanessa atalanta* Linnaeus, 1758) (Fig. 2B–D), a nymphalid butterfly widely admired for its striking aesthetic beauty.



**Figure 3.** Details of Bouguereau's paintings highlighting the wings of Psyche: A, *Psyche et L'Amour* (1889) showing the wings probably modeled after a species of *Junonia* (Linnaeus, 1758); B, *The Abduction of Psyche* (1895) depicting symbolic wings with conspicuous eyespots near the apex; C, *L'Amour et Psyché* (1899) depicting schematic wings attributable to *Calopteryx splendens*.

In some of his later paintings, Bouguereau shifted his focus by emphasizing the aesthetic effects of the eyespots rather than the realism of the depicted butterfly. In *Psyche et L'Amour* (1889), Psyche's wings are of a stylized butterfly with a partially concealed eyespot on the underside of the forewings (Fig. 3A). The eyespot shows a yellow outer ring and a solid black center, while the underside of the hindwings are in various shades of gray and without any markings. There are no exact equivalents to this butterfly in real world, however, it is somewhat reminiscent of the females of *Junonia* species (e.g. *J. orithya* or *J. coenia*). If so, this should be considered as another example of the “shifting location bias” phenomenon (sensu Simbula et al. 2024), since in the real *Junonia* butterflies, the position of the

eyesspots on the underside of the forewing are quite different (e.g. see Mahdi et al. 2011; Cong et al. 2020). In subsequent paintings of the same subject (1895 and 1899), Bouguereau drifted even further from realistic butterflies by focusing more on the aesthetic effect of the eyespots, depicting a highly stylized butterfly to portray Psyche's wings (Fig. 3B), or by modelling the wings after the damselfly *Calopteryx splendens* (Fig. 3C).

## 5. Discussion

The use of butterfly wings as the wings of mythological figures dates back to the Roman era (Brewer 1978). Since then, artists have faithfully continued this tradition into modern times. In Roman and Greek antiquity, the butterfly metamorphosis symbolized the transcendent immortal life and the rebirth of human soul after death ([Blatchford] 1889). During the Renaissance, artists incorporated real butterflies in still life and other types of paintings primarily as symbols of reincarnation, and some of these butterflies also showed prominent eyespots (Carvalho 2010; Kritsky & Mader 2011). Bouguereau's genre of realism is arguably a direct descendent of the classical Flemish and Italian Renaissance schools, however he placed additional emphasis on the prominence of eyespots in his paintings.

The function of butterfly eyespots in deterring predators such as birds is well documented (Blest 1957). Images of eyes as talismanic symbols to that ward off evil have also been used in countless human cultures since the dawn of time, with well-known examples such as the Egyptian eye of Horus and the myth of Medusa. The eyespot as a symbol of terror has also been used in art, for example in Paolo Uccello's painting of *St. George and the Dragon* (1470), where the evil dragon is shown with eyespots on its bat-like wings (Howse 2010). The common denominator in all these cases, however, is the fact that the eyespots are primarily meant to capture the immediate attention of the viewer.

Our analysis of Bouguereau's paintings reveals that he frequently used real nymphalid butterflies in his artwork, likely because their distinctive wing eyespots serve as powerful visual stimuli that enhance aesthetic appeal. In the case of *L'Amour au Papillon* (1888), the depicted butterfly was likely modeled after the swallowtail *Papilio machaon* (Papilionidae), however the focus in this case is also on the eyespot on the hindwing of the butterfly. Eyespots are known to increase the appeal of an animal by humans and may even promote positive attitudes toward its conservation (Manesi et al. 2015). The prominence of eyespots in butterflies has long been a subject of interest, not only in art but also in ecological, evolutionary, and developmental biology research. Humans have an innate tendency to respond to face-like markings in nature, such as eyespots, which Bouguereau skillfully incorporated them into his work. By doing so, he not only enhanced the visual beauty of his paintings but also, perhaps inadvertently, highlighted the capacity of eyespots to elicit emotional engagement and foster appreciation for living species.

Overall, this study demonstrates that Bouguereau's incorporation of eyespots in his paintings reflects not only aesthetic and cultural significance but also a broader connection to human perception, ecological appreciation, and conservation. His work highlights how art can engage viewers with natural beauty in ways that resonate with both scientific understanding and environmental stewardship.

## Acknowledgements

We are grateful to David Jutzeler for his assistance with the identification of *Hipparchia fagi* and for his helpful comments. We also thank Franck Boue for the photograph of *Hipparchia fida*, and Nick Greatorex-Davies for granting permission to use his butterfly photographs in this article.

## Bibliography

- [ALD 12] ALDINI A., PANTALEONI R., “Zephyr’s wings: Tiepolo’s imagination or the antlion *Pseudimares Kimmins*, 1933 (Neuroptera, Myrmeleontidae) as his model?”, *Biodiversity Journal*, vol. 3, n° 2, p. 132–136, 2012.
- [BLA 89] BLATCHFORD C. H., “The butterfly in ancient literature and art”, in S. H. SCUDDER (ed.), *The butterflies of the Eastern United States and Georgia, with special reference to New England, Vols 1–3*, Author, Cambridge (Massachusetts), 1889, p. 1257–1263.
- [BLE 57] BLEST A. D., “The function of eyespot patterns in the Lepidoptera”, *Behaviour*, vol. 11, n° 2/3, p. 209–256, 1957.
- [BOU 85] BOUGUEREAU W. A., VENDRYES C., *Catalogue illustré des œuvres de W. Bouguereau*, Librairie d’Art L. Baschet, Paris, 1885.
- [BRE 78] BREWER J., *Butterflies*, Henry N. Abrams, New York, 1978.
- [CAR 10] CARVALHO A. D. L., “Butterflies at the mouth of Hell: Traces of biology of two species of Nymphalidae (Lepidoptera) in European paintings of the fifteenth century”, *Filosofia e História da Biologia*, vol. 5, n° 2, p. 177–193, 2010.
- [CON 20] CONG Q., ZHANG J., SHEN J., CAO X., BRÉVIGNON C., GRISHIN N. V., “Speciation in North American *Junonia* from a genomic perspective”, *Systematic Entomology*, vol. 45, n° 4, p. 803–837, 2020.
- [EFE 25] EFETOV K. A., YENA A. V., “Plants and insects in the realistic masterpiece *Haymaking (1945)* by Arkady Plastov”, *Ecologica Montenegrina*, vol. 84, p. 41–47, 2025.
- [GAG 76] GAGLIARDI R. A., *The butterfly and moth as symbols in Western art*, MSc Dissertation, Southern Connecticut State College, New Haven, 1976.
- [HOW 10] HOWSE P. E., *Butterflies: Decoding their signs and symbols*, Firefly Books, 2010.
- [HSU 22] HSU Y. F., “Butterflies and moths in insect paintings: A dialogue between ancient romantic imagination and modern science”, *Palace Museum Monthly*, n° 474, p. 72–87, 2022.
- [KRI 11] KRITSKY G., MADER D., “The insects of Pieter Bruegel the Elder”, *American Entomologist*, vol. 57, n° 4, p. 245–251, 2011.
- [MAH 11] MAHDI S. H. A., YAMASAKI H., OTAKI J. M., “Heat-shock-induced color-pattern changes of the blue pansy butterfly *Junonia orithya*: Physiological and evolutionary implications”, *Journal of Thermal Biology*, vol. 36, p. 312–321, 2011.
- [MAN 15] MANESI Z., VAN LANGE P. A. M., POLLET T. V., “Butterfly eyespots: Their potential influence on aesthetic preferences and conservation attitudes”, *PLoS ONE*, vol. 10, n° 11, e0141433, 2015.
- [MAN 00] MANOS-JONES M., *The spirit of butterflies: Myth, magic, and art*, Harry N. Abrams, New York, 2000.
- [MAN 25] MANDRIJ V. E., SIMONINI G., *Insects and colors between art and natural history*, Brill, Leiden, 2025.
- [NAZ 14] NAZARI V., “Chasing butterflies in medieval Europe”, *Journal of the Lepidopterists’ Society*, vol. 68, n° 4, p. 223–231, 2014.
- [NAZ 21] NAZARI V., “Lepidoptera in Upper Palaeolithic art”, *Antenna*, vol. 45, n° 2, p. 66–72, 2021.
- [NAZ 24] NAZARI V., *Butterflies in paintings*, online publication, 2024.
- [NAZ 15] NAZARI V., EVANS L., “Butterflies of ancient Egypt”, *Journal of the Lepidopterists’ Society*, vol. 69, n° 4, p. 242–267, 2015.
- [RAU 06] RAUSCH S., “Zephyrus”, in H. CANCIK, H. SCHNEIDER (eds.), *Brill’s New Pauly*, Brill Reference Online, 2006.
- [SIM 24] SIMBULA G., ZINGARO V., PORTERA M., DAPPORTO L., “The enchanted gaze: Modification of butterfly eyespots in Flemish art”, *Art & Perception*, vol. 12, n° 2, p. 1–16, 2024.
- [STA 88] STANDEN E. A., “Ovid’s *Metamorphoses*: A Gobelins tapestry series”, *Metropolitan Museum Journal*, vol. 23, p. 149–191, 1988.
- [STA 71] STAUDINGER O., WOCKE M. F., *Catalog der Lepidopteren des europæischen Faunengebiets. I. Macrolepidoptera*, Dresden, 1871.
- [VAC 99] VACHON M., *W. Bouguereau, A. Lahure*, Paris, 1899.
- [VAN 19] VAN HUIS A., “Cultural significance of Lepidoptera in sub-Saharan Africa”, *Journal of Ethnobiology and Ethnomedicine*, vol. 15, n° 26, p. 1–13, 2019.
- [VAN 23] VAN TONGEREN E., SISTRI G., ZINGARO V., CINI A., DAPPORTO L., PORTERA M., “Assessing the aesthetic attractivity of European butterflies: A web-based survey protocol”, *PLoS ONE*, vol. 18, n° 5, e0283360, 2023.