Faculty of Resource Science and Technology

Distribution and Habitat Associations of the Genus *Diplommatina* (Gastropoda: Diplommatinidae) in Sarawak

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DECLARATION

I declare that the work in this thesis was carried out in accordance with the regulations of Universiti Malaysia Sarawak. Except where due acknowledgements have been made, the work is that of the author alone. The thesis has not been accepted for any degree and is not concurrently submitted in candidature of any other degree.

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ABSTRACT

The formation of the South China Sea separated Peninsular Malaysia and Borneo, influencing the evolutionary paths of many species, including land snails, which serve as excellent models for biogeographical studies. Land snails, particularly those of the genus *Diplommatina*, mainly found in limestone habitats due to the abundance of calcium carbonate, resulting in high levels of endemism and restricted distribution ranges. The habitat association of land snails is influenced by environmental factors such as soil pH, moisture, and calcium levels, with minute land snail species being particularly sensitive to changes to in habitat conditions. Despite the focus on limestone habitats, recent studies have shown that some *Diplommatina* species are also found in non-limestone areas, highlighting the need for more research on their distribution and ecological preferences in these regions. Hence, the main objectives of this study are to determine the distribution of the genus *Diplommatina* in Sarawak and the habitat association of selected species. The study was conducted across eight sites in Sarawak, Malaysia, including limestone areas such as Gua Rumbang, Gua Rambus, Gunung Silabur, and Niah National Park, as well as non-limestone areas like Gunung Gading National Park, Kiyau Campsite in Sapit, Mutiara Campsite in Baleh, and Lambir Hills National Park. Fieldwork for this study was conducted from October 2022 to January 2024 across six 20 × 20 m plots per site, where both living snails and empty shells were collected using direct searching method and soil floatation habitat assessment focused on substrate types (e.g., leaf litter, vegetation, and limestone), abiotic factors (e.g., leaf litter depth, soil pH, soil temperature, ambience temperature, humidity, luminosity) and biotic factors (e.g., canopy cover and diameter of tree at breast heigth). A total of 23 *Diplommatina* species, including both living snails and empty shells, were recorded for distribution mapping. 16 out of 23 species found alive were included in the habitat association analysis.

The findings of this study suggest the distribution of *Diplommatina* species in Sarawak is primarily influenced by the presence of limestone outcrops, species chirality, and shell size, leading to region-specific endemism which allows the understanding of the current distribution of this genus. Additionally, most living *Diplommatina* individuals were found to be significantly abundant in leaf litter compared to limestone or vegetation habitats. Notable observations, such as the presence of *D. baritensis* on banana tree trunks in non-limestone areas, provide valuable insights into the occurrence of this genus beyond limestone outcrops and emphasise the need to include these areas in future surveys. Furthermore, the discovery of a new species, *D. rumbangensis*, highlights the potential for further taxonomic discoveries in the region and underscores the importance of conserving the areas. Soil pH was the only factor that significantly affected species, with *D. onyx* favoring lower pH levels and *D. baritensis* associated with near-neutral soils. The other tested biotic and abiotic factors did not show significant differences between species ($p > 0.05$). These findings underscore the importance of further exploring the ecological factors that contribute to the unique distribution patterns of this genus in Sarawak.

Keywords: Terrestrial gastropods, diversity, habitats selection, Borneo, Diplommatinidae

Taburan Genus Diplommatina di Sarawak dan Hubungannya dengan Habitat

ABSTRAK

Pembentukan Laut China Selatan telah memisahkan Semenanjung Malaysia dan Borneo, lalu mempengaruhi evolusi spesies, termasuk siput darat, yang menjadi model untuk kajian biogeografi. Siput darat, terutamanya genus Diplommatina*, kebanyakannya ditemui di habitat batu kapur disebabkan oleh kandungan kalsium karbonat, justeru mengakibatkan tahap endemisme yang tinggi dan julat taburan yang terhad. Perkaitan habitat siput darat dipengaruhi oleh faktor persekitaran seperti pH tanah, kelembapan, dan kandungan kalsium, khususnya bagi spesies siput darat bersaiz kecil yang sangat sensitif terhadap perubahan keadaan habitat. Walaupun genus* Diplommatina *ini kebanyakkannya dijumpai di habitat batu kapur, kajian terbaru telah menunjukkan bahawa beberapa spesies* Diplommatina *juga ditemui di kawasan bukan batu kapur, yang menekankan keutamaan untuk lebih banyak kajian mengenai taburan dan ekologi species ini. Oleh itu, objektif utama kajian ini adalah untuk menentukan taburan genus* Diplommatina *di Sarawak dan perkaitan habitat bagi spesies-spesies terpilih. Kajian ini dijalankan di lapan kawasan di Sarawak, Malaysia, termasuk kawasan batu kapur seperti Gua Rumbang, Gua Rambus, Gunung Silabur, dan Taman Negara Niah, serta kawasan bukan batu kapur seperti Taman Negara Gunung Gading, Tapak Perkhemahan Kiyau di Sapit, Tapak Perkhemahan Mutiara di Baleh, dan Taman Negara Bukit Lambir. Kerja lapangan telah dijalankan dari Oktober 2022 sehingga Januari 2024 di enam plot bersaiz 20 × 20 m bagi setiap lokasi kajian, di mana siput hidup dan cangkerang kosong dikumpul menggunakan kaedah pencarian secara langsung dan pengapungan tanah. Penilaian habitat melibatkan jenis substrat (contohnya, serasah daun, tumbuh-tumbuhan, dan batu kapur), faktor abiotik (contohnya, kedalaman serasah daun, pH tanah, suhu tanah, suhu persekitaran, kelembapan, pencahayaan), dan* *faktor biotik (contohnya, litupan kanopi dan diameter pokok pada ketinggian dada). Sebanyak 23 spesies Diplommatina, termasuk siput hidup dan cangkerang kosong, telah direkodkan untuk pemetaan taburan. Daripada jumlah tersebut, 16 spesies yang didapati hidup disertakan di dalam analisis perkaitan habitat. Hasil kajian ini mendapati bahawa taburan spesies Diplommatina di Sarawak dipengaruhi oleh kawasan batu kapur, keunikan pusingan cangkerang, dan saiz cangkerang yang menjurus kepada endemisme serta menyumbang kepada pengetahuan mengenai taburan genus ini. Selain itu, kebanyakan individu Diplommatina yang hidup didapati jauh lebih banyak dijumpai di serasah daun berbanding di habitat batu kapur atau tumbuh-tumbuhan. Penemuan-penemuan penting seperti rekod D. baritensis pada batang pokok pisang di kawasan bukan batu kapur, memberi maklumat tentang keberadaan genus ini di luar habitat batu kapur serta keperluan untuk memasukkan kawasan tersebut bagi tujuan kajian masa hadapan. Tambahan pula, penemuan spesies baharu, D. rumbangensis, berpontensi untuk terdapat lebih banyak penemuan taksonomi di rantau ini serta kepentingan untuk memelihara kawasan-kawasan di rantau tersebut. pH tanah merupakan satu-satunya faktor yang memberi kesan signifikan terhadap spesies, iaitu D. onyx lebih memilih tanah dengan pH rendah manakala D. baritensis dikaitkan dengan tanah yang hampir neutral. Faktor biotik dan abiotik lain yang diuji tidak menunjukkan perbezaan yang signifikan antara spesies ($p > 0.05$). Penemuan ini menekankan kepentingan untuk terus meneroka faktor ekologi yang menyumbang kepada corak taburan unik genus ini di Sarawak.*

Kata kunci: *Gastropod darat, kepelbagaian, pemilihan habitat, Borneo, Diplommatinidae*

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LIST OF ABBREVIATIONS

°C	Degree Celsius
cm	Centimetre
CSV	Comma-Separated Value
DBH	Diameter of Tree at Breast Height
GPS	Global Positioning System
ha	Hectare
IQR	Interquartile Range
km	Kilometre
L	Limestone
LL	Leaf Litter
m	Metre
mm	Millimetre
MZU	Zoological Museum of University Malaysia Sarawak
NP	National Park
QGIS	Quantum Geographic Information System
UNIMAS	Universiti Malaysia Sarawak
V	Vegetation

CHAPTER 1

GENERAL INTRODUCTION

1.1 Study Background

Peninsular Malaysia and the states of Sabah and Sarawak in Borneo was once part of the ancient landmass Sundaland (Advokaat & Hisbergen, 2023). The separation of these regions was caused by the formation of the South China Sea which shaped Malaysia's present-day geography. The differing tectonic histories of Peninsular Malaysia and Borneo have driven the evolutionary paths of many faunas, including the land snail (Webster et al., 2012). Thus, land snail is an excellent model organism for biogeographical studies that effectively highlights the impact of geographical barriers on species distribution (Hausdorf & Hennig, 2007).

Land snails are particularly abundant in limestone landscapes due to the abundance of calcium carbonate ($CaCO_3$), which is essential for their growth (Clements et al., 2006). This preference causes land snail communities to thrive on limestone outcrops, which serve as habitat for these snails. Limestone outcrops across most parts of Southeast Asia are formed in patchy distributions, resulting in a high level of endemism among land snails (Schilthuizen & Rutjes, 2001). In general, it is predicted that the median distribution range for land snail species is less than 100 km^2, and possibly less than 50 km^2 (Solem, 1984). Additionally, several endemic land snail species have restricted range of less than 1 km^2 (Vermeulen & Junau 2007; Marzuki et al., 2021; Lee et al., 2024; Nasir et al., 2024). This offers a fascinating model of diversity and distribution study.

The distribution and abundance of terrestrial land snails are also influenced by various environmental factors and essential resources (Pulliam, 2000; Moreno-Rueda, 2006). This group exhibit opportunistic habitat selection, influenced by key resources like soil pH, moisture, and calcium (Silvan et al., 2000; Martin & Sommer, 2004; Bernadett et al., 2018). Minute land snails are sensitive to shifts in habitat conditions (Nicolai & Ansart, 2017; Sullivan, 2022). The complex combination of these ecological factors leads to differentiation in habitat selections for this group. Whenever the current habitat becomes inadequate in supplying the necessities, land snail species might relocate to another suitable habitat (Pulliam, 2000). For this reason, general knowledge of spatiotemporal and habitat selection could aid in the management and protection of habitats and resources required by a species (Noss et al., 1997; Morrison, 2001; Miller & Hobbs, 2007).

Nevertheless, the specific ecological influences that affect the habitat selection of land snails at the species level remain unclear, especially for members of the genus *Diplommatina* Benson, 1849. This genus is widespread across Asia and the Indo-Australian Archipelago, with significant diversity in Borneo (Vermeulen, 1993; Vermeulen, 1994; Schilthuizen et al., 2002). Currently, there are 29 species of *Diplommatina* have been identified on Sarawak (Vermeulen, 1993; Vermeulen, 1996; Marzuki, 2019; Marzuki et al., 2021; Nasir et al., 2024). Species identification within this genus primarily relies on detailed descriptions and diagnostic keys based on shell morphology (Vermeulen, 1993; Vermeulen, 1996), as molecular studies remain limited in this region (Vermeulen & Liew, 2022).

Members of *Diplommatina* are minute in size, characterised by their conical shells. They predominantly inhabit leaf litter in forested areas, particularly in limestone habitats. They are commonly found in uneven distributions, often restricted to individual hills or small clusters (Vermeulen, 1993; Gittenberger, 1995; Vermeulen, 1996). Nevertheless, recent studies have documented the presence of this genus in non-limestone habitats, such as dipterocarp forests (Schilthuizen & Rutjes, 2001; Liew & Huong, 2009; Schilthuizen, 2017; Marzuki, 2019). This challenges previous assumptions that *Diplommatina* species are restricted to limestone areas, albeit in limited numbers, as predicted by distribution patterns (Tweedie, 1961) and population genetics (Schilthuizen et al., 1999).

1.2 Problem Statement

The distribution of the genus *Diplommatina* is primarily abundant in limestone areas, due to high calcium concentration. In Borneo, the scope of malacofauna surveys conducted in non-limestone regions remains notably limited. This creates a significant gap in understanding the terrestrial gastropods distributions outside limestone-rich environments especially for the genus *Diplommatina*.

Previously, there are several studies that documented the occurrences of this genus in non-limestone areas (Schilthuizen & Rutjes, 2001; Liew & Huong, 2009; Schilthuizen, 2017). The most recent survey was carried out by Marzuki (2019) that revealed the presence of *D. azlani* at Gunung Santubong NP. This research suggests possibilities of the ability of land snails to adapt or disperse beyond the karstic region.

Moreover, a significant portion of existing literature of the genus *Diplommatina* primarily delves into taxonomy, leaving ecological aspects relatively understudied. Although most of the species within this genus are typically associated with leaf litter (Liew et al., 2014), several individuals have been observed foraging on alternative substrates, such as various parts of vegetation, including tree trunks, leaf surfaces, and branches. This behaviour is particularly notable in non-limestone areas. Despite the diversity in habitat utilisation, there is lacking comprehensive documentation regarding the specific habitats favoured by these snails, and the environmental parameters defining their ideal habitats. Understanding the population gap is crucial for researchers to discern the environmental conditions, both biotic and abiotic, associates with the snails and to identify the potential factors that influence their habitat selection.

1.3 Objectives

This research aimed to conduct a comprehensive analysis of the distribution of the genus *Diplommatina* while investigating their habitat association. These were achieved through the following set of objectives:

i. To determine the species distribution of the genus *Diplommatina* in Sarawak, and

ii. To determine the habitat association of selected *Diplommatina* species.

This study provides an overview of the distribution, and habitat selections of the genus *Diplommatina* in Sarawak. The study is composed of five chapters. The first chapter is the introduction on the general outline of the thesis, followed by the second chapter of literature review based on the related studies. Chapter three is for results section, followed by the discussion of the result in chapter four. Finally, the general conclusion and recommendations is written in chapter five.

CHAPTER 2

LITERATURE REVIEW

2.1 Geographical History of Malaysia

Malaysia is composed of Peninsular Malaysia and the states of Sabah and Sarawak in Borneo. During the Mesozoic era, these regions were part of a unified landmass known as Sundaland, which belonged to the supercontinent Gondwana (Advokaat & Hisbergen, 2023). It was only during the late Cretaceous to early Cenozoic periods that the opening of the South China Sea contributed to the separation of landmasses within Sundaland, shaping the present geographical land (Advokaat & Hisbergen, 2023).

Presently, Sarawak's regions are generally divided into two: I) the Kuching Zone located in the southwest, and II) the Rajang-Crocker Accretionary Complex that represent the central and northeast sections (Advokaat & van Hisbergen, 2023). The Kuching zone is a part of the Sundaland core and known as the oldest part of Sarawak due to ancient geological formations such as upper carboniferous limestones and marble intruded by granites dating back 320 - 204 million years (Williams et al., 1988). In contrast, Northeast Sarawak is a part of the younger Rajang-Crocker Accretionary Complex, formed at a south-dipping subduction zone below north Borneo from the Middle Eocene to the Middle Miocene (Honza et al., 2000; Hall et al., 2008; van Hattum et al., 2013).

The different tectonic histories exhibited in both Peninsular Malaysia and Borneo have led to distinct evolutionary paths for land snail populations on these islands. This can be seen in the genus *Diplommatina* as individuals from Borneo forms its own distinct lineage separate from Peninsular Malaysia (Webster et al., 2012). Moreover, this geographic isolation has resulted in high levels of endemism. The limestone regions, in particular, are known for their high endemic snail species due to the unique habitats provided by the karst landscapes.

2.2 Limestone Hills as a Source of Biodiversity

A total of 264 limestone outcrops have been identified in Sarawak, covering a total area of 27,836 ha (Liew et al., 2021a). These outcrops support high species diversity due to its complex terrain and variable climatic conditions, that create a range of ecological niches (Clements et al., 2006). The limestone formations in Sarawak are characterised by their isolated and dispersed nature, each with distinct geological ages and varying sizes (Pearce, 2003). Additionally, these limestone areas are surrounded by acidic forests, which limit the dispersal of certain flora and fauna, leading to the confinement of species to the limestone bedrock (Berry, 1963; Vermeulen & Whitten, 1998). Among the fauna species, several land snails are site-endemic (Vermeulen, 2003; Vermeulen & Junau, 2007; Marzuki et al., 2021), thriving in the limestone environment.

Land snails disperse only a few meters per generation, causing local populations to occupy areas of just tens of square meters (Schilthuizen & Lombaerts, 1994; Pfenninger et al., 1996). Notably, the genus *Plectostoma*, member of the family Diplommatinidae, is comprise of obligate calcicoles (i.e., species that are restricted to limestone). Species within this genus are highly endemic, found only in specific limestone clusters (Liew et al., 2014). The high calcium carbonate content in these ecosystems provides an ideal habitat for these calcium-dependent snails (Schilthuizen et al., 2003).

Moreover, the abundance of land snails in karstic areas is known to be higher than in non-karstic areas (Sullivan, 2022). Thus, studies on land snail inventory of Sarawak were mainly conducted in limestone outcrops. For example, malacofauna survey done at Niah NP and Gunung Mulu NP (Vermeulen, 2003) found 108 species and 97 species of land snails, respectively. Meanwhile in Bukit Sarang, there are 83 species of land snails recorded (Vermeulen & Junau, 2007). The description of various land snail species from limestone regions show that this area is perceived as unique and potentially comprises many undescribed species.

2.3 Occurrence of Land Snails in Non-Limestone Areas

A conspicuous gap exists in the survey coverage of non-limestone regions, particularly in the interior areas of the second and third divisions, such as in the districts of Kapit and Song. This discrepancy arises from various factors, notably the prevalent notion that land snails are generally infrequent and less diverse in such environments (Schilthuizen & Rutjes, 2001). Solem (1984) considered that these areas tend to provide less conducive conditions for snail sustenance due to limited nutrient availability, minimal litter cover, and higher presence of predators. He further mentioned that rainforests often deal with excessive rainfall, causing essential nutrients to be leached, and the seasonality of rainfall trigger diapause in snails.

Nevertheless, few malacofauna surveys done in non-karst areas in Sarawak offers interesting prospects for further study. A study by Liew and Huong (2009), documented an impressive count of 43 land snail species, noteworthy for a moderately disturbed and uniform habitat within Eastern Lanjak Entimau, a region comprising lowland dipterocarp and alluvial forests. If the sampling scope were expanded to encompass the entirety of the Lanjak Entimau Wildlife Sanctuary, the species tally could potentially reach 100 species. Next, Schilthuizen (2017) reported 25 species at Mount Penrissen. The land snail collected encompassed several species from the families of Cyclophoridae and Diplommatinidae, which were previously found exclusively in limestone hills. In Bako NP and its surrounding environs, three surveys yielded 12 species, an impressive count that included ten previously unrecorded land snail species for the locality (Khalik & Marzuki, 2023). Meanwhile, Gunung Santubong NP recorded nine species and a new species of the genus *Diplommatina* (Marzuki et al., 2019) which the genus was previously assumed to be obligate calcicoles.

Non-limestone regions particularly in Sarawak hold the potential insights despite the limited scope of initial surveys conducted, such as land snail's families that necessitate urgent taxonomic revisions. Other than that, the discovery of variability in morphological appearances (i.e., colouration, and coiling directions) in certain land snail species shed light for the future research on the evolution of such variability. Due to that, malacofauna occurred in non-limestone areas offers interesting prospects for further study.

2.4 Habitat Associations of Land Snails and its Important Parameters

Land snails demonstrate opportunistic behaviour in habitat selection, driven by the availability of essential resources and various ecological factors (Moreno-Rueda, 2016; Pulliam, 2000). The intricate interplay of these factors leads to differences in habitat preferences among species. However, species with similar ecological requirements often converge in favourable locations rather than outcompeting each other (Waldén, 1981). This pattern within land snail communities has been highlighted by Hylander et al. (2005) as an example supporting the nested habitat quality hypothesis, wherein higher quality habitats sustain a more diverse assemblage of species, including those found in lower-quality habitats.

Most land snails inhabit leaf litter, with the majority feeding on decaying plant material (Locasciulli & Boag, 1987). Forests rich in leaf litter create ideal conditions for thriving land snail communities (Solem et al., 1981; de Winter & Gittenberger, 1998). For example, species of the genus *Opisthostoma* in Borneo, part of the family Diplommatinidae, have been found exclusively in the forest's leaf litter, living as soil-dwelling organisms (Schilthuizen et al., 2003). This habitat type offers essential resources such as food (Locasciulli & Boag, 1987), moisture, and shelter, particularly due to the presence of woody debris (Gheoca et al., 2021).

The presence of deadwood is crucial for determining snail diversity, as it supports snails living in woody debris and those preferring leaf litter. Wood logs serve as a shelter and food source for some species that feed on the microflora that develop there (Gheoca et al., 2021). Furthermore, the bark of old trees and the interior of decaying branches and trunks retain moisture for extended periods, benefiting species sensitive to low humidity (Müller et al., 2005).

Other than that, most of land snail's communities exhibit a strong preference for calcium carbonate, a key component of limestone. This preference leads the communities to inhabit limestone outcrops, which effectively act as habitat islands for these snails. Additionally, land snails can be found feeding on microvegetations present on the limestone rock surfaces. For example, species from the Vertiginidae family and several *Diplommatina* (Diplommatinidae) are commonly located on the dry sections of rocks where lichen coverage is sparse, while *Plectostoma* (Diplommatinidae) favour wetter, moss-covered areas. Moreover, *Acmella* (Assimineidae) tend to inhabit crevices more often than other species (Hendriks et al., 2021).

Other than limestone, calcium can also be found in vegetation parts. One example of a tree with calcium content is the wild banana tree, which has particularly high concentrations of calcium in its peels and blossoms (Kumari et al., 2023). Calcium plays a crucial role in plants by regulating nutrient and water movement, supporting cell division, and contributing to cell wall construction (McLaughlin & Wimmer, 1999). However, the calcium content in plant parts varies significantly among different species. These variations lead to differences in tree species composition, which in turn affects the calcium content in the upper soil horizons through leaf litter (Plice, 1934; Boettcher & Kalisz, 1990; Vesterdal & Raulund-Rasmussen, 1998).

2.4.1 Characteristics of the Abiotic Parameters.

There is not a singular or limited set of characteristics that define an ideal habitat, rather, the distribution of these snails is shaped by the complex interplay of both biotic and abiotic factors (Bernadett et al., 2018). An abiotic factor is a non-living thing or condition that influences or affects an ecosystem and the organisms in it. When considering abiotic factors, soil pH, calcium concentration, and soil moisture emerge as primary predictors for the abundance of terrestrial gastropods.

Snails are particularly sensitive to soil conditions, such as pH levels (Hotopp, 2002; Martin & Sommer, 2004; Kappes et al., 2006). This sensitivity is due to their frequent contact with the soil and the decomposing organic material on it (Kappes & Topp, 2014). Additionally, most of snails lay their eggs in soil crevices, where the young develop and hatch (Kappes & Topp, 2014). They also favour alkalinity which is typically associated with higher calcium content, aiding in growth and shell development.

Conversely, soil acidification has been shown to reduce the abundance and richness of various litter-dwelling organisms, including land snails, in northwest European forests

(Kappes et al., 2006). Similarly, in Europe, land snail faunas have become increasingly uneven in their abundance distributions with rising soil acidity (Cameron & Pokryszko, 2005). Due to the very small calcium pools in such acidic habitats (Binkley et al., 1992), land snails extract and utilise calcium from calcium salts, such as calcium citrate and calcium oxalate (Wäreborn, 1970), which are leached from various tree and shrub species (Nekola, 2012). Despite these challenges, several acidophilic snails have been recorded in low pH environment (Ondina et al., 1998; Ondina et al., 2004; Nekola, 2012).

Nutrients in litter are essential for altering soil pH and impacting the overall chemical balance within tropical rainforest ecosystems (Mishra et al., 2019). Millar and Waite (2002) found a connection between the presence of calcitic granules produced by earthworms and the abundance of certain snail species. Calcitic granules can contribute to higher soil pH, making the environment more suitable for certain snail species.

Additionally, Zhang et al. (2018) demonstrated that both annual mean precipitation and annual mean air temperature are strong predictors of regional soil pH levels. Within temperate monsoon climate, average soil pH was higher during dry season compared to wet season (Jia et al., 2021).

Soil pH and calcium content are closely related, with soil pH serving as an indicator of diverse soil chemical properties, including calcium concentration. A higher alkaline pH level, assuming to be higher in calcium content, provides a conducive environment for gastropods to thrive (Schilthuizen et al., 2002; Hylander et al., 2005; Müller et al., 2005; Bernadett et al., 2018). This is due to calcium holds pivotal importance, not only for shell formation but also for various physiological processes, including maintaining a balanced pH, reproduction, and acting as a component of permeable cell membranes (Robertson, 1941; Juřičková et al., 2008).

Wäreborn (1979) identified significant linear relationships between snail populations and calcium content in the litter layer across two distinct forest types in southern Sweden. Similarly, Juřičková et al. (2008) found that calcium levels in the topsoil were the primary factor influencing the composition, structure, species diversity, and abundance of land snail communities.

Land molluscs are highly dependent on moisture, as it serves essential functions such as respiration, reproduction (Coney et al., 1982), and the production of mucus (Cameron, 1970). This led to their selections of habitat, where Hernández and Reyes-Tur (2017) revealed that the number of land snail species is notably higher in leaf litter during the dry season, while rock habitats become favourable during the wet season in tropical settings. These two habitats lower the risk of dehydration, providing the necessary and suitable moisture conditions for gastropods.

Soil moisture plays a pivotal role in shaping mollusc diversity (Silvan et al., 2000; Pflug & Wolters, 2001; Morecroft et al., 2002; Martin & Sommer, 2004). Martin and Sommer (2004) found that increased soil moisture levels were associated with higher snail density and species diversity, and particularly noticeable in extremely arid sites. Additionally, in soils that are moist, both soil moisture and soil pH together influence these patterns. It demonstrates that the interplay between multiple factors influences the overall density and richness of land snail species.

2.4.2 Characteristics of the Biotic Parameters

Biotic factors are defined as the living components or factors that affect an ecosystem or other organisms living in that ecosystem. Essentially, while soil conditions shape overall snail populations and diversity, the specific species present are also significantly influenced by the surrounding environment and available resources the type of vegetation and the quality of the leaf litter in the habitat (Martin & Sommer, 2004).

The thickness of leaf litter often correlates with greater snail species diversity, a relationship shaped by a complex set of indirect factors. The composition of the plant species and the abiotic properties of the soil influence the characteristics of the litter layer. For instance, in the southern Appalachian region, the diversity of land snail communities is significantly affected by the variety of plant species contributing to the forest floor litter. This diversity enhances the availability of soluble calcium, which in turn enriches the snails' food resources (Bishop, 1977; Getz & Uetz, 1994).

Additionally, the depth of leaf litter aids in moisture retention on the forest floor, shielding gastropods from desiccation during dry periods (Locasciulli & Boag, 1987). Chiba (2007) observed that land snail species, once confined to shallow broad-leaved litter, tend to retreat to deeper layers where they face reduced predation risks.

Since most land snails are litter dweller, thus, it is indirectly affected by the DBH or with canopy cover. Larger trees tend to have bigger and broader canopies, which contribute more significantly to the overall canopy cover of a forest, hence, reducing the amount of light that penetrates to the forest floor. This affects the microclimate and the types of vegetation that can grow underneath, influencing the forest's overall structure and ecology (Korhonen et al., 2006).

Large DBH of trees signifies long-term stability and a consistent microclimate within the stand, both of which are crucial for snail colonisation (Müller et al., 2005). Larger trees attributed to the availability of resources and habitats. For instance, a greater surface area of trees able the snails to attach and move on, including branches and trunks, which can support a larger snail population (Falkner, 1991; Utschick & Summerer, 2004).

Dead wood has generally shown a positive influence on the snail fauna. Decomposing wood logs foster the growth of fungi, which serve as a crucial food source for detritivores organisms including land snails (Kappes, 2005). Müller et al. (2005) found that the pH and calcium content were significantly higher at the base of large snags and beneath pieces of fallen dead wood compared to the litter layer, upper mineral soil, and the substrate at the base of living trees.

Dead wood also provides sustainable habitat or shelter (Addison & Barber, 1997), attributed to the capacity to absorb, and hold moisture for extended periods (Kappes, 2005). For instances, large-bodied land snails have found to exhibit greater abundance and diversity near woody material. Beyond dead wood and litter habitats, specialised species also find homes in other structures, notably living wood and rock, nevertheless, these habitats tend to be drier and possess fewer diverse food sources such as lichens and mosses, primarily due to surface runoff from rainfall (Sólymos et al., 2009).

Other than that, coarse woody debris can help reduce the impacts of disturbances. Post-fire management that involved spreading branches on the ground led to a positive response for snails, possibly due to the accumulation of wood debris created moist refuges (Bros et al., 2011).

Predation pressure can drive shifts in the habitat preferences of land snails (Rosin et al., 2011). For example, land snails often ascend tree trunks not only to forage but also to evade predators (Corsmann, 1989; Lefcort et al., 2006; Saeki et al., 2017). Furthermore, land snails also showed higher abundance in shaded micro-habitat plots, suggesting a deliberate preference to avoid direct sunlight and/or minimise predation risk (Ozgo & Kubea, 2005; Rosin et al., 2011).

These snails face diverse predation pressures from various groups across different habitats, resulting in regulatory effects on their communities (Němec & Horsák, 2019). Some of the predator groups include beetles, which pose a major threat to snails (Konuma et al., 2011; Baalbergen et al., 2014). Moreover, additional predators include other vertebrates such as small mammals (Rosin et al., 2011), reptiles (Hoso et al., 2010), as well as invertebrates including terrestrial flatworms (Sugiura et al., 2006), slugs (Schilthuizen et al., 2006) and dipteran flies (Vala et al., 2000; Knutson & Vala, 2011). This is due to land snails can be water sources for predators, especially in arid conditions (Yom-Tov, 1970; Shachak et al., 1981), and they provide essential energy and nutrients, including calcium (Graveland & van Gijzen, 1994).

2.5 The Genus *Diplommatina* Benson, 1849

The classification of the genus *Diplommatina* places it within the class Gastropoda (Cuvier, 1795), specifically under the superorder Caenogastropoda (Fry, 1928) and the order Littorinimorpha (Golikov & Starobogatov, 1975). It belongs to the superfamily Cyclophoroidea (Gray, 1847) and the family Diplommatinidae (L. Pfeiffer, 1856). *Diplommatina* is a large genus that is widely distributed from eastern and southern continental Asia, Japan, to the Indo-Australian Archipelago (Kobelt, 1902; Greķe, 2017). This genus is known to be diverse in Borneo (Vermeulen, 1993; Vermeulen, 1994; Schilthuizen et al., 2002) in terms of species numbers and shell morphology. Out of more than 400 described species of *Diplommatina* (Kobelt, 1902; Thiele, 1929; Wenz, 1939; Vermeulen, 1993), there are 29 species of *Diplommatina* recorded in Sarawak, followed by 27 species in Sabah, and 17 species in Kalimantan, Indonesia (Vermeulen, 1993; Vermeulen, 1996; Schilthuizen, 2017; Marzuki, 2019; Vermeulen & Khalik, 2021). Members of this genus are characterised by their conical shape shells, featuring radial ribs, a lipped aperture, and an operculum (Panha & Burch, 2005; Yamazaki et al., 2015; Nurinsiyah & Hausdorf, 2017). This genus consists of micro land snail's species, having typically less than 10 mm of spire length (Kohler & Kessner, 2020).

Like all other land snails, diplommatinids exhibit in distinct sexes (Neubert & Bouchet, 2015). This genus also exhibits in distinct chirality forms, which are dextral and sinistral shells. Phylogenetic analysis suggests that the Diplommatinidae family likely originated with sinistral chirality, as supported by ancestral state reconstruction (Webster et al., 2012). Regardless of the ancestral chirality, phylogenetic data indicate that chirality reversals are rare but do occur, providing an opportunity to analyse the selective factors involved in these reversals (Webster et al., 2012). A sinistral origin would require three shifts to dextrality, whereas a dextral origin would need four shifts (Webster et al., 2012). Although this genus typically displays a single form of chirality throughout their populations, there is recent study that discovered differences in chirality among several island populations of a species of this genus (Rundell, 2008).

The genus *Diplommatina* occur in different types of forests, ranging from lowland to montane forests (Marzuki, 2019) with the highest diversity of species can be found in limestone habitats (Vermeulen, 1993; Nurinsiyah & Hausdorf, 2017). Most members of this genus are typically found in leaf litter, but they can also occasionally be observed on other substrates such as limestone bedrock, vegetation, and deadwood.

Given that many malacofauna surveys in Borneo have focused on limestone areas, it is often assumed that species of this genus are restricted to limestone habitats. Nevertheless, recent discoveries have shown *Diplommatina* species to exist beyond limestone areas. In

Sarawak, recent discovery of a new species, *D. azlani* were found near a rocky stream in lowland mixed dipterocarp forest of Santubong NP (Marzuki, 2019). In Sabah, *D. centralis, D. soror, D. sykesi*, and *D. whiteheadi* were found in forest floor of undisturbed, mainly lowland dipterocarp rainforest of Danum Valley Conservation Area (Menno & Rutjes, 2001). Meanwhile in Philippines, *D. antheae* and *D. microstoma* were found in non-karstic tropical forest of Mount Makiling (Bernadett et al., 2018). In Singapore, *D. concinna* was found among leaf litter at the foothill of primary lowland rainforest of Bukit Timah, near granite quarry (Chan & Lau, 2020). These implies that several species believed to be exclusive in limestone area can occur in low densities in non-limestone area, as foreseen by distribution patterns (Tweedie, 1961) and population genetics (Schilthuizen et al., 1999).

CHAPTER 3

MATERIALS AND METHODS

3.1 Study Sites

The study sites involved fieldwork activities in eight areas located in the divisions of Lundu (one), Padawan (three), Serian (one), Kapit (one), and Miri (two) (Figure 3.1). Four sites are situated within limestone area, while another four are non-limestone areas. The selection of these study sites hinged on factors such as safety, area accessibility, and the study duration. There were instances where certain sites yielded no recorded species such as Gunung Gading NP and Lambir Hills NP.

The four limestone areas sampled in this study are Gua (= Cave) Rumbang, Gua Rambus, Gunung (= Mountain) Silabur, and Niah NP. The first location, Gua Rumbang (1°16'48.0"N 110°15'41.0"E), is positioned on the northern flank of Gunung Temugan. This limestone outcrop resides near Kampung (= Village) Semadang and Kampung Karu, along the Sarawak Kanan River, Padawan. The area features lowland dipterocarp and riparian forests alongside limestone vegetation. The second location is Gua Rambus (1°12'30.3"N 110°16'23.3"E), located near Kampung Temurang, along the Semadang River, Padawan. The cave lies on the northwest side of Gunung Babu. The area is surrounded by a mix of lowland dipterocarp forest and limestone forest. The third site is Gunung Silabur (0°57'27.9"N 110°30'16.5"E), located in Kampung Lobang Batu, Serian. There are two caves on the mountain, namely Gua Sius and Gua Siturib. The area is characterised by dense lowland dipterocarp forest interspersed with limestone vegetation. Lastly, Niah NP (3°49'29.1"N 113°47'49.6"E), which located in the division of Miri. The area encompasses diverse forest types, including mixed dipterocarp forest, seasonal swamp forest, riparian forest, and limestone forest.

Four non-limestone areas included for this study are Gunung Gading NP, Kiyau Campsite in Sapit, Lambir Hills NP, and Mutiara Campsite in Baleh. Firstly, Gunung Gading NP (1°42'33.4"N 109°49'33.4"E) located in Lundu, Sarawak. The surveys were conducted along the Waterfall 7 trail and near the waterfalls within lowland dipterocarp and riparian forests. Secondly, Kiyau Campsite (1°10'45.4"N 110°11'54.4"E) is situated in Kampung Sapit, Padawan. The surveys were established amidst the shrubby vegetation and forest trails. The third site is Mutiara Campsite (1°43'14.5"N 113°27'56.5"E) in Baleh, Kapit. The areas surveyed included dipterocarp forest trails, around salt licks, and along riparian forests near riverbanks. Lastly, the sampling was done in Lambir Hills NP in Miri division. Searches were carried out along the trails and in the area of waterfalls within dipterocarp and riparian forests.

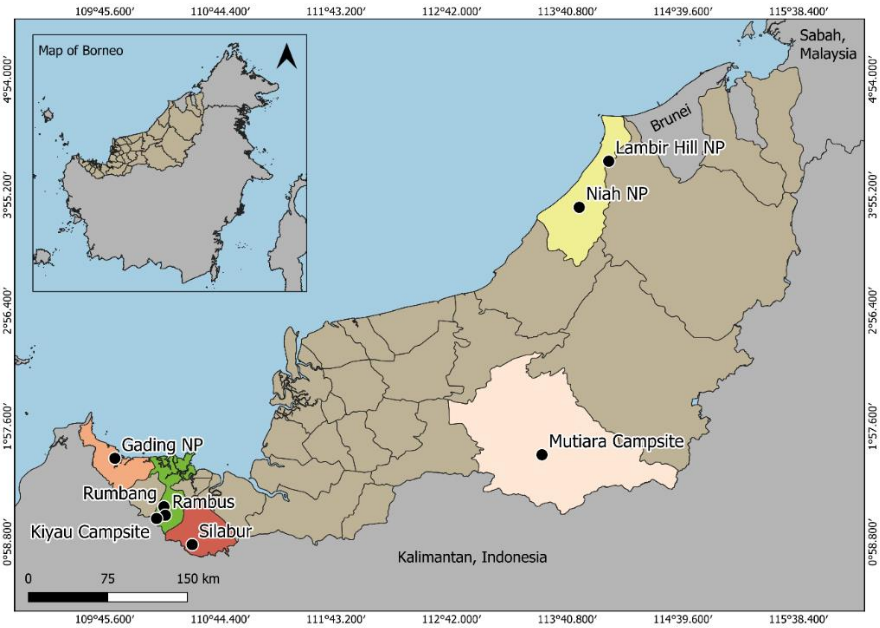


Figure 3.1: Map of Sarawak (Brown) showing the study sites location in Lundu (Orange), Padawan (Green), Serian (Red), Kapit (Beige) and Miri (Yellow) generated using QGIS v.3.34.5

3.2 Data Collection

Fieldwork was carried out from October 2022 until January 2024 based on accessbility of the areas and scheduling opportunities (Table 3.1). The coordinates of each plot were marked using the Garmin Hand-held Global Positioning System (GPS) Map 64s. Six 20 × 20 m plots were established in each eight site, where four persons spent an hour for each plot, totalling 192 man-plot/hour (6 plots × 4 man × 1 hour × 8 sites). All living snails and empty shells were collected during the search. Active searching includes sifting through leaf litter, scanning the surface of limestone rocks, and the surrounding karst vegetation. The search for living *Diplommatina* snails was conducted at the ground level up to a height of two metres (Figure 3.2). For the passive method, five litres of loose-leaf litter and soil were collected from the area and submerged in water for a floatation process (Vermeulen & Whitten, 1998; Cameron, 2008). The materials that floated, presumed to contain micro snails and shells, were then left to dry overnight. Living specimens were stored in sample vials containing 70% ethanol. Empty shells were cleaned and dried prior to storage in the museum collection. The material and specimens of holotype and paratypes were deposited at the Zoological Museum of Universiti Malaysia Sarawak (MZU).

Table 3.1: Sampling dates and duration for each study site

Sites	Date	Duration (Days)
Gua Rumbang	2 September 2022 and 28 June 2023	2
Gua Rambus	20 February and 15 March 2023	2
Gunung Silabur	27 February – 3 March 2023	5
Niah NP	22 – 26 October 2022	5
Gunung Gading NP	7 – 11 May 2023	5
Kiyau Campsite	13 – 17 March 2023	5
Lambir Hills	22 – 26 January 2024	5

Figure 3.2: Searching for the land snails on the vegetation and limestone wall surfaces

3.3 Habitat Assessment Between Species of the Genus *Diplommatina*

The habitat assessment of the genus *Diplommatina* involved three main components (Table 3.2). The first component focused on the substrates where the snails were found. The substrate types where the land snails were found were characterised with respect to their leaf litter, limestone, and vegetation (Figure 3.3). Leaf litter is the surface litter of the outermost layer of the ground. Limestone refers to the vertical and horizontal limestone wall surfaces, pockets, and crevices as well boulders and small limestone rocks. Vegetation encompasses various plant structures, including leaf surfaces, tree trunks, branches, vines, shrubs, saplings, and vascular plants (Figure 3.3, C and D). Most of the vegetation examined does not exceed eye level. The second component is the abiotic component, where the assessed parameters are soil pH and soil temperature that were measured using a pH meter, ExStik PH 100 (Anderson & Ingram, 1994). Additionally, the depth of the leaf litter (cm) was measured by inserting a ruler into the layer of leaf litter until it reached the ground. Next, humidity (%), ambience temperature (°C), and luminosity (lux) were measured using a 4-in-

1 Environmental meter, Extech 45170. The last component is the biotic component. The assessed parameters include tree diameter at breast height (DBH) (m) and canopy cover (%). Tree diameter at breast height was ascertained using a measuring tape, and canopy cover was quantified by capturing images of green vegetation through Canopeo mobile application (Android 1.1.7, Oklahoma State University). Each abiotic and biotic parameters were taken in a plot with the presence of *Diplommatina* species. Three readings taken per plot were averaged to ensure comprehensive coverage.

Only living snails sampled during fieldwork were included in the habitat association study to accurately assess their current ecological requirements and habitat associations (Liew et al., 2021b). This approach avoided potential biases toward calcium-rich sites, where empty shells persist longer due to the habitat's properties (Schilthuizen, 2011). Meanwhile, both live and empty shells were utilised for mapping distribution. This approach provides a more comprehensive understanding of species presence and historical changes (Cernohorsky et al., 2010), as well as enhances sampling efficiency for studies where observing live specimens is challenging (Stankowski, 2014). Additionally, distribution data included from specimens stored at the Zoological Museum UNIMAS, which were obtained from previous sampling efforts and published datasets, including checklists of land snail species in Sarawak (Vermeulen, 2003; Vermeulen & Junau, 2007; Liew & Huong, 2009; Schilthuizen, 2017; Marzuki et al., 2021).

Table 3.2: List of components and parameters measured for habitat assessment

Component	Parameter	Unit
Substrate	Leaf litter, limestone, and vegetation.	-
Abiotic	Leaf litter depth	cm
	Soil pH	-

	Soil temperature	°C
	Ambience temperature	°C
	Humidity	%
	Luminosity	lux
Biotic	Canopy cover	%
	Diameter of tree at breast height (DBH)	m

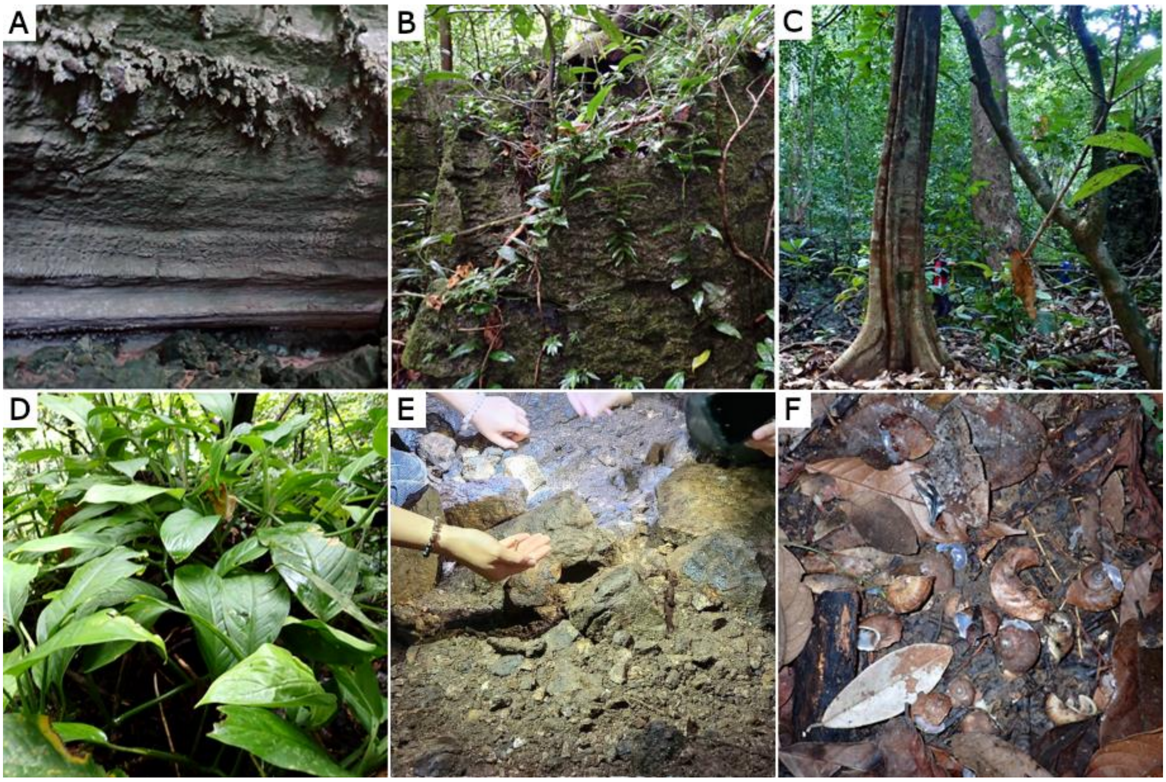


Figure 3.3: Habitat types where the snails were found which are **A** Limestone wall **B** Limestone rock **C-D** Vegetation **E-F** Leaf Litter

3.4 Species Identification of the Genus *Diplommatina*

Identification to the species level based on shell morphology followed established methods outlined in published literature, with references to studies on Bornean land snails (Vermeulen, 1993; Vermeulen, 1996; Vermeulen & Liew, 2022). Differentiation between species was based on the external appearance of the shells, including shell size (i.e., shell height and shell width), number of whorls, coiling direction, and shell sculpture. A more detailed examination of shell characteristics, such as the umbilicus opening, and the aperture, which includes its shape, dentition, peristome, and level of constriction, was also conducted. Additionally, species distribution records were referenced.

3.5 Imaging and Scanning Electron Microscopy

A representative shell of each species was selected for imaging. A set of stacked images were taken using a Nikon DSLR with CaptureOne 15.0.0 software. Then, the composite images were generated in Helicon 8.2.0 software. Later, these images were edited using Adobe Photoshop 24.1 and GIMP 2.10.34 software. Scanning electron microscopy (JEOL, JSM-6390LA) was used to obtain detailed images of *Diplommatina* species. Prior to this, the shells were coated with platinum to enhance image quality and protect the sample from damage caused by the electron beam.

3.6 Data Analysis

3.6.1 Distribution of the Genus *Diplommatina* in Sarawak

All 405 distribution records of *Diplommatina* were compiled in Microsoft Excel 365 v.2411. Data consisting of latitude, longitude, species names and districts were organised in CSV format for constructing a distribution map. The distribution map of *Diplommatina* species was created using several R packages: I) `ggplot2` (Wickham, 2011) for plotting, II) `scatterpie` (Yu & Yu, 2018) for adding scatter pie charts to the plots, III) `tidyr` (Wickham et al., 2023b) for pivoting data from long to wide format, IV) `dplyr` (Wickham et al., 2023a) for data grouping and summarising, and V) `sf` (Pebesma, 2018) for reading and handling spatial data, including shapefiles (Appendix B). A shapefile of Malaysia with state and division borders (MYS_adm2.shp) was downloaded from DIVA-GIS (https://www.diva-gis.org/gdata) and imported into RStudio 4.2.2 (RStudio Team, 2022). The maps were then imported into GIMP 2.10.34 software for further refinement, which included organising map elements and adding a legend.

Additionally, the distribution data of *Diplommatina* species were categorised based on chirality and size. Chirality was classified into two forms: dextral and sinistral, which describe the direction of shell spirals when viewed from the apex with the shell opening (aperture) facing forward. A dextral shell spirals clockwise when viewed from the apex, with the aperture positioned on the right-hand side, whereas a sinistral shell spirals counterclockwise, with the aperture on the left-hand side. Size was determined by measuring shell height and shell width. Shell height was divided into three forms: small (less than 3 mm), medium (3 mm to 6 mm), and large (greater than 6 mm). Shell width was also divided into three forms: small (less than 1mm), medium (1 mm to 2 mm), and large (greater than 2 mm). These measurements were based on adult snails.

Subsequently, the species were mapped based on these categories utilising the Infomap Bioregion application (Edler et al., 2017). To summarise bioregions, 'combined' grids were included, representing areas where both forms (e.g., dextral and sinistral) within a category (e.g., chirality) coexist. The application constructs a bipartite network connecting each species to the grid cells where it is found, subsequently aggregating these cells into larger geographic regions with similar species compositions. This process yields detailed maps delineating distinct bioregions characterised by unique species assemblages.

Data consisting of species name, latitude and longitude was organised in Microsoft Excel in CSV format. The document then uploaded to the website (https://www.mapequation.org/bioregions2/). Experimentation with various parameter combinations was necessary to determine the optimal appearance of the map. Each size of the grid cell was standardised to 48 square kilometres to ensure a detailed map. Setting this parameter too high may lead to the creation of large, uninformative regions that encompass areas where species do not typically coexist (Rivera et al., 2021), while smaller grid sizes might produce fragmented, discontinuous bioregions. The cell capacity minimum was fixed at 1, while adjustments to the maximum capacity had minimal impact on the results. This capacity represents the number of occurrence points per cell, influencing the granularity of the map.

The generated bioregions higlighted the most common and indicative species. The indicative score is calculated as the ratio of the species frequency in the region to its frequency in all regions. A higher score indicates the species is found in greater relative abundance. The resulting bioregion maps were exported as a shapefile and imported into QGIS Desktop 3.34.5 for further editing.

3.6.2 Habitat Association of the Genus *Diplommatina* Based on Utilisation of Habitat Types

The associations between *Diplommatina* species and habitat types were illustrated with bipartite network analysis using `bipartite` package (Dormann, 2011). This analysis included bipartite link graph, interaction matrix, and modularity plot (Appendix C). The data matrix for bipartite network consists of rows representing three habitat types and columns representing 16 species of *Diplommatina*. Bipartite link graph using the `plotweb` function with the default method cca. This graph consisting of nodes and links. The nodes represent the upper and lower levels, while the links indicate the connections between them. The width of the nodes and links corresponds to the number of individuals of each species. Interaction matrix using the `visweb` function with nested type of network. Modularity plot used `plotModuleWeb` function. The network's modularity was calculated using Newman's modularity measure (Newman, 2006) combined with the Beckett method (Beckett, 2016) and plotted to visualise the interlinked subsets of species (modules) within the bipartite network (Olesen et al., 2007). Connection (c-values) and participation (z-values) metrics for each species were derived from the modularity analysis, illustrate their functional roles within the network (Guimerà et al., 2005; Olesen et al., 2007). Connection metric measures how evenly a species' interactions are distributed across different modules while participation metric quantifies a species' importance within its own module. A high c-value indicates that the species interacts with members of multiple modules, making it a connector species. A connector species are often characterised by their connection metric (c-values more than 0.62) than their participation metric (z-values less than or 2.5) as their primary role lies in linking rather than dominating within a single module (Olesen et al., 2007).

Next, non-parametric Friedman test was computed to determine the significance of habitat chosen by the snails using `friedman.test` command in `stats` package (Appendix C). All 16 species of *Diplommatina* were organised on Microsoft Excel in the first column, followed by their corresponding habitat types in the second column, and the number of individuals of that species in the third column. Then, Conover post hoc test was carried out as follow-up procedure to the Friedman test to identify which specific groups differ from each other after a significant overall test result (p-values were set at 0.05). This was done using `frdAllPairsConoverTest` computation in `PMCMRplus` package (Pohlert, 2021). Then Chi-square test was conducted on each six species of *Diplommatina* found in two and more habitat types identify the habitat most closely associated with that species where the p-value were set to 0.1 and 0.01. The test was conducted using `chisq.test()` function. Next, species that has significant differences was subjected to pairwise comparison. The p-values were set at 0.1 and 0.01. All statistical analyses were done in RStudio 4.2.2 (RStudio Team, 2022).

3.6.3 Habitat Associations of the Genus *Diplommatina* Based on Abiotic and Biotic Components

Box plot was generated for each habitat parameters utilised the `ggplot2` package (Wickham, 2011)(Appendix D). The construction of the graph employed a data matrix, with the first column representing seven species of *Diplommatina* and the second column is the average reading for each parameter. Subsequently, normality tests were applied to all eight parameters to ascertain whether the datasets followed a normal distribution. This analysis was conducted using `qqPlot` function from the car package (Fox & Weisberg, 2019). Following this, Kruskal-Wallis tests were conducted on each eight parameters to identify any statistically significant differences between species where p-value was set to 0.05. These tests were conducted using `kruskal.test()` function in `stats` package (R Core Team, 2022). Next, parameters showing significant differences were subjected to Dunn's post hoc test with Bonferonni method using `dunnTest()` function from the `FSA` (Fisheries Stock Assessment) package (Ogle et al., 2023). This analysis aimed to identify species of *Diplommatina* that significantly different at 0.05 p-value. All analyses were done in RStudio 4.2.2 (RStudio Team, 2022)(Appendix D).

CHAPTER 4

RESULTS

4.1 Distribution of the Genus Diplommatina in Sarawak

A total of 23 *Diplommatina* species across Sarawak were successfully compiled in this study. Based on Figure 4.1, the distribution of these species is divided into three regions which are southwestern, central, and northeastern Sarawak. Specific districts within these regions are labeled A through K, each represented with pie charts showing the relative occurrences of the species in those districts. In the southwestern region, District A (Bau) is the most diverse, with 12 species present. District B (Padawan) and District E (Siburan) are the second most diverse, each with eight species. This is followed by Districts C (Kuching) and F (Serian) in southwestern Sarawak, and District H (Kapit) in central Sarawak, each hosting four species. District G (Simunjan) and District D (Samarahan) have lower species occurrences, with two and one species, respectively. In northeastern Sarawak, District J (Miri) and District K (Mulu) each exhibit eight species, while District I (Marudi) has two species. Six species were found to be regionally endemic, appearing only in the northeast (i.e., *D. sulphurea, D. moluensis, D. maduana nefrens, D. strongyla, D. niahensis,* and *D. subglaber subisensis*) or only in the southwest (i.e., *D. goliath, D. rumbangensis, D. busanensis, D. azlani, D. spinosa, D. isseli, D. toretos, D. whiteheadi,* and *D. subglaber subglaber*). Eight species have a broader distribution, occurring in both the southwestern and northeastern regions (i.e., *D. concinna, D. onyx, D. maduana maduana, D. adversa, D. calcarata, D. stibara, D. baritensis,* and *D. lygipleura*).

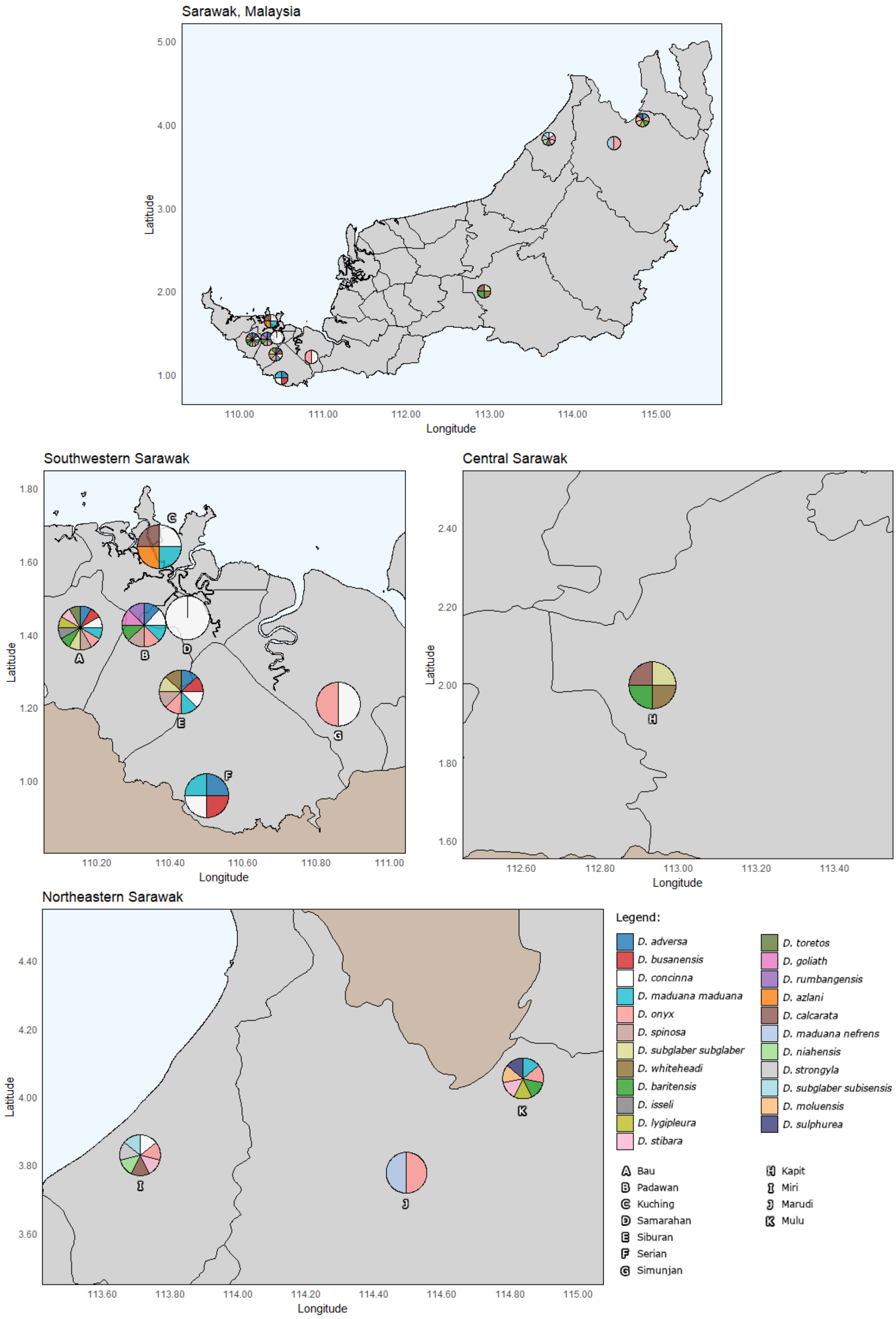


Figure 4.1: Distribution map of 23 *Diplommatina* species in Sarawak. The maps are categorised into three regions: Southwestern, central, and northeastern sarawak. Coordinates for each species are grouped by districts, labelled **A** through **K**. Each pie chart represents the occurrences of a species within these districts

4.1.1 Distribution of the Genus *Diplommatina* Based on Chirality

Based on the chirality form of *Diplommatina* species, several distinct bioregions were identified (Figure 4.2). The infomaps based on the dextral, sinistral and combined forms were summarised. The summarised infomap shows that combined forms are represented throughout Sarawak and are not exclusive to any of the different regions (i.e., southwestern, central or northeastern). Specifically, eight bioregions were established for both dextral and sinistral forms. Some bioregions identified in central Sarawak, such as Bioregions 1 and 4, overlap with those in the southwestern region for both dextral and sinistral orientations. Unique to the southwestern part of the state are Bioregions 2, 6, and 8 for dextral species and Bioregions 2, 6, 7, and 8 for sinistral species. In northeastern Sarawak, unique bioregions include Bioregions 3 and 7 for dextral species and Bioregions 3 and 5 for sinistral species. Bioregion 1 for dextral form species is found across all three parts of the state, while no sinistral form species are present in bioregions common to all regions.

The produced bioregions take into account the most common and indicative species (Table 4.1). *Diplommatina concinna* is the most common species for six out of the eight bioregions for dextral form (Table 4.1). The most common species for the other two bioregions are *D. niahensis* (Bioregion 3) and *D. maduana neferens* (Bioregion 8). These two species are also the most indicative species for their respective bioregions. *Diplommatina adversa* is the predominant species in three out of the eight bioregions for the sinistral form. The remaining five bioregions feature species that are both common and indicative of their respective regions (Table 4.1).

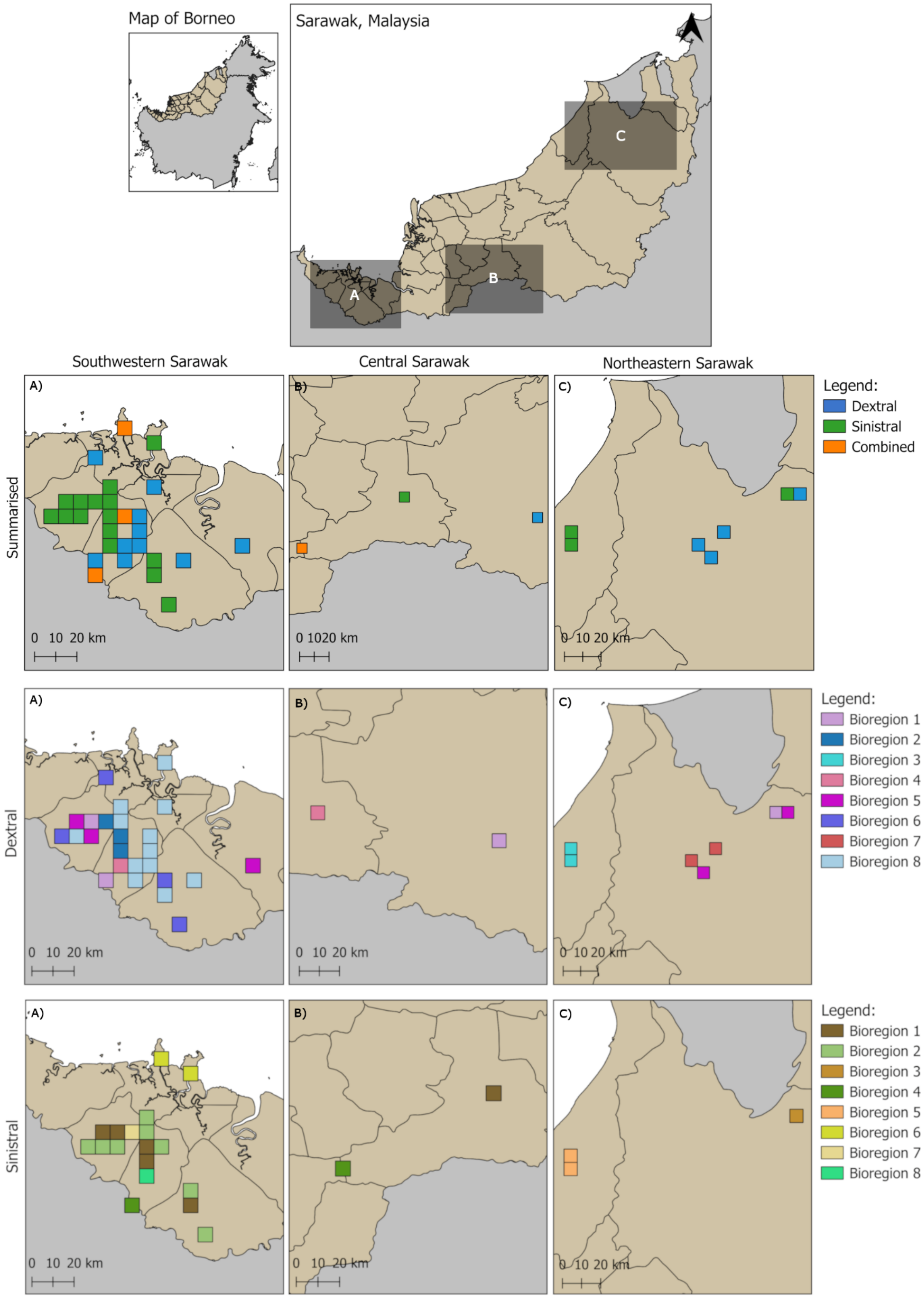


Figure 4.2: Bioregions Map Categorised by Chirality Form. The map is Organised Into Three Columns, Each Representing A) Southwestern B) Central C) Northeastern Sarawak.

Maps Depicting the Dextral Form are in the First row, Those Illustrating the Sinistral Form are in the Second row and Summarised of Dextral and Sinistral Forms are in the Third Row. Legends Identifying Each Bioregion are Located on the Right Side

Table 4.1: List of bioregions for dextral and sinistral forms. The 'species' column shows the number of species found in each bioregion. The most common species are listed by their individual count, whereas the most indicative species are represented by a score. Bold texts indicate the highest value

Chirality	Bioregion	Species	Most common species (count)	Most indicative species (score)
Dextral	1	6	*D. concinna* (27)	*D. baritensis* (3.4)
	2	7	***D. concinna*** **(37)**	*D. spinosa* (3.3)
	3	6	*D. niahensis* (21)	*D. niahensis* (8.4)
	4	6	*D. concinna* (11)	*D. rumbangensis* (10.3)
	5	3	*D. concinna* (16)	*D. maduana maduana* (1.6)
	6	2	*D. concinna* (14)	*D. maduana maduana* (2)
	7	1	*D. maduana nefrens* (2)	***D. maduana nefrens*** **(144)**
	8	1	*D. concinna* (24)	*D. concinna* (2.1)
Sinistral	1	4	***D. adversa*** **(38)**	*D. subglaber subglaber* (6)
	2	1	*D. adversa* (12)	*D. adversa* (6)
	3	2	*D. sulphurea* (2)	*D. sulphurea* (135)
	4	2	*D. whiteheadi* (2)	D. *whiteheadi* (135)
	5	1	*D. subglaber subisensis* (13)	*D. subglaber subisensis* (28.9)
	6	1	*D. azlani* (6)	*D. azlani* (27.5)
	7	4	*D. adversa* (17)	*D. isseli* (18.4)
	8	1	*D. goliath* (1)	***D. goliath*** **(405)**

4.1.2 Distribution of the Genus *Diplommatina* Based on Shell Sizes

Based on variations in shell height among *Diplommatina* species, several bioregions were identified (Figure 4.3). Specifically, nine bioregions were established for species with small shell heights, six for species with medium shell heights, and five for species with large shell heights. In the southwestern part of the region, unique bioregions for small shell height species include 3, 4, 6, 7, and 8; for medium shell height species, 1, 3, 4, and 5; and for large shell height species, 3 and 4. In the central part, no bioregions were recorded for medium shell height species. The northeastern part features unique bioregions 9 for small shell height species, 2 and 6 for medium shell height species, and 5 for large shell height species. Some bioregions overlapped across the three parts of the state, which are bioregions 1 and 2 for small shell height species.

Based on the shell width variations, multiple distinct bioregions were identified (Figure 4.4). Specifically, three bioregions were designated for small shell width species, eight for medium shell width species, and five for large shell width species. Several bioregions were overlapped across the three regions. Unique to the southwestern region are Bioregion 7 for medium shell width species and Bioregion 5 for large shell width species. In northeastern Sarawak, the unique bioregions include Bioregion 2 for small shell width species, Bioregion 2 for medium shell width species, and Bioregions 2 and 3 for large shell width species. As for the summarised sizes form infomap, species of all different width sizes are distributed throughout the same three regions of Sarawak, with southwestern Sarawak having the most overlap of *Diplommatina* species with differing sizes.

Among the small shell height species, *D. concinna* was the most common species in seven out of nine bioregions (Table 4.2). Only Bioregion 8 showed *D. concinna* as both the most common and indicative species. The other two bioregions had species that were both common and indicative of their respective bioregions: *D. whiteheadi* in Bioregion 7 and *D. maduana nefrens* in Bioregion 9. For the medium shell height species, *D. spinosa* was the most common species in Bioregions 3 and 4. In Bioregion 4, *D. spinosa* was also the indicative species, while in Bioregion 3, *D. isseli* was the indicative species, with a score of 5.5. The remaining four bioregions had species that were both the most common and indicative. Among the large shell height species, *D. adversa* was the most common species in two out of five bioregions (Bioregions 1 and 3). *Diplommatina adversa* was also the indicative species in Bioregion 3, but in Bioregion 1, *D. subglaber subglaber* was the indicative species. The remaining three bioregions featured the same species as both common and indicative for their respective bioregions.

All three bioregions for small shell width species record the same species as both the most common and most indicative for their respective regions (Table 4.2). Similar to the dextral bioregions map, *D. concinna* is the most common species in six of the eight bioregions for the medium shell width species. However, the most common species in the other two bioregions are instead *D. niahensis* (Bioregion 2) and *D. azlani* (Bioregion 7). These two species are also the most indicative for their respective bioregions. *Diplommatina adversa* is the predominant species in two of the five bioregions for large shell width species. The remaining three bioregions feature species that are both common and indicative of their respective bioregions (Table 4.2).

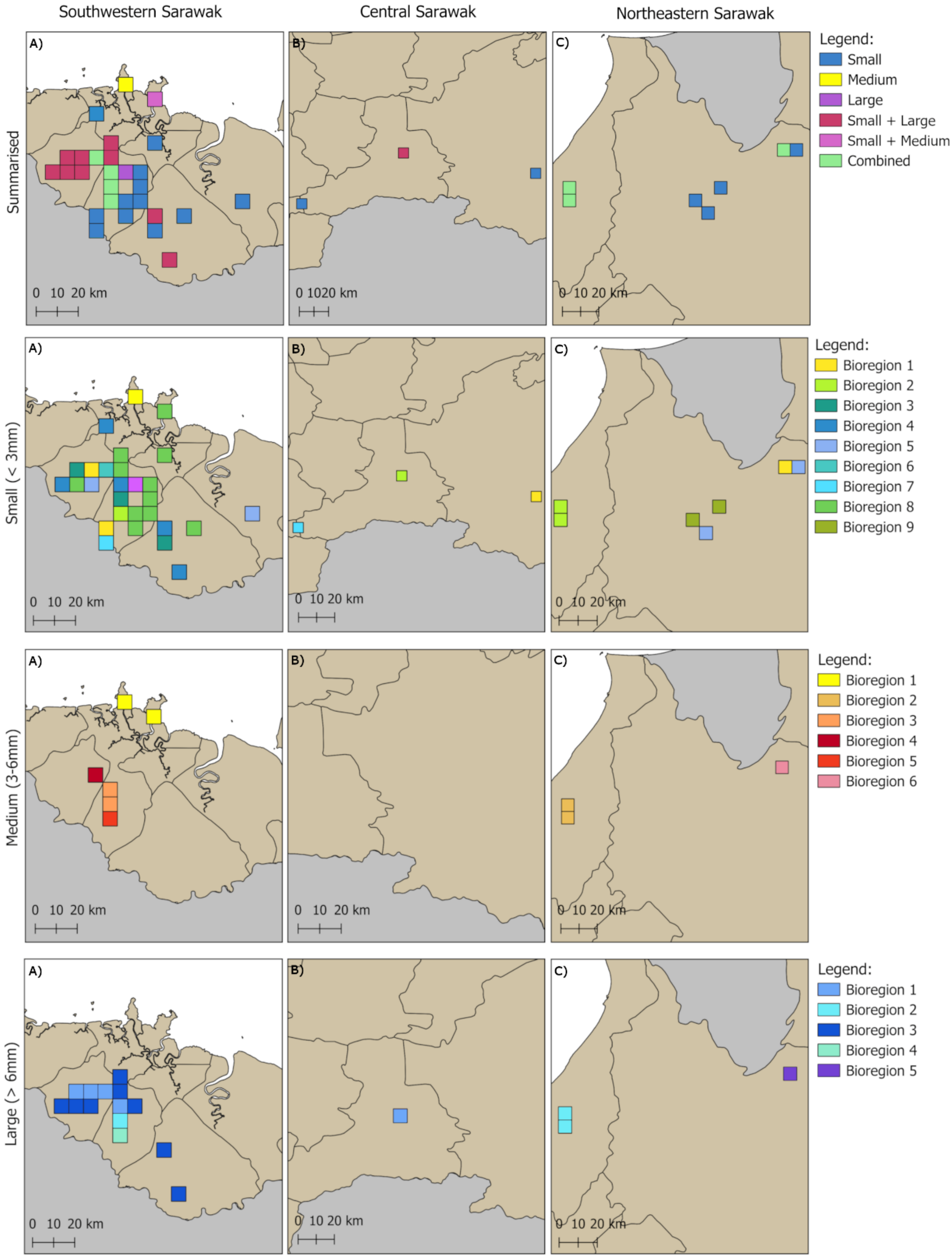


Figure 4.3: Bioregions map categorised by shell height. The map is organised into three columns, each representing A) Southwestern B) Central C) Northeastern Sarawak. Maps depicting the small shell height are in the first row, medium shell height in the second row and large shell height in the third row. Legends identifying each bioregion are located on the right side

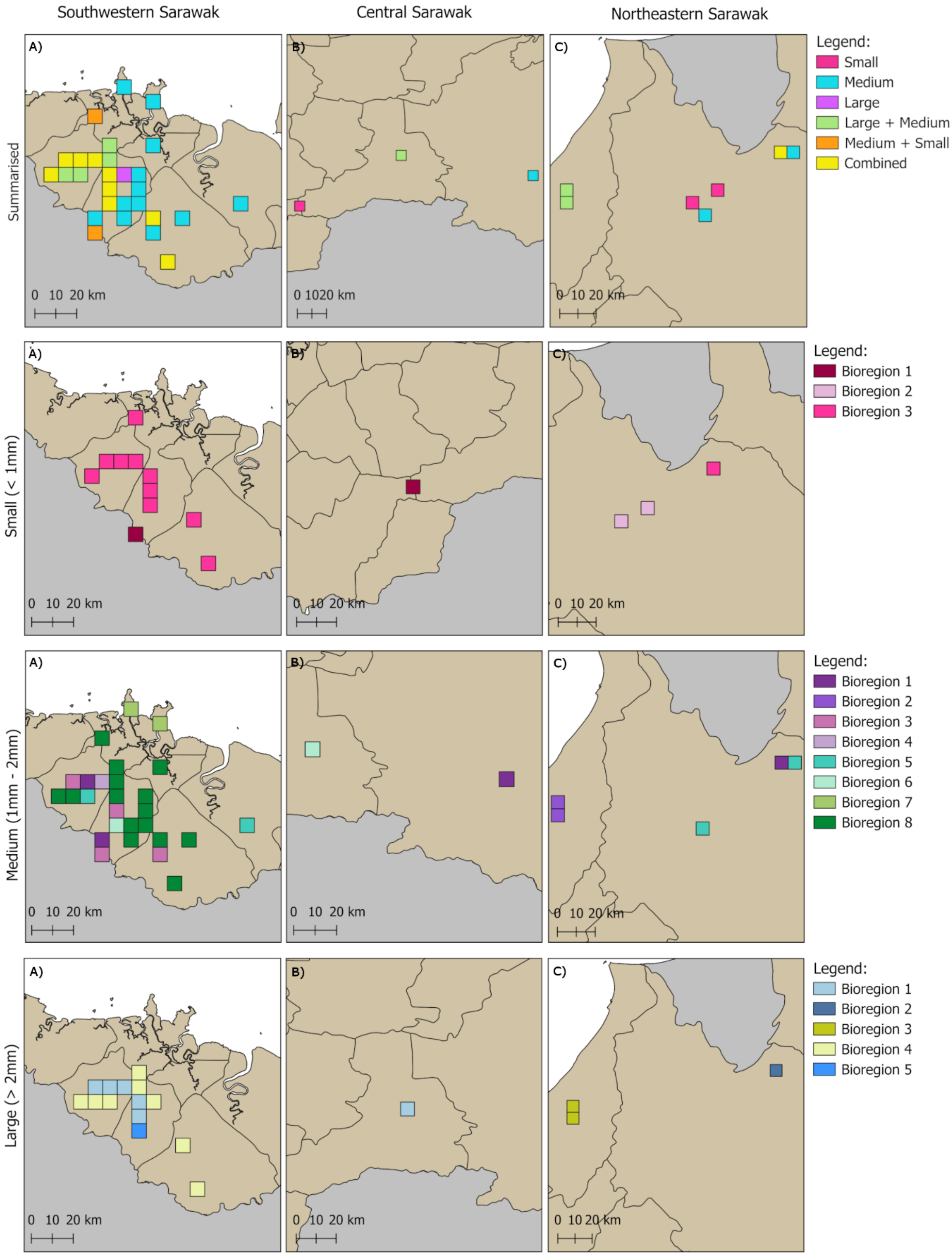


Figure 4.4: Bioregions map categorised by shell width. The map is organised into three columns, each representing A) Southwestern B) Central C) Northeastern Sarawak. Maps depicting the small shell width are in the first row, medium shell width in the second row, large shell width in the third row and summarised of shell width forms are in the fourth row. Legends identifying each bioregion are located on the right side

Table 4.2: List of bioregions for small, medium, and large sizes. The 'species' column shows the number of species found in each bioregion. The 'most common species' column are listed by their individual count, whereas the 'most indicative species' column are represented by a score. Bold texts indicate the highest value

Sizes	Bioregion	Species	Most common species (count)	Most indicative species (score)
			Shell height	
Small	1	7	***D. concinna* (27)**	*D. baritensis* (3.4)
	2	7	*D. concinna* (16)	*D. strongyla* (8.5)
	3	5	*D. concinna* (27)	*D. busanensis* (2.5)
	4	2	*D. concinna* (21)	*D. maduana maduana* (2.3)
	5	3	*D. concinna* (6)	*D. onyx* (3.3)
	6	6	*D. concinna* (14)	*D. toretos* (8.7)
	7	2	*D. whiteheadi* (2)	***D. whiteheadi* (105)**
	8	1	*D. concinna* (23)	*D. concinna* (2.3)
	9	1	*D. maduana nefrens* (2)	*D. maduana nefrens* (157)
Medium	1	1	*D. azlani* (6)	*D. azlani* (7.3)
	2	1	***D. niahensis* (21)**	*D. niahensis* (2.1)
	3	1	*D. spinosa* (4)	*D. spinosa* (4)
	4	2	*D. spinosa* (7)	*D. isseli* (5.5)
	5	1	*D. rumbangensis* (4)	*D. rumbangensis* (11)
	6	1	*D. moluensis* (1)	***D. moluensis* (44)**
Large	1	2	***D. adversa* (42)**	*D. subglaber subglaber* (1.6)
	2	3	*D. subglaber subisensis* (14)	*D. subglaber subisensis* (3.3)
	3	1	*D. adversa* (12)	*D. adversa* (1.4)
	4	1	*D. goliath* (1)	***D. goliath* (91)**
	5	1	*D. sulphurea* (2)	*D. sulphurea* (45.5)
			Shell width	
Small	1	1	*D. whiteheadi* (2)	*D. whiteheadi* (403)
	2	1	*D. maduana nefrens* (2)	*D. maduana nefrens* (403)
	3	1	*D. maduana maduana* (44)	*D. maduana maduana* (18.3)
Medium	1	6	*D. concinna* (27)	*D. baritensis* (9.6)
	2	6	*D. niahensis* (21)	*D. niahensis* (22.3)
	3	4	*D. concinna* (27)	*D. busanensis* (9.1)
	4	6	*D. concinna* (14)	*D. toretos* (25.3)
	5	2	*D. concinna* (6)	*D. onyx* (8.7)
	6	4	*D. concinna* (11)	*D. calcarata* (22)
	7	2	*D. azlani* (6)	***D. azlani* (108)**
	8	1	***D. concinna* (43)**	*D. concinna* (5.7)
Large	1	4	***D. adversa* (55)**	*D. spinosa* (6.7)

2	2	*D. sulphurea* (2)	*D. sulphurea* (169)
3	1	*D. subglaber subisensis* (13)	*D. subglaber subisensis* (36.3)
4	1	*D. adversa* (12)	*D. adversa* (7.6)
5	1	*D. goliath* (1)	***D. goliath* (508)**

4.2 Habitat Associations Between Species of the Genus *Diplommatina*

4.2.1 Utilisation of Habitat Types

A total of 16 living *Diplommatina* species with their respective habitat association were recorded. The associations between *Diplommatina* species and their habitats were represented as a bipartite link graph (Figure 4.5). In total, 19 bipartite weighted networks were constructed from 1,153 individuals belonging to 16 *Diplommatina* species (Appendix A). All 16 species were found in leaf litter, with ten of them found exclusively in this habitat. Five species (i.e., *D. adversa*, *D. busanensis*, *D. concinna*, *D. baritensis*, and *D. onyx*) were found on vegetation. Four species (i.e., *D. adversa*, *D. concinna*, *D. subglaber subglaber*, and *D. onyx*) were found on limestone surfaces. Among 16 species, *D. concinna* and *D. onyx* were present in all three habitat types. Friedman test indicates that there is a significant difference in means at p-values less than 0.01 (p-value: 4×10^{-7}) between three habitat types (Table 4.3). The Conover post hoc test showed a significant difference at p-values less than 0.01 between leaf litter and vegetation (p-value: 1.3×10^{-14}), as well as between leaf litter and limestone (p-value: 4.4×10^{-15}), but not between vegetation and limestone (p-value: 1).

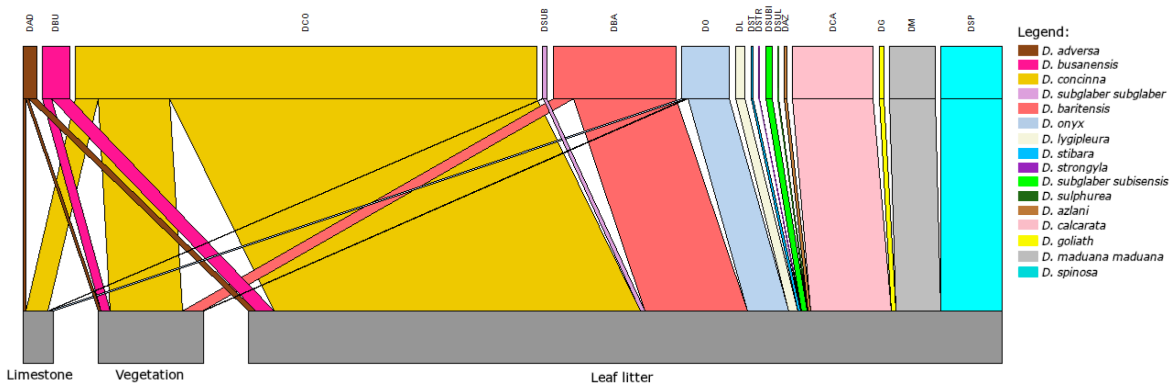


Figure 4.5: Weighted network of land snail species and habitats sampled. The upper level shows the 16 species of live-taken land snail. The lower level indicates three (3) habitats (Limestone, vegetation, and leaf litter) and the relative density of each species is illustrated by the width of its block

Table 4.3: Friedman test and Conover post hoc test results between three habitat types showing its p-value less than 0.01. L: Limestone, LL: Leaf litter, V: Vegetation

	Habitat	p-values
Friedman test	L - LL - V	4×10^{-7}
Conover post hoc test	V - LL	1.3×10^{-14}
	L - LL	4.4×10^{-15}
	L -V	1

Six *Diplommatina* species were found in two or more habitat types which are *D. adversa*, *D. baritensis*, *D. busanensis*, *D. concinna*, *D. onyx*, and *D. subglaber subglaber*. Among all six species, only *D. adversa* showed no significant difference among three habitat types, while the other five species showed significant differences. Pairwise comparisons following a chi-squared test revealed that the observed number of individuals in leaf litter for the five species exceeded the expected individual number. This indicates a stronger association with leaf litter compared to the other two habitat types, where observed individual numbers were lower than expected (Table 4.4).

Table 4.4: Chi-square test (X^2) and pairwise comparison result. As for habitat, LL: Leaf litter. L: Limestone. V: Vegetation. Observed is the total number of individuals present in their respective habitat. Highlighted boxes indicate preferred habitat types. The asterisk symbol indicates p-values, *: p-values at less than 0.01. **: p-values less than 0.1

Species	X^2	Habitat	Observed	Expected	p-values	Total indi.
D. adversa	0.14	LL	10	6	0.14	18
		L	4		0.32	
		V	4		0.32	
D. baritensis	0.00*	LL	133	53	0.00*	159
		L	26		0.00*	
		V	0		0.00*	
D. busanensis	0.00*	LL	23	11.67	0.00*	35
		L	12		0.9	
		V	0		0.00*	
D. concinna	0.00*	LL	475	199	0.00*	597
		L	93		0.00*	
		V	29		0.00*	
D. onyx	0.00*	LL	54	20.67	0.00*	62
		L	2		0.00*	
		V	6		0.00*	
D. subglaber subglaber	0.03**	LL	5	2	0.03**	6
		L	0		0.12	
		V	1		0.39	

An interaction matrix was used to visualise the associations between *Diplommatina* species abundance and the sampled habitats (Figure 4.6). The colour gradient from pale to dark indicates the strength of the interactions between the land snails and the habitats. *Diplommatina concinna* was highly abundant and frequently found in leaf litter (475 individuals) as indicated by the darkest cell colour. In contrast, *D. strongyla* and *D. sulphurea* on the right were represented by fewer individuals, as indicated by the lighter cell colours (one individual).

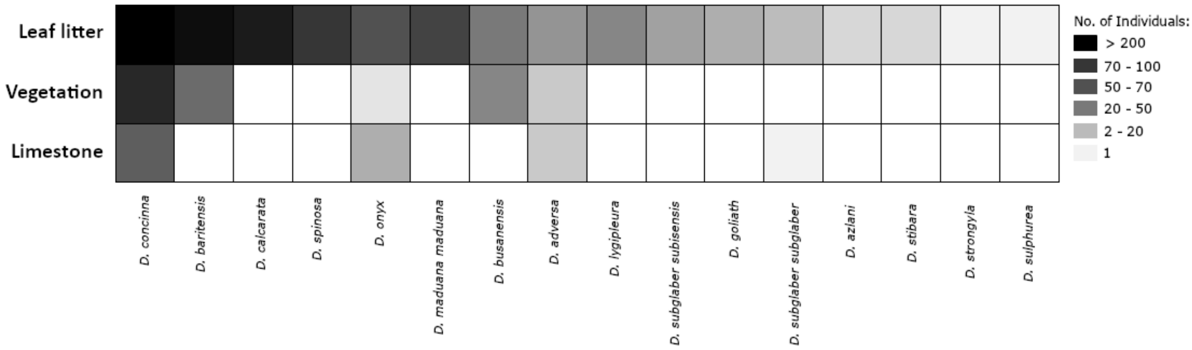


Figure 4.6: A visualisation of the adjacency matrix of land snail species and habitats sampled. The x-axis shows the 16 species of live-taken land snail. The y-axis indicates the three (3) habitats (Limestone, vegetation, and leaf litter) and the relative density of each species is illustrated by the tone of its cell

Next, modularity plot was generated to produce modules based on different *Diplommatina* species and their sampled habitat (Figure 4.7). The modules refer to the tendency for a network to form closely interacting communities. In this study, the modules indicate species that have similar habitat associations. Colour indicates the presence or absence of the interaction and the intensity of the colour in the cells reflects the strength of the interaction. Strong interactions (more than 70 individuals) are shown with the brightest colour, moderate interactions (20–70 individuals) with a medium brightness, and weak interactions (fewer than 20 individuals) with the faintest colour. Leaf litter habitat type includes several species that have a weak association with leaf litter. However, *D. concinna* show a stronger association (dark blue) with leaf litter. Vegetation habitat type shows some species have a weak to moderate association with vegetation. Similarly, *D. concinna* shows a particularly strong association with vegetation. Limestone habitat type shows fewer species associated compared to leaf litter and vegetation and the associations with limestone are generally weaker (light blue or white).

There are three modules shown in the modularity plot. Module 1 encompasses a group of species that are all associated, albeit weakly, with the leaf litter habitat, namely *D.*

azlani, *D. calcarata*, *D. goliath*, *D. lygipleura*, *D. maduana maduana*, *D. spinosa*, *D. stibara*, *D. strongyla*, *D. subglaber subisensis*, and *D. sulphurea*. This suggests these species might prefer or depend on leaf litter, even if the association is not particularly strong. Additionally, the data suggests that if a species from this module is found in a leaf litter habitat, there is a likelihood of finding other species from the same module in the leaf litter habitat as well. Module 2 highlights species that are associated with vegetation type which are *D. baritensis*, *D. busanensis*, and *D. concinna*. Module 3 shows a group of species associated with limestone such as *D. adversa*, *D. onyx*, and *D. subglaber subglaber*. The associations are generally weaker compared to vegetation but still significant enough to form a noticeable cluster.

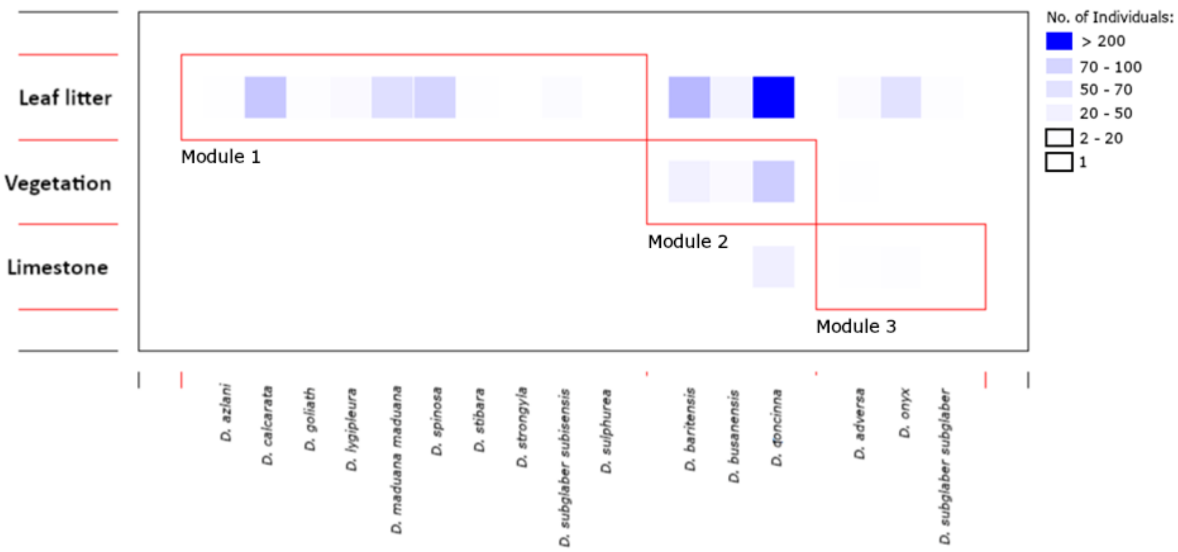


Figure 4.7: Interaction matrix featuring nested modules for the data of land snail species and habitats sampled. The x-axis shows the 16 species of live-taken land snail. The y-axis indicates the three (3) habitats (Limestone, vegetation, and leaf litter) and the relative density of each species is illustrated by the tone of its cell. Red coloured box delineates three (3) modules

The standardised connection (c values) and participation (z values) metrics for module members are displayed in the Table 4.5. According to Guimerà et al. (2005), the critical values for c and z are 0.625 and 2.5, respectively. A species with a high c value

(>0.625) and a low z value (<2.5) is identified as a connector, serving to connect the modules together and thus playing a vital role in maintaining network coherence. In this study, *D. concinna* is the connector species (c-value: 0.66 (> 0.625) and z-value: 1.14 (<2.5)).

Table 4.5: The 'c' and 'z'- values of the module members: Snail species. *Diplommatina concinna* with high c value (>0.62) and low z value (<0.25) is regarded as connector species

Species	c values	z values
D. adversa	0.44	0.13
D. azlani	>0.0	-0.64
D. baritensis	0.49	-0.41
D. busanensis	0.33	-0.73
D. calcarata	>0.0	1.99
D. concinna	0.66	1.14
D. goliath	>0.0	- 0.56
D. lygipleura	>0.0	-0.41
D. maduana maduana	>0.0	0.82
D. onyx	0.47	0.93
D. spinosa	>0.0	1.34
D. stibara	>0.0	-0.64
D. strongyla	>0.0	-0.69
D subglaber subglaber	0.28	-1.05
D. subglaber subisensis	>0.0	-0.51
D. sulphurea	>0.0	-0.69

4.2.2 Abiotic Components

The boxplots revealed distribution patterns of seven *Diplommatina* species with abiotic parameters (Figure 4.8). Parameter's readings were represented as ranges in a boxplot. Each box shows the interquartile range (IQR), with the middle line representing the median. Whiskers extend to the smallest and largest values within 1.5 times the IQR from the quartiles. Any dots outside these lines indicate outliers that placed outside the adjacent value range.

Out of all the tested physical parameters, only pH had a significant difference at p-value less than 0.05 between species. This includes *D. onyx* which had a median pH of 4 and *D. baritensis* at 6 pH. Although the other species (i.e., *D. goliath*, *D. niahensis*, *D. maduana maduana*, and *D. adversa*) were found in environments with varying ranges of pH values, they were not found to be significantly different from each other. *D. concinna* exhibited the broadest range of pH levels (pH 4 to pH 6) with a median of around 4.6.

For the other physical parameters, namely soil temperature, leaf litter depth, humidity, ambience temperature and illuminance, no significant differences were found between *Diplommatina* species. The species showing the highest and lowest median for these parameters do not adhere to a specific pattern and varies for each boxplot. For soil temperature, *D. baritensis* recorded the lowest median at approximately 24.4°C, while *D. maduana maduna* was the highest at around 30.2°C. Also, *D. baritensis* had the broadest range of recorded temperature (23.2°C to 30.8°C). The other *Diplommatina* species such as *D. onyx*, *D. concinna*, *D. adversa* and *D. maduana maduana* had varying smaller ranges when compared with *D. baritensis*.

All seven species of *Diplommatina* are found in areas with varied leaf litter depths. *Diplommatina concinna*, *D. baritensis*, and *D. onyx* inhabit regions with a wide range of leaf litter thicknesses. *Diplommatina baritensis* was found in areas where the leaf litter depth varies from 5 cm to 8 cm, with a median depth of approximately 8 cm. *Diplommatina concinna* occupies regions with leaf litter depths ranging from 5 cm to 10 cm, and a median depth of about 7.9 cm. *Diplommatina onyx* was observed in the deepest leaf litter, spanning up to 12.2 cm, with a median depth around 10.3 cm. Meanwhile, *D. maduana maduana* and *D. adversa* were found in shallow leaf litter, with median depths of approximately 4 cm and 5 cm, respectively.

The obtained humidity levels slightly vary in terms of median among *Diplommatina* species. Among them, *D. baritensis* had the highest humidity range and median, with values around 66% to 88% and a median around 89% respectively. Conversely, *D. niahensis* has the lowest median humidity value at approximately 78%.

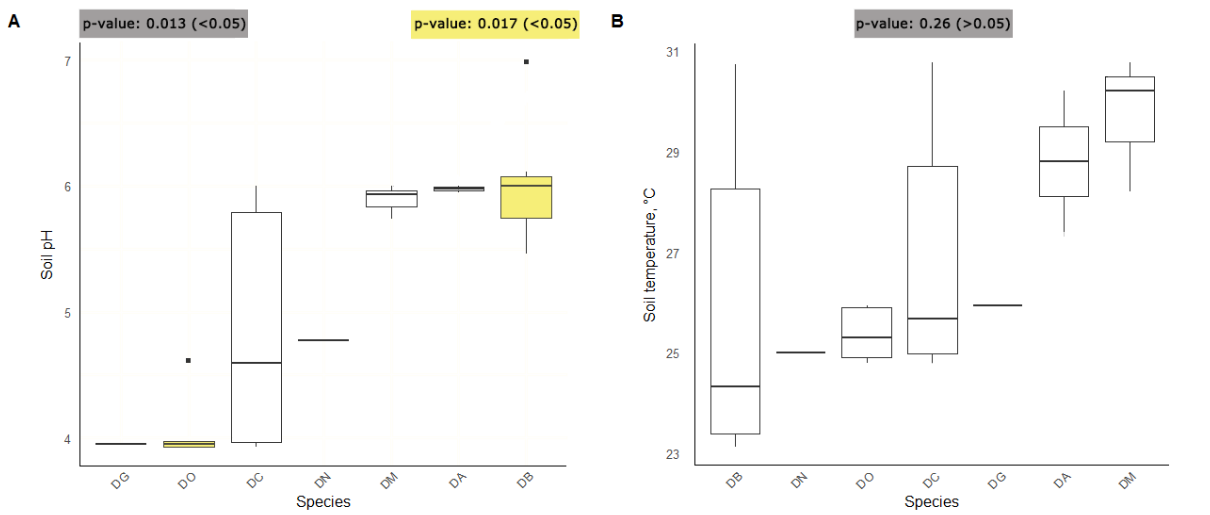
Based on the ambience temperature parameter, the median of all *Diplommatina* species varies between approximately 28.9°C to 30.9°C. *Diplommatina baritensis* has the largest spread of ambient temperature, ranging from 26.4°C to 32.2°C, with a median around 30.3°C. The highest and lowest median for this parameter were occupied by *D. niahensis* (30.9°C) and *D. goliath* (28.9°C) respectively.

As for illuminance, six out of seven species were found in an area with range below 1000 lux, except for *D. baritensis*, which has the highest range of illuminance, going up to 2500 lux, with a median around 240 lux. Meanwhile, *D. adversa*, *D. maduana maduana*, *D. concinna* and *D. onyx* had consistently lower illuminance values, with medians below 500 lux.

Table 4.6: Summary of abiotic parameters with median, minimum, maximum, and range values for each species labelled DA: *D. adversa*, DB: *D. baritensis*, DC: *D. concinna*, DG: *D. goliath*, DM: *D. maduana maduana*, and DO: *D. onyx*

Parameter		**Species**						
		DA	**DB**	**DC**	**DG**	**DM**	**DN**	**DO**
Soil pH	**Median**	5.99	6	4.6	3.95	5.9	4.75	4
	Min	5.95	5.5	3.9		5.7		3.85

	Max	6	7	6		6		4.6
	Range	5.9-6	5.8-6.1	4-5.85		5.8-5.95		3.8-3.95
Soil temperature (°C)	**Median**	28.8	24.4	25.7	26	30.2	25	25.4
	Min	27.4	23.2	24.8		28.2		24.8
	Max	28.2	30.9	30.8		30.8		25.8
	Range	28.1-29.5	23.2-30.8	25-28.7		29.2-30.5		24.9-25.9
Leaf litter depth (cm)	**Median**	5	8	7.9	10.5	4	4	10.3
	Min	4	4	4		4		5
	Max	6	12	11		5.8		12.2
	Range	4.5-5.5	5.4-8	5.3-10.6		4-4.9		8.8-10.8
Humidity (%)	**Median**	86	89	81	80.5	78.5	78	81
	Min	78	78	77.5		78		77.5
	Max	93	86	90		90		84.9
	Range	82.5-89	66-88	78-82.5		78-84		80-81
Ambience temperature (°C)	**Median**	29	30.3	30.2	28.9	30.3	30.9	29.4
	Min	27.8	26.4	28.1	28.2	29.2		28.1
	Max	30.2	32.1	30.8	30.6	30.8		30.6
	Range	28.4-29.6	26.4-32.2	29.2-30.7	28.4-29.7	29.7-30.5		28.4-29.5
Illuminance (lux)	**Median**	116	240	244	766	196	376	459
	Min	36	149	149		149		179
	Max	194	2500	766		241		926
	Range	52-180	152-750	162-282		162-225		250-766



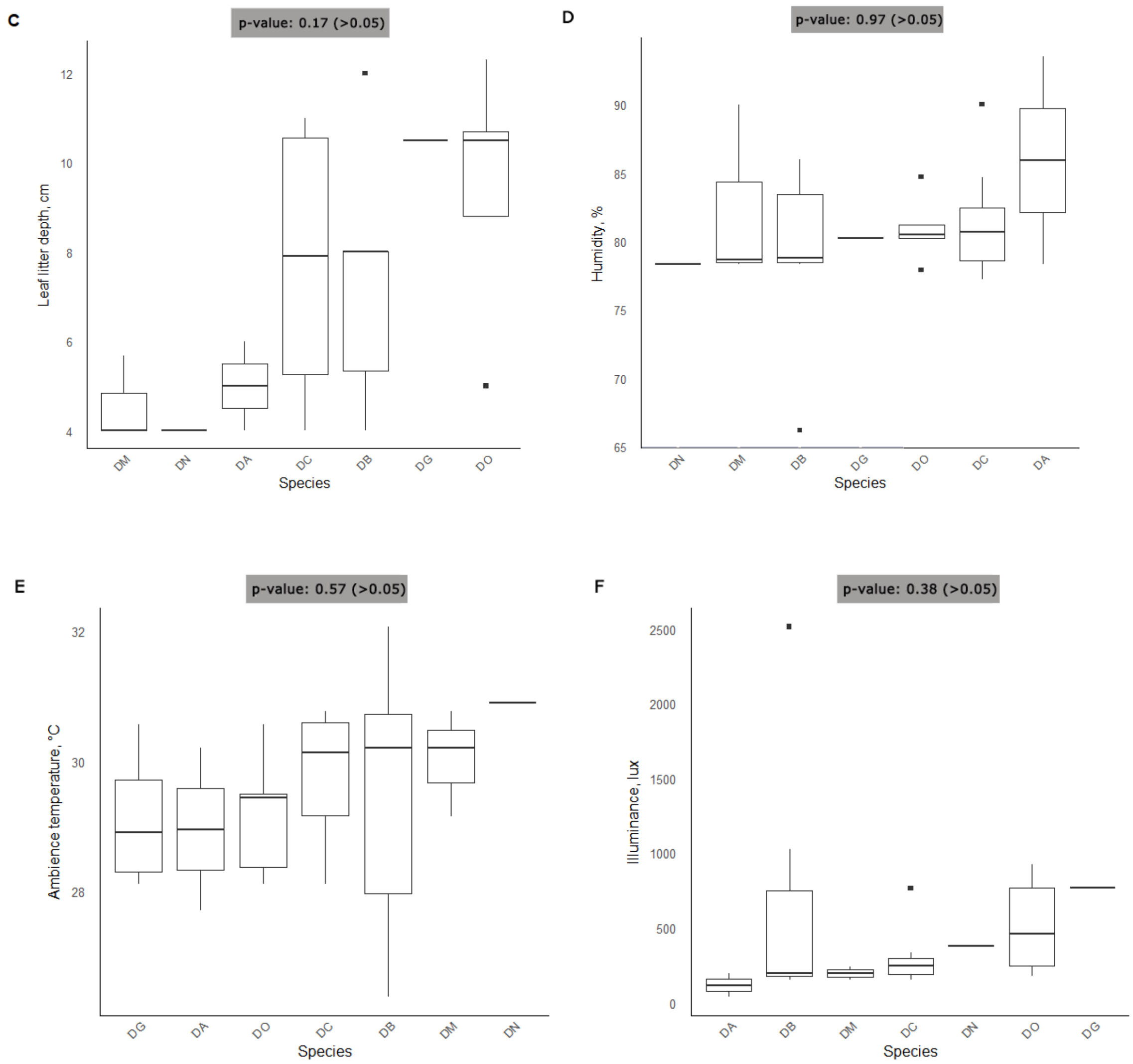


Figure 4.8: Boxplot of measured value of the abiotic parameters (y-axis) for seven *Diplommatina* Species (x-axis) labelled as DG (*D. goliath*), DO (*D. onyx*), DC (*D.concinna*), DN (*D.niahensis*), DM (*D. maduana maduana*), DA (*D. adversa*), and DB (*D. baritensis*). Black boxes showed p-values for Friedman test while red box showed p-value for Dunn post hoc test. Only soil pH has p-values less than 0.05, depicted significance difference. **A** Soil pH **B** Soil temperature **C** Leaf litter depth **D** Humidity **E** Ambience temperature **F** Illuminance

4.2.3 Biotic Components

The relationship between seven *Diplommatina* species and two biotic parameters was assessed using boxplots (Figure 4.9). The biotic parameters examined are the diameter of trees at breast height (DBH) and canopy cover. However, no significant differences were found among the *Diplommatina* species for either parameter (Table 4.7). In terms of DBH, *D. baritensis*, *D. maduana maduna* and *D. concinna* exhibited the widest range, from approximately 0.25 m to 1.8 m. *Diplommatina goliath* had the largest median diameter, around 1.2 m, while *D. adversa* showed the smallest median, approximately 0.5 m. As for canopy cover, *D. baritensis* again showed the broadest range, between 38% and 68%, and had the highest median at about 48%. In contrast, *D. adversa* had the lowest median canopy cover, around 33%.

Table 4.7: Summary of biotic parameters with median, minimum, maximum, and range values for each species labelled DA: *D. adversa*, DB: *D. baritensis*, DC: *D. concinna*, DG: *D. goliath*, DM: *D. maduana maduana*, and DO: *D. onyx*

Parameters		**Species**						
		DA	**DB**	**DC**	**DG**	**DM**	**DN**	**DO**
DBH (m)	**Median**	0.5	0.6	0.7	1.2	0.6	0.7	0.6
	Min	0.3	0.2	0.2		0.2		0.4
	Max	0.6	1.8	1.8		1.8		1.2
	Range	0.38-0.5	0.28-1.1	0.4-0.96		0.38-1.2		0.4-1.1
Canopy cover (%)	**Median**	33	48	34.89	39.9	32.5	33.23	36.73
	Min	31.35	32.5	28.77		28.77		30.11
	Max	32.5	78	65.44		37.79		58.91
	Range	31.5-32	38-68	32-38				34-40

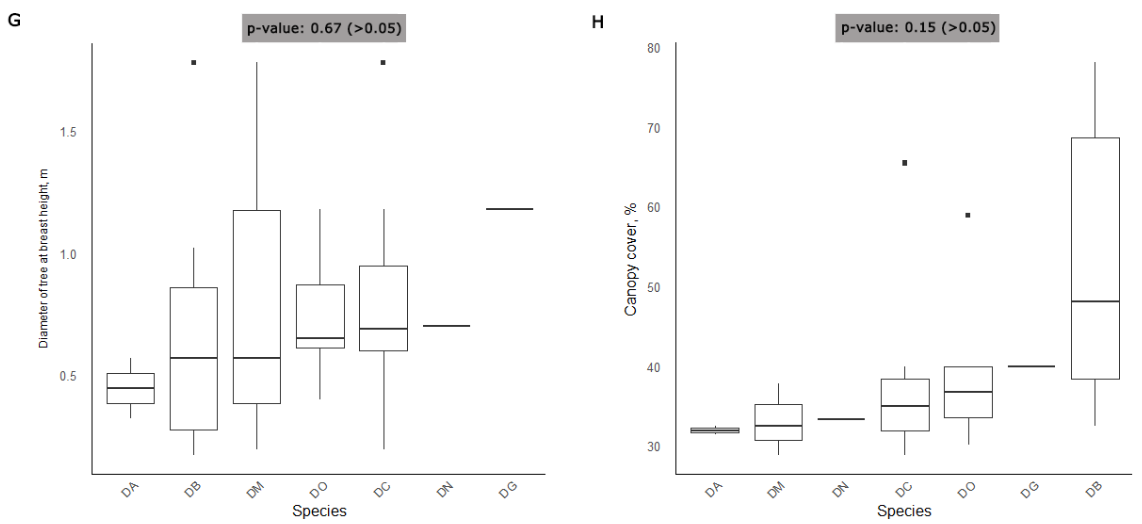


Figure 4.9: Boxplot of biotic parameters (y-axis) for seven *Diplommatina* species (x-axis) namely *D. goliath*, *D. onyx*, *D.concinna*, *D.niahensis*, *D. maduana maduana*, *D. adversa*, and *D. baritensis*. **G** Diameter of tree at breast height **H** Canopy cover

4.3 Species Account of Genus *Diplommatina* in Sarawak

To date, a total of 29 species of *Diplommatina* have been discovered in Sarawak, including a newly described species, *D. rumbangensis*. Among these, 18 species are documented in the MZU collection, with photographs provided (Figures 4.10 until 4.33). For species not available in the MZU collection, photographs were extracted from Vermeulen (1993; 1996). Descriptions of these species were also extracted from Vermeulen (1993; 1996), Marzuki (2019) and Nasir et al. (2024) and supplemented by additional information gathered during our species identification process.

***Diplommatina rumbangensis* Nasir, Lee, Marzuki, Vermeulen, Mohd-Azlan, & Khalik, 2024**

Figures 4.10, 4.11

Description. Shell: Dextral, fusiform to moderately conical, reddish orange, shining and translucent, with the penultimate whorl widest, convex, well rounded. Suture: Impressed. Protoconch: $1\frac{1}{2}$, whorls, punctate with small pits, without radial and spiral lines. Constriction nearly level with the edge between the parietal and columellar side of the peristome. Parietales: 2. Longitudinal palatales: 2, upper, which are not covered by the peristome on the outer surface of the shell. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards and positioned at the start of the constriction together with the longitudinal palatales. Tuba: $\frac{3}{4}$ whorl. Radial ribs: On the top whorls only, widely spaced, inconspicuous, but halfway the whorl with an almost tubular projection, in adults sometimes abraded to a semi-circular scar. Spiral striation: Inconspicuous, on top whorls only. Aperture: Hardly tilted regarding the coiling axis. Peristome: Double, expanding. Palatal side: Hardly sinuous, without edge. Basal side: With an edge. Basal edge: Hardly sinuous, rounded. Inner peristome: Expanding beyond the outer, with a palatal lip, free and erect on the columellar side, and expanding on the parietal side. Umbilicus: Open, narrow.

Habitat. The living snails were not observed. Empty shells were found in the leaf litter.

Distribution. It is known from the type locality only.

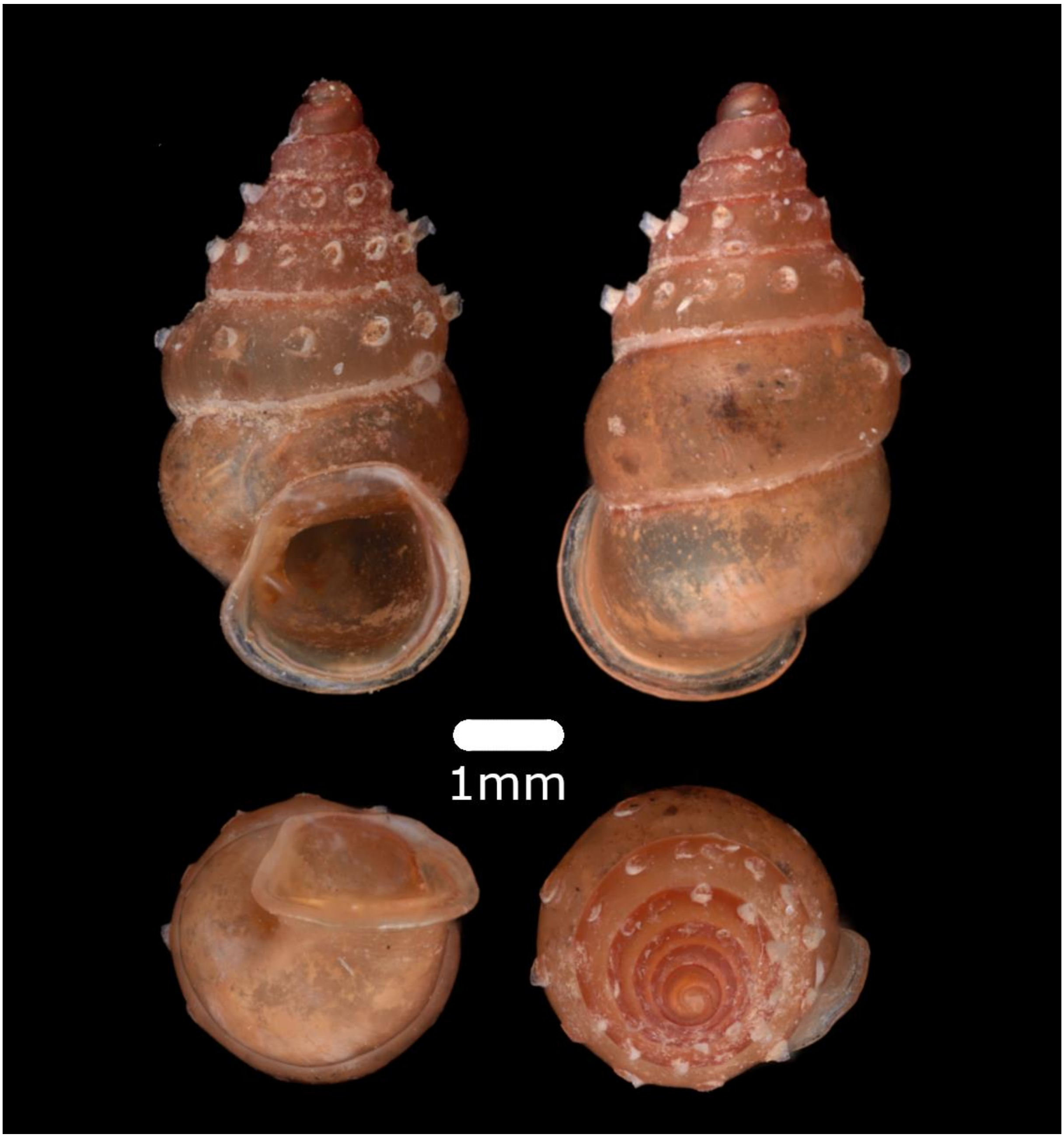


Figure 4.10: *Diplommatina rumbangensis* Nasir, Lee, Marzuki, Vermeulen, Mohd-Azlan & Khalik, 2024 in aperture, side, posterior, apical and umbilical point of views

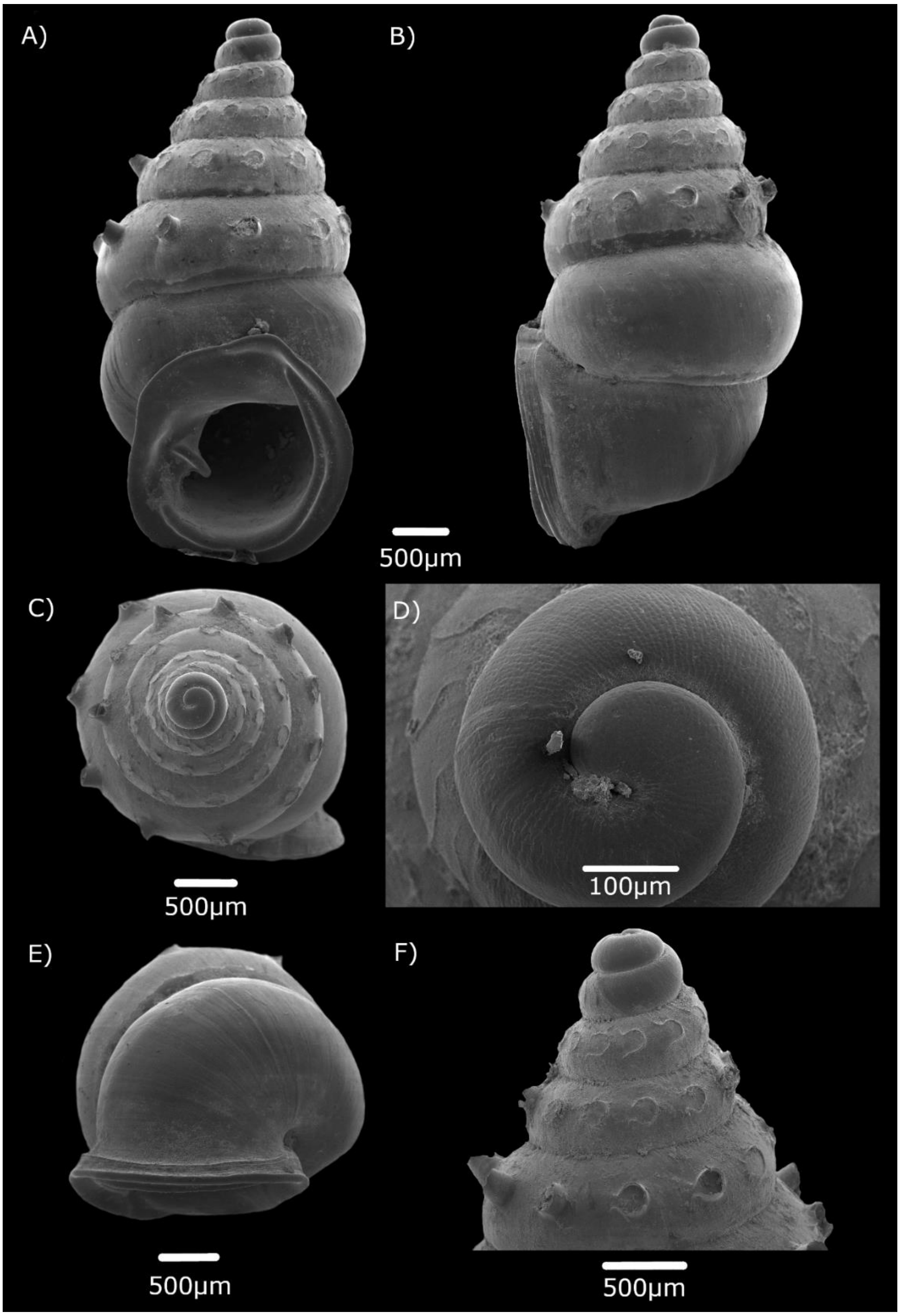


Figure 4.11. Scanning Electron Microscope images of *Diplommatina rumbangensis*. **A–F** Paratypes (ME 14471). **A** Apertural view **B** Side view **C** Apical view **D** Enlargement of apical view showing the apex with radial ribs **E** Umbilical view **F** Top whorls view showing the tubular projection and semi-circular scars

***Diplommatina adversa* (Adams & Adams, 1851)**

Figure 4.12

Description. Shell: Sinistral, fusiform, last two whorls widest, sides slightly concave. Whorls $6\frac{1}{8}$-$7\frac{3}{8}$, slightly convex. Suture: Impressed. Constriction level with the parietal side of the peristome. Parietalis: 1. Longitudinal palatales: 3. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards. Tuba: $\frac{3}{4}$ - $\frac{7}{8}$ whorl. Radial ribs: Absent or inconspicuous, not sinuous, low, thin, densely placed. Spiral striation: Absent. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Simple, palatal side not sinuous, without edge. Basal side: Without edge. Basal edge: Not sinuous, rounded. Peristome: A palatal lip, expanding but free and slightly erect on the columellar side, and expanding up to the suture of the previous whorl on the parietal side.

Habitat. Living snails were observed foraging on limestone rocks, vegetation, and in the leaf litter.

Distribution. Malaysia, western of Sarawak: Scattered localities between Bau and Serian-Padawan limestone hills. Malaysia, Sabah: Ulu Segama (Marzuki et al., 2021; Vermeulen & Liew, 2022). West Malaysia and Singapore (Laidlaw, 1949).

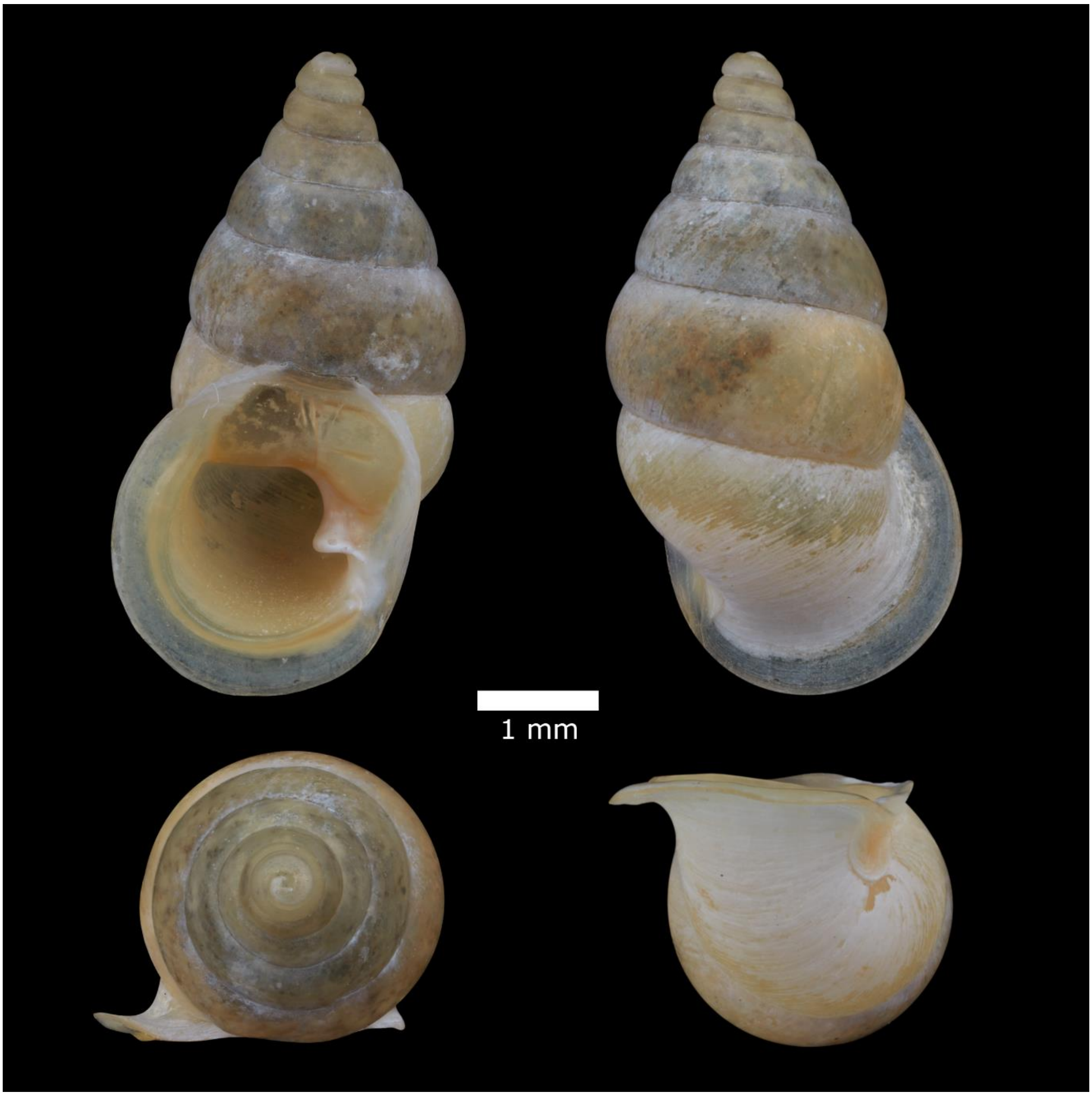


Figure 4.12: *Diplommatina adversa* (Adams & Adams, 1851) in aperture, posterior, apical and umbilical point of views

Diplommatina azlani **Marzuki, 2019**

Figure 4.13

Description. Shell: Sinistral, fusiform to moderately conical, dark ruby red, moderately shiny, and translucent. Whorls: 6, last whorl widest, top whorls almost flat, others convex, well rounded. Suture: Impressed. Protoconch: $1\frac{1}{2}$ whorls, punctate with small pits, without radial and spiral lines. Constriction level with angular edge of peristome. Long transversal palatalis: 1. Columellaris: 1, distinct, slightly directed downwards. Tuba approximately ¾ whorl. Radial ribs: Oblique, inconspicuous, and densely placed. Spiral striation: Present, inconspicuous. Aperture: Tilted about 45° relative to the coiling axis. Peristome: Double, thickened, expanding. Palatal side: Sinuous, without edge. Basal side: Sinuous with sharp edge. Umbilicus: Closed. Living animal observed with creamy white head and a pair of black tentacles.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Gunung Santubong NP.

Figure 4.13: *Diplommatina azlani* Marzuki, 2019 in aperture, posterior, apical and umbilical point of views

***Diplommatina baritensis* Smith, 1893**

Figure 4.14

Description. Shell: Dextral, fusiform, penultimate whorls widest, sides slightly concave. Whorls: $6\frac{1}{2}$ - $7\frac{1}{4}$, convex. Suture: Impressed. Constriction level with the parietal side, or with the angular edge of the peristome or slightly beyond this point. Parietalis: 1. Longitudinal palatalis: 1 at the level of the peristome. Transversal palatalis: 1. Columellaris: 1, distinct, not, or slightly directed downward. Tuba: $\frac{7}{8}$ - 1$\frac{1}{8}$ whorl. Radial ribs: Straight, distinct, high, thin, widely spaced to densely placed near the top, widely spaced on the other whorls. Spiral striation: Absent or inconspicuous, on the top whorls only. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Sinuous, with a protrusion. Basal side: Without edge. Basal edge: Sinuous, protruding. Outer peristome: Slightly hardly to distinctly expanding beyond the inner. Inner peristome: A palatal lip, expanding over the shell on the columellar side, and on the parietal side.

Habitat. Living snails were observed foraging on wild banana tree trunk and in the leaf litter.

Distribution. Malaysia, Sarawak: Scattered localities between Padawan limestone hills at western Sarawak and Mulu limestone hills in northern Sarawak (Smith, 1895; Vermeulen, 1993).

Figure 4.14: *Diplommatina baritensis* Smith, 1893 in aperture, posterior, apical and umbilical point of views

Diplommatina busanensis **Godwin-Austen, 1889**

Figure 4.15

Description. Shell: Sinistral, conical with the last whorl moved inwards but still widest, sides flat. Whorls: $5\frac{1}{2}$ - $6\frac{1}{8}$, convex. Suture: Impressed. Constriction about level with the edge between the parietal and columellar side of the peristome. Parietalis: 1. Transversal palatalis: 1. Columellaris: 1, inconspicuous. Tuba ¾ whorl. Radial ribs: Not sinuous, distinct, high, thin, widely spaced. Spiral striation: Present. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Simple, expanding. Palatal side: Not sinuous, without edge. Basal side: Without edge. Basal edge: Hardly sinuous, protruding. Outer peristome: Slightly expanding beyond the inner. Inner peristome: A palatal lip, free and slightly erect on the columellar side, expanding on the parietal side.

Habitat. Living snails were observed foraging on vegetation and in the leaf litter.

Distribution. Malaysia, Sarawak: Kuching Division. Endemic to Borneo (Marzuki et al., 2021)

Figure 4.15: *Diplommatina busanensis* Godwin-Austen, 1889 in aperture, side, posterior, apical and umbilical point of views

***Diplommatina calcarata* von Möellendorff, 1897**

Figure 4.16

Description. Shell: Dextral, fusiform, penultimate whorl widest, sides flat or slightly concave. Whorls: $5\frac{3}{4}$ - $6\frac{1}{4}$, convex. Suture: Impressed. Constriction level with the angular edge of the peristome or slightly beyond this point. Parietalis: 1. Longitudinal palatalis: 1, at the level of the peristome. Transversal palatalis: 1. Columellaris: 1, distinct, not, or slightly directed downwards. Tuba: 1 - $1\frac{1}{8}$ whorl. Radial ribs: Straight, distinct, low, thin, densely placed near the top, moderately spaced to densely placed elsewhere. Spiral striation: Present. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Moderately sinuous or not, with a rather distinct edge. Basal side: Two more edge which are sometimes fused to a single. Basal edge: Not sinuous, rather sharp to slightly protruding. Outer peristome: Expanding beyond the inner or not. Inner peristome: A palatal lip, expanding but partly free on the columellar side, and on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Scattered localities between limestone hills at western Sarawak, central Sarawak, and Niah limestone hills in northern Sarawak. Indonesia: Kalimantan and Java.

Figure 4.16: *Diplommatina calcarata* von Möellendorff, 1897 in aperture, side, posterior, apical and umbilical point of views

***Diplommatina concinna* Adams, 1872**

Figure 4.17

Description. Shell: Dextral, conical to fusiform, last two whorls widest, sides flat to concave. Top usually decollate. Whorls: $6\frac{5}{8}$ - $8\frac{1}{8}$, convex. Suture: Impressed. Constriction level with the parietal side of the peristome. Parietalis: 1. Longitudinal palatalis: 1. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards or not. Tuba: $\frac{3}{4}$ - $\frac{7}{8}$ whorl. Radial ribs: Slightly sinuous, with a slight edge to the right, distinct, high, wide, widely spaced to densely placed. Spiral striation: Present. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Not or slightly sinuous, with or without edge. Basal side: With or without edge. Basal edge: Sinuous or not, protruding. Outer peristome: Expanding beyond the inner. Inner peristome: With or without palatal lip, expanding over the shell on the columellar side, and little on the parietal side.

Habitat. Living snails were observed foraging on limestone rocks, vegetation, and in the leaf litter.

Distribution. Malaysia, Sarawak: Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Niah, in northern Sarawak. Indonesia: Bunguran (Marzuki et al., 2021). And in Singapore (Chan & Lau, 2020)

Figure 4.17: *Diplommatina concinna* Adams, 1872 in aperture, side, posterior, apical and umbilical point of views

Diplommatina goliath **Vermeulen, 1996**

Figure 4.18

Description. Shell: Sinistral, fusiform, last two whorls widest, sides flat or slightly convex.

Whorls: $6\frac{3}{8}$ - $6\frac{7}{8}$, slightly convex. Suture: Impressed. Constriction level with the parietal side of the peristome. Parietalis:1. Longitudinal palatales: 2. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards. Tuba: $\frac{3}{4}$ whorl. Radial ribs: Often absent on the top whorls, not sinuous, low, thin, moderately spaced. Spiral striation: Absent. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Simple, widely expanding, palatal side not sinuous, without edge. Basal edge: Not sinuous, rounded. Peristome: A palatal lip, expanding but free and slightly erect on the columellar side, up to the suture of the previous whorl on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Gua Rambus, Temurang, Padawan.

Figure 4.18: *Diplommatina goliath* Vermeulen, 1996 in aperture, side, posterior, apical and umbilical point of views

Diplommatina lygipleura **Vermeulen, 1993**

Figure 4.19

Description. Shell: Dextral, fusiform, penultimate whorls widest, sides or slightly concave.

Whorls: $5\frac{7}{8}$ - $6\frac{1}{4}$, convex. Suture: Impressed. Constriction $\frac{1}{8}$ whorl beyond the angular edge of the peristome. Parietalis: 1. Longitudinal palatalis: 1, at the level of the peristome. Transversal palatalis: 1. Columellaris 1, distinct, not directed downwards. Tuba $1\frac{1}{8}$ whorl, rounded. Radial ribs: Sinuous, with a slight edge to the left on the upper half of the whorls, distinct, high, wide, densely placed. Spiral striation: Absent. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Sinuous, with an edge. Basal side: Without edge. Basal edge: Slightly sinuous, sharp, or slightly protruding. Outer peristome: Expanding beyond the inner. Inner peristome: A palatal lip, expanding over the shell on the columellar side, and on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Scattered localities between Bau limestone hills at western Sarawak and Mulu and Niah limestone hills in northern Sarawak.

Figure 4.19: *Diplommatina lygipleura* Vermeulen, 1993 in aperture, side, posterior, apical and umbilical point of views

Diplommatina maduana maduana **Laidlaw, 1949**

Figure 4.20

Description. Shell: Dextral, fusiform, last two whorls widest, sides convex. Whorls: 5 - 5 $\frac{5}{8}$, convex. Suture: Impressed. Constriction level with the parietal side of the peristome. Parietalis: 1. Longitudinal palatalis: 1. Transversal palatalis: 1. Columellaris: 1, not or hardly visible. Tuba: $\frac{3}{4}$ - $\frac{7}{8}$ whorl. Radial ribs: Straight, distinct, low, thin, densely placed, often wider spaced on the tuba. Spiral striation: Inconspicuous. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Not or hardly sinuous, usually with a slight edge. Basal side: Without edge. Basal edge: Not sinuous, sharp, or slightly protruding. Outer peristome: Slightly expanding beyond the inner. Inner peristome: A palatal lip, expanding over the shell on the columellar side, and little on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Scattered localities between Bau and Serian-Padawan limestone hills in western Sarawak to Mulu hills in northern Sarawak (Marzuki et al., 2021). West Malaysia (Laidlaw, 1949).

Figure 4.20: *Diplommatina maduana maduana* Laidlaw, 1949 in aperture, side, posterior, apical and umbilical point of views

***Diplommatina maduana nefrens* Vermeulen, 1993**

Figure 4.21

Description. As the type subspecies, constriction with often 1 inconspicuous pariatelis, 1 transversal palatalis, 1 inconspicuous columellaris present half-way the tuba.

Habitat. Unrecorded.

Distribution. Malaysia, Sarawak: Baram Valley.

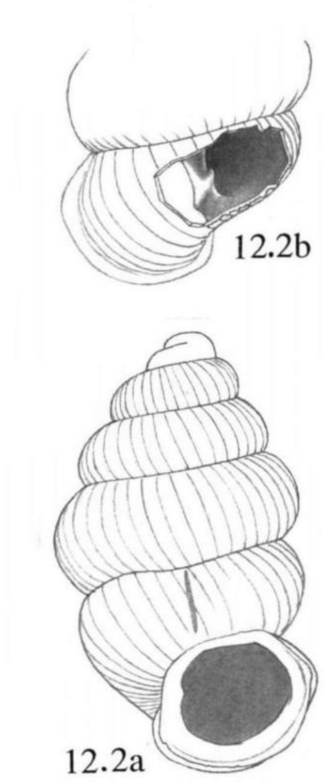


Figure 4.21: *Diplommatina maduana nefrens* Vermeulen, 1993 in aperture and side extracted from Vermeulen (1993)

***Diplommatina moluensis* Smith, 1893**

Figure 4.22

Description. Shell: Sinistral, almost conical, with the last whorl slightly moved inwards but still widest, sides flat. Whorls: 7, convex. Suture: Impressed. Constriction level with the parietal side of the peristome. Parietalis: 1. Longitudinal palatales: 2, the upper parallel with the suture. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards. Tuba: $\frac{7}{8}$ whorl. Radial ribs: Sinuous, distinct, high, widely spaced. Spiral striation: Absent.

Umbilicus: Closed. Aperture: Slightly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Not sinuous, with a wing. Basal side: Without edge. Basal edge: Moderately sinuous, sharp. Outer peristome: Expanding beyond the inner. Inner peristome: Without palatal lip, free and erect on the columellar side, and on the parietal side.

Habitat. Unrecorded.

Distribution. Malaysia, Sarawak: Gunung Mulu NP.

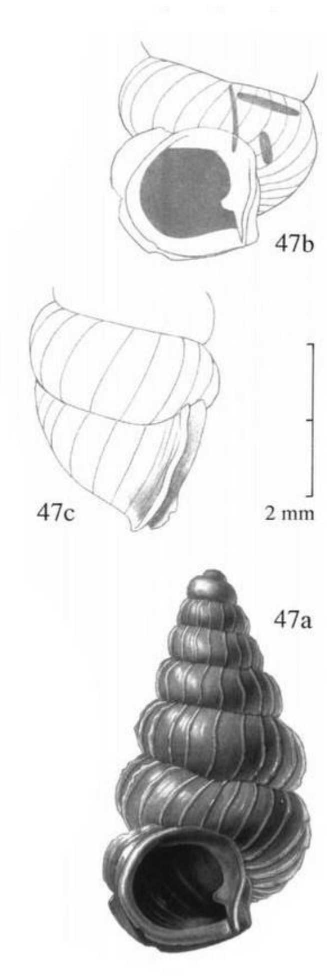


Figure 4.22: *Diplommatina moluensis* Smith, 1893 in aperture, side and dentition positions extracted from Vermeulen (1993)

***Diplommatina niahensis* Godwin-Austen, 1889**

Figure 4.23

Description. Shell: Dextral, fusiform, penultimate whorl widest, sides concave. Whorls: $6\frac{1}{2}$ - $7\frac{3}{4}$, top whorls flat, others convex. Suture: Impressed. Constriction about level with the angular edge of the peristome. Parietalis: 1. Longitudinal palatalis: 1, at the level of the peristome. Transversal palatalis: 1. Columellaris: 1, distinct, not, or hardly directed downwards. Tuba: 1 whorl. Radial ribs: Straight, inconspicuous, low, thin, densely placed, on the top whorl only, or continuing up to the penultimate whorl. Spiral striation: Absent. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Sinuous, with a slight to distinct edge. Basal side: Without edge. Basal edge: Hardly sinuous, sharp. Outer peristome: Expanding beyond the inner. Inner peristome: A palatal lip, expanding over the shell on the columellar side, and on the parietal side.

Habitat. Living snails were observed foraging on limestone rocks and in the leaf litter.

Distribution. Malaysia, Sarawak: Niah NP.

Figure 4.23: *Diplommatina niahensis* Godwin-Austen, 1889 in aperture, side, posterior, apical and umbilical point of views

***Diplommatina onyx* Fulton, 1901**

Figure 4.24

Description. Shell: Dextral, fusiform, penultimate whorl widest, sides flat to concave. Whorls $6\frac{1}{8}$, - 7, top whorls convex, next whorls convex, body whorls convex. Suture:

Impressed. Constriction level with the angular edge of the peristome or slightly beyond this point. Parietalis: 1. Longitudinal palatalis: 1, at the level of the peristome. Transversal palatalis: 1. Columellaris, distinct, not, or slightly directed downwards. Tuba: 1 whorl. Radial ribs: Straight, inconspicuous to distinct, low, wide, often densely placed near the top, moderately spaced to densely placed elsewhere, inconspicuous on the penultimate whorl or towards the constriction. Spiral striation: Absent or inconspicuous, on the top whorls only. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Sinuous, with and edge. Basal side: Without edge. Basal edge: Slightly to distinctly sinuous, sharp, or protruding. Outer peristome: Not or hardly expanding beyond the inner. Inner peristome: A palatal lip, expanding over the shell on the columellar side, and on the parietal side.

Habitat. Living snails were observed foraging on limestone rocks, vegetation, and in the leaf litter.

Distribution. Malaysia, Sarawak: Kuching, Serian, and Miri divisions. Endemic to Borneo (Marzuki et al., 2021).

Figure 4.24: *Diplommatina onyx* Fulton, 1901 in aperture, side, posterior, apical and umbilical point of views

Diplommatina spinosa **Godwin-Austen, 1889**

Figure 4.25

Description. Shell: Dextral, fusiform, or conical, if conical with the tuba distinctly moved inwards, last, or penultimate whorl widest, sides flat. Whorls: $7\frac{1}{4}$ - $8\frac{1}{8}$, convex. Suture:

Impressed. Constriction about level with the edge between the parietal and columellar side of the peristome. Parietales: 2. Longitudinal palatalis: 1, which is not covered by the peristome on the outer surface of the shell. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards. Tuba $\frac{3}{4}$ - $\frac{7}{8}$ whorl. Radial ribs: Continuing up to the peristome, widely spaced, hardly visible but halfway the whorl with a tubular projection, in adults sometimes abraded to a semi-circular scar. Spiral striationl: Absent. Umbilicus: Open, narrow. Aperture: Tilted up to 40° about the coiling axis. Peristome: Double, expanding. Palatal side: Not sinuous, without edge. Basal side: Without edge. Basal edge: Not sinuous, rounded. Inner peristome: Expanding beyond the outer, with a palatal lip, free and erect on the columellar side, and expanding on the parietal side.

Habitat. Living snails were observed foraging on limestone surfaces and in the leaf litter.

Distribution. Malaysia, Sarawak: Kuching and Serian divisions. Endemic to Borneo (Marzuki et al., 2021).

Figure 4.25: *Diplommatina spinosa* Godwin-Austen, 1889 in aperture, side, posterior, apical and umbilical point of views

Diplommatina stibara **Vermeulen, 1993**

Figure 4.26

Description. Shell: Dextral, fusiform, penultimate whorls widest, sides flat or slightly concave. Whorls: $5\frac{5}{8}$ - $6\frac{1}{8}$, convex. Suture: Impressed. Constriction $\frac{1}{8}$ - $\frac{1}{4}$, whorl beyond the angular edge of the peristome. Parietalis: 1. Longitudinal palatalis: 1, at the level of the peristome. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards or not. Tuba $1\frac{1}{8}$-$1\frac{1}{4}$ whorl, last half whorl obtusely angular at the periphery. Radial ribs: Sinuous, with a slight edge to the left on the upper half of the whorls, distinct, high, wide, densely placed. Spiral striation: Absent or inconspicuous. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Sinuous, with a protrusion. Basal side: Without edge. Basal edge: Sinuous, sharp, or slightly protruding. Outer peristome: Slightly expanding beyond the inner. Inner peristome: A palatal lip, expanding over the shell on the columellar side, and expanding on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Scattered localities between Bau limestone hills at western Sarawak and Mulu, Niah and Limbang limestone hills in northern Sarawak.

Figure 4.26: *Diplommatina stibara* Vermeulen, 1993 in aperture, side, posterior, apical and umbilical point of views

Diplommatina strongyla **Vermeulen, 1993**

Figure 4.27

Description. Shell: Dextral, fusiform, penultimate whorl widest, sides flat. Whorls: $5\frac{1}{8}$ - $6\frac{3}{8}$, convex. Suture: Impressed. Constriction level with the angular edge of the peristome or slightly beyond this point, sometimes level with the parietal side of the peristome. Parietalis: 1. Longitudinal palatalis: 1, at the level of the peristome. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards. Tuba: 1 whorl. Radial ribs: Straight, distinct, low, thin, densely placed. Spiral striation: Inconspicuous. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, moderately expanding. Palatal side: Sinuous, without edge. Basal side: Without edge. Basal edge: Sinuous, sharp. Outer peristome: Hardly expanding beyond the inner. Inner peristome: A palatal lip, expanding over the shell on the columellar side, and little expanding on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Niah NP.

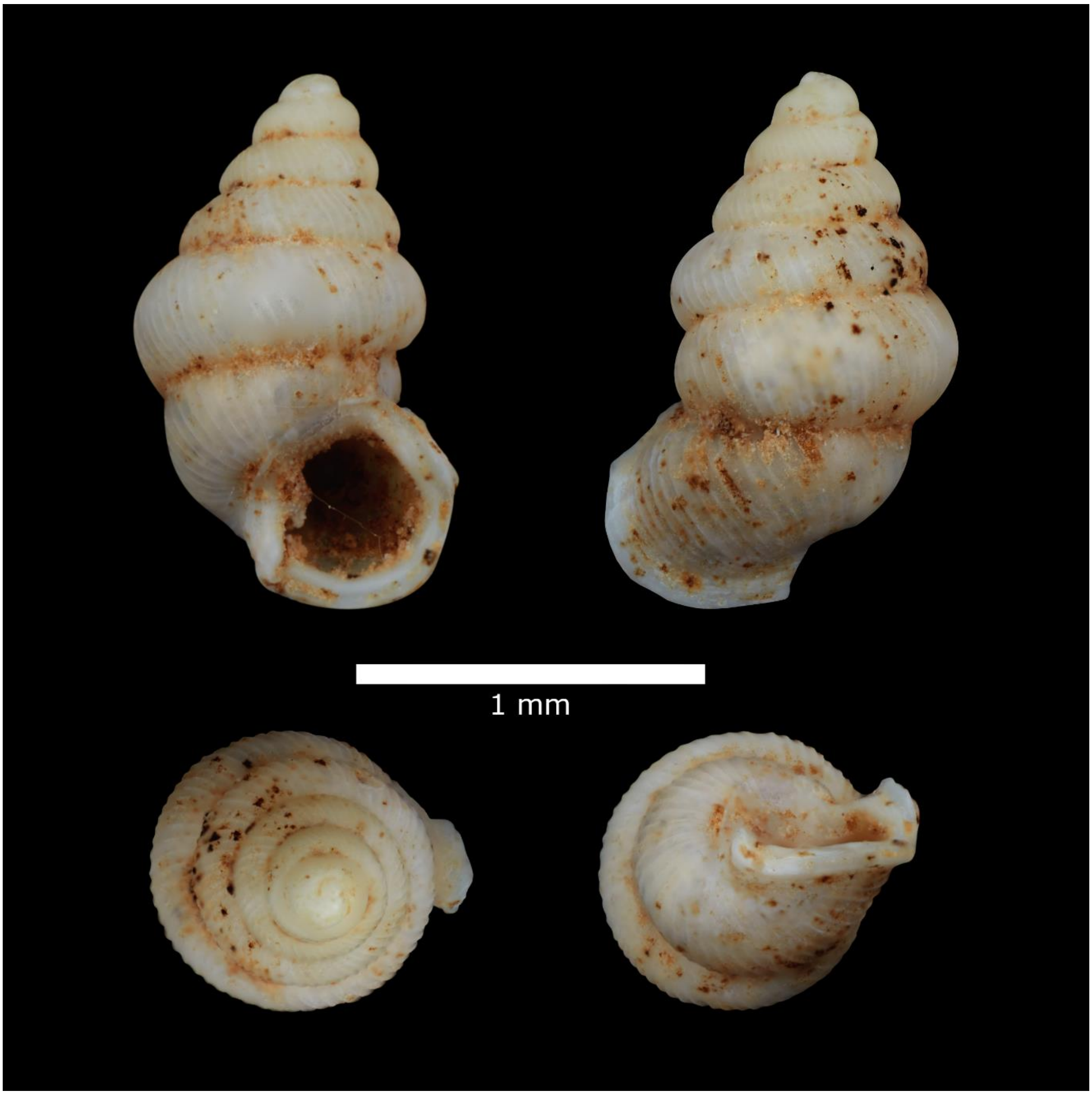


Figure 4.27: *Diplommatina strongyla* Vermeulen, 1993 in aperture, side, posterior, apical and umbilical point of views

Diplommatina subglaber subglaber **Vermeulen, 1993**

Figure 4.28

Description. Shell: Sinistral, fusiform to almost conical, with the last whorl slightly moved inwards but still widest, sides flat or slightly concave. Whorls: $6\frac{1}{8}$ - $7\frac{7}{8}$, top whorls convex, next whorls almost flat, body whorls slightly convex. Suture: Impressed. Constriction level with the parietal side of the peristome. Parietalis: 1. Longitudinal palatalis: 1, obliqued. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards. Tuba $\frac{7}{8}$ whorl. Radial ribs: Inconspicuous, low, wide, densely placed. Spiral striation: Absent. Umbilicus: Closed. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Sinuous, without edge. Basal side: Without edge. Basal edge: Not sinuous, sharp. Outer peristome: Expanding beyond the inner, inner peristome without palatal lip, free and erect on the columellar side, and expanding on the parietal side.

Habitat. Living snails were observed foraging on limestone rocks and in the leaf litter.

Distribution. Malaysia, Sarawak: Scattered localities between Kuching limestone hills at western Sarawak and Lubok Bedil in central Sarawak. Indonesia: Kalimantan.

Figure 4.28: *Diplommatina subglaber subglaber* Vermeulen, 1993 in aperture, side, posterior, apical and umbilical point of views

Diplommatins subglaber subisensis **(Vermeulen, 1993)**

Figure 4.29

Description. Shell: Sinistral, fusiform, last two whorls widest, sides flat or slightly concave.

Whorls: $6\frac{1}{2}$ - $7\frac{1}{8}$, top whorls convex, next whorls flat, body whorls slightly convex. Suture:

Impressed. Constriction level with the parietal side of the peristome. Parietalis: 1. Longitudinal palatalis: 1, obliqued. Transversal palatalis 1. Columellaris: 1, distinct, directed downwards. Tuba: $\frac{3}{4}$ - $\frac{7}{8}$ whorl. Radial ribs: Inconspicuous, not sinuous, low, wide, densely placed. Spiral striation: Absent. Umbilicus: Closed. Aperture: Slightly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Not sinuous, without edge. Basal side: Without edge. Basal edge: Not sinuous, somewhat angular. Outer peristome: Expanding beyond the inner. Inner peristome: Without palatal lip, free and erect on the columellar side, and expanding on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Scattered localities between Padawan limestone hills in western Sarawak and Niah limestone hills in northern Sarawak (Vermeulen, 1993; 1996).

Figure 4.29: *Diplommatina subglaber subisensis* (Vermeulen, 1993) in aperture, side, posterior, apical and umbilical point of views

Diplommatina sulphurea **Smith, 1894**

Figure 4.30

Description. Shell: Sinistral, fusiform to almost conical, with the last whorl slightly moved inwards but still widest, sides flat. Whorls 8 - 8$\frac{1}{4}$, moderately convex. Suture: Impressed.

Constriction level with the parietal side of the peristome. Parietalis: 1. Longitudinal palatalis: 1, obliqued. Transversal palatalis: 1. Columellaris: 1, distinct, directed downwards. Tuba $\frac{7}{8}$ whorl. Radial ribs: Inconspicuous, not sinuous, low, wide, densely placed. Spiral striation: Absent. Umbilicus: Closed. Aperture: Tilted about the coiling axis. Peristome: Simple, expanding. Palatal side: Not sinuous, without edge. Basal side: Without edge. Basal edge: Not sinuous, rounded. Peristome: Without palatal lip, free and erect on the columellar side, and expanding on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter.

Distribution. Malaysia, Sarawak: Gunung Mulu NP.

Figure 4.30: *Diplommatina sulphurea* Smith, 1894 in aperture, side, posterior, apical and umbilical point of views

***Diplommatina whiteheadi* Smith, 1898**

Figure 4.31

Description. Shell: Sinistral, about cylindrical, penultimate whorl widest, sides convex. Whorls: $4\frac{1}{4}$, - $4\frac{5}{8}$, convex. Suture: Impressed. Constriction level with the parietal side of the peristome. Parietalis: 1. Transversal palatalis: 1. Columellaris: 1, distinct, not directed downwards. Tuba: $\frac{3}{4}$ - $\frac{7}{8}$, whorl. Radial ribs: Straight, distinct, high, thin, densely placed. Spiral striation: Distinct. Umbilicus: Open, narrow. Aperture: Slightly tilted about the coiling axis. Peristome: Double or triple, expanding. Palatal side not sinuous, without edge. Basal side: Without edge. Basal edge: Not or hardly sinuous, rounded or slightly angular. Outer peristome: Expanding beyond the inner. Inner peristome: Without palatal lip, expanding over the shell on the columellar side, and little expanding on the parietal side.

Habitat. Living snails were observed foraging in the leaf litter (Schilthuizen, 2017).

Distribution. Malaysia, Sarawak: Penrissen and Lanjak Entimau. Malaysia, Sabah: Kinabalu Mountain, Crocker Range, and Kinabatangan basin.

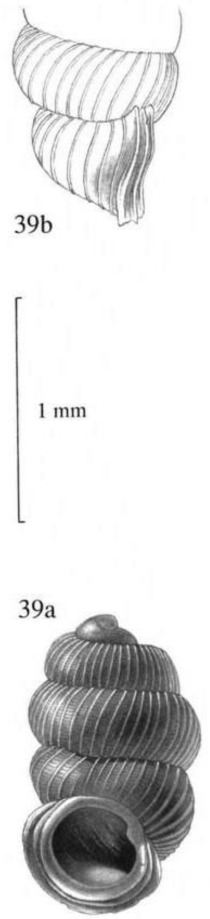


Figure 4.31: *Diplommatina whiteheadi* Smith, 1898 in aperture and side extracted from Vermeulen (1993)

Diplommatina isseli **Godwin-Austen, 1889**

Figure 4.32

Description. Shell: Sinistral, strictly conical, sides flat. Whorls: $6\frac{7}{8}$ - $8\frac{1}{4}$, convex. Suture: Impressed. Constriction level with the columellar side of the peristome. Parietalis: 1, short, obliqued, and close to the suture. Transversal palatalis: 1. Columellaris: 1, distinct, not directed downwards. Tuba: $\frac{5}{8}$ whorl. Radial ribs: Not sinuous, distinct, low, thin, densely. Spiral striation: Present or not. Umbilicus: Open, narrow. Aperture: Tilted about 45° about the coiling axis. Peristome: Simple or double, moderately expanding. Palatal side: Not sinuous, without edge. Basal side: Without edge. Basal edge: Not sinuous, rounded. Outer peristome: Hardly expanding beyond the inner. Inner peristome: Without palatal lip, expanding but free on the columellar side, and little expanding on the parietal side.

Habitat. The living snails were not observed. Empty shells were found in the leaf litter (Marzuki et al., 2019).

Distribution. Malaysia, Sarawak: Kuching Division. Malaysia, Sabah: Interior and West Coast divisions. Endemic to Borneo (Marzuki et al., 2021)

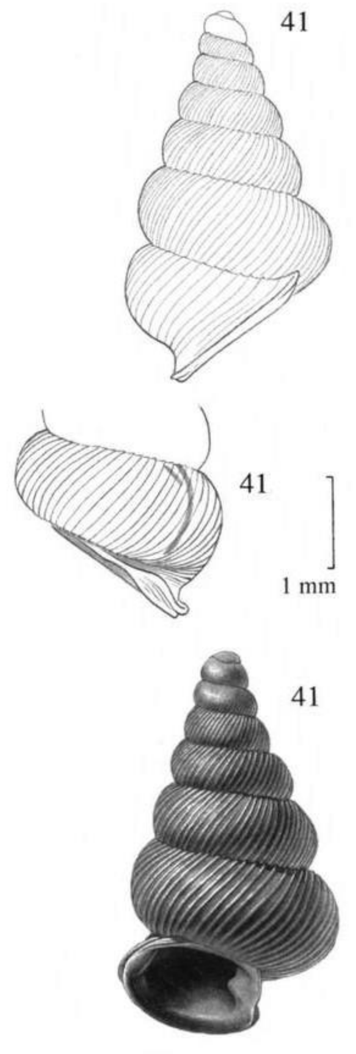


Figure 4.32: *Diplommatina isseli* Godwin-Austen, 1889 in aperture, side and dentition positions extracted from Vermeulen (1993)

Diplommatina toretos **Vermeulen, 1993**

Figure 4.33

Description. Shell: dextral, conical, last two whorls widest, sides concave. Whorls: $6\frac{1}{8}$ - $7\frac{1}{2}$, convex. Suture: Impressed. Constriction about level with the edge between the parietal and the columellar side of the peristome. Parietalis: 1. Longitudinal palatalis: 1. Transversal palatalis: 1. Columellaris: 1, usually not visible. Tuba $\frac{3}{4}$ whorl. Radial ribs: Sinuous, distinct, high, wide, widely spaced to densely placed. Spiral striation: present. Umbilicus: open, deep, narrow. Aperture: Hardly tilted about the coiling axis. Peristome: Double, expanding. Palatal side: Not to slightly sinuous, with a moderate edge. Basal side: With or without a slight edge. Basal edge: Sinuous, sharp. Outer peristome: Expanding beyond the inner. Inner peristome: Convex but usually without palatal lip, expanding, free and sinuous on the columellar side, and little expanding on the parietal side.

Habitat. The living snails were not observed. Empty shells were found in the leaf litter (Marzuki et al., 2019).

Distribution. Malaysia, Sarawak: Kuching, Serian and Miri divisions. Endemic to Borneo (Marzuki, et al., 2021).

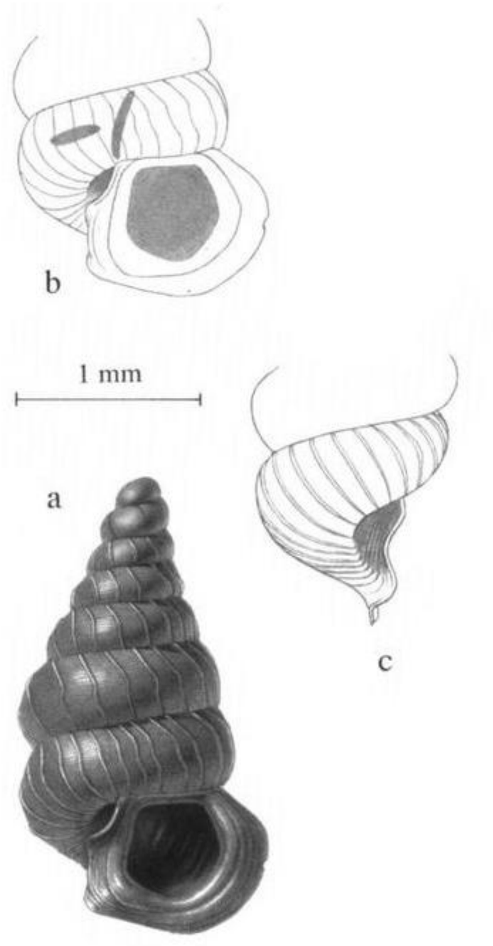


Figure 4.33: *Diplommatina torestos* Vermeulen, 1993 in aperture, side and dentition positions extracted from Vermeulen (1993)

CHAPTER 5

DISCUSSION

5.1 Distribution of the Genus *Diplommatina* in Sarawak

A total of 29 species of *Diplommatina* have been recorded in Sarawak, primarily distributed in limestone areas. This concentration is largely due to extensive malacofauna surveys, particularly in the southwestern region of the state. At least three species of *Diplommatina* that are present in Borneo such as *D. concinna*, *D. adversa*, and *D. maduana maduana*, can also be found outside of Borneo. For example, *D. concinna* is found in Singapore (Chan & Lau, 2020) and Indonesia (Marzuki et al., 2021), while *D. adversa* occurs in both West Malaysia and Singapore (Laidlaw, 1949). Additionally, *D. maduana maduana* is also present in West Malaysia (Laidlaw, 1949). The geological history of these regions likely played a significant role in the distribution of these species beyond Sarawak. The Kuching Zone, originally part of the Sundaland core (Williams et al., 1988), remained connected until the formation of the South China Sea during the Eocene (Advokaat & Hinsbergen, 2023), which may have influenced the dispersal patterns of the genus across Southeast Asia.

The studied species of the genus *Diplommatina* are mostly endemic to Borneo, with several species widely distributed across the island, such as *D. onyx*, *D. baritensis*, *D. busanensis*, *D. calcarata*, *D. stibara*, *D. subglaber subglaber*, *D. subglaber subisensis*, *D. whiteheadi*, *D. isseli*, and *D. toretos* (Figure 4.1). This distribution can be explained in part by the geological history of Borneo, particularly involving the Rajang-Crocker Accretionary Complex and the surrounding Sundaland region. The Rajang-Crocker Accretionary

Complex, formed during the subduction processes under north Borneo between the Eocene and Miocene periods, created significant uplift and structural complexity in the region (Advookat & Hinsbergen, 2023). This led to the development of various mountain ranges and river systems. Rivers could have contributed to the distribution of land snails as they could be dispersed along running water (Baur & Gosteli, 1986).

Furthermore, the tectonic activity and geological shifts in Borneo may have created intermittent land bridges and ecological corridors (Liew et al., 2020). These features could have facilitated the spread of land snails, especially *Diplommatina* across what is now a fragmented landscape as seen in Figure 4.1. The descend and spread of montane forest in Borneo due to the cooler temperature during the last glacial maximum could have increased the connectivity among mountains and facilitated the dispersal of once geographically isolated highland species (Manthley et al., 2017). Additionally, the fluctuating sea levels associated with Sundaland's tectonic activity would have allowed species to colonise different areas of Borneo at various times. This was also mentioned by Liew et al. (2020) that current species diversity and distribution patterns of the genus *Everettia* in northern Borneo have been influenced by the climatic fluctuation which caused uplift of mountain ranges that occurred during the Pleistocene epoch.

In contrast, some species are restricted to specific regions or limestone outcrops. For instance, species such as *D. sulphurea, D. moluensis, D. maduana nefrens, D. strongyla, D. niahensis,* and *D. subglaber subisensis* are endemic in the northeast while species such as *D. goliath, D. rumbangensis, D. busanensis, D. azlani, D. spinosa, D. isseli, D. toretos, D. whiteheadi,* and *D. subglaber subglaber* are endemic in the southwest (Figure 4.1). This pattern of endemism is likely influenced by Sarawak's distinct geological divisions: the

Kuching zone in the southwest and the Rajang-Crocker Accretionary Complex in the northeast (Advokaat & van Hinsbergen, 2023). The earlier formation of the Kuching Zone, during the Late Jurassic to Late Cretaceous periods (Gradstein et al., 2012), provided a stable environment that may have allowed certain species in the southwest to evolve in isolation. In contrast, the Rajang-Crocker Accretionary Complex, which developed during the Upper Cretaceous (Maastrichtian stage) and into more recent periods, represents a younger and distinct geological setting, further contributing to the divergence and specialisation of species in the northeast (Tongkul, 1997; Cullen, 2010).

These differences in geological history are intertwined with the nature of the limestone outcrops in Sarawak, which exist as small fragments of exposed karst surrounded by sandstone or mudstone areas. The karst ecosystem provides varying climatic conditions (Clements et al., 2006) and calcium carbonate deposits, serving as a habitat for numerous calcium-dependent organisms, including land snails (Schilthuizen et al., 2003). The Diplommatinidae family, which includes species often restricted to small areas due to limited active dispersal capabilities, is frequently confined to a single limestone hill (Vermeulen, 1993). The combination of the unique geological history and the isolated, calcium-rich limestone habitats has likely shaped the evolution and persistence of these region-specific *Diplommatina* species, contributing to the endemism observed in both the northeast and southwest regions of Sarawak.

5.1.1 Distribution of the Genus *Diplommatina* Based on Chirality and Sizes

Most of the produced bioregions for both chirality and size are concentrated in southwestern Sarawak, likely due to extensive sampling in that area. Meanwhile, the central region of Sarawak shows shared bioregions with the southwestern region for both categories.

These shared bioregions indicates that these regions share a common species composition (Figures 4.2, 4.3, 4.4). The Infomap algorithm builds a bipartite network between species and grid cells, clustering grid cells representing localities into bioregions based on shared species assemblages (Edler et al., 2017). It is assumed that grids within a bioregion might have similar environmental conditions. Multiple environmental factors, including soil pH, soil moisture, and vegetation, play significant roles in supporting diverse species compositions in specific habitats (Martin & Sommer, 2004). Additionally, this similarity could be attributed to the presence of non-limestone areas in the southwestern part of Sarawak where *Diplommatina* species were sampled. The sampling sites in central Sarawak were located in non-limestone areas, suggesting that these sites may share comparable environmental conditions with other non-limestone regions. However, some bioregions in central Sarawak overlap with limestone areas in the southwestern region. This overlap indicates that *Diplommatina* species can inhabit both limestone and non-limestone environments, as recently documented through multiple malacofaunal surveys.

The presence of *Diplommatina* species endemic to specific limestone hills has created bioregions unique to both southwestern and northeastern Sarawak. This endemism highlights their role as indicative species for their respective bioregions (Tables 4.1, 4.2). Indicative species are identified based on their strong association with specific bioregions or ecological clusters, reflecting the unique environmental conditions and biodiversity patterns of these areas (Edler et al., 2017). Understanding and designating indicative species is crucial for studying ecological dynamics, monitoring environmental changes, and prioritising conservation efforts (Chan & Grismer, 2021). For instance, *D. niahensis* is found exclusively in Niah NP in northeastern Sarawak, making it an indicative species for Bioregion 2 (Table 4.2). Similarly, *D. rumbangensis* is restricted to the Serian-Bau-Padawan limestone cluster in southwestern Sarawak, serving as an indicative species for Bioregion 4 (Table 4.1). These findings align with observations of other minute land snail genera, such as *Georissa* (*Hydrocenidae*), in Borneo. For example, *Georissa silaburensis* occurs exclusively in the caves of Mount Silabur, part of the Serian-Bau-Padawan limestone cluster (Khalik et al., 2019). In contrast, *G. hadra* and *G. muluensis* are confined to Mulu NP in northeastern Sarawak (Khalik et al., 2018).

In contrast, no unique bioregions have been identified in central Sarawak, as no *Diplommatina* species endemic to that region have been discovered thus far. This reflects the lower sampling effort in this region. Furthermore, central Sarawak is comparatively larger than the other regions. Due to that, the Infomap algorithm was chosen because it uses an adaptive spatial grid that adjusts to the density of occurrence records (Edler et al., 2017). This is particularly advantageous in this study that has unevenly distributed data, such as those from the central and northeastern regions of Sarawak. A low number of recorded occurrences for a given species may not indicate rarity or accurately represent the species' true abundance or diversity in those areas. Instead, the limited number of occurrence records often reflects the lower sampling effort in these regions, rather than the actual diversity present.

Based on the summarised chirality Infomap (Figure 4.2), most grids are composed exclusively of either dextral or sinistral *Diplommatina* species. This indicates that the composition of *Diplommatina* species in an area tends to exhibit only one type of chirality. In contrast, there are few grids contain both dextral and sinistral species. Selection against hybridisation and reproductive character displacement likely play roles in instances where species with opposite coiling directions coexist (Schilthuizen & Davison, 2005), as observed in this genus (Peake, 1973). A similar phenomenon is seen in *Amphidromus inversus*

(Camaenidae) in Borneo, where the coexistence of both dextral and sinistral forms is likely maintained by a combination of genetic and possibly environmental factors (Schilthuizen et al., 2012).

In addition to chirality, observations were made on shell sizes, including shell height and shell width (Figures 4.3, 4.4). Based on the summarised maps of the shell height and shell width forms, a total of 39 out of 76 bioregion grids display the coexistence of small, medium, or large species, suggesting areas of higher biodiversity with diverse environmental features that support multiple species. Heller (1987) found that in Mediterranean and desert fauna, shell shape and size were closely linked to habitat type. Different environments favour distinct shell morphologies, allowing species with varying shell sizes to coexist. Khalik et al. (2020) discovered that the larger shell size of *G. saulae* and *G. filiasaulae* in northern Borneo, compared to their southern counterparts, is likely shaped by ecological factors unique to the tropical cave environment. Similarly, Baur (1988) found that shell size positively correlated with dense vegetation and local population density of conspecifics.

However, another study found that coexisting snail species were significantly more similar in body size, suggesting that body size plays a key role in structuring these communities (Schamp et al., 2010). The study also explored how the strength of these patterns varied across environmental gradients, such as pH and conductivity. Results indicated that convergence in body size was more pronounced in habitats with higher pH, implying that smaller snail species have an advantage in calcareous habitats.

5.2 Habitat Association of the Genus *Diplommatina*

5.2.1 Utilisation of Habitat Types

According to Figure 4.5 and Table 4.3, leaf litter hosts the majority of the sampled *Diplommatina* species and is more significantly associated compared with limestone and vegetation habitats. This finding is similar to Marzuki et al. (2021). This could be due to the leaf litter having a positive effect on snail abundance. Similar to other minute land snails from the family Diplommatinidae such as *Opisthostoma*, the genus *Diplommatina* are also detritivores (i.e., feed upon microbial decomposer such as fungi and bacteria) (Bishop, 1977; Fog, 1979; Corsmann, 1990; Bernadett et al., 2018). Schamp et al. (2010) found that diet plays a significant role in shaping land snail community assemblages. While the specific species were not mentioned, detritivores and herbivorous snails living in leaf litter were more represented within land snails' communities.

Other than that, an increase in leaf litter thickness can enhance land snail species diversity (Solem et al., 1981; de Winter & Gittenberger, 1998). In temperate climates, leaf litter is known to provide suitable habitat for snails due to the readily soluble form of calcium such as calcium citrate (Wäreborn, 1969), availability of food (Locasciulli & Boag, 1987), additional shelter due to the presence of woody debris within (Gheoca et al., 2021), and moisture from decaying organic matter (Gheoca et al., 2021). Soil moisture is the most crucial factor in determining snail density and species richness (Martin & Sommer, 2004), since moisture is important in preventing the dehydration of land snails to move, grow and produce mucus (Baur & Baur, 1993; Kappes, 2005; Jordan & Black, 2012; Hernández & Reyes-Tur, 2017).

Apart from leaf litter, vegetation also associates with moisture. Based on Figure 4.5, *D. baritensis* was found exclusively in non-limestone areas, foraging on the pseudo-stem (i.e., tightly packed overlapping leaf sheath) or trunk of wild banana trees. This behaviour is likely due to the high moisture content of banana pseudo-stems, as demonstrated by multiple studies examining moisture levels across various banana types (Mydhili et al., 2022; Kumari et al., 2023). It is known that several plant species can absorb calcium from the soil (Dijkstra & Smits, 2002; Nation, 2007). Calcium is present in banana pseudo-stems, albeit in smaller amounts, compared to the fruit peel and blossoms (Kumari et al., 2023). In general, a minimum amount of calcium is necessary for the survival of any snail species, as it is essential for their shell formation (Martin & Sommer, 2004). This might be the reason for the land snails to forage on vegetation such as leaves and trunk (Schilthuizen & Rutjes, 2001; Schilthuizen et al., 2003).

It is also known that rock or limestone habitats capable to reduce the possibility of dehydration of land snails (Hernández & Reyes-Tur, 2017). This is due to the irregular surface of rocks, that are able to store rain (MacKinnon et al., 1996). During our fieldwork for data collection, all living *Diplommatina* species found on limestone (*D. adversa, D. concinna, D. subglaber subglaber, D. onyx*) were on wet limestone crevices, that are covered in mosses or lichens. Besides, limestone rocks are considered as high-quality habitat that can support the coexistence of multiple land snail species (Kemencei et al., 2014). This is due to the availability of calcium (Schilthuizen et al., 2013), optimal conditions, and shelter, along with the durability of rocks, which may play a crucial role in the long-term persistence of land snail populations (Kemencei et al., 2014). This habitat type is known to host high number of land snail species and abundance of individuals (Schilthuizen, 2003; Bernadett et al., 2008; Liew et al., 2008; Schilthuizen, 2011). However, in this study, limestone recorded the fewest number of *Diplommatina* species and individuals compared to other habitat types (Figure 4.5). No studies had been conducted specifically on the habitat association of *Diplommatina* in Borneo. Other studies included different land snail genera, and since many of these are abundant in limestone, the results of those studies were directed that way. Additionally, other research included empty shells found in the litter beneath the limestone, which might have caused a bias towards considering limestone as the most associated habitat type.

Diplommatina concinna, D. adversa, and *D. onyx* can be found across all three habitat types, indicating their ability to distribute in various habitats. For instance, *D. concinna* has been observed not only in limestone areas but also in acidic soil at the base of a granite quarry (Chan & Lau, 2020). Additionally, *D. concinna* is recognised as a connector species, linking the three modules of the bipartite network (Figure 4.7, Table 4.5). This highlights the species' significance; its loss could disrupt the network's integrity and lead to a cascade of extinctions within the land snail community (Olesen et al., 2007). In contrast, although *D. adversa* and *D. onyx* also inhabit multiple habitats, they are not considered connector species. This is due to the lower number of individuals sampled for these species, as the analysis is based on density.

5.2.2 Abiotic and Biotic Components

Among the abiotic and biotic parameters, only soil pH parameter showed significant between species, specifically between *D. baritensis* and *D. onyx* (Figure 4.8). This observation may be attributed to *D. baritensis* is predominantly found in non-limestone areas, where the soil pH is generally expected to be in the acidic to neutral range. However, several individuals of this species were found in limestone areas with an acidic to neutral soil pH. This could be due to the period of sampling that was conducted during rainfall season. Additionally, soil alkalinity is significantly influenced by the monsoon climate (Li et al., 2016). Soil tends to be more acidic during the wet season than the dry season (Jia et al., 2021). Acid precipitation is thought to affect soil calcium levels in eastern North America and Europe due to acid rain and logging (Graveland et al., 1994; Huntington et al., 2000). Other than that, annual mean precipitation and annual mean air temperature could have affected soil acidity as both are strong predictors of regional soil pH level (Zhang et al., 2018).

For the other abiotic and biotic parameters tested, no significant differences were found between the *Diplommatina* species. This may be attributed to the small sample size collected for certain species in this study. Additionally, several species, such as *D. goliath* and *D. niahensis*, are endemic to specific locations, which may have affected the results. The sampling was predominantly conducted in limestone areas, suggesting environmental homogeneity that might have minimised variation in environmental conditions. Furthermore, several species recorded from different localities were found in similar habitats. This uniformity in habitats may result in comparable environmental conditions, leading to similar values across the measured variables.

CHAPTER 6

CONCLUSION AND RECOMMENDATION

6.1 Conclusion

In conclusion, the distribution of *Diplommatina* species is influenced by a combination of factors, including the distribution of limestone outcrops, the chirality of certain species and the variations in their sizes. These factors collectively contribute to the existence of *Diplommatina* species that are endemic to specific regions of Sarawak, either in the southwest or northeast. Also, the majority of living *Diplommatina* individuals observed in this study were found to be significantly more common in leaf litter compared to those in limestone or vegetation habitats. Interestingly, in non-limestone areas, we were able to collect *D. baritensis* on banana tree trunks. Additionally, we were able to describe a new species, *D. rumbangensis* (Nasir et al., 2024). Lastly, pH was the only tested parameter that significantly affected the presence of certain *Diplommatina* species. For instance, *D. onyx* was predominantly found in areas with lower pH levels, whereas *D. baritensis* was more commonly associated with soils that were closer to neutral pH. The other tested biotic and abiotic did not show any significant differences between *Diplommatina* species.

6.2 Recommendation

One limitation of the study is that the presence of *Diplommatina* individuals in leaf litter may not necessarily indicate a preference for that habitat. It is possible that these individuals were originally present on other habitats prior to their falling. Future studies could involve a comparative analysis of *Diplommatina* species targeting other habitats such as limestone and vegetation with those found in the leaf litter. Additionally, the sampling effort might have impacted the results, as locating *Diplommatina* species in the forest can be challenging due to their small size and the difficulty of finding them in leaf litter. Prolonging the sampling period would allow for more plots to be sampled, providing a more comprehensive assessment of the genus. The initial sampling method for this study considered other genera of land snails. Hence, systematic and comprehensive plotting techniques should be carried out to focus only on *Diplommatina* species. Lastly, field work was predominantly conducted in the southwestern areas of Sarawak, leaving the central and northeastern regions underrepresented. Further studies should prioritise sampling these regions, including both limestone and non-limestone habitats, to enable effective comparisons with the southwestern region.

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APPENDICES

Appendix A: List and total individuals of 16 living *Diplommatina* sampled for habitat association analysis.

Species	Habitat		
	Leaf litter	Vegetation	Limestone
D. adversa	10	4	4
D. azlani	3	0	0
D. baritensis	133	26	0
D. busanensis	23	12	0
D. calcarata	104	0	0
D. concinna	475	93	29
D. goliath	6	0	0
D. lygipleura	12	0	0
D. maduana maduana	59	0	0
D. onyx	54	2	6
D. spinosa	79	0	0
D. stibara	3	0	0
D. strongyla	1	0	0
D. subglaber subglaber	5	0	1
D. subglaber subisensis	8	0	0
D. sulphurea	1	0	0

Appendix B: The distribution map of *Diplommatina* species

```
library(ggplot2)
library(ggmap)
library(scatterpie)
library(maps)
library(dplyr)
library(tidyr)
library(sf)

#Load data
my_data <- read.csv("C:/")

#Aggregate the data by locality
agg_data <- my_data %>%
group_by(latitude, longitude, species) %>%
summarise(count = n()) %>%
pivot_wider(names_from = species, values_from = count, values_fill
= list(count = 0))

#Adding a region column (unique identifier for each point)
agg_data$region <- factor(1:nrow(agg_data))

#Set a fixed radius for each pie chart
fixed_radius <- 0.06 #Adjustable value for map’s scale
agg_data$radius <- fixed_radius

#Ensuring longitude and latitude columns are named correctly
names(agg_data)[names(agg_data) == 'latitude'] <- 'lat'
names(agg_data)[names(agg_data) == 'longitude'] <- 'long'
```

```
#Define custom colors for each species
species_colors <- c(
  "DW" = "#8c6d31"     # Dark Brown
)


#Load the shapefile for Sarawak divisions
sarawak_divisions <- st_read("C:/")


#Map of Sarawak
p <- ggplot() +
geom_sf(data = sarawak_divisions, fill = "lightgrey", color =
"black") + # Sarawak divisions
coord_sf(xlim=c(112.5, 113.5), ylim=c(1.6, 2.5)) +
theme_minimal() + # Use a minimal theme
theme(panel.background = element_rect(fill = "aliceblue", color =
NA), # Sea color
panel.grid = element_blank(), # Remove grid lines
panel.border = element_rect(fill = NA, color = "black")) + # Black
border for the panel
labs(title = "Northeastern",
x = "Longitude", y = "Latitude") +
scale_x_continuous(labels = scales::number_format(accuracy =
0.01)) + # Adjust x-axis labels to decimal form
scale_y_continuous(labels = scales::number_format(accuracy =
0.01))   # Adjust y-axis labels to decimal form


#List of species columns for the pie charts
species_columns <- colnames(agg_data)[!(colnames(agg_data) %in%
c('lat', 'long', 'region', 'radius'))]


#Adding scatter pie charts using the data
p + geom_scatterpie(aes(x = long, y = lat, group = region, r =
radius),
```

```
data = agg_data, cols = species_columns, color = "black", alpha =
.8) +

scale_fill_manual(values = species_colors) +

theme(legend.position = "right") +

geom_scatterpie_legend(agg_data$radius, x = 113.50, y = 3.55)
```

Appendix C: Bipartite network analysis and mean significance test.

```
library(readxl)

library(bipartite)

#Load data and bulid the plot

Bipartite = read_excel("C:\\")

plotweb(Bipartite)


#Improve plot appearance

bpok <- as.matrix(sapply(Bipartite, as.integer))

row.names(bpok) <- c("Leaf litter", "Vegetation", "Limestone")

par(cex = 0.9)  # Set the text size to 1.5 times the default


plotweb(bpok, method = "cca", empty = TRUE, labsize = 1, ybig = 1,
y.width.low = 0.1, y.width.high = 0.1, low.spacing = NULL,
high.spacing = NULL,arrow = "no",

col.interaction =
c("saddlebrown","peru","indianred1","deeppink","pink","gold2","yel
low","beige","grey","slategray2","cyan","deepskyblue","purple","pl
um","green","green4"),

col.high =
c("saddlebrown","peru","indianred1","deeppink","pink","gold2","yel
low","beige","grey","slategray2","cyan","deepskyblue","purple","pl
um","green","green4"),

col.low = "grey59",  bor.col.interaction = "black", bor.col.high =
"black",

bor.col.low = "black", high.lablength = NULL, low.lablength =
NULL,sequence = NULL, low.abun = NULL,

low.abun.col = "green", bor.low.abun.col = "black", high.abun =
NULL, high.abun.col = "red", bor.high.abun.col = "black",

text.rot = 90,    # Specify the rotation angle of the text

text.high.col = "black", text.low.col = "black", adj.high = NULL,
adj.low = NULL,

plot.axes = FALSE,low.y = 0.5, high.y = 1.5, add = FALSE,

y.lim = NULL, x.lim = NULL, low.plot = TRUE, high.plot = TRUE,
```

```
high.xoff = 0, low.xoff = 0, high.lab.dis = NULL, low.lab.dis =
NULL, abuns.type = "additional"
)
#Bipartite Interaction matrix
visweb(Bipartite, type="nested", plotsize=8,
square="interaction",outerbox.border="white",
outerbox.col="white", box.border="black", box.col="black")

#Bipartite Modularity plot
mod <- computeModules(Bipartite)
plotModuleWeb(mod)
czvalues(mod, weighted=FALSE, level="higher")

?computeModules

#Significant test
library("stats")
Bipartite<-data.matrix(BP)
friedman.test(BP$No, BP$Habitat, BP$Species)

#Conover test
library(PMCMRplus)
frdAllPairsConoverTest(y = pH$No, groups = pH$Habitat,
blocks = pH$Species, p.adjust.method = "bonf")

#Chi-square test.
library(chisq.posthoc.test)
chisq.test(sub)
```

Appendix D: Box plot and mean significance test.

```
#Box plots
library(readxl)
pH = read_excel("C:\\")

library(dplyr)
library(ggplot2)
library(hrbrthemes)
data_ordered <- pH

#Calculate median pH for each species and reorder the Species
factor levels
species_order <- data_ordered %>%
  group_by(Species) %>%
  summarize(median_pH = median(pH)) %>%
  arrange(median_pH) %>%
  pull(Species)

#Reorder the Species factor levels based on the calculated order
data_ordered <- data_ordered %>%
  mutate(Species = factor(Species, levels = species_order))

pH_plot <- ggplot(data = pH, mapping = aes(x = Species, y = pH,
fill = type, alpha = type)) +
    geom_boxplot(outlier.shape = "square") +
    scale_fill_manual(values = c("red", "grey")) +
    scale_alpha_manual(values = c(1, 0.1)) +
    theme_ipsum() +
    theme(legend.position = "none",
          axis.text.y = element_text(size = 10, margin = margin(r
= 5)),  # Adjusts the margin on the right side of the y-axis text
```

```
          axis.title.y = element_text(size = 12, hjust = 0.5, margin = margin(r = 10)),  # Adjusts the margin on the top side of the y-axis title and centers it vertically
          axis.title.x = element_text(size = 12, vjust = -0.5, hjust = 0.5),  # Adjusts the size, vertical justification, and centers the x-axis title horizontally
          axis.text.x = element_text(size = 10, angle = 45, hjust = 1)) +  # Adjusts the size, angle, and horizontal justification of the x-axis text
    xlab("Species") +
    ylab("Soil pH")


#Normality test
library("car")
qqPlot(BP$DBH)


#Kruskal-Wallis test
test <- aov(pH~Species, data = BP)
summary (test)
CC <- kruskal.test(CC~Species, data = CC)


#Dunn test
library(FSA)
dunnTest(pH~Species, data=pH, "bh")
```