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The Shell evolution of the hydrocenidae of Malaysian Borneo

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Chapter 6

Discussion and future prospects

Discussion

Tropical land snails are known to possess high allopatric and sympatric diversity, especially those inhabiting limestone karsts (as discussed in **Chapters 2 and 3**). The spatial isolation of limestone hills greatly contributes to this diversity and ultimately leads to the high incidence of local endemism (Clements et al., 2008). A few studies have shown that this isolation does not only induce endemism, but also leads to cryptic diversity in land snails (e.g., Köhler and Burghardt, 2016; Rundell, 2008; von Oheimb et al., 2019). This study was conducted to understand the evolutionary history of the genus *Georissa* of Borneo, which is particularly distributed in karst areas.

Land snails of the genus *Georissa* Blandford 1864 were collected at various localities in Malaysian Borneo (Sabah and Sarawak). I then applied molecular and morphological approaches to understand (i) the systematics, taxonomy, and biogeography, (ii) morphological variation, and, (iii) shell character evolution. In this chapter, I will summarize the most important findings of this study. In addition, I will briefly discuss the future prospects and potential further studies of *Georissa*.

Systematics, taxonomy, and biogeography

In general, species identification in *Georissa* and other minute land snails is done by applying detailed morphological assessment and biogeographic data. By doing so, a geographically and morphologically coherent species can often be defined. For the Bornean *Georissa*, our study shows that these two approaches could be improved by adding molecular data in species delimitation, because I found:

- a. cryptic molecular diversity of two or more morphologically similar species, and
- b. high degrees of morphological variation within a single, genetically uniform population, suggesting morphological plasticity.

Therefore, I did a comprehensive systematic evaluation of the Bornean *Georissa* by combining these three approaches in species delimitation. Initially, I grouped the species into two informal groups, namely, (i) the “scaly group” (**Chapter 2**) and (ii) the “non-scaly group” (**Chapter 3**). As a result, I

identified a total of 13 scaly species, of which six were new to science (i.e., *Georissa anyiensis* sp. n., *Georissa muluensis* sp. n., *Georissa bauensis* sp. n., *Georissa silaburensis* sp. n., *Georissa kinabatanganensis* sp. n., and *Georissa sepulutensis* sp. n.) and 16 non-scaly species, of which three were new to science (i.e., *Georissa corrugata* sp. n., *Georissa insulae* sp. n., and *Georissa trusmadi* sp. n.).

Overall, the defined species show strong bootstrap support (**Chapters 2 and 3**). On the one hand, high *COI* genetic divergences were observed between species with similar features (e.g., *Georissa bauensis* and *Georissa hosei*). On the other hand, I found species with very distinct morphological features that might be genetically closely related (e.g., *Georissa hadra* and *Georissa muluensis*). This already suggests that morphological evolution is not neutral, and may include both stasis and rapid divergence (see further below).

In **Chapter 2**, I carried out web-based delimitation by using Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2012) and Poisson Tree Processes (PTP) (Zhang et al., 2013) on the “scaly” group *Georissa*. I found that ABGD divided the Bornean *Georissa* into 6 species, while PTP divided the species into at least 15 species. These results were obtained based on the molecular data of what I argue are in fact 11 species of the “scaly” *Georissa*. Therefore, I could conclude that it is not advisable to identify a species of the Bornean *Georissa* based on molecular data alone. Moreover, it is widely known that many land snails have a highly fragmented population structure (see Liew et al., 2014; Rundell, 2008; Tongkerd et al., 2004), which increases the possibility of cryptic diversity of the *Georissa*. For this reason, I further refrained from algorithm-based species delimitation in the “non-scaly” *Georissa* (**Chapter 3**).

Despite the many challenges in species delimitation in the Bornean *Georissa*, the approaches that I took eventually provided a comprehensive and pragmatic arrangement into species. Therefore, I would suggest that future species delimitation of *Georissa* would best be done by complementing morphological assessment and biogeographic data with molecular analysis.

Morphological variation

The Bornean *Georissa* show two distinct shell surface sculpture types. First, there is the “scaly group”, which comprises species with scale-like protuberances on the shell surface, and second, the “non-scaly group” which comprises species without such scales; instead, there may be raised and/or weak radial and/or spiral sculpture in this latter group.

Georissa species vary based on their morphological features. This could be observed even within small populations. For this reason, I conducted a molecular study to understand the shell variation of *Georissa* in a small-scale geographical area (**Chapter 4**). Interestingly, I found that the seemingly high shell variation of *Georissa silaburensis* is in fact due to a morphological parallelism in two sympatric species (i.e., *G. silaburensis* + *G.* “sp. Silabur”). These sympatric species are derived from ancestors from the outer part of the cave (**Chapter 4**). This finding is similar to Haase and Schilthuizen (2007), who found a sister species (*Georissa filiasaulae*) of *Georissa saulae*, which had strongly diverged from a “scaly” to a smooth (non-scaly) shell. In addition, the findings also highlight the fact that locally endemic species may render the ancestral species paraphyletic (Schilthuizen et al., 2005).

Shell character evolution

Based on shell morphology, the two informal groups of the Bornean *Georissa* show distinct shell characteristics, as stated earlier in this chapter. The phylogenetic approach with which I studied the shell evolution of *Georissa* (**Chapter 5**) showed that both groups to a large extent correspond with monophyletic groups (the “scaly” and “non-scaly” groups). The only exception is *Georissa saulae*, the only “scaly” species that is phylogenetically contained within the “non-scaly” clade of *Georissa*.

Furthermore, the phylogenetic reconstruction (**Chapter 5**) shows little geographic structure, with species from Sabah, Sarawak, and non-Bornean species mixed across the tree. This further indicates their long history of dispersal. However, some shell traits seem to be geographically restricted. For example, I found *Georissa hadra* and *Georissa niahensis* are the largest forms of Bornean *Georissa* (adult shell height > 2.5 mm) and they are both found in

the northern part of Sarawak (Miri district). On the other hand, *Georissa xesta*, *Georissa nephrostoma*, *Georissa flavescens*, and *Georissa bangueyensis* are the smallest Bornean species with shell heights around 1.0 mm or less. These species are mainly distributed in the Kinabatangan region (Sabah).

Additionally, I found that shell coloration of *Georissa* varies widely, even among individuals of the same species (as discussed in the taxonomy sections in **Chapters 2 and 3**). The cause of this variation remains unknown. Future research could possibly investigate associations between shell coloration and the environment to unravel this variability, which may be genetic or phenotypically plastic. I did, however, find that *Georissa* which inhabit the hypogean environment show less pigmentation as compared to the epigeal species. For example, the hypogean *G. filiasaulae* is white in color, while the ancestral species *G. saulae* is orange to red. A similar situation is seen in epigeal *G. pyrroderma* with orange to red shells and the hypogean *G. silaburensis* with less pigmentation, rendering it light orange (**Chapter 4**). In both cases, the hypogean species also have larger shell size as compared to the epigeal species. Such shifts in shell color and size in cave snails might be due to the effects of a combination of ecological factors, such as the abiotic environment (Baur, 1988; Cameron and Cook, 1989; Chiba, 2004; Chiu et al., 2002; Goodfriend, 1986; Haase and Misof, 2009), predation pressure (Moreno-Rueda, 2009; Schilthuizen et al., 2006), and physical restrictions (Okajima and Chiba, 2009). It is also not known by what developmental means *Georissa* shell color can change. Recent papers on snail shell coloration provide indications of the chemical compounds that could play a role (e.g., Jordaens et al., 2006; Schilthuizen et al., 2018).

Future prospects

Haase and Schilthuizen (2007) described the genitalia structures of *G. saulae* and *G. filiasaulae*, and this is the only complete description of a *Georissa*'s genitalia. Given the genus's uniformity in shell shape, an additional set of soft anatomy characters could certainly help improving the taxonomy. Moreover, a focus on the evolution of their genitalia might give indications of reproductive isolating mechanisms in sympatric species. Additionally, molecular studies that focus on the genus *Georissa* at a larger geographical

scale could improve our understanding on their phylogeographic pattern and mode of dispersion.

References

- Baur, B. (1988). Microgeographical variation in shell size of the land snail *Chondrina clienta*. *Biological Journal of the Linnean Society*, 35(3), 247–259.
- Cameron, R. A. D., and Cook, L. M. (1989). Shell size and shape in Madeiran land snails: do niches remain unfilled? *Biological Journal of the Linnean Society*, 36(1-2), 79–96.
- Chiba, S. (2004). Ecological and morphological patterns in communities of land snails of the genus *Mandarina* from the Bonin Islands. *Journal of Evolutionary Biology*, 17(1), 131–143.
- Chiu, Y. W., Chen, H. C., Lee, S. C., and Chen, C. A. (2002). Morphometric analysis of shell and operculum variations in the viviparid snail, *Cipangopaludina chinensis* (Mollusca: Gastropoda), in Taiwan. *Zoological Studies*, 41(3), 321–331.
- Clements, R., Ng, P. K., Lu, X. X., Ambu, S., Schilthuizen, M., and Bradshaw, C. J. (2008). Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts. *Biological conservation*, 141(11): 2751-2764.
- Goodfriend, G. A. (1986). Variation in land-snail shell form and size and its causes: a review. *Systematic Biology*, 35(2), 204–223.
- Haase, M., and Misof, B. (2009). Dynamic gastropods: stable shell polymorphism despite gene flow in the land snail *Arianta arbustorum*. *Journal of Zoological Systematics and Evolutionary Research*, 47(2), 105–114.
- Haase, M., and Schilthuizen, M. (2007). A new *Georissa* (Gastropoda: Neritopsina: Hydrocenidae) from a limestone cave in Malaysian Borneo. *Journal of Molluscan Studies*, 73(3), 215-221.
- Jordaens, K., De Wolf, H., Vandecasteele, B., Blust, R., and Backeljau, T. (2006). Associations between shell strength, shell morphology and heavy metals in the land snail *Cepaea nemoralis* (Gastropoda, Helicidae). *Science of the Total Environment*, 363(1-3), 285-293.
- Köhler, F., and Burghardt, I. (2016). Cryptic diversity in a widespread land snail: revision of the genus *Xanthomelon* Martens, 1860 from the Australian Monsoon Tropics (Pulmonata, Camaenidae). *Zoologica Scripta*, 45(2), 127-144.
- Liew, T. S., Vermeulen, J. J., Marzuki, M. E., and Schilthuizen, M. (2014). A cybertaxonomic revision of the micro-landsnail genus *Plectostoma* Adam (Mollusca, Caenogastropoda, Diplommatinidae), from Peninsular Malaysia, Sumatra and Indochina. *ZooKeys*, 393, 1–107.
- Moreno-Rueda, G. (2009). Disruptive selection by predation offsets stabilizing selection on shell morphology in the land snail *Iberus* g. *gualtieranus*. *Evolutionary Ecology*, 23(3), 463-471.
- Okajima, R., and Chiba, S. (2009). Cause of bimodal distribution in the shape of a terrestrial gastropod. *Evolution: International Journal of Organic Evolution*, 63(11), 2877-2887.
- Puillandre, N., Lambert, A., Brouillet, S., and Achaz, G. (2012). ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, 21(8), 1864-1877.

- Rundell, R. J. (2008). Cryptic diversity, molecular phylogeny and biogeography of the rock- and leaf litter-dwelling land snails of Belau (Republic of Palau, Oceania). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1508), 3401-3412.
- Schilthuizen, M., Cabanban, A. S., and Haase, M. (2005). Possible speciation with gene flow in tropical cave snails. *Journal of Zoological Systematics and Evolutionary Research*, 43(2), 133-138.
- Schilthuizen, M., Sipman, I., and Zwaan, H. (2018). Sexual dimorphism in shell coloration of *Plectostoma* (Caenogastropoda: Diplommatinidae) is caused by polyenes. *Journal of Molluscan Studies*, 84(1), 108-110.
- Schilthuizen, M., Til, A. V., Salverda, M., Liew, T. S., James, S. S., Elahan, B. B., and Vermeulen, J. J. (2006). Microgeographic evolution of snail shell shape and predator behavior. *Evolution*, 60(9), 1851–1858.
- Tongkerd, P., Lee, T., Panha, S., Burch, J. B., O'Foighil, D. (2004). Molecular phylogeny of certain Thai gastrocoptine micro land snails (Stylommatophora: Pupillidae) inferred from mitochondrial and nuclear ribosomal DNA sequences. *Journal of Molluscan Studies*, 70(2), 139-147.
- von Oheimb, K. C., von Oheimb, P. V., Hirano, T., Do, T. V., Ablett, J., Luong, H. V., Pham, S. V., and Naggs, F. (2019). Cryptic diversity of limestone karst inhabiting land snails (*Cyclophorus* spp.) in northern Vietnam, their evolutionary history and the description of four new species. *PLoS one*, 14(10), e0222163.
- Zhang, J., Kapli, P., Pavlidis, P., Stamatakis, A. (2013). A general species delimitation method with applications to phylogenetic placements. *Bioinformatics*, 29(22), 2869-2876.

