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Chapter 1

Introduction and summary

Thesis Outline

Mollusca form an important animal phylum that first appeared in the Cambrian, and today is, after Arthropoda, the second largest animal phylum, with more than 100,000 extant species (Bieler, 1992, Brusca and Brusca, 2003), with the class Gastropoda accounting for 80% of the extant species in the Mollusca. Despite its species-richness, a generalised gastropod shell architecture is maintained because of conserved developmental processes. All of the shelled-gastropods grow by adding, in a unidirectional accretionary way, shell material with the mantle edge organ, usually at different deposition rates around the existing aperture. This shell ontogeny, or to be more specific aperture ontogeny, gives the general spiral form for the shells. However, spiral forms can vary when there are changes in any one of the aspects in the aperture ontogeny profiles, namely, the rate and direction of shell deposition around the aperture, size and shape of the aperture (i.e. mantle edge), and the total length of the shell ontogeny processes. The interplays between these developmental parameters have generated a great diversity in shell form, for which taxonomists and evolutionary biologist are now trying to accurately characterise and to understand with regard to its evolution.

The variability in shell form is one of the cornerstones of gastropod taxonomy. Usually, shell form variability between species at genus level is quite small, and taxonomists frequently describe a species based on subtle differences in shell characters, such as size, height-width proportions, coiling direction, shell surface ornamentation, or aperture morphology. However, species in several land snail genera, such as *Plectostoma* and *Opisthostoma* (Diplommatinidae), exhibit a greater diversity in shell forms, largely due to the last whorl, which, in some species is coiled irregularly (van Benthem Jutting, 1952; Vermeulen, 1991; Vermeulen, 1994). Such disparity, poses a challenge to describe and compare the shell accurately, because homologisation and the determination of shell synapomorphies in these taxa is problematic (van Benthem Jutting, 1952).

In **Chapter 2**, I revise non-Borneo *Plectostoma* species, which are more diverse in their shell form than Bornean *Plectostoma*. I appraise the shell characters on the basis of developmental homology, genetic and 3D morphometric data. As a result, the subgenus *Plectostoma* is elevated to genus status based on the genetic and ecological data, and 10 new *Plectostoma* species are described together with the existing 21 species, based on the redefined shell characters and genetic data. This chapter suggests that more biologically informative shell characters can be obtained when the shell is viewed as a petrified ontogeny, rather than as a solid geometrical object.

The shell forms of *Plectostoma* and their underlying aperture ontogeny differences can be characterised and compared in a qualitative manner as shown in **Chapter 2**. However, it remains unknown how changes in the aperture ontogeny profile may generate a particular shell form. To complicate matters further, the size and shape of a shell are known to have a close association with the shell growth rate. Thus, few empirical data are available on how the aperture ontogeny profiles and shell growth rates determine shell form because growth and form are difficult to quantify and examine simultaneously.

Hence, I attempt to fill this gap in **Chapter 3** by examining how growth and form change along the shell ontogeny in one particular species, *Plectostoma concinnum*. Its shell consists of three shell parts: the regularly-coiled spire phase, the transitional constriction phase, and the distortedly-coiled tuba phase. I use a newly defined ontogeny axis to simultaneously analyse the associations between and changes in growth rates and aperture ontogeny profile. As a result, I show how the changes in the aperture ontogeny profiles in terms of aperture shape, size and growth trajectory, and the changes in growth rates, are associated with different shell forms at different stages of the shell ontogeny. In other words, shell form can be quantified as an aperture ontogeny profile. This chapter also highlights the fact that while a plausible roles for mantle edge and columellar muscle can be inferred from the record of aperture ontogeny profiles contained in a shell, it is important to study the anatomy and behaviour of these two organs to understand the underlying mechanisms that create the profiles.

The outcome of **Chapter 3** also highlights the limitation of the traditional linear measurement and geometric morphometrics in the quantification of shell form. While these quantification methods can provide measurable form differences between shells, these differences can hardly be interpreted directly from the aspect of aperture ontogeny. Linear measurements, on the one hand, give absolute size of a shell but cannot capture the shape of the spiral shell. Geometric morphometrics (GM), on the other hand, provide shape information of a shell by comparing homologous landmark points, lines or surfaces. However, these homologies, either developmental, evolutionary or geometric cannot be universally defined across different shell forms, different species, and different studies. Geometric morphometrics was developed by Bookstein (1977, 1980) who formalised the idea of Thompson (1917: Chapter 17, “On the theory of transformations, or the comparison of related form”). Ironically, while recent biologists have quickly adopted GM to compare shell forms, Thompson (1917) himself did not compare shell forms with his own transformation method, instead using a logarithmic spiral approach, which may suggest he was aware of the limitations in addressing shell shape analysis with GM.

In view of these limitations, I develop a new method for quantifying, visualising and analysing gastropod shell form in **Chapter 4**. I would not have been able to develop this method, which is based on ideas from theoretical modelling of shell form and from **Chapter 3**, without the development of state-of-the-art technology in computer graphic hardware, flexible 3D modelling software, and 3D scanning instrumentation. First, the shell was retopologised according to the aperture ontogeny. Then, the aperture ontogeny profiles were extracted by calculation of aperture growth trajectory, aperture form and ontogeny axis. Lastly, the similarities between shell forms were determined by comparing their aperture ontogeny profiles. The underlying changes in the aperture ontogeny profile that have caused the differences between shell forms can be examined with this method. Moreover, the reopotologised shell mesh model can be used for functional-morphological analysis and for the evaluation of theoretical shell models. In addition, the similarity matrix for shells as based on the aperture ontogeny profiles can be analysed together with other distance matrixes, such as phylogenetic distance, geographical distance or environmental distance.

After the growth and form of morphologically diverse and unusual shells have been analysed in the preceding two chapters, I examine the functional aspects of the more striking shell traits in *Plectostoma* species, such as the protruding radial ribs and the distortedly-coiled tuba. In general, land snail shells serve for protection against predation and desiccation. In marine snails, shell traits similar to those in *Plectostoma* are known to have anti-predation function (Vermeij, 1993; Allmon, 2011). Hence, in **Chapter 5**, I explore whether these *Plectostoma* shell traits may act as defensive adaptations against one of its identified predators, namely the slug *Atopos*.

Atopos slugs have two predatory strategies, namely, shell-apertural entry and shell-drilling, to attack *Plectostoma concinnum*, *P. cf. inornatum*, *P. fraternum*, and other closely-related species in Sabah, Malaysian Borneo. The twisted tuba part of the shells of these snails is an effective defensive trait against shell-apertural entry attack. However, when the slug fails to enter the shell via the aperture, it will shift to the energetically more costly shell-drilling strategy. I found indications that the slug prefers to drill holes on shell surfaces without ribs. In any case, the twisted tuba and the protruding ribs do not guarantee the survival of the snails. Further analysis reveals that the lack of full effectiveness of these anti-predation shell traits may be caused by a functional trade-off between both traits under selection by two different predatory strategies.

In **Chapters 2 – 5**, I give insight into how *Plectostoma* shell forms can differ between species, how shell forms change between different developmental stages in a species, and how the properties of different shell traits can have anti-predation functionality. One of the remaining questions is how the *Plectostoma* shell forms have changed and diversified in the course of evolution. The rampant convergent and parallel evolution in shell form in the Gastropoda is well known. Many studies have investigated this pattern from the perspective of adaptive significance of the shell forms, which implies shell functionality under selection pressures. In fact, evolutionary changes in shell form are only possible when the underlying shell ontogeny changes as well. However, there is a scarcity in studies that aim at understanding shell form evolution with respect to the required changes in their ontogeny.

In **Chapter 6**, I investigate the evolution of shell forms in *Plectostoma* from the viewpoint of shell ontogeny. First, I obtain aperture ontogeny profiles as in **Chapter 3** and **Chapter 4**, characterise the shell characters as in **Chapter 2**, and finally estimate the phylogeny of *Plectostoma* species. I collate all these three data sources, and discuss the patterns of character evolution for shell form from an ontogenetic morphospace perspective. The results suggest that the phylogenetic history does not constrain changes in shell ontogeny, and the resultant *Plectostoma* shell forms. Also, species that are similar in shell shape may have their individually unique aperture ontogeny profile, while certain developmental aspects of shell size retain a conserved developmental program among species.

Summary

In summary, this thesis reveals several hitherto unknown aspects of *Plectostoma* shell forms, in terms of the developmental homology, the aperture ontogeny profile, anti-predation functionality, and evolutionary pattern in shell characters and ontogenetic morphospace evolution. In fact, these are the issues that have been targeted by biologists for centuries in order to improve the way shell shape is characterised and to improve understanding of shell form evolution. In many scientific fields, technology advancement has offered a new way to address old questions. This is also true for this thesis. The 3D technology that has been used intensively in every chapter of this thesis has, to some extent, opened new dimensions in the way we address these old questions, and provides important insight in the study of shell form.

Hence, I suggest three topics for future studies, which are essential to improve our understanding of the evolution of gastropod shell form:

- *Which shell characters should be used in the taxonomy?*
When the taxonomy of snail taxa relies heavily on the shell characters, it is important that the chosen shell characters represent certain biological information in terms of developmental, ecological, or functional aspects of the shell.
- *What are the roles of anatomy, behaviour, and development of snail columellar muscle and mantle edge in the determination of the snail's shell form?*
In order to understand the development and evolution of a gastropod solid shell, the animal's soft body organs, particularly the mantle edge that produces the shell and the columellar muscle that supports the shell, must be understood.
- *What are the quantifiable biological and physical properties of different shell forms and how do these quantitative properties influence a snail's fitness?*
The current state of 3D technology, in terms of hardware and software, allows not only comparisons of the geometrical shape of a shell form, but it also allows comparisons of the biological and physical properties of a shell form in an accurate and quantitative manner. Thus, these quantified biological and physical properties should be used in the functional, ecological and phylogenetic analysis of the shell forms.

