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UNDERSTANDING THE BIOLOGY OF *WILHELMINA NEPENTHICOLA* SCHMITZ ET VILLENEUVE (DIPTERA: CALLIPHORIDAE) INHABITING *NEPENTHES* IN SARAWAK (PART 1)

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ABSTRACT

During a field survey at Matang Wildlife Centre, Sarawak in 2019, two third-instar larvae of *Wilhelmina nepenthicola* (Diptera: Calliphoridae) were collected from the pitcher plant *Nepenthes ampullaria*. These plants provide a unique microhabitat where various dipteran species complete their life cycles. The collected larvae were subsequently reared under controlled laboratory conditions to document their developmental progression and biological behaviours. Observations revealed that the larvae exhibited both predatory and scavenging feeding behaviours, suggesting a degree of ecological plasticity in their feeding strategy. They actively preyed upon other invertebrates within the pitcher fluid while also utilising decaying organic matter as a food source. Under natural conditions of 29 ± 1 °C and 70 ± 10% relative humidity, the pupariation period lasted for 11 days, after which adult emergence was observed. This study provides a detailed examination of the morphology and biology of *W. nepenthicola* larvae, contributing to a better understanding of their ecological role within *Nepenthes* pitcher habitats. The findings also highlight the potential adaptation of this species to specialised environments, offering insights into the survival strategies of necrophagous and predatory dipterans in nutrient-limited ecosystems.

Keywords: *Wilhelmina nepenthicola*, Calliphoridae, pitcher plant, *Nepenthes ampullaria*, Sarawak, Borneo

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INTRODUCTION

Nepenthes, commonly known as pitcher plants, constitute a diverse genus of carnivorous plants comprising approximately 180 recognised species (Christenhusz & Byng, 2016; Mansur *et al*., 2021, Fitmawati *et al*., 2023). A substantial proportion of these species is distributed throughout the Malay Archipelago – particularly in Borneo, Sumatra, and the southern Philippines – which is regarded as a biogeographical hotspot due to its exceptional complexity and high levels of endemism (Jebb & Cheek, 1997; Clarke *et al*., 2018). Sarawak, situated on the island of Borneo, is especially renowned for its *Nepenthes* diversity, with at least 25 species recorded to date (Clarke & Lee, 2004). Notable species found in the region include *N. ampullaria* Jack (1835), *N. bicalcarata* Hook.f. (1873), *N. gracilis* Korth. (1839), *N. mirabilis* (Lour.) Druce (1869), *N. rafflesiana* Jack (1835), *N. albomarginata* T.Lobb ex Lindl. (1849), and *N. northiana* Hook.f. (1881) (Adam, 2002). These carnivorous plants have adapted to oligotrophic environments by developing specialised pitcher structures that function as passive pitfall traps. These modified leaves collect rainwater, forming phytotelmata — self-contained aquatic microhabitats rich in organic material. The primary function of these structures is the entrapment of prey, predominantly insects, which succumb to submersion within the pitcher fluid. Following entrapment, enzymatic digestion facilitates the breakdown of organic matter, enabling the assimilation of essential nutrients such as nitrogen and phosphorus, which are otherwise scarce in their natural habitats (Clarke, 2006).

Beyond their role in nutrient acquisition, *Nepenthes* pitchers harbour a complex assemblage of aquatic organisms, including bacteria, protozoa, and a variety of invertebrates, thereby sustaining a microecosystem within the phytotelmata. Dipteran larvae are particularly well-documented inhabitants of these microhabitats, exhibiting varying degrees of ecological dependence on the *Nepenthes* environment. These larvae are taxonomically classified as inquilines, or more specifically, as nepenthebionts, indicating their specialised adaptation to phytotelmata. Nepenthebionts complete a significant portion of their life cycle within the pitcher fluid, exploiting the organic detritus and microbial communities present. The interaction between nepenthebionts and *Nepenthes* plants is often regarded as mutualistic, as larval activity contributes to the decomposition of captured prey, thereby facilitating nutrient cycling within the pitcher. However, the degree of specialisation varies among taxa, with some dipterans exhibiting strong host specificity, suggesting possible co-evolutionary relationships between certain *Nepenthes* species and their associated inquilines (Adlassnig *et al*., 2011). Despite extensive documentation of these interactions, the ecological and evolutionary dynamics governing pitcher-nepenthebiont relationships remain incompletely understood.

Among the dipteran taxa associated with *Nepenthes, Wilhelmina nepenthicola* Schmitz et Villeneuve (1932) represents a particularly distinctive species within the family Calliphoridae. Unlike most calliphorid flies, whose larvae are predominantly terrestrial and necrophagous, *W. nepenthicola* is an obligate aquatic nepenthebiont, developing exclusively within the water-filled pitchers of *Nepenthes*. This unique ecological adaptation distinguishes it from other members of Calliphoridae and suggests a specialised evolutionary trajectory. The precise functional role of *W. nepenthicola* larvae within the phytotelmata remains unclear; however, observations indicate a combination of scavenging and predatory feeding behaviours, suggesting an ecological role in regulating the microfauna within the pitcher environment.

Despite its ecological distinctiveness, the taxonomic placement of *W. nepenthicola* has been a subject of considerable debate. Kurahashi and Omar (2007) proposed an affinity with the genus *Bengalia* based on abdominal morphology and pigmentation patterns, whereas Kurahashi and Leh (2009) classified it within the subfamily Melanodexiinae. Earlier classifications by Schmitz and Villeneuve (1932), Fan (1965), Rognes (1991) and Verves (2005) placed it within Polleniinae. However, Rognes (2011) presented a detailed morphological analysis supporting its inclusion in Phumosiinae, citing key diagnostic characteristics, including the presence of yellowish-white, upstanding hairs on the supraspiracular convexity in males (Schmitz & Villeneuve, 1932; Kurahashi & Omar, 2007; Kurahashi & Tan, 2010) and the occurrence of small setulae on the mediana (facial plate) (Kurahashi & Omar, 2007; Kurahashi & Tan, 2010). These conflicting taxonomic interpretations underscore the necessity of further morphological and molecular analyses to resolve the phylogenetic placement of *W. nepenthicola* within Calliphoridae.

The present study aims to elucidate the biological characteristics of *W. nepenthicola* through controlled rearing experiments in an artificial environment. Specific focus is directed towards larval development, feeding behaviour, and ecological interactions within the phytotelmata. By systematically documenting its life history traits under laboratory conditions, this study seeks to enhance our understanding of its ecological role and adaptive strategies within the *Nepenthes* microhabitat. These findings contribute to the broader understanding of dipteran nepenthebionts and their ecological significance, offering novel insights into the specialised adaptations governing their survival within these unique carnivorous plant ecosystems.