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A revision of
Strombus urceus Linné, 1758

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Ad maiorem Dei gloriam
in extollendo naturæ magneitudinem

Acknowledgments

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Statement of Contributions of Others

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Limitations

This research was significantly affected by COVID-19 in three ways: 1) It was impossible for me to travel to collect material for the study, and limited access to international collections for locality data sourcing; 2) There was a heavy reliance on local fishermen in the Asia-Pacific to obtain specimens. These collectors lacked suitable preservation materials (discussed below), had long localised restrictions on movement and, in some cases, the shipping systems were closed for extended periods; and 3) The laboratory that performed the genetic analyses was located in a jurisdiction that underwent significant ongoing lockdowns, leading to long delays (> 6 months) in the processing of samples.

A secondary consequence of the problems associated with COVID-19 was the compromised nature of many samples when they arrived having disintegrated in part, which limited detailed genetic and anatomical studies. In many cases, while the level of preservation still enabled sexing, the foot and body of the animal was poorly preserved, and the visceral masses had mostly disintegrated, making detailed anatomical studies impossible. This poor preservation also resulted in quality issues for the genetic studies, with over 50% of samples failing extraction quality controls.

One further limitation was the reliance on others to examine institutional material and, in particular, there was a propensity for some to limit information sharing, particularly in relation to fossil material. This significantly limited the ability to describe new taxa, as others have commenced work on the material and have indicated their intention to publish, making it ethically problematic for me to pursue further research in those specific domains.

List of Publications

Publications, the text of which has, in part, been extracted and added to this thesis, and the level of author contribution for each article (in alphabetical order).

Contribution

SM – primarily carried out by Stephen Maxwell (> 90%)
AA – all authors contributed in part (SM > 50%) and cited within the text appropriately.
OA – Work where authors other than Stephen Maxwell contributed significantly (SM < 50%) and cited within the text appropriately.
T – taxonomic descriptions conjointly written and cited within the text appropriately.

Publication	Author of text of manuscripts used in thesis	Conception and design	Analysis and interpretation	Drafting	Critical revision	Materials (specimens)	Submission and administrative
Dekkers AM, Dekker H, **Maxwell** SJ (2022) Studies in *Canarium urceus* (Linné, 1758) Part 5*:* a new *Canarium* species from the Andaman Sea (Gastropoda: Strombidae). The Festivus 54(1), 29-35.	T	AA	AA	OA	OA	OA	OA
Dekkers AM, **Maxwell** SJ (2020). Studies in *Canarium urceus* (Linnaeus, 1758) Part 3: new species from the western Pacific (Gastropoda: Neostromboidae: Strombidae). The Festivus 52(4), 345-358.	T	AA	AA	AA	AA	AA	SM
Liverani V, Dekkers AM, **Maxwell** SJ (2021) Resolving phylogenetic and classical nomenclature: a revision of *Canarium* Schumacher, 1817 (Mollusca, Neostromboidae, Strombidae). The Festivus 53(1), 26-43.	T	AA	SM	SM	AA	AA	SM
Maxwell SJ (2022) A new putative hybrid in *Conomurex* Fischer, 1884 (Mollusca, Neostromboidae, Strombidae) with notes on the types of hybrids. European Journal of Applied Sciences 10(1), 401-408.	SM	SM	SM	SM	SM	SM	SM
Maxwell SJ, Dekkers AM (2021). Studies in *Canarium urceus* (Linné, 1758) Part 5: a new species from the northern Pacific Ocean (Gastropoda: Neostromboidae: Strombidae). The Festivus 53(4), 282-287.	T	SM	SM	SM	SM	AA	SM
Maxwell SJ, Rymer TL (2022) Population Structure of *Canarium* (*Canarium*) *urceus* (Mollusca, Strombidae) from Nha Trang, Vietnam. Strombus, 28(1-2), 1-5.	SM	SM	AA	SM	AA	SM	SM

Maxwell SJ, Rymer TL, Congdon BC (2022) A theoretical composite model for population sex-specific shell size dynamics in Strombidae (Gastropoda, Neostromboidae). Journal of Natural History 55(41-42), 2661-2672.	SM	SM	SM	SM	AA	SM	SM
Maxwell SJ, Todd SJ, Rymer TL (2022) Population structure and morphology of *Canarium* (*Canarium*) *incisum* (Wood, 1828) and *Canarium* (*Canarium*) *esculentum* (Maxwell, Rymer, Congdon and Dekkers 2020) (Mollusca: Neostromboidae: Strombidae) from the Philippines with preliminary notes on aperture colouration based on DArTseq Data. Acta Zoologica 124, 1-7.	SM	SM	AA	SM	AA	SM	SM
Maxwell SJ, Watt J, Rymer TL, Congdon BC (2021) A checklist of near-shore Strombidae (Mollusca, Gastropoda, Neostromboidae) on Green Island, Queensland. Biogeographia – The Journal of Integrative Biogeography 36, a004.	SM	SM	AA	SM	AA	SM	SM
Maxwell SJ (2021). Registration of Neostromboidae clades in the RegNum of the PhyloCode and errata. The Festivus 53(3), 282-287.	SM	SM	SM	SM	SM	n/a	SM
Maxwell SJ (2021) Recognising and defining new crown clades in Stromboidea Rafinesque, 1815. Bulletin of the Russian Far East Malacological Society 25(1/2), 9-16.	SM	SM	SM	SM	SM	n/a	SM
Maxwell SJ, Bordon AV, Rymer TL, Congdon BC (2019) The birth of a species and the validity of hybrid nomenclature demonstrated with a revision of hybrid taxa within Strombidae (Neostromboidae). Proceedings of the Biological Society of Washington 132(1), 119-130.	SM	SM	SM	SM	AA	n/a	SM
Maxwell SJ, Congdon BC, Rymer TL (2020) Essentialistic pluralism: The theory of Spatio-temporal positioning of species using integrated taxonomy. Proceedings of the Royal Society of Queensland 124, 83-97.	SM	SM	SM	SM	AA	n/a	SM
Maxwell SJ, Dekkers AM (2019) A new name for *Altivasum typicum* Hedley, 1916 fide Dekkers and Maxwell, 2018 and the description of *Altivasum clarcksoni nov. sp.* The Festivus 51(2), 171-176.	SM	SM	AA	SM	AA	AA	SM
Maxwell SJ, Dekkers AM (2021) Studies in *Canarium urceus* (Linné, 1758) Part 4: *Canarium* (*Canarium*) *orrae* (Abbott, 1960) (Gastropoda: Neostromboidae: Strombidae) and a new species from the Northern Territory, Australia. The Festivus 53(4), 270-281.	T	SM	SM	SM	SM	AA	SM
Maxwell SJ, Dekkers AM, Rymer TL, Congdon BC (2020) Towards resolving the American and West African Strombidae (Mollusca: Gastropoda: Neostromboidae) using integrated taxonomy. The Festivus 52(1), 3-38.	SM	SM	AA	AA	AA	AA	SM
Maxwell SJ, Rymer TL (2021) Are the ICZN and PhyloCode that incompatible? A summary of the shifts in Stromboidean taxonomy and the definition of two new subfamilies in Stromboidae (Mollusca, Neostromboidae). The Festivus 53(1), 44-51.	SM	SM	SM	SM	AA	n/a	SM

Maxwell SJ, Rymer TL, Congdon BC, Dekkers AM (2020) Studies in *Canarium urceus* (Linné, 1758) Part 2: *Strombus anatellus* Duclos, 1844, *Strombus crassilabrum* Anton, 1839, *Strombus incisus* Wood, 1828 and *Strombus ustulatus* form *laevis* Dodge, 1946 (Neostromboidae: Strombidae). The Festivus 52(4), 335-344.	T	SM	AA	SM	AA	AA	SM
Maxwell SJ, Rymer TL, Dekkers AM (2020) *Canarium urceus* (Linné, 1758) Studies Part 1: The recircumscription of *Strombus urceus* Linné, 1758 (Neostromboidae: Strombidae). The Festivus 52(2), 113-127.	T	SM	SM	SM	AA	n/a	SM
Maxwell SJ, Rymer TL, Rowell MK, Hernandez Duran LC, Berschauer DP, Underdown M, Petuch EJ, Dekkers AM (2021) Defining and bringing relevance of meaning to species group-level taxa. Proceedings of the Biological Society of Washington 134, 27-28.	SM	SM	SM	SM	AA	n/a	SM

Abstract

This dissertation presents a classical revision of *Strombus urceus* Linné, 1758 post Abbott 1960 (Mollusca, Neostromboidae, Strombidae) and has resolved this monospecific group into twelve species. This involved a review and the presentation of novel theories in the areas of speciation, hybridisation and clade recognition. The species concept was reviewed and a new theory for species conception was generated, essentialistc pluralism, which frees the taxonomist from the rigidity of a species conceptuality and enables the taxonomist to define a taxon based on the taxonomist's perceived necessity. The novel idea of species and subspecies was reconceptualised such that subspecies is a rank that is restricted to those organisms where differences in genetic sequence data are the only way to distinguish organisms. If organisms can be differentiated without the use of genetics, then these are to be considered full species. The novel theory of how hybridisation leads to recognisable speciation, in particular when a set of organisms become identifiable as distinct species in real time, is identified. At the supraspecies level, the principles for clade recognition is presented. These principles are applied to circumscribe and define the clades that contain the target species below the level of superfamily using phylogenetic nomenclature. This is the first work to demonstrate that morphologically generated clades are acceptable in the diagnostic process required under the PhyloCode, demonstrated by their accepted registration by that body. This study is also the first to use phylogenetic nomenclature in the Mollusca. In order to achieve this recognition, the internal clades within Stromboidae were recognised and defined, something all workers on the complex have failed to do. These are supported by morphological differences and fall into discrete biogeographical regions. This thesis also presents a novel model that seeks to explain the spatiotemporal expression of sexual size dimorphism in stromboidians. Females show significant differences in the shape of the shell, which is reflected in the shape of the body whorls and width of the anterior aperture. Historically, the presence of a black aperture in what is now considered different species was an argument for the synonymisation of them. Using morphometric data and DArTseq data, I demonstrate that this phenotype does not define a species, and is considered a historical phylotypic remnant of a speciation or hybridisation event. The phylogeography of the species complex is presented with reference to interglacial periodicity, current dispersal potential, ecological barriers, and DArTseq data and morphometrics. At the species and intraspecies taxonomic levels, the type of *Strombus urceus* was identified and the species taxonomically stabilised after 200 years of instability. The synonymy of *Strombus urceus* was found to contain four valid species, one of which required recircumscription. Two subspecies were recognised prior to this study, both of which have now been recircumscribed as species. A total of six new taxa were recognised, resulting in the deconstructing of the once monotypic complex into twelve species. This thesis demonstrates that Abbott (1960) greatly underestimated stromboidean diversity and that, with biogeography and classical morphological analyses, species can be robustly described and radiation patterns postulated.

Contents

Premier

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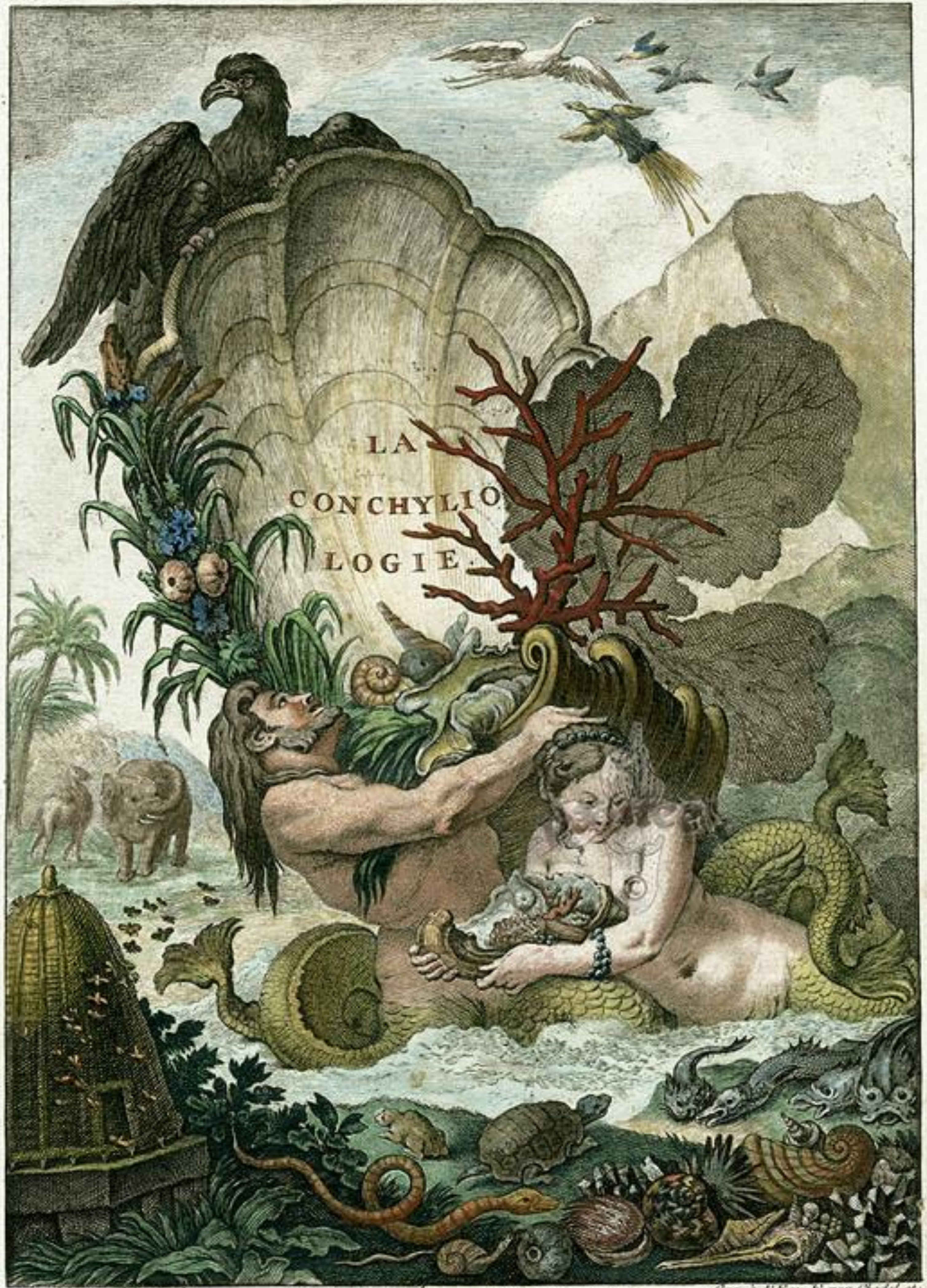

Retouché et conduit par Jac. De Favanne.

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Chapter 1 Introduction

Strombidae is a tropical marine gastropod family with a global distribution, and the family has experienced a great many taxonomic revisions through time (Hanley 1855; Sowerby 1839; Duclos 1844; Swainson 1823; Tryon 1883, 1885; Abbott 1960). Within the Strombidae, *Canarium* represents a collection of small strombs that has often confounded reviewers, particularly in relation to the taxonomic irregularities surrounding Linné's "urceus". The "urceus" irregularities have been exposited in earlier works such as Hanley (1855), Dodge (1946, 1956) and Abbott (1960). However, these revisions lacked the full gamut of evidence that technological advances now provide to the modern reviewer, such as access to rare literature online, rapid communications between institutions, and the ability to draw on material held in collections world-wide with ease and from the comfort of a desk. Therefore, where once the taxonomic complexity to determine the meaning of what is "urceus" led to a capitulation into either a belief of insolvability or a tactical resolution to enable taxonomic continuity, both of which are without a mindset of absolute correctiveness (Dodge 1946; Abbott 1960), this recircumscription seeks to bring satisfactory resolution.

While *Canarium urceus* (Linné, 1758) has challenged taxonomists through the centuries, it remains an enigma in terms of the understanding of the relationships between the distinctive regional forms that appear to be aggregated in certain regions of the Indo-Pacific, for example the central Philippines. It is this aggregation of what could be definable and distinctive forms that has led to the reluctance of many taxonomists to recognise the various regional names that have been historically erected (Schumacher 1817; Anton 1839; Duclos 1844; Dodge 1946).

To address the historical taxonomic conundrum surrounding "urceus", it is necessary to examine the complete type records and review the collective assumptions and errors that have been applied to the determinations of what is “urceus”. These assumptions and errors may be in terms of failure to recognise the duplicity of the Linnaean types, often only having observed one and not the other, or reflect a taxonomic imperative to enable the completion of a broader revision (Hanley 1855; Dodge 1956; Abbott 1960), or assigning type material and locality based on an acquiescence to the taxonomic understanding of what “urceus” was at that time, rather than what it ought to be (Abbott 1960).

This thesis works to resolve the taxonomic conundrum that is *Strombus urceus* Linné, 1758 (= *Canarium urceus* (Linné, 1758)) through identifying the type and explicitly defining a range for that phenotype by first principles. This is achieved by bringing together the physical type material and lectotypes to provide a sound resolution to the taxonomical enigma of what Linné (1758, 1764, 1767) intended when describing “urceus”, and to review its synonymy in the context of modern systematic understanding. The geographical range of “urceus” is identified and differing biogeographical regions are then sampled. These samples are compared morphologically and genetically, and new species identified and described where appropriate. Finally, the biogeography and radiation are discussed for all taxa that were once considered “urceus’ prior to this revision. Where appropriate, taxa that have historically been synonymised, but are considered to be valid species, are recircumscribed and reinstated.

Layout of the thesis

The second chapter of the thesis presents the rationale, hypotheses and research questions that guide the thesis. Chapter 3 deals with the theoretical ideas of what a species is. It presents the species theory of essentialistic pluralism (Maxwell et al. 2020a), and presents a rationale on how infra-species ranks are chosen. This chapter forms the basis from which the systematics were derived. It also provides an explanation of why *purpose* or *why* questions are essential to understand why to discerning *how* they are named. This ensures that species as explanatory hypotheses are given priority over personal taxonomic prejudices. The next chapter (Chapter 4) explores speciation processes, and highlights the many evolutionary potentialities that can give rise to novel taxa, while exploring the role of hybridisation in taxonomic demarcation and the place of hybrids in the nomenclature. I define the speciation processes, demonstrate how radiation theories correspond to different speciation processes, and explore the biogeographic influences that affect marine species radiations. Three types of hybrids are defined, and their place in the nomenclature is discussed. The following chapter (Chapter 5) discusses how higher taxonomic principles are outlined. It moves the discussion from the species and infra-species ranks to higher taxonomy, where inter-species relationships are explored in terms of when and why these relationships should be considered for identification formally within the nomenclature. Following from the theoretical discussions related to species conception, the remaining chapters of the thesis are related to the physical revision of "urceus".

The methods for morphological analyses and materials are outlined in Chapter 6, and examine how the selection of organisms was made for the inclusion within the revision of "urceus", which comprises the main focus of the thesis. This chapter outlines how material from public and private collections was processed, the identification of regions that were selected for sampling, and the classification of those samples. Details of locality validation and the assessment of samples are also outlined, and the summary statistics are provided for larger samples of preserved material obtained. Chapter 7 details the taxonomic processes used in the systematics part for the identification of the true "urceus", its synonyms, and species that have previously been defined and buried within that synonymy that need to be drawn out and recircumscribed. The morphological characters and computational analyses used to discern species based on that morphology are outlined, and the components used in the presentation of clades and species are presented. The next chapter (Chapter 8) examines and explains the morphological variability in size and colour within ”urceus”, presents the summary statistics for large wet and dry samples examined, and morphometrically tests the species hypotheses contained in the chapter. Morphometrics are used to examine morphological variability between the sexes. A model is developed to explain the size variability between males and females, and sexual size dimorphism in “urceus”, and how this size is regulated between populations of the same species. Colour variability is discussed, and shared characteristics between species that have often led to taxonomic confusion and synonymisation, such as the black colouration in some species and its sporadic occurrence in others, is explored genetically. Chapter 9 investigates the biogeography of the species identified in the thesis and, in particular, the glacial cycles, land dispersal barriers, ocean current mediated dispersal and environmental barriers that have influenced the distribution of these animals. Chapter 10 presents the systematics part of this thesis. It seeks to resolve the intra- and inter-species relationships, and the classification is hypothesised to epifamily, with twelve species once considered “urceus” being designated. Notes on the paleontological record are also presented. The thesis concludes with chapter 11.

Chapter 2 Questions, Aims, Hypotheses and Rationale

There are three main themes to this thesis. Theme 1 focuses on Abbott's (1960) review and the question of over synonymisation. Theme 2 focuses on the value of classical taxonomy. Theme 3 focusses on the robustness of phylogenies, and how biogeography may inform on the nomenclature.

Theme 1: Abbott and over synonymisation

Did Abbott (1960) over-synonymise in his revision? For this theme, the aim was to review *Canarium urceus* (Linné, 1758) (s.l.) from the revision of Abbott (1960) using essentialistic pluralism. I hypothesised that *Canarium urceus* (Linné, 1758) (s.l.) after Abbott (1960) was over synonymised because Abbott (1960) had a limited of understanding of the extent of the distribution and localised distinctive morphotypes.

Theme 2: Value of classical taxonomy

Can classical taxonomy contribute to the formulation and construction of sound phylogenies? For this theme, the aim was to compare and contrast molecular and classical techniques in resolving phylogenies. I hypothesised that comparing phylogenetic analyses to morphological similarity analyses on the same set of organisms would provide a greater understanding of the radiation and evolutionary process that are currently affecting the family because both analyses contribute differing sets of information.

Theme 3: Robustness of phylogenies and biogeography

If there are two alternative species hypotheses for a set of organisms, can biogeographic analyses indicate the most robust hypothesis to integrate into the nomenclature, with the observed speciation process used as a causal argument? For this theme, the aim was to use biogeographic evidence to determine if this provided robustness to the nomenclature through the justification of the taxonomy that the nomenclature reflects. I hypothesised that biogeographic methods can enable the determination of a robust model of radiation history of a complex of organisms, and once the modes of speciation have been determined, these biogeographic methods can then be used to justify a rewriting of the nomenclature because the classification is grounded in evolutionary evidence.

Rationale

Canarium urceus (Linné, 1758) meets the five rationales for a species in need of revision (Schlick-Steiner et al. 2010, p. 429): 1) *Long standing taxonomic dispute*: the understanding of what Linné intended to be "urceus" has been debated for over 150 years, with conclusions ranging from it being invalid to the now broad inclusivity of a large range of phenotypes, often with distinct regional forms (Hanley 1855; Dodge 1946, 1956; Abbott 1960); 2) *Ambiguous delimitation in morphology based on primary exploration*: the distinctive regional forms and high degree of variability of "urceus" has led to much confusion of the true nature of the species, resulting in both lumping and splitting of the complex based on the personal nuanced explanation of the taxonomist (Link 1807; Schumacher 1817; Wood 1828; Anton 1839; Watson 1885; Dodge 1946); 3) *Pronounced life history variability or broad geographic or ecological space occupied by nominal species*: while little is known of the variability in life history across the range of "urceus", it has a wide distribution from the west coast of Thailand through to the central South Pacific, with many regions acting as unique, disconnected glacial maxima refugia, or having stable island-based populations that have largely been free of global sea-level upheavals through time; 4) *Occupies biodiversity hotspots*: the range of "urceus", occupies the central Indo-Pacific, which is universally recognised for its concentration of marine diversity and complex evolutionary history (Santini and Winterbottom 2002; Spalding et al. 2007; Carpenter et al. 2011; Kulbicki et al. 2013; Veron et al. 2015; Borsa et al. 2016; Yang et al. 2016; Wainwright et al. 2018a); and 5) *Outstanding importance of organisms to progress in other fields*: resolving the phylogeography and taxonomy will help shape our understanding of the broader evolutionary history that has given rise to the biodiversity of the Indo-Pacific through provision of new evidence for radiation patterns and biogeographic dispersal influences on marine organisms and, in particular, molluscs. The combination of the taxonomic complexity, as well as meeting all five of Schlick-Steiner et al.'s (2010) criteria, make "urceus" a model species for intensive revision. Importantly, that this taxon meets all of Schlick-Steiner et al.'s (2010) criteria for addressing *why* this recircumscription is necessary (as outlined in Chapter 3).

Chapter 3 Choice of Species Concept

Maxwell SJ, Congdon BC, Rymer TL (2020) Essentialistic Pluralism: The theory of Spatio-temporal positioning of species using integrated taxonomy. *Proceedings of the Royal Society of Queensland* 124, 83-97.

Maxwell SJ, Dekkers AM (2019) A new name for *Altivasum typicum* Hedley, 1916 fide Dekkers and Maxwell, 2018 and the description of *Altivasum clarcksoni nov. sp. The Festivus* 51(2), 171-176.

Maxwell SJ, Rymer TL, Rowell MK, Hernandez Duran LC, Berschauer DP, Underdown M, Petuch EJ, Dekkers AM (2021) Defining and Bringing Relevance of Meaning to Species Group-Level Taxa. *Proceedings of the Biological Society of Washington* 134, 27-28.

This chapter explores the concept of species and subspecies, and provides a defining conception on how both these taxonomic levels are discerned and applied. Species are hypothetical constructs used to describe a collection of organisms that share a distinguisable trait(s). What a species is, therefore, is a matter for the taxonomist to discern, and is fundamentally constructed from the standpoint of their opinion on the value of the observed differences of the group of organisims at that point in time. The differences that a taxonomist uses depend on their chosen philosophical approach to species conception. The choice of concept needs to be applicable to the data being tested (Schlick-Steiner et al. 2010). For example, undertaking a study on morphology and then basing the taxonomy on biological conceptionality because of hybridisation patterns would result in a fundamental theoretical flaw in conceptional application. Similarly, using genetic distance to establish species and then basing descriptions on observable morphology would generate the same philosophical issue.

This thesis is conceptionally grounded in essentialistic pluralism, which is based on the use of integrated taxonomy, with its unrestricted approach to conceptualisation of what a species is. This allows the taxonomist the freedom to express a unique approach to exploring phylogeny without the shackles of rigid necessity to declare adherence to a single species concept (Yeates et al. 2011; Pavan and Marrioig 2016; Solari et al. 2019;

Pardo-Diaz et al. 2019). The essentialistic pluralist approach enables a choice in definition to be applied based on the uniqueness of the characteristics of the organism as a set, and thus is an extension of the reality that taxa represent entities that currently exist, or have existed, within a temporal space and are in need of demarcation and explanation (Kitcher 1984a, 1984b). Essentialistic pluralism provides a theoretical underpinning for integrative taxonomic practice, bringing a universality in the choice of criteria with maximum defensibility of demarcation (Yeates et al. 2011; Schutze et al. 2017).

3.1 Essentialistic Pluralism

The natural world is classically ordered according to hierarchical relationships that are constructed in a manner that does not reflect modern evolutionary principles and the new biological essentialist paradigm. The historical pursuit of inferring the natural relationships between organisms is primarily a by-product of human intellectual inquisitiveness, and reflects a pseudo-theological search for understanding the natural order of life, a quest that has challenged philosophers and those interested in the sciences before the Common Era (Lewis 1963; Henry 2011). As scientific understanding and shifts in theological influence have changed over time, so too have the processes and doctrines underpinning methodological approaches among those disciplines concerned with finding an optimal system of nomenclature (Moritz 2013).

The shift from theocratic creationism towards an evolutionary necessity in taxonomy has challenged the hierarchical orthodoxy conceptualised and instituted by Linné (1735, 1758). This challenge has led to conflict and a rigorous defence of systems of nomenclature based on personal ideology rather than theoretical optimisation (Cantino et al. 1999; Brummitt 2002). Irrespective of the ideological stance taken, any system of nomenclature needs to impart a sense of ontology, or reality, as well as possess an inherent epistemology that enables a delineation of how derived taxonomic conceptional entities reflect the taxonomic needs of the classifier (Szalay and Bock 1991). Consequently, taxonomists are drawn towards particular taxonomic schools of thought based on their personal understanding of evolutionary theory, taxonomical needs and predisposition towards an ideological stance on a particular taxonomic or species concept (Cracraft 1987).

In order to re-engage the wider scientific community in the species debate, there needs to be an acceptance that the term “species” has fundamentally different meanings (Schlick-Steiner et al. 2019). The use of integrated taxonomy, with its unrestricted approach to conceptualisation of what a species is free the taxonomist to use any evidence in their discernment (Yeates et al. 2011; Pavan and Marrioig 2016; Pardo-Diaz et al. 2019; Solari et al. 2019). The broader scientific community can be brought back to the species debate only when there is an acceptance that there is no correct or incorrect conceptuality in species definition, with all proposed species concepts theoretically having a usefulness (Schlick-Steiner et al. 2019). Many scientists have avoided species debates in evolutionary biology as a consequence of the semantics surrounding many of the current issues (Noor 2002). Much of this avoidance can also be attributed to conceptual misunderstandings and ignorance of the theoretical basis for what actually constitutes a species.

Species need to be conceptualised outside of taxonomic classification systems as they fall outside of systematic hierarchical arguments, being fundamentally hypothetical (Dubois 2011). Although hypothetical in nature, a species hypothesis is represented by a real set of organisms. Thus, because species are representaive of real entities and not just intentional meanings derived by the taxonomist, they differ innately from higher classifications, which are subjective in that there is no physical representation of the hypothetical rank (Ghiselin 1974; Hull 1976). This raises a point of contention: if species are based on the real, why are many of the concepts that are used to define them based on unreal or non-causal criteria? This leads to a complexity in conceptual realisation and invariably to conceptual misunderstanding, a problem again absent in higher taxonomic arguments that have no physical reality (Stamos 2003). There is a need for criteria to give a sense of a “touchstone” to the real.

One of the problems with engaging a taxonomist in the species conceptual debate is that the taxonomist is often at a loss to explain their meaning of species, falling into the trap of conceptual adherence and associated rhetoric, and overlooking the hypothetical nature of the reference point in nature they seek to demarcate. Such rigidity to a conceptual belief invariably ends with the taxonomist at a loss when faced with contra-arguments (Hey 2001). This adherence to a conceptual framework also loses sight of the primary mission of the taxonomist, which is, according to Mayden (1999, p. 115), “to discover, describe, and classify biological diversity, regardless of how much there may really be out there”. It is also irrational for a taxonomist to bind themselves to any concept due to its convenience in application or acceptance by the wider collective scientific community (Nadachowski 1993). Furthermore, the long-term species debate has failed to enunciate the significance of the nuances of the species concept applied by the practising biologist. The application of species concepts is used to make critical decisions that affect universal biodiversity and macroecological assessments, as well as providing the support for evolutionary understanding in fields well apart from the narrow frame of their activities (Hey et al. 2003; Tan et al. 2008; Naomi 2011; Frankham et al. 2012). This has never been more relevant than in contemporary taxonomic practice, with the rise of conservation orientated systematic arguments that seek to limit the ability of the taxonomist to undertake wide-ranging revisions, with such revisions seen as a threat to global diversity (Garnett and Christidis 2017; Thomson et al. 2018; Gangloff 2019).

Taxonomic descriptions of new species are often fundamentally flawed, as there is generally no explicit statement of the species concept used to delineate the taxon (Tan et al. 2008). This lack of conceptual explicitness leads invariably to three primary errors in the systematic demarcation of species: 1) Type I errors occur when there has been an overestimation of the number of species within a particular organism complex; 2) Type II errors occur when the number of species in the organism-complex has been underestimated; and 3) Type III errors occur when there has been a misrepresentation of the systematic relationships between the organisms within the complex (Adams 1998). These errors have serious implications for understanding evolutionary history, where "irrational" species could lead to a misrepresentation of the evolutionary progression of a clade (Adams 1998), or in the conservation of endangered organisms (Garnett and Christidis 2017). When determining a species, a taxonomist has an obligation to nominate the species conceptual approach being followed, to ensure a clear understanding of the criteria that are necessary and sufficient to determine the population (Hausdorf 2011). The need for explicitness in criteria brings the theoretical species recognition problem back within the scope of the rules of nomenclature that govern the application of names (Knapp 2008). In addition, the taxonomist has an obligation to inform on the actual process of speciation that has taken place, giving insight into the ontogeny and causation of organismic differentiation (Miller 2001; Losos and Glor 2003). The use of integrated taxonomy enables the taxonomist the freedom to choose species criteria that are most appropriate for the set of organisms, irrespective of definitions that may have been applied to their sister taxa. However, this freedom in descriptive modality needs to be coupled with conception explicitness; that is, not just state the methodology used to discriminate a taxon, but answer the causal question(s) as well.

In this thesis, I redefine biological essentialism through the differentiation of the two concepts of kind and essence that have become erroneously synonymised in modern evolutionary theory. I argue that a *kind* is a part of an organism state, which is a fixed discrete entity within a spatio-temporal framework that is defined by essences. The edges of the organism state represent the phylogenetic constrained boundaries of an organism at a particular point in time. I also consider the pluralist approach to understanding what constitutes an essence; that is, the integrative taxonomic freedom to determine the criteria or species delimitation. I specifically describe two discrete forms of essence, namely the character essence (Box 1), which is a spatio-temporally fixed character, and the structural essence (Box 1), which is mutable and has an evolutionary context, a distinction that has yet to be fully explored in the literature. The essence matrix confines the organism state to a discrete set of boundaries of evolutionary potential for an organism to reticulate and evolve within through time. Furthermore, I demonstrate essentialistic pluralism as a standard for universality, and address the need for species demarcation at its core.

Box 1: Glossary of new and revised significant taxonomic terms

Character essence - the immutable attribute of an individual that reflects a spatio-temporal expression of structural essences.

Essence matrix - the entire collection of structural essences that unifies the ancestral and descendant taxa, and is used to define the higher clade from which an organism state has evolved. It bounds that organism’s potential for evolutionary divergence in form into the future.

Kind - a region within an organism state that represents a conflux of an organism's structural essences, and reflects the nature of an organism at a point in its evolutionary progression, an immutable semaphoront.

Organism state - the phylogenetically constrained boundary of all potentially expressed essences that a biological population (considered a species) exhibits at a static point in its spatio-temporal evolution, that is, a holomorph, and contains the expressed morphological boundaries, otherwise known as the diktyzonos, of an organism (Maxwell 2022).

Structural essence - an evolutionary trait that may represent a phenotypically plastic form, or an ecological boundary, which defines some intrinsic or extrinsic aspect of the organism.

Many scientists have avoided species debates in evolutionary biology because of the semantics surrounding many of the current issues, or because of a lack of training in the codes of nomenclature and species descriptive writing (Noor 2002; Pante et al. 2015). Much of this avoidance can also be attributed to conceptual misunderstandings and ignorance of the theoretical bases for what actually constitutes a species.

3.1.1 Essentialist Taxonomy

Essentialism has a valuable role to play in providing an understanding of evolutionary processes, as it explains the evolution of both the intrinsic and extrinsic natures of taxa (Walsh 2006). Understanding the dualistic nature of taxa requires an acceptance of the evolutionary reality that organisms evolve subordinate monophyletic groups that have an ancestry determined by the linking of real organism states (Box 1) and not some evolutionary ideology (Brundin 1972). Organism states are, in turn, defined by kinds (Box 1), which are created by the congruence of structural essences (Box 1).

Many of the reviews of species concepts fail to explore essentialist arguments or, when this exploration is carried out, it is with the basic premise that all essentialist arguments are phenetic. One of the major failings of the modern essentialist approach to species criteria is the decision about which species concepts are valid and acceptable to be used taxonomically (Hey 2006). However, there is no reason that essentialists should not take an integrated approach, given there is the necessity to use all criteria to uncover the greatest diversity (Schlick-Steiner et al. 2010). This clearly is the crux of the problem. Taxonomists fail to recognise that species have two parts: a separate criterion with the distinctive process of species delimitation often linked with the rigidity to a concept; and the conception itself, which is hypothetical (Paul 2002). The natural consequence of failing to recognise these two parts explains why the treatment of complex taxonomic clusters, such as agamics, is overlooked in conceptual formulations. It is only with integrated taxonomy that the taxonomist is freed from the theoretical constraints of taxonomic rigidity imposed by doctrinal adherence to a single hypothetical species concept, and is thus able to explore the criteria of the real organism necessary to impart taxonomic meaning (Schlick-Steiner et al. 2010).

Kind and essence have often been used interchangeably, although they are different concepts. Consequently, they have been maligned in the arguments against immutability that have been used to support the drive toward neo-Darwinism and the modern evolutionary synthesis (Mayr 1987; Amundson 1998; Okasha 2002). There has been considerable debate on the nature of what actually constitutes an essence. First, historically to taxonomists, such as Linné, the term essence simply meant that which is taxonomically useful (Winsor 2006). Second, many contemporary essentialist arguments are pseudo-Aristotelian, based on either shared salient morphology or innate intrinsic properties that have explicit and rigid taxonomic meaning (Wallace 2002; Oderberg 2007). Third, the essence of an organism has also been linked to its genotype, which is then expressed in the observable morphological, physiological or behavioural characters it displays (Kitts and Kitts 1979). Fourth, the genotypical approach was further refined into the extended phenetical approach, where the definition of essence included ancestry and relational biology (Walsh 2006; Elder 2008). Fifth, the more minimalist approach to defining the essence, is based on the character trait, is outside of historical necessity and is not intrinsic to the definition of an individual (Dumsday 2012). Finally, the phylogenetic approach seeks to shift the focus of essentialism from a categorical basis to a historical one, thus enabling the essence to be used in evolutionary biology through the incorporation of both intrinsic and extrinsic characters, or relational essences as part of a wider holistic view of the organism (Devitt 2010; Dumsday 2012). Irrespective of the approach taken to defining the essence, one of the failings of these theories is the inability to distinguish between two distinctive essence forms, namely the structural and character essences (Box 1).

The structural essences of an organism state arise from the collective essence matrix, which defines the morpho-space of inclusivity of the higher taxonomy to which the organism, in all possible phenotypically plastic forms and ecological boundaries, belongs. This organism state can be viewed simply as the boundary of a species variability at an exact point in space and time, that is, a species is an affixed cross-section of a continuum chosen by the taxonomist to give it a reference point to advance an explanation of the observable natural world. In contrast, the character essences are the immutable attributes of an individual and the spatio-temporal expression of the structural essences at the point at which the species is circumscribed. Importantly, it is the character essences of a taxon that are used to provide the restricted definition of the kind within the broader organism state, and these character essences are used to formulate the diagnosis of a species.

In the current essentialist debate, the concept of a kind refers to an immutable form and is not linked to a particular end point in the hierarchical tree typology (Pavlinov 2021). Therefore, it is theoretically incorrect to refer to species, in the classical sense, in terms of discrete classes of natural kinds with an implicit immutability. Rather, species should be viewed as distinct representatives along a continuum, thus being evolutionarily plastic, rather than temporality variable. Kinds need to be viewed in terms of a convergence of structural essence axes within the organism matrix, which enables the discernment of a collective type with an explicit taxonomic definition, albeit at the arbitrary judgement of the taxonomist (Forey 2002). In this context, kinds represent the collection of units of change within an organism state that result from the subjective assessment of the unbroken chain of divergence (Dobzhansky 1935). The kind forms a statement of evolutionary position chosen by the taxonomist to reflect a more inclusive organism state comprised of evolving structural essences.

Mayr (1987) rejected kinds, arguing that natural kinds were sterile and, consequently, this terminology should be restricted to inanimate objects, such as metals. However, this is an incorrect assumption based on an innate restrictiveness and lack of historicity that has been applied to the classical definition of a kind. Furthermore, Mayr's (1987) approach is a rejection of the premise that species are capable of evolving, which is not upheld under the revised definition.

3.1.2 Historical Perceptions of Species

Darwin (1859) argued that species are arbitrary constructs of convenience selected from a fluctuating evolutionary pond of forms. This argument mirrors the belief that species are not discrete, but rather become indistinguishable within a merging metapopulation, where essences reticulate between individuals as populations (Lamarck 1801). This idea was extended in the adaptive field theories of Wright (1932) and Dobzhansky (1951), in which discernment of taxa occurs at topological peaks of adaptational success. The valleys between the combination of genes indicate a point at which a discrete organism can be delineated from one another (Dobzhansky 1951). Species, therefore, are hypothetically derived with the choice of demarcation, a decision made by the taxonomist.

The determination of a method to demarcate species is a complex argument that has lasted centuries. Species need to be contextualised as a direct and discernible product of evolution, constructed on a set of unifying essences chosen by the taxonomist. This currently occurs under guides of a theoretical concept chosen by the taxonomist. It is worth noting that the word species *senso stricto* has two primary uses: it is used by taxonomists to delineate the forms within nature and create hypothetical hierarchies and, at the same time, it is used as a definition by the taxonomist to form a discernible immutable kind that acts as a hypothetical name-bearing reference point from which the process of evolution can be described (Mayr 1987, 1996; Ereshefsky 1992; Pleijel and Rouse 2000). However, a species has a unique evolutionary history, and forms the more inclusive individual taxon with characteristics that are often not exhibited by the kind (Wiley 1980; Mishler and Donaghue 1982; Nixon and Wheeler 1990). In contrast, higher taxa are multidimensional, existing within a spatio-temporal continuum in which the shared characteristics, or structural essences, are acting as axes that reflect their unique evolutionary direction (Andersson 1990; Szalay and Bock 1991). When these axes converge, there is a forming of a discrete kind that can be given a formal definition (Dupré 1981). Furthermore, it is the relationship and clustering of these organism states, based on shared ancestry, that form the basis for the definition of higher taxa.

The birth of a new species, or delineation of two taxa, occurs in two ways. First, via the process of heterochronic cladogenesis, where two distinct convergences arise in the organism state and the cleavage of new identifiable species with new identified phylogenetic constraints is deemed appropriate by the taxonomist (Huxley 1957; Gould 1977; Aze et al. 2013). Second, via the process of anagenesis, where a particular set of essences consistently converge outside the parameters of the parental metapopulation, as defined by the kind, requiring a redefinition of the kind (Huxley 1957; Aze et al. 2013). While the acceptance of stasiogenesis implies that there is no multiplication of species and evolutionary failure, it may also reflect internal reticulation of the kind that reflects a convergence about a conflux of evolutionary optimisation (Huxley 1957; Crusafont-Pairó and Truylos-Santonja 1958; Figure 1).

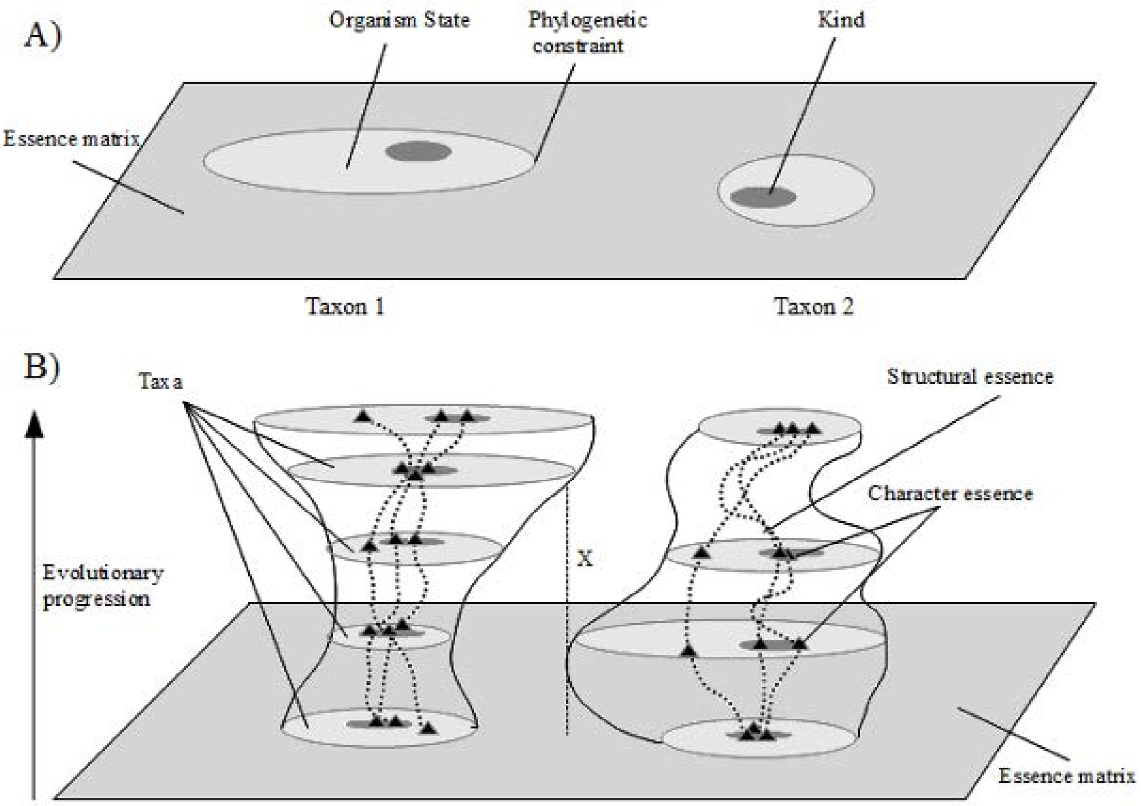


Figure 1: The two fundamental essentialist ideologies: A) the phenetic approach, which does not include evolutionary progression; and B) the essential pluralist approach, in which structural essences are used to delineate an organism state with character essences in temporal stasiogenesis within the evolutionary continuum. Where differing organisms show similar structural essences (X) through mechanisms as a consequence occupying the same position within the essence matrix arising from mechanisms such as convergence, but can be readily distinguished from each other through an understanding of the evolutionary progression they should be recognised as species. The essence matrix is the limited potential for evolutionary forms to exist within.

Reticulation has significant implications for phylogenetic reconstruction, where only one gene tends to be used, and the results may only reflect gene evolution, rather than the true state of the historical relationships between organisms. Evolution is more than the addition or subtraction of genetic material, but rather reflects an interaction of gene systems: the transitional valleys between gene clusterings represent taxic exploration of evolutionary possibilities rather than the initial stages of a genetic conflux giving rise to a new taxon (Dobzhansky 1951).

Notwithstanding the mode of speciation, there is a necessity for the generation of artificial temporal evolutionary stasigenesis for the delimitation of an organism state for the purpose of generating systematic understanding. This artificial stasiogenesis introduces an explicitness into the definition of species that then enables the production of real propositions on the historicity of the evolution of organisms. Taxa are explicitly defined in terms of kinds to avoid ambiguity and facilitate effective communication of the biological entity reflecting the convergences of the axes, even if these kinds are only representative of the wider, more inclusive organism state (Dupré 1981; Bryant 1996). In point of fact, kinds represent nothing more than the adaptive peaks of an organism state.

Avise et al. (1987) highlight the complexity of gaining an understanding of the evolutionary significance and determining within an organism state when, from the extrapolation of a number of microevolutionary events, macroevolution is said to have occurred. Avise et al. (1987) saw macroevolutionary patterns as a substrate that is formed by the branches and twigs of intergenerational pedigrees within the complexity of phylogeny. One of the major theoretical standards for the delineation of a species from the myriad of branching possibilities is the simultaneous establishment of joint possession of structural essences, or synapomorphies, in each line (Bremer and Wanntorp 1979). However, strict adherence to this method of differentiation is problematic in delineating taxa when dealing with a novel structural essence, from the time of origin to fixation, which gives rise to a new kind in a spatio-temporal organism state. This can be resolved by the defining of ancestry in terms of the absence of structural essences. However, the problem with this approach to the delineation of ancestor-descendant relationships is determining the temporal points of divergence, or when an adaptive peak deserves taxonomic isolation from its sister peaks. A particular characteristic may be more frequent in one taxon than another, absent altogether, or cryptic, and an assumption is made by the taxonomist practising a level of pattern cladistics when a new species has arisen (Brady 1982). If this is accepted, then it is the taxic homologies, which are based on descendants rather than transformational homologies, that are defining the phylogeny, rather than just seeking to explain the genealogy.

Taxonomists must also deal with a level of contingency in delineating taxa (Chambers 2012). There is a level of inference, based on evidence at hand, that is used to generate the essences that define the organism state and then are restricted further into the kind. This involves a shift from a search for differences to an examination of commonality and the seeking of sub-patterns, or character essences, which form the conflux of axes unifying them (Kitcher 1981). The determination of which essences form the best guide to the determination of an organism state and the kind is a matter of relational taxonomic subjectivity (Okasha 2002; Devitt 2008). This reflects the reality that structural essences are innately ambiguous, comprised of an unknown number of transitions, and possess an often-cryptic singular origin that may have undergone a level of evolutionary reversal (de Pinna 1991). Therefore, the approach taken in the determination of a discrete kind, which represents a wider organism state, will be highly dependent on the species conceptual approach that is being used by the taxonomist. Again, it is worth noting that the conceptual approach to species is often restricted by a rigid adherence to an ideological stance that blinds the taxonomist to the real phylogeny.

There are a plethora of rigid methodological approaches enabling discrimination of the kind. Many of these methodological approaches to species conception are based on the single individual, and are mereologically formulated, and all have the underlying drive to find exclusivity in definition (Hull 1980; Kornet 1993; de Pinna 1999). This gives rise to the problem of defining the evolutionary unit and the nature of a species itself. Notwithstanding the need for definitional exclusivity, species can also be considered as a set of organisms with a unique relationship that forms a natural heterogeneous individual (Kitcher 1984b; Ereshefsky 1992).

Irrespective of the species concept that is chosen by the taxonomist, there are four basic characteristics that must be met in order to fulfil the need of communication of the natural world. First, there needs to be a reality, or an actual spatio-temporal existence, even if this is unobservable (Cracraft 1987). Second, the species needs to have a level of individuation and mutual exclusivity, enabling a demarcation of it from other organisms (Cracraft 1987; Kornet 1993). Third, there needs to be irreducibility, so that the entity cannot be further divided and, therefore, forms a basal unit of taxonomy (Cracraft 1987), with subspecies used as recognisable cryptic forms of a species complex and not basal taxonomic units in themselves (Maxwell and Dekkers 2019). Finally, the species must offer a level of recognisable comparability to allow for systematic evaluation and the discernment of evolutionary history (Cracraft 1987). The individualisation of a species can be problematic, particularly at the boundaries, where the descriptive essences are chosen to create the definition stray from the those of the kind obscuring the recognisable compatibility needed to generate a phylogeny. However, taxonomic realism can be achieved only when the taxonomist rejects limiting the definition of a species by adherence to dogma and accepts that nature does not differentiate itself by a single unique classificatory unit or set of definitions inherent to a particular species concept (Ruse 1998). Therefore, species-as-taxa are individuals formed out of a class consisting of a population, reflecting the reality that species are a taxonomic concept and not a category (Wiley 1980).

The need to adhere rigidly to a single concept, and the ideology that once a species has been defined it is immutable, can hinder the greater understanding of the natural world (Knapp 2008; Lugadha et al. 2018). There is a long historical acceptance that no single concept best encapsulates the idea of a species, and that there is a need to use the way it is optimised to achieve comprehensibility and usefulness for the species that the applied concept gives rise to (Grout 1938). Therefore, the approach to defining a species and its operation must, as a priority, grant the wider community outside the realm of semantic taxonomy a greater understanding of nature (Cracraft 1987). Each of the monist species concepts relies on a single universal level of evolutionary units, but each is fundamentally unable to account for the diversity between organisms (Mishler and Donaghue 1982; Rosindell et al. 2010; Alitto et al. 2019). It is only with a broad pluralist approach to the idea of a species, as the collective individual, that evolutionary relationships can be explained taxonomically (Matos-Marví et al. 2019).

Dealing with a subspecies is problematic, and this is reflected in the lack of reference to them in the conceptual literature. This is in part a consequence of the definition given to these lower taxonomic ranks, such as temporarily isolated populations that are arbitrarily delimited and fated to reticulate back within other lineages (Frost and Kluge 1994). However, the problem arises when the taxonomist is faced with making a subjective decision on whether a population is an arbitrary subspecies or a distinctive allopatric population with a distinct evolutionary trajectory (Frost and Kluge 1994). This leads to the argument that subspecies are not objective concepts (Groves 2012). Subspecies should be restricted to cryptic species where there are no physically observable boundaries to distinguish between populations and, where boundaries are observable, a species rank is justified (Maxwell and Dekkers 2019; Maxwell et al. 2021a).

The elevation of subspecies to full species ranking and redrawing existing phylogenies has consequences for the allocation of great reputational capital for the taxonomist. This has a direct impact on all fields of biology, particularly the highly politicised areas of ecology and conservation biology (Hey et al. 2003; Tan et al. 2008; Frankham et al. 2012). Therefore, the arguments on the treatment of subspecies are even more controversial than debating any singular particular species concept, which is why it is so often omitted from species debates. Notwithstanding, both species and subspecies are taxonomically terminal in nature, and they both have taxonomical importance irrespective of conception (Maxwell and Dekkers 2019; Maxwell et al. 2021a).

3.1.3 Historical Species Conceptual Overview

The number of species concepts that are in current use is a reflection of the treatment of the level of subtle distinctive phrasing that authors apply to a preferred concept, and its conceptual refinement is reflective of the lumping and splitting debates over species themselves (Mayden 1999; Groves 2012). The major conceptual frameworks proposed to delineate a species are each subdivided *ad infinitum* by individual graduation and augmentation as taxonomists have sought theoretical ascendancy and have been driven to find the one true universal species theory. Fundamentally, all historical species concepts fall into one of four categories: 1) morphological or phenetical (primarily ahistorical); 2) biological (attribute or mechanism); 3) historical (common descent as the primary delineating factor); and 4) genetic, where nature is viewed as continuous and not discrete (Wheeler 2007).

Phenetist, or morphological, based species concepts are those in which physical characters are used to formulate the fundamental division, or class, that is used to generate a species. This is fundamentally a classical approach in which there is an innate essence that distinguishes the organism (Mayr 1987). Phenetic methodologies can be divided into two schools: Typological or Linnaean Species Concepts and Morphological or Diagnostic Species Concepts.

The biological methodologies all have, at their core, a determination of species based on fitness and inheritance. The argument may be couched in terms of current or future biological isolation, depending on the methodological approach taken, or the current selective benefits a cline may have to its current environment. However, a considerable failure of the biological species methodologies is the need for the redefining of many of the currently accepted species, the lumping of reticulating populations and the application of these concepts to asexual biota (Hausdorf 2011). There are four principle schools of biological species conception: Biological or Mixological Species Concepts; Behavioural or Recognition Species Concepts; Ecological or Differential Fitness Species Concepts; and Geographical Species Concepts.

The historical species concepts are based on cladistic analyses. They use cladistic tree divisions and are grounded in cleavage in the lineage of an organism, which can be traced, providing a temporal aspect to the definition (Hennig 1965; Kornet 1993). Historical concepts can be divided into two approaches: one in which the continuity is the fundamental driver of differentiation; and the other in which the recognition of distinctiveness predominates. The distinctiveness of the species as an individual in the historical context is conceptualised in fundamental ways, such as morphologically differentiable, adaptively distinct, geologically isolated or tokogenetically isolated (Mishler and Donoghue 1982). However, even more fundamental is the decrement of species from a delimiting point of divergence, and whether the original species is said to continue is extinguished in the divergence event (Miller 2001). A secondary fundamental issue for all historical methodologies concerns the treatment of reticulation among organisms, and this gives rise to many of the symptomatic issues concerning the biological concepts (Hausdorf 2011). There are four primary schools of historical speciation: Evolutionary or Unified Species Concepts; Hennigian General Lineage Species Concepts; Historical Continuity or Purist Phylogenetic Species Concepts; Historical Tokogenesis Species Concepts; and Phylogenetic or Historical Semphorantry Species Concepts.

Dissimilarity models have an ideology that species should be considered in terms of the smallest delineation, a mereological approach to the delineation of entities based on similarities contained within the DNA, which has given rise to a plethora of physically indistinguishable cryptic species that should be treated as subspecies (Mishler and Donaghue 1982; Baker and Bradley 2006; Maxwell and Dekkers 2019; Stauffer-Olsen et al. 2019; Maxwell et al. 2021a). Ahistorical species concepts seek to find processes of speciation that differentiate sets of organisms. Notwithstanding the approach made to the species concept, there is an underlying commonality (intrinsic essence) based on a shared analogy and parallel evolution that creates a fundamental natural kind, which is delineated and classifiable (Hull 1987). There are four principle schools of speciation based on genetic dissimilarity: Structural Species Concepts; Genetic or Genic Species Concepts; Cohesion or Continuous Stochastic Block Model Species Concepts; and Genotypic or Functional Clustering Species Concepts.

3.1.4 Why Should a Species be Circumscribed?

When considering the validiaty of a species, we must first consider *why* a species is circumscribed by the taxonomist before focusing on *how* it is circumscribed. Debates on the viability of species hypotheses are often framed with the *how* focus in mind, questioning *how* the taxon was circumscribed, rather than *why* the taxonomist deemed it necessary to delimitate the organism. If we understand *why* a taxonomist circumscribed a species, then the *how* that was applied in terms of conceptionally becomes less important.

From the time Mayr’s (1942, 1946b) biological taxonomic conception challenged the two centuries old Linnaean phenetic orthodoxy, the debate has raged without satisfaction for those seeking a universal conception (Maxwell et al. 2020). The failure to reach an accepted synthesis in species conceptionality is based on a lack of understanding of what I call the *purpose* of taxa. *Purpose* in terms of taxonomic recognition deals only with the perceived rationale that the author brings to the table during the descriptive process. Fundamentally, *purpose* answers the *why* questions that should be asked of a taxonomic work. There is a focus on the determination of what the intended *purpose* was in describing the taxon. It does not look at the *how* questions. The *how* questions lie in the depths of conceptionality and criteria, and do not indicate *purpose*. Therefore, in the determination of *purpose*, there is no implied assessment of validity.

The decision of whether taxa are valid or not is a discretionary decision made by the taxonomist based on the evidence that they consider important to systematic determination (Maxwell et al. 2020d). Through time, these decisions are reviewed and tested, resulting in periodic shifts in the determination of taxonomic position of organisms (Stromboidea – Abbott 1960; Maxwell et al. 2021c). There is often a conflict between philosophical approaches to choosing the criteria upon which species are described, and this can have profound impacts on the way we see the natural world (Daru et al. 2020). This is colloquially referred to as the war of the “lumpers”, those who seek similarity, and the “splitters”, those who seek uniqueness, between taxa. Which side of the conflict a taxonomist chooses is often arbitrary and based on their personal preference of a species conception model and how it is applied. However, very little consideration is given to the reasons *why* a species is being delineated or aggregated with others in the first instance. If the *purpose* of the taxonomist is considered, then the rationale should negate the lumper/splitter conundrum.

In dealing with purpose, taxa are seen as tools designated to provide a framework for the taxonomist to draw a more complex understanding of the world around them. This is quite different to the conception that is used to delimit the criteria that guide the formulation of the description or definition of taxa. I postulate that there are four possible categorical functions of a species that need to be considered when considering the purpose for species delimitation, any one of which guide us to understand the author's possible intent. The first function is to provide evolutionary markers upon which a hypothesis of evolutionary and radiation theory can be grounded (e.g., Brassicales – Hohmann et al. 2015; Orthoptera – Nolen et al. 2020). The second function is to bring greater awareness to some ecological dilemma that might be resolved through the defining of the organism (Morán-Ordóñez 2020), which is often the focus in matters of conservation biology (e.g., Artiodactyla – Coimbra et al. 2021). The third function is to increase the value of an organism, thereby enabling improved marking of forms or varieties that command premiums in commercial markets (e.g., Littorinimorpha – Lorenz 2002). Finally, the fourth function is the demarcation of an organism on a purely relational basis of difference (e.g., Cichliformes – Vranken et al. 2020).

If the *puropse* of the author in naming taxa is clearly identified, then a clear perspective of its taxonomic usefulness can be assessed by those who seek to understand the role of taxa in providing a greater understanding of nature. The taxa are therefore treated in accordance with the objective explanatory need of the taxonomist rather than the subjective opinion of the audience with conceptional biases. At the same time, *purpose* should not be given as an overarching excuse to take or leave a taxonomic assessment but should rather act as the starting point from which we gauge the value of the taxonomic hypothesis that is presented.

3.1.5 The Complexity of Demarcation

One of the challenges facing taxonomists is the determination of the level of difference that is considered significant enough to warrant the demarcation of a species from its sister taxa (Adams 1998; Schutze et al. 2017). The adherence to a particular species concept limits the potential for the naming of new species (de Meeûs et al. 2003; Schlick-Steiner et al. 2010; Pante et al. 2015). Key to the determination of what constitutes a species is the understanding of the evolutionary trajectory of an organism and the level of reticulation with sister taxa that they may undergo (Adams 1998; de Queiroz 2005). However, the determination of future evolutionary trajectories is fraught with the danger of speculation and is often undertaken with a level of subjective evidence of directional change based on comparative phylogeny (Adams 1998). There is now almost universal consensus that, irrespective of the choice of species concept chosen by the taxonomist, it is the demarcation of a distinctive evolutionary trajectory that unifies all concepts (de Queiroz 2007).

The construction of phylogenies and the determination of species are often based on the sampling of taxa from an existing preconceived pool of organisms. These pools are derived from taxonomic assumptions that are based on existing notions of what species exist and characters are drawn from a checklist of that group (Barraclough and Nee 2001). This invariably opens the process of phylogenetic reconstruction to be based on the existing taxonomy, and invariably leads to the confounding and completely arbitrary splitting-lumping conundrum (Barraclough and Nee 2001). The taxonomist seeks out the patterns of recurrence in nature and then makes the internal judgement of the significance of that pattern (Hey 2001). Whether species are lumped together, or the level of variation is significant enough to enable the distinguishing of separate entities, it is conducted at the subjective judgement of the taxonomist, and their weighting given to differing characteristics they determine to be consequential (Casanova 2013). The approach taken in the determination of consequential characteristics is often biased by the discipline or taxonomic group that the taxonomist is working with, and their need for taxonomic indicators (Kunz 2002; Frankham et al. 2012). This invariably leads to a set of conditions, or criteria, that are used to generate the concept that is applied to the species diagnosis, often to the exclusion of all other species concepts. If species are comprised of multiple populations that are spatio-temporally separated with individual destinies, either to reticulate, speciate, or to go extinct, then it is clear that there is no one conceptualised force that explains all the potentialities of divergence. Consequently, no one single species concept is able to encapsulate the entirety of the collective essences of the amalgamated organism clade to meet the needs of the taxonomic masses (Haveman 2013).

One major failing with a hypothetical species is the historical clustering of organisms that can be well defined and used to generate the spatio-temporal point at which a species is delimited, creating the problem of omitting transitional forms (Girard and Renaud 2011). Similarly, populations may be heterospecific and may be part of more than one species by definition (González-Forero 2009). Heterospecificity is one of the major problems when demarcating the boundaries of agamic groups and is a primary reason that most species concepts omit an argument on asexuality (Hausdorf 2011; Haveman 2013).

Discrete discernment of kinds, which are sound in their spatio-temporal position and are not singularly based upon particular apomorphs, will give rise to the collective individual, and offer basal soundness to any clade (de Queiroz and Gauthier 1994; Baum and Donoghue 1995). The monist argument that pluralism leads to confusion through a lack of intrinsic meaning in the term *species* can be overcome when the taxonomist is explicit in the methodology and conceptionality (Schlick-Steiner et al. 2010). The use of essentialistic pluralism delineates a set of organisms from the natural world at a particualar spatio-temporal point and that contains enough meaning to enable discrimination and thus allow for an organism's taxonomic discernment. It is the failing of hierarchical taxonomic theory that, even if kinds are well defined, there remains a distinct lack of evolutionary theory in the relationships between higher taxa.

3.1.6 Reviewing Pluralism

Many of the reviews of species concepts fail to explore essentialist arguments or, when this exploration is carried out, it is with the basic premise that all essentialist arguments are phenetic. Taxonomists fail to separate the criteria, which involves the distinctive process of species delimitation from the rigidity to a concept often based on the biological (Paul 2002), when an intergrated approach in needed to understand maximum diversity (Schlick-Steiner et al. 2010). The natural consequence of rigidity of critera explains why the treatment of complex taxonomic clusters, such as agamics, is overlooked in conceptual formulations. It is only with essentialistic pluralism that the taxonomist is able to explore the criteria necessary to impart taxonomic meaning using integrative taxonomy (Schick-Steiner et al. 2010; Solari et al. 2019).

The essentialistic pluralist approach does not seek to tie the taxonomist down to one species concept but rather enables a choice in definition to be applied based on the uniqueness of the characteristics of the organism as a set, and thus is an extension of the reality that taxa are entities that currently exist, or have existed, within a temporal space and are in need of demarcation and explanation (Kitcher 1984a, 1984b). This is the theoretical underpinning for integrative taxonomic practice, with its universality in the choice of criteria having maximum defensibility of demarcation (Yeates et al. 2011; Schutze et al. 2017), and further adding a spatio-temporal constraint. This temporalism must still include innate references to the organisms that are historically related, as the removal of the historical context itself reduces the meaning of species and is a major cause of inconsistency, even in the face of disconnectivity of lineages (Ereshefsky 1992).

Ereshefsky (1992) noted that pluralistic species concepts allow for the coverage of the multiplicity of evolutionary forces that drive divergence, such as interbreeding, selection, genetic homoeostasis, common descent and developmental and ecological isolation, and this conceptional approach formed the basis for integrated taxonomy (Schlick-Steiner et al. 2010; Pante et al. 2015; Solari et al. 2019). Mayr (1987, p. 149) argues that the pluralist approach failed through the inability to distinguish the species category and the species organism: "mammals, hairy caterpillars, hairy seeds of certain plants and other hairy objects, would make a legitimate set" and therefore a heterogeneous species. Mayr (1987) failed to recognise that pluralist species are discrete individuals, a collective set unbounded in time and having a real meaning used to describe the observable characteristics, and are not categorical abstractions. True pluralism needs to be free from any structural boundaries, and it overcomes the underlying complexities of the species argument to enable a taxonomist to enunciate a greater accuracy in the phylogenetic classification process. This is achieved through the enabling of individuality through the recognition of set complexity (Lomabrd et al. 2010).

Mishler and Donaghue (1982) argued that a species should not be separated from higher ranks, but form a natural extension of them, and should be viewed as assemblages united by descent, and not as individuals. However, the acceptance of individuality enables a line to be drawn, upon which the kinds used in classification can be decided. These kinds then enable the understanding of higher ranks based on evolutionary relationships. Not accepting species as individuals means that the basis of higher taxonomy is grounded in arbitrariness and thus rendered meaningless. The term 'exclusivity' can be associated with kinds and is the foundation of the coalescence theory that biological entities are closely related to a particular group and, thus, objectively discernible (Baum and Donoghue 1995).

Mayden (1999) conceived the consistent approach of species delimitation, in which there was an encouragement of co-operation in the understanding of diversity and for conceptual monism. At the heart of this monist approach is the recognition of the species based on a description or diagnosis that is used as the criterion for demarcation, which is then defined by a concept (Mayden 1999). However, one universal failure of species concepts is the lack of conceptual definition, which should be resolved before the population can be determined (Hausdorf 2011). This is probably more relevant to species delineation than any conceptual approach. Hey (2006, p. 459) argued that "detection protocols are not concepts" and the taxonomist needs to separate the criteria for delineating species from the "theoretical understanding of the way species exist", that is, the concept. This idea places the recognition of a species outside the confines of any preconception of how a species should be conceptualised. There is a need for species pluralism, which is the overarching monist concept, and has been the underlying goal of all species conceptual arguments.

A fundamental pluralistic approach seeks to bring an overarching conceptuality to the differing species concepts, in which the goal is not an abandonment of any one concept *per se*, but rather an acceptance that each concept is an operational tool to be used in the discovery of the species (Mayden 1999). The determination of the evolutionary trajectory has a priority in species demarcation, and the species concept applied is merely the tool to enable recognition of that evolutionary event at a point in time.

One of the major issues that distinguishes species concepts is the determination of where the process of evolutionary separation has been finalised, or is an on-going process marked with a lack of complete biological separation of the populations. There is a growing shift to accept species as evolutionary populations and a realisation that criteria for delimiting these species cannot be restricted but rather need to be based on factors that are outside the confines of any one isolating biological property (Naomi 2011); that is, under essentialist pluralism, the taxonomist may be aware of an essential characteristic that makes a species unusual and distinctive. This then forms the basis for a criterion, and integrated taxonomy allows the taxonomist to be free to determine a conceptual approach that provides the framework for naming a new taxon based on that distinctiveness. Therefore, under essentialist pluralism, there is no restriction on which concept is used to delineate an organism. However, there is a need to restrict the species to a point in time with defined morphospace. Thus, this conceptual freedom demands that taxonomists accept an obligation to be true to the phylogeny, and thus must justify the choice of a species concept, both in terms of a criterion for distinction and an explanation for the cause of that species existence, as well as state its relationships with others, placing the organism in context.

3.1.7 Implications for Discerning Species

Recent evolutionary essentialism has, at its core, a sense of indeterminacy in the definition of what constitutes a species (Devitt 2010). This indeterminacy can be countered if a species is first viewed as an individually unified population representing hypotheses that explain the convergence of both intrinsic and extrinsic structural essences. The acceptance of essences as having intrinsic and extrinsic properties highlights one of the theoretical failings of the current anti-essentialism debate, where species are delineated based primarily on intrinsically pseudo-phenetically inclined parameters (Lewens 2012). The intrinsic and extrinsic structural essences of collective higher taxa particular to a clade are used to form a continuum, the essence matrix, from which the organism state is then delineated. This organism state represents a static cross-section in the evolutionary history of a real population that contains all the phylogenetic restricted character essences that are exhibited by the organism and allows for group delineation (Pleijel and Rouse 2000; Figure 2).

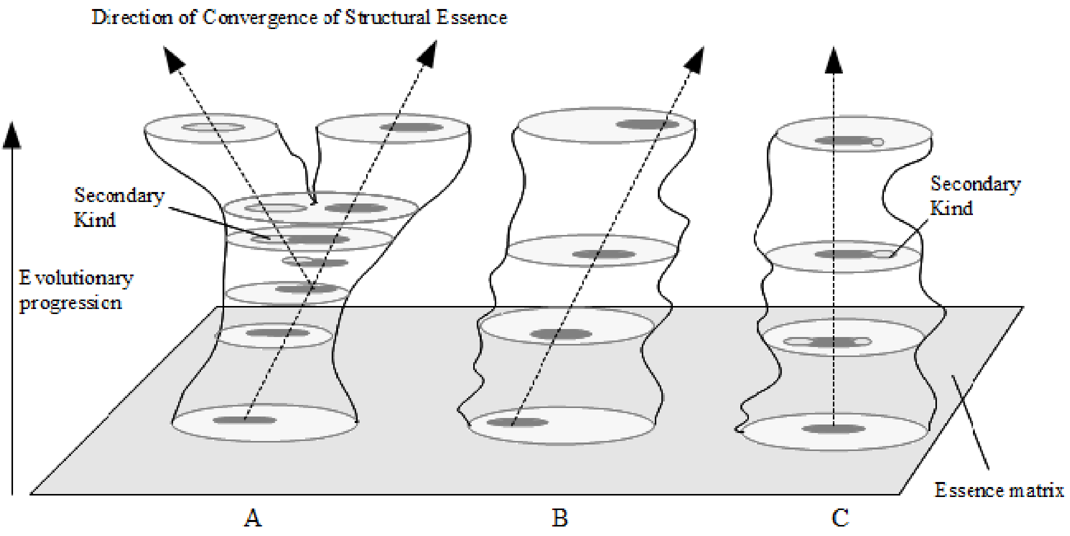


Figure 2: The use of structural essences and the organism state to illustrate how the delineation of a kind can reflect modes of evolutionary phylogenesis: A) cladogenic evolution, in which there are two distinctive kinds created, each with individual phylogenetic constraints; B) anagenic evolution, where there is a shift in the structural essence convergence giving rise to distinctive changes in the kind within relatively constant phylogenetic constraints; and C) stasiogenic evolution, in which there is with no change in the kind, illustrating also that, while phylogenetic constraints remain relatively stable, there may be reticulation.

The evolutionary progression of the organism is phylogentically constrained by the evolving and limiting structural essences. This idea of structural essences forming a unified entity is in the true Aristotelian tradition (Dumsday 2012). Notwithstanding this, the concept of phylogeny generated by the new evolutionary synthesis necessitates that these structural essences are viewed as spatio-temporally mutable. Therefore, structural essences are to be seen as historical and, possibly, changingly pluralistic in nature and, in turn, reference the wider immutable spatio-temporal.

3.2 Assigning Species or Subspecies Ranks

The choice of species rank over form or subspecies for this taxon reflects a more nuanced understanding of the role of infraspecific ordering. At the lower taxonomic levels, a "form" reflects a consistent variant within a wider population. Páll-Gergely et al. (2019)

argued that the rank of subspecies was arbitrarily applied based on “human factors”. These factors reflect the choices that the taxonomist has to make with regards to the differentiation of taxa in terms of morphology, homology and pre-existing taxonomic hypotheses (Páll-Gergely et al. 2019). However, Páll-Gergely et al. (2019) offer no practical solution as to how subspecies should be identified; rather, they are seeking a rule to regulate taxonomic decisions to avoid uneven subspecies rates between taxonomic groups. This raises the serious question of what is a “subspecies” and, in particular, once you move away from the biological species concept, how do you demarcate between subspecies and full species? Subspecies should be restricted to cryptic species, where the difference between taxa are grounded on the unobservable genetic distance; there is no morphological difference and typically no test for biological isolation between isolated populations or their clines. That is, the rank of subspecies should be applied to reflect genetic differences within a species complex, rather than used to distinguish unique taxonomic entities with observable differences. These are species. Subspecies, therefore, is a rank that should be restricted to cryptic species (Dekkers and Maxwell 2020; Maxwell et al. 2021a). This approach would provide a level of taxonomic stability to the species rank and, at the same time, address the issues identified by Páll-Gergely et al. (2019). Where a taxon can be readily identified based on observable differences, as is the case of the species in this thesis, the rank of species is justified.

3.3 Species and Their Evolutionary Context

The reliance on species relational concepts without an evolutionary context, and the linking of phenetic ideology with the concept of essence, is a failing in much of current essentialist and anti-essentialist arguments (Lewens 2012). It is only the understanding of the structural essence itself, and knowledge of the driving forces and processes that gave rise to that essence, which enables the discernment of analogies and reveals the true phylogenesis of an organism. It is how the cladist or taxonomist deals with the delineation of stages in the evolutionary progression of structural essences that then forms the basis of the restriction of the organism state and how the kind is defined. This is then consequently reflected in the criteria used in the choice of model of speciation and conception that is used to impart taxonomic meaning to all hypothetical entities called "species".

Once the taxonomist has distinguished the evolutionary trajectory of an organism based on any criterion, there is freedom to determine an appropriate conceptual approach to justify the recognition of the new species. The only requirement that is placed on the taxonomist is the need for explicitness in the justification for that conceptual choice. Essentialistic pluralism generates hypothetical terminal taxonomic units from which phylogenies are then constructed. Therefore, delimitation of species has a critical impact on the understanding of evolutionary biology where they form the spatio-temporal kind within an essence matrix, the continuum of evolutionary descent. The use of essentialistic pluralism, with its unrestricted approach to conceptualisation of what a species is using integrated taxonomy, with spatio-temporal limitations, provided the taxonomist with all the tools necessary to describe the obervable world. Essentialist pluralism is, therefore, the gold standard for universality and is the conceptual monist "Holy Grail" that has underpinned the rhetoric of species debates for centuries. It is only the fear of reputational capital loss by taxonomists who have spent their lives arguing for one concept that implicitly holds back integrated taxonomy from achieving universal acceptance.

The conceptual monist argument that pluralism leads to confusion through a lack of intrinsic meaning in the term *species* can be overcome when the taxonomist is explicit. The use of essentialist pluralism delineates a set of organisms from the natural world that contains enough meaning to enable discrimination and thus allow for an organism's taxonomic discernment. It is the failing of hierarchical taxonomic theory that, even if kinds are well defined, there remains a distinct lack of evolutionary theory or the conceptual idea of what the describing author had for the relationships between higher taxa. Therefore, essentialistic pluralism addresses the issue of species demarcation at its core. Once the taxonomist has "uniqueness" of an organism based on its distinctiveness compared to other species (or any other criterion), there is freedom to determine an appropriate conceptual approach to justify the recognition of the new species. The only requirement that is placed on the taxonomist is the need for explicitness in the justification for that conceptual choice. This leads to an argument for the use of mononomial terminal taxonomy. In addition, this new taxonomic approach to species conceptualisation has significant implications for the assignation of higher taxonomy, which is being challenged with the introduction of phylogenetic nomenclature under the PhlyoCode (2020).

The Linnaean system is a set of informal hierarchies that are simply groupings of organisms into clusters based on taxonomic preference. These are then named relative to each other without the need for historic consideration of any higher relationships. This lack of relational meaning can be traced back to the fact that relational understanding of higher systematics fundamentally eluded Linné. The need to explain evolutionary trends has become an important facet in the modern evolutionary synthesis, and such evolutionary processes and patterns need to be reflected in the nomenclature. This contextual ambiguity has left Linnaean taxonomy struggling to demonstrate true historical relationships between the taxa within clades. Therefore, there is a strategic need to revise the lower order taxonomy and, in particular, revisit the idea of uninomials to avoid arbitrary cladistics rankings.

3.4 Summary

In this chapter, I argued that essentialistic pluralism addresses the issue of species demarcation at its core. There is a systematic imperative to understand the need to identify the *why* question when evaluating taxonomic hypotheses, with four proposed *purpose* functions associated with the evaluation of *why*. If we seek to focus on understanding *why* a species was named, rather than *how* it was named, this is its conceptional validity, then species as explanatory hypotheses are given priority over personal taxonomic prejudices, relegating the lumping/splitter debate to meaningless semantics. Ideally, *purpose* should be taken out of the *how* decision-making process, and should be independent to the objective species concept applied to all taxonomic work. In the case of this thesis, the why is answered with the taxon meets the five rationales indicative for the need of a revision (Schlick-Steiner et al. 2010).Once the taxonomist has distinguished the evolutionary trajectory of an organism based on any criterion, there is freedom to determine an appropriate conceptual approach to justify the recognition of the new species. The only requirement that is placed on the taxonomist is the need for explicitness in the justification for that conceptual choice. This invariably makes sub-specific ranks taxonomically meaningless and invariably recognises all ranks below species as individual evolutionary lines worthy of full species recognition. This leads to an argument for the use of terminal taxonomy to be declared to anchor all levels of nomenclature. Furthermore, this new taxonomic approach to species conceptualisation has significant implications for the assignation of higher taxonomy, which is often more a reflection of the lack of "room" at the lower cladistic levels under the draconian Linnaean rigid methodology. Essentialistic pluralism and terminal taxonomy present a new approach to species, and is a natural extension of using rank free phylogenetic taxonomy in higher classification.

Chapter 4 Reviewing Speciation Processes

Maxwell SJ (2022) A new putative hybrid in *Conomurex* Fischer, 1884 (Mollusca, Neostromboidae, Strombidae) with notes on the types of hybrids. *European Journal of Applied Sciences* 10(1), 401-408.

Maxwell SJ, Bordon AV, Rymer TL, Congdon BC (2019) The birth of a species and the validity of hybrid nomenclature demonstrated with a revision of hybrid taxa within Strombidae (Neostromboidae). *Proceedings of the Biological Society of Washington* 132(1), 119-130.

Once the question of what a species is has been hypothesised, it is then necessary to understand *how* they arose in order to fully understand the diversification of an organism complex that has been presented for revision. Speciation processes that govern population differentiation are complex and highly particular to individual organisms, making a broad theoretical model for the global radiation and diversification of taxa difficult to achieve (Moura et al. 2014; Pérez-Escobar et al. 2018; Wainwright et al. 2018b; Crandall et al. 2019). Notwithstanding, there are key biogeographic events that have effects on marine radiations universally, which help uncover larger scale regionally-based radiation patterns. In particular, the inter-glacial mediated sea level oscillations have had profound impacts on a wide range of shallow water marine taxa, particularly in relation to species distribution patterns with each oscillation (Borsa et al. 2013; 2016). At present, we are experiencing an inter-glacial minimum, and this has led to large areas of continental landmasses, that would otherwise be exposed, being inundated. These inundations have provided avenues for taxa dwelling within inter-glacial maxima refugia to rapidly colonise newly created niches, and have facilitated secondary contact, both processes thus providing the opportunity for rapid and ongoing speciation (Bae et al. 2016; Borsa et al. 2016; Neiva et al. 2017).

There are two primary driving forces in speciation (Figure 3): 1) sympatric, where a greater population internally fragments; and 2) allopatric, where a population expands and diverges across a range gradient leading to speciation. Allopatric speciation may also take different forms, namely 3) peripatric, where a section of a population found a new colony disjunct to the main population, and 4) parapatric, or the riving of a population

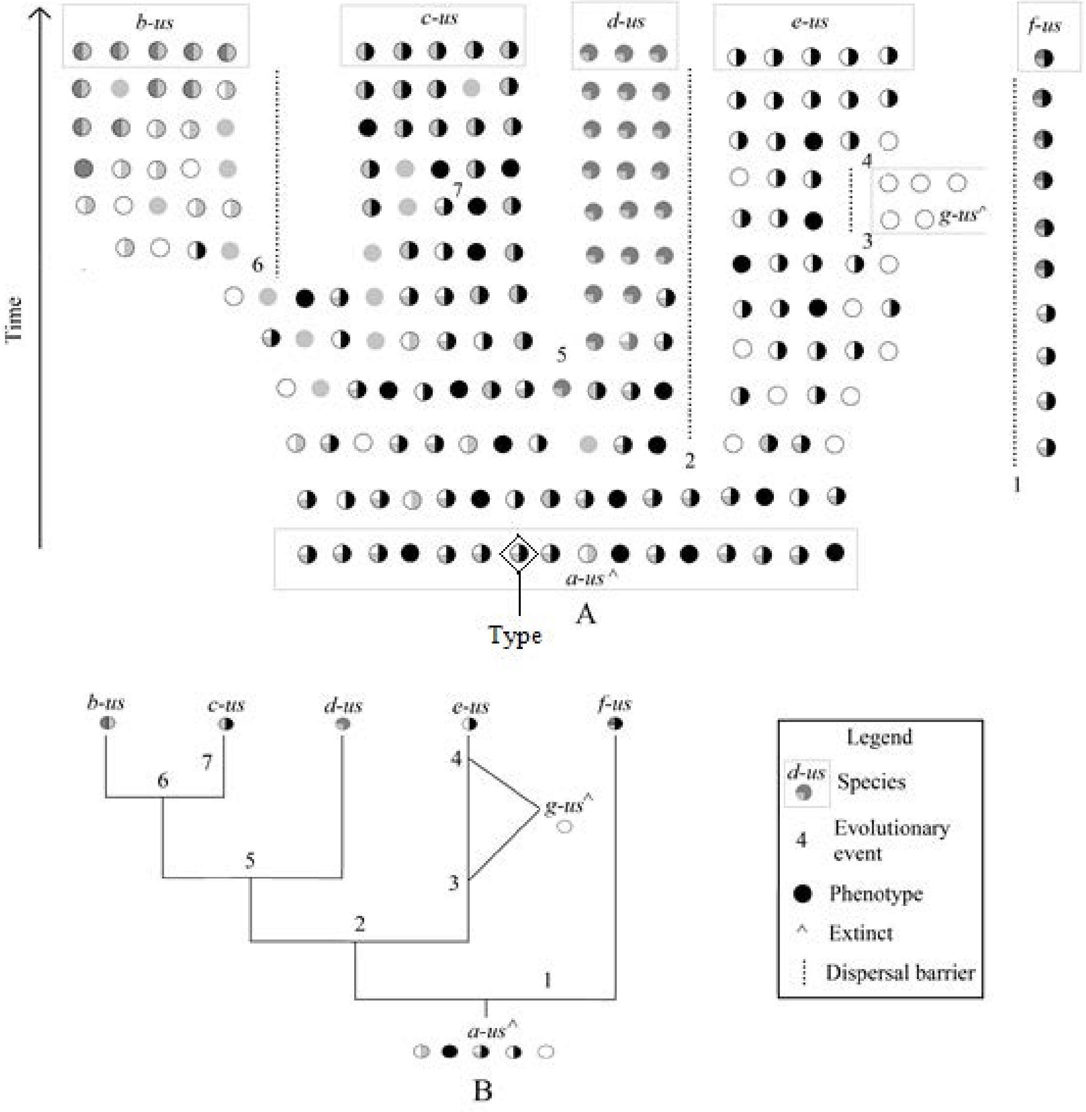


Figure 3: A simplified phenotypic map showing (A) the seven modes of cladogenic and anagenic speciation and (B) the resultant phylogeny over twelve theoretical generations. The ancestral species, a-us, has a wide distribution and extensive phenotypic variability. (1) Peripatric speciation is shown as the ancestral, a-us, a population colonises a remote location that then returns to being isolated, which in this case has resulted in either drift or selection acting to result in f-us. (2) Allopatric speciation is shown through time, and how the loss of gene flow with the parent population results in a reduction in diversity leading to the appearance of the crown taxon e-us. (3) This population also underwent a bottleneck event, which led to the formation of g-us, (4) which later reticulated back into the main e-us lineage after the barrier was removed, and this unification resulted in the extinction of g-us. (5) Sympatric speciation is demonstrated with the arrival of a novel phenotype, which may have resulted from a hybridisation event or a spontaneous mutation. This becomes regionally fixed inside the wider a-us complex, leading to reproductive isolation through time and the formation of d-us. (6) Parapatric speciation is shown as the radiation of a-us, resulting in drift and the arising of a new phenotype b-us. (7) Anagenisis through drift is also shown with the extinction of a-us and the rise of c-us.

into separate populations, leading to diversification. Vicariant speciation has been associated with three forms of speciation, namely allopatric, peripatric, and soft-vicariance, which is a form of sympatric speciation. Speciation is both passive, in terms of drift and anagenisis, and reactionary, such as with cladogenesis through ecological change, with the subsequent effects of that change on the life histories of the organism leading to lineage splitting.

The rules governing the application of names to hybrids in zoology is problematic. In terms of nomenclature, I have two further aims that involve testing the validity of taxa that are now considered invalid, due to their putative hybrid roots, through: 1) presenting an argument for justification as taxonomically valid those established taxa that can be demonstrated to have been derived from ancestral reticulation; and 2) presenting an argument for taxonomic invalidity of names that have been applied to random or sporadic putative hybrids that represent an evolutionary anomaly, rather than a reticulatory tokogenic event.

4.1 Fragmentary (Sympatric) Speciation

While sympatric speciation occurs mostly as a consequence of disruptive selection within a population, resulting in polymorphism and isolation from the parent taxon (Barton and Charlesworth 1984), another form of sympatric speciation occurs through ecological disruptive selection at the micro-habitat level (Whitney et al. 2018). Historically, sympatric speciation was thought to be driven by ecological factors affecting regions of an organism’s range, leading to localised adaptation (Mayr 1947). This adaptation then led to the evolution of new taxa (Thorpe 1945). Mayr (1946a) further suggested that sympatric speciation had occurred when two overlapping populations with the same ancestry had achieved complete reproductive isolation. Furthermore, Mayr (1946b) suggested that, no matter how close sympatric species were, there would be some level of differentiation observed due to niche differentiation or behavioural modification driving the speciation process.

A form of sympatric speciation is soft-vicariance, or shifting balance, which is defined as the fragmentation of wide-ranging ancestral taxa, giving rise to a low number of weak polygenetic mutations that lead to gradual isolation (Barton and Charlesworth 1984; Hickerson and Meyer 2008). Hickerson and Meyer (2008) argued that marine populations less than one migrant per one hundred population per generation are subject to potential soft-vicariance driven speciation. Planes and Fauvelot (2002) demonstrated that a level of stability in population structure through time on island chains is achieved where a small level of outside recruitment enables local genetic differentiation from surrounding populations, but at a recruitment level large enough to prevent fixation of those differences, with gene flow preserving the species cohesion despite geographic isolation. In cases where gene flow does not prevent fixation of genetic differences, speciation may occur naturally through time as a consequence of drift. Soft-vicariant species are often circumscribed based on genetic distances giving rise to cryptic species; these taxa may reticulate through time (Cheng and Sha 2017; Liu et al. 2019). Where reticulation is insufficient to maintain cohesion, these cryptic species may develop morphological differences (Ravago-Gotanco et al. 2018).

4.2 Vicariant (Allopatric) Speciation

A vicariant species occurs when the population gradually divides and loses effective gene flow between larger populations through time. Often there is a zone of reticulation, but these hybrids never establish, and the two parental populations eventually become isolated. This form of speciation is the result of shifting selection pressures resulting in drift, with a slow to moderate rate of polygenic mutation (Barton and Charlesworth 1984).

The earliest practical use of allopatry was in terms of describing forms within an already divided greater population, and these forms were then used as reference points to discuss reticulatory theory (Epling 1947; Hairston and Pope 1948; Chapin 1948; Ripley 1949). Epling (1947) illustrated two examples of allopatric species. These were based on a common ancestry, rather than the cladagenic process, but Epling (1947) struggled theoretically with taxa that had reticulated in the region of distributional overlap, preferring the term to be used for clearly demarcated populations. Mayr (1949) found it necessary to reinforce the distinct nature of species in the light of the imprecise application of the term by botanists in particular (*cf.* Epling 1947; Heiser 1947), without regions of hybridisation as allopatric, and that if there were regions of hybridisation, they should be considered sympatric rather than allopatric. This necessity to have a hybrid-free criterion was a natural consequence of the rise of reproductive isolation as the new theory for species delimitation (Mayr 1942). Therefore, the concept of allopatric species was introduced to distinguish species that had three evolutionary qualities: "(1) it continually moulds all the populations of a species to be adapted to their local environment, (2) it remodels isolated portions of a species while they are protected against gene flow from the main body of the species, and (3) it perfects isolating mechanisms after the two populations have re-established contact and eliminates individuals with imperfect isolating mechanism" (Mayr 1949, p. 519). This approach was then followed by later workers, who defined allopatric species as those belonging to distinct populations of unique species without regions of overlap that generated viable offspring (Clay 1949).

White et al. (1967 in Key 1968, p. 14) defined stasipatric speciation as "the direct conversion of an essentially continuous population into a number of contiguous taxa…

by the spread of chromosomal rearrangements around which isolating mechanisms develop”. Stasipatric speciation is based on the post-allopatric reconnection of two divergent populations; in that sense, it straddles both allopatric and geographic isolation, or parapatric, ideas of species evolution (Key 1968). In theory, stasipatric conceptions for speciation explain how diverged allopatric species have come together and reticulated, rather than being a model mechanism for speciation (Patton 1969).

4.3 Founder (Peripatric) Speciation

Founder, or peripatric speciation, occurs when an organism colonises a new geographically isolated area, and is generally applied to smaller populations that break away from the parent stock. Early founder theory was based on the idea of complete biological reproductive isolation and homeostatic disruption in order to facilitate change (Mayr 1963; Mayr in Mayr and Provine 1980). Similarly, Carson (1968) proposed that speciation could occur via complete isolation where epistasis would lead to the expression of traits that would otherwise be masked by the expression of a dominant trait: this is post-isolation drift and fixation in conception. Templeton (1977, 1979) argued that effective founder populations needed to go through a bottleneck, where extreme inbreeding drove disequilibrium in the Hardy-Weinberg equilibrium, allowing for isolation mechanisms such as mutation, restrictive mating, lack of gene flow, a small population and a form of natural selection driving the loss of genotypes, to occur. However, it was the seminal work of Endler (1977) on the need for understanding geographic variation and clines in the determination of species that pushed the idea of founder speciation back into the mainstream of evolutionary biology discourse. Kaneshiro (1980) shifted the focus in founder theory away from the purist biological conception, and this shift enabled the development of alternative hypotheses for speciation, such as the behavioural isolation model.

The early use of the term *peripatric* speciation was in relation to explaining the origin and reticulation of subspecies within a wider organism complex, rather than complete cladogenesis (Levin 1983). Barton and Charlesworth (1984) brought together the divergent founder theories (Mayr 1963; Carson 1968; Templeton 1977, 1979; Kaneshrio 1980) and systemised the term *peripatric*, formally defining the characteristics of the theory in terms of two isolationist drift models. The first model, known as Fisherian, or pure peripatricy, occurs where there is spatial differentiation, limiting the number of mutations in the diverging population and leading to background homozygosity derived from strong epistatic polymorphic selection. The second model, known as Wrightian, or founder-flush, occurs where selection is relaxed and there is only moderate epistatic polymorphic selection. However, the failing of Barton and Charlesworth (1984) was the contextualising of founder theory only in terms of the biological conception of species, explicitly backing Mayr (in Mayr and Provine1980) during a period of increased debate on what and how species are defined.

4.4 Parapatric Speciation

Parapatric speciation involves the breakdown and dividing of a distribution of an organism by rapid environmental change (Jain and Bradshaw 1966; Yamaguchi and Iwasa 2017). In particular, to be considered parapatric speciation, there needs to be spatial variation in selection, with limited mutations, and genetic transience, where there is a disruption in the Hardy-Weinberg equilibrium, with limited epistatic events (Barton and Charlesworth 1984).

Smith (1955, 1965) refined the term *parapatric* for situations where ranges are in some form of contact. This is in contrast to dichopatry, where populations are not in contact.

This was done to overcome the idea of a seamed separation that is necessary by the definition of parapatry. Thus, due to Smith (1965), the idea of allopatric speciation is the divergence of two neighbouring populations that do not have overlaying regions of viable hybridisation. It was Jain and Bradshaw (1966) who refined the term *parapatric* to mean the separation of a population by very narrow zones occurring as a result of rapid environmental change, which left two populations isolated and diverging as a consequence of drift and possible shifts in selection pressures.

4.5 Hybridisation

Hybridisation is the functional pathway to achieving reticulate evolution, and is a process that has profound effects on speciation theory (Hegarty and Hiscock 2005; Mallet 2005; Schwarz et al. 2005; Mavárez et al. 2006; Mallet et al. 2007; Abbott et al. 2013; Eroukhmanoff et al. 2013; Kang et al. 2013; Amaral et al. 2014; Xing et al. 2014; Capblancq et al. 2015; Suzuki et al. 2016; Lamichhaney et al. 2018; Maxwell et al. 2019a). Trace evidence of hybridisation appearing as discordant signals in molecular evidence occurs in the majority of taxonomic groups (Pons et al. 2014; Toews et al. 2014; Bernal et al. 2017). This highlights the need for reticulation processes to be considered in phylogenetic analyses (Soltis and Soltis 2009). This is particularly the case when there is inter-generic hybridisation, where the impact of unidentified hybrid character-states has an effect on the generation and interpretation of phylogenies.

Classifying hybrid entities has been problematic, and the process of classification has been primarily driven by the systematic bias of the taxonomist (Barton 2001, Schwenk et al. 2008; Amaral et al. 2014). Historically, most hybrids have been viewed as everything from anecdotal abnormalities (Canestrelli et al. 2017) and evolutionary noise that can blur species boundaries (Mallet 2008; Soltis and Soltis 2009; Capblancq et al. 2015), to significant threats to biodiversity (Allendorf et al. 2001; Seehausen 2006; Gilman and Behm 2011). Each perspective treats the validity of a hybrid based on a disciplinary approach, rather than an indicator of potential or current speciation. The level of reproductive isolation of hybrids is often difficult to ascertain (Buerkle et al. 2000). The only exception to this ability to discern offspring isolation from its parental stock is allopolyploid hybridisation, where instantaneous speciation occurs, as backcrossing between diploid parents and tetraploid hybrids cannot produce fertile offspring (Seehausen 2006; Abbott et al. 2013). Other non-reproductive isolating mechanisms that may lead to speciation, typically through spatial or ecological separation, or by behavioural divergence, such as assortative mating, are unlikely to be driven by a hybridisation event, but rather are likely to be the consequence of drift (Gross and Rieseberg 2004; Meyer et al. 2006; Amaral et al. 2014). As a result, conceptionally, it is difficult to classify a hybrid where the process of reticulation leads to a large variation in form, particularly when the reticulation is both historical and an ongoing event between two periodically connected populations. Hybridisation poses a significant complication to the taxonomy of extinct species because of the necessity of using morphology in studying fossils. Hybridisation can result in an overestimation of species boundaries, making systematic reconstruction problematic, particularly when hybrids become re-absorbed into the parental line and affect its phenotypes. Furthermore, whenever hybridisation is common between taxa, the resulting crosses will have an impact on the fossil record, even when the hybrids are infertile, due to the weight in numbers within the record. In extant taxa, hybrid-mediated speciation is well documented, although there is some level of confusion on how species derived from hybridisation should be treated in the literature (ICZN 1999; Newcombe et al. 2000; Vallejo-Marín and Hiscock 2016; Cruywagen et al. 2017).

4.5.1 Taxonomy and Hybrids

The treatment of hybrids in terms of nomenclature is largely dependent on the species concept that is applied at the time the definition of the species is made. Hybrids are not seen as problematic to the phylogenetic species concept, which uses total genetic distance as the primary determinant of species status (Baum et al. 2009; Cruywagen et al. 2017). In contrast, hybrid species clearly conflict with the biological species concept, which uses reproductive isolation as the main criterion of taxa separation (Taylor et al. 2000). The phenetic species concept, which is based on morphological similarity, is not in direct conflict with hybrid speciation, but the use of this framework can lead to infertile or non-persistent hybrids being identified as new taxa (Cruywagen et al. 2017). The phenetic concept, however, fails to provide a reliable means of hybrid species recognition when hybrids are morphologically similar to one of their parental species (Amaral et al. 2014). The rules that govern taxonomy are not so bound up by the debates on species conception regarding hybrids, but rather sideline them in a framework outside the formal literature.

4.5.2 The Rules and Hybrids

There is clear conflict between the necessity to record the reticulatory process within the nomenclature and the recognition of an established hybrid in the International Code of Zoological Nomenclature (ICZN 1999). Primarily, there is provision for recognition of hybrid names. However, it is unclear whether the named organism is considered a valid species *senso stricto*. There are three articles of the ICZN (1999) that deal with hybrids:

> 1.3. Exclusions. Excluded from the provisions of the Code are names... . 1.3.3. for hybrid specimens as such for taxa which are of hybrid origin see Article 17.2;
>
> Article 17. Names found to denote more than one taxon, or taxa of hybrid origin, or based on parts or stages of animals or of unusual specimens. The availability of a name is not affected

> even if it is applied to a taxon known, or later found, to be of hybrid origin (see also Article 23.8);
>
> Article 23.8. Application to species-group names established on hybrids. A species-group name established for an animal later found to be a hybrid [Article 17] must not be used as the valid name for either of the parental species, even if it is older than all other available names for them. Such a name may enter into homonymy. For names based on taxa which are of hybrid origin see Article 17.2.

At this point, the intersection of nomenclatural acceptance of names given to hybrids with their general use outside the literature, and the ICZN (1999) rules on the acceptance of hybridisation names and their accepted use in the literature, becomes problematic. While the name may be considered valid, the organism may not, in fact, be considered a species. It is critically important at this point to revise the original description, and determine the taxonomic intent of the author. This intent needs to be classified either as a description of: 1) a hybrid with no indication of population establishment; 2) an established population that has arisen post-hybridisation, which may include an ongoing process of reticulation with the progenitors, as well as internal reproductive viability; and 3) a new species then not recognised as a hybrid. In terms of the ICZN (1999), under the first point, a name is taxonomically invalid, given that there was no intention to erect a valid taxon, but merely to recognise an organism of interest. Under the second point, the reference to the ancestry as being of hybrid stock should not preclude the validity of a taxon to gain recognition as a species. Finally, under the third point, there was clear intent to describe a new species, whereas article 23.8 makes it clear that the name given to a hybrid should not be applied to either of the parent species and is not relevant to the recognition of the hybrid. Article 17 makes names given to hybrids invalid taxonomically. However, this gives rise to an ancestral question: at which point in the process of reticulation are parental stock deemed to be hybrids? In other words, there needs to be a determination of a point of taxonomic divergence where the entity can gain recognition in its own right. For a hybrid to be recognised as a new species, it has to: a) establish a persistent population; b) overcome inbreeding depression; and c) attain reproductive isolation (Lamichhaney et al. 2018). An established hybrid species population must demonstrate continuous breeding within itself with minimum to no backcrossing (Zhou et al. 2005; Zhang et al. 2017).

4.5.3 Hybrid Derived Species

When undertaking a systematic revision into a set of organisms, it is imperative that consideration is given to the representative taxa in the fossil record to identify those that may represent an episodic hybridisation event or an ongoing reticulation process. Similarly, when seeking to estimate the potential impact of hybridisation on a phylogeny, it is worth examining descendant extant taxa to determine the current level of hybridisation across a clade, and extrapolate that back down the phylogeny. Thus, there is a necessity to consider the reticulatory potential of a set of organisms when defining clades, and also in the determination of their phylogenetic internal resolution.

There also needs to be an understanding of the potential role of hybridisation when seeking to understand the evolution of a set of organisms. Is the hybridisation a random infertile mating event? Do the hybrids represent the reticulation of two species? Or is the hybridisation the birth of a new species? One way to answer these questions is to visualise hybrids in terms of the diktyzonos, or organism states, the parental and hybrid taxa fill (Maxwell et al. 2019a; Maxwell 2022; Figure 4).

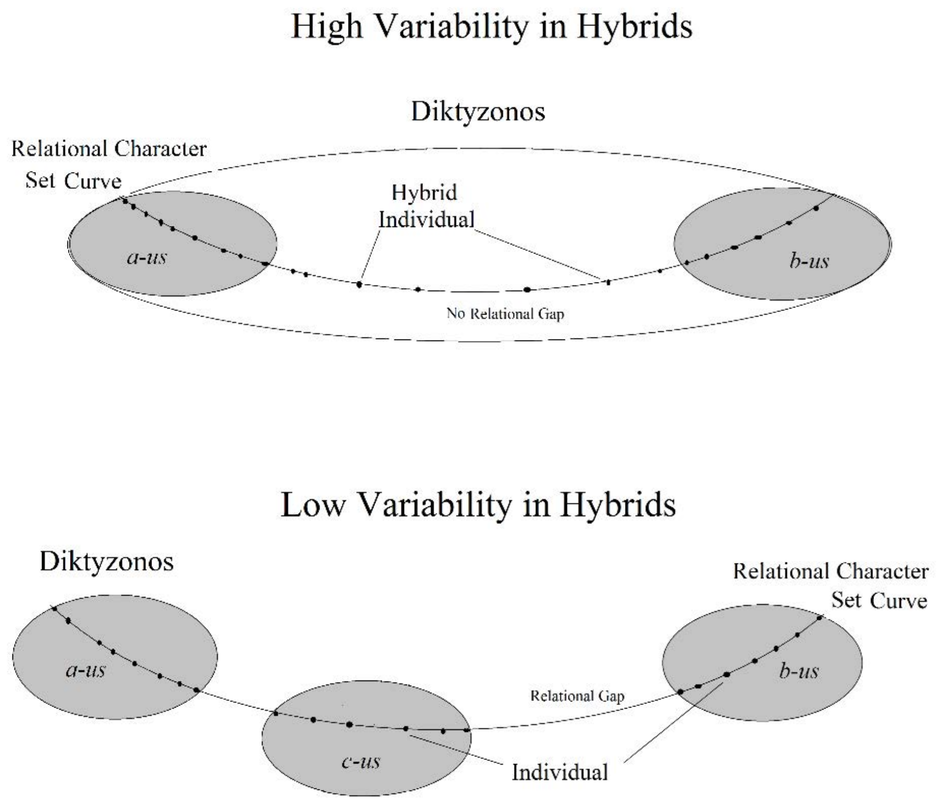


Figure 4: The two forms of expressed hybridisation between species: a level of high variability with a large diktyzonotic region that may blur the character set limits for each of the parental taxa; and low variability hybrids, which may lead the taxonomist to concur that there are three distinct regions of diktyzonos, indicating that there maybe three species, and a test of establishment needs to be considered to determine if a speciation event has occurred (Maxwell 2022).

The classification of hybrids into distinct classes, each of which has a potentially different outcome for the evolution of a set of organisms, enables a robust understanding of how hybrids are affecting evolutionary trends. This is particularly important when considering taxa that have a high propensity to hybridise, and when considering the morphological variability of the resulting hybrids. In populations where there is a high degree of variability in the hybrid offspring, and the hybrids differ in the morphological characters they express leading to some tendency to favour the morphology of either parent, the diktyzonos between the two parental organism states tends to become blurred. In contrast, where there is low variability in the morphospace occupied by hybrids and they form and cluster somewhere between the parental stock, this gives rise to three distinct regions of clustered organisms with differing morphological characteristics, and may lead the taxonomist to infer that there are three regions of diktyzonism and an inference that there are three species within the morphospace.

In clades where there is evidence for strong hybridisation in extant taxa, these hybrids will generate a plethora of forms and varieties in the clade, each of which may indicate processes of reticulation, where two species are introgressing, and/or speciating, or may just be indicators of random mating events. While three forms of hybridisation are well recognised in the literature among a diverse set of organisms, these have not been clearly delineated or defined. To address this, Maxwell (2022) proposed the following terms (Figure 5): 1) t*rue hybrids*, which are isolated examples of the congruence of two species and not reproductively viable; 2) *reticulatory hybrids*, which are evidence of the merging of two species; and 3) *diversificatory hybrid*s, which are the product of hybridisation between two species that results in a new species being formed. The question then is, when is a hybrid to be recognised in the literature as a new species? Maxwell (2022) suggested that it is *diversifacatory hybrids*, where the hybrid population has established a permanent presence alongside parental stock giving rise to a new taxonomic entity, which should be given taxonomic status within the nomenclature (Grant and Grant 1993, 1996; Kraak et al. 2001; Lamont et al. 2003; Bettles et al. 2005; Mercaderm et al. 2009; Maxwell et al. 2019a).

Failure to include hybridisation in speciation modelling for a set of organisms will potentially have a negative impact on the determination of a phylogeny because of the consequence of trickle-down discordance (Baum et al. 2009). When seeking to estimate

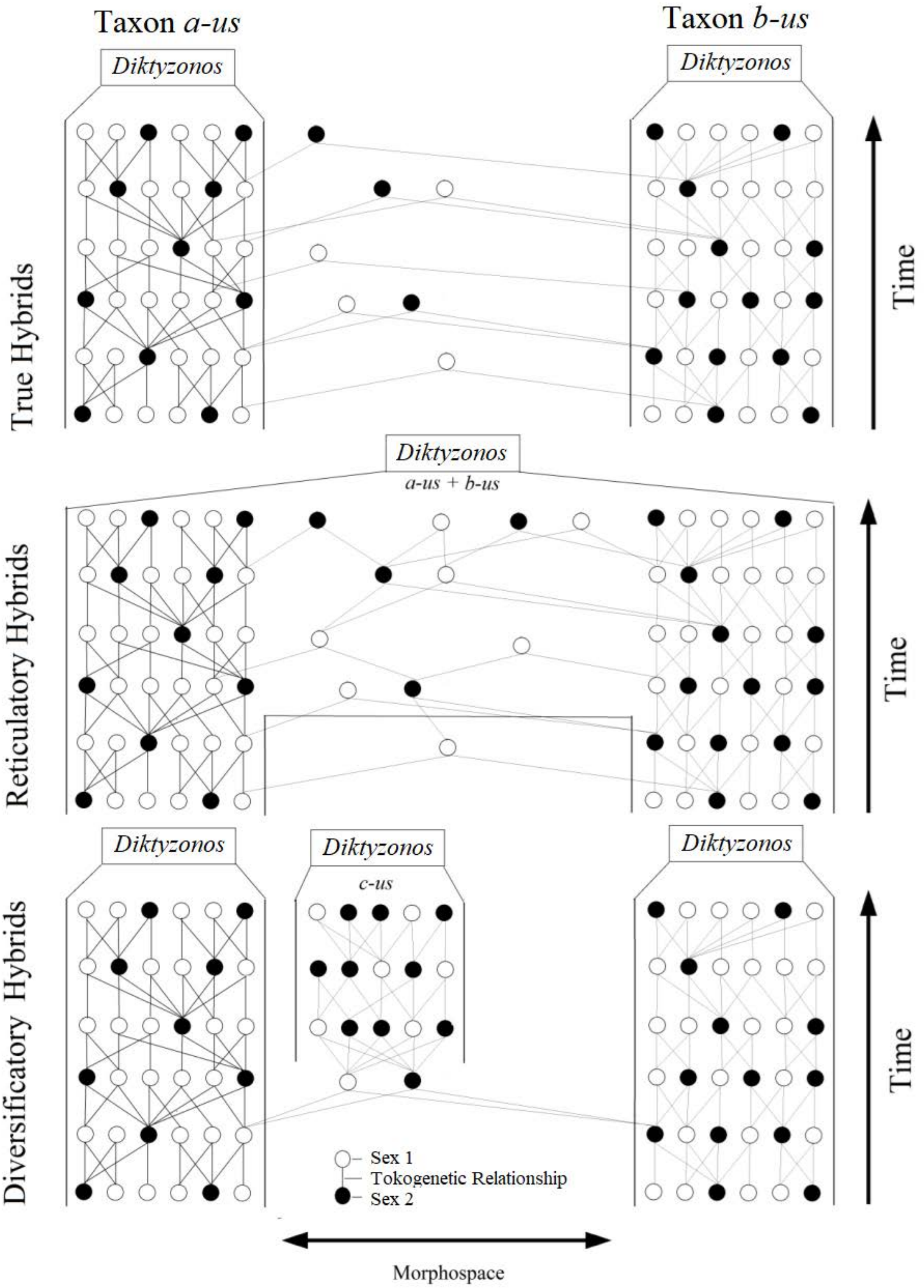


Figure 5: Three forms of theoretical hybridisation: true hybrids, which are sporadic infertile outcomes of the mating of two taxa; reticulatory hybrids, which are generated when two species come together and generate viable offspring that then cause the merging of the two parental taxa; and diversifactory hybrids where two species hybridise and produce viable offspring that then form a taxon that is distinguishable from both of the parental taxa. Mapping hybridisation across a phylogeny will enable a more accurate assessment of reticulatory potential, and facilitate a more comprehensive understating of the relationships between reticulation-driven speciation reflected in fossil taxa (Maxwell 2022).

the potential impact of hybridisation on a phylogeny, it is worth examining descendant extant taxa to determine the current level of hybridisation across a clade, and extrapolate that back down the phylogeny. Thus, there is a need to consider the reticulatory potential of a set of organisms when defining clades, and in the determination of their phylogenetic internal resolution (Maxwell et al. 2019a; Maxwell 2022).

Hybridisation poses a significant complication to the taxonomy of extinct species because of the necessity of using morphology in studying fossils. Hybridisation can result in an overestimation of species boundaries, making systematic reconstruction problematic, particularly when hybrids become reabsorbed into the parental line(s), affecting its(their) phenotype(s) (Maxwell et al. 2019a). Furthermore, whenever hybridisation is common between taxa, the resulting crosses will have an impact on the fossil record, even when the hybrids are infertile, due to the weight in numbers within the record.

Mapping hybridisation across a phylogeny will enable a more accurate assessment of the reticulatory potential between species, and facilitate a more comprehensive understating of the relationships between reticulation-driven speciation reflected in the fossil taxa. This will also enable the discernment of new species, with narrow diversicatory diktyzonotic parameters, from a broader diktyzonos of true hybrids between the putative parental stock. Futhermore, it allows those spcies that are undergoing a process of reticulation with a broad spread of hybrid forms without a region of morphologically stable clustering to be identified.

4.6 Summary

This chapter examined the modalities of speciation, and explored the role hybrids play in species evolution. While there is extensive literature on hybridisation, the placement of these in the nomenclature has not been fully explored. To address this, three forms of hybrid are defined in relation to the diktyzonotic regions that the hybrid and the parental stock occupy. This then provides the criteria for the classification of a hybrid, and guides the taxonomist to how that organism is to be dealt with in terms of the literature.

Chapter 5 The Theory of Higher Classification

Maxwell SJ, Dekkers AM, Rymer TL, Congdon BC (2020) Towards Resolving the American and West African Strombidae (Mollusca: Gastropoda: Neostromboidae) Using Integrated Taxonomy. *The Festivus* 52(1), 3–38.

Revision of organism complexes must also examine their relationships to the sister taxa, and how they fit into the more general higher classification matrix. Higher classification in biology has two fundamental roles: it provides a practical definition for the ordering of the reference list of species, and it provides a diagnosis that describes how that list can be derived (Benton 2000). Therefore, the role of higher classification is to elucidate the evolutionary relationships between organisms and serve to provide a tool for comparative evolutionary analyses (de Queiroz and Gauthier 1990; Benton 2000). Furthermore, the diagnosis is supplemented with a description that states the innate characteristics of the organisms that are to be included within a particular rank, enabling a high level of clarity on what is, or is not, to be included within the erected clades (de Queiroz and Gauthier 1990).

Ranks have historically been based on a need to recognise the phenotypic variability of organisms that are included under each classification, and these ranks have sought to encapsulate the innate breadth and uniqueness of the characters of the organisms included (Ereshefsky 2002). However, the problem with characters is that they create ambiguity, and this leads to problems of delineation in what is naturally a continuous process of evolutionary linkage within a phylogenetic system. Hennig (1965) argued for, but later abandoned, the idea that higher taxa need to be grounded by a taxon drawn from the particular time from which the lineage arose. The lack of explicit time grounding avoids arguments for the need to identify monotypic origins of higher taxa and limits the subsequent inferred nature of nodal taxa to the organisms used in its definition (Platnick

1977). Cladistic analyses need to find the point of equivalence at which there is maximum descriptive ability and maximum explanatory power, providing the optimal delineation of a taxon (Platnick 1986).

Rank hierarchy seeks to achieve a level of positioning of a taxon relative to another that allows for the creation of a class of taxa that then forms the underlying argument for ranking and subsequent ordering of the natural system (Stevens 2002). Therefore, taxa and their ancestral relationships cannot be discerned from assigned higher Linnaean ranks, which are necessary under the restrictions of that system, as they are not grounded in the phylogeny of the organisms. Linnaean ranks serve no other purpose than to group 'like' organisms. The nineteenth century concepts of adaptation, in particular the ideas of Lamarck and Darwin, were yet to be formalised when Linné formulated the system of nomenclature. This lack of theoretical importance given to the asymmetry of ranks under the Linnaean system of nomenclature has led to the lack of evolutionary justification in tree topology and nomenclature, resulting in the assignment of higher taxa within the nomenclature that provide no insights as to the evolution of the organisms that are being classified. Therefore, there is a need for a complete restructure of the higher nomenclature (de Queiroz and Gauthier 1990, 1992, 1994; de Queiroz 1996). That is, under the Linnaean system of nomenclature, when a genus is compared to other genera, there is an implicit equality in rank that, in terms of an evolutionary grounded phylogeny, may not actually be equal.

In contrast to Linnaean nomenclature, phylogenetic nomenclature is designed to show relationships based on a historically or evolutionary generated phylogeny. This hierarchical approach to the ordering of nature creates taxon-bearing reference points that then form the basis for relative comparisons, without any implications for the existence of ranks (Stevens 2002). Brochu and Samrall (2001) emphasise the benefit of explicitness and that universal meaning needs an explicit taxon name definition. That is, under phylogenetic nomenclature, name-bearing reference-points are used in formal definitions that are restricted by a diagnosis, thus enabling stable internal tree reconstruction (Schander 1998). This is in contrast to Linnaean nomenclature, where the assignment of taxa is singularly explicit in all definitions lacking relational explanations, thus giving rise to inherent paraphyletic problems. In contrast, phylogenetic nomenclature is fundamentally implicit. Instability in definition as a result of implicit description, where relationships are given priority, is only found if the definition fails to fulfil all the requirements needed to satisfy that formal definition (Benton 2000).

The use of structured or formulaic styled definitions for cladistic relationships brings clarity to the relationship between name and taxon in taxonomic definitions (Benton 2000). Much of the opposition to the acceptance of phylogenetic nomenclature is related to the misconception that it causes a loss of taxonomic freedom to deviate taxa outside the definitional framework (Lidén and Oxelman 1996; Lidén et al. 1997; Bryant and Cantino 2002). The disruption to the use of the nomenclature in the real world that may occur with the adoption of a phylogenetic rank-free system, and the subsequent changes in nomenclature that result from different approaches to the construction of phylogenies, can be minimised if the existing type-based taxa have priority in determining the named regions of inclusivity. The use of types can avoid such instability by providing stable markers for defining the limits of inclusivity (Blackwell 2002).

Recent works that apply phylogenetic nomenclature to biological revisions have demonstrated that streamlined transitions from traditional Linnaean nomenclature to relationship-based phylogenetic nomenclature can be achieved (Cantino et al. 1997; Pleijel 1999; Härlin and Härlin 2001). In order to avoid ambiguity in the definition of a clade there needs to be accuracy in the wording of the definition, avoidance of reference inspecificity, and provision of phylogenetic definitions of included taxa (Bryant 1996).

5.1 Practical Definitions in Higher Taxonomy

With the PhyloCode (2019) revolutionising the way in which definitions are used in taxonomy, a review of the principles that govern the defining of clades needs to be explored. There are three ways a clade can be defined in higher taxa: first, node-based, where the most common ancestor of two terminals or clades and all their descendants are included; second, stem-based, where all taxa more closely related to an organism than to another are included; and third, apomorphy-based, where all taxa that share particular unique characters are included (de Queiroz and Gauthier 1990, 1992, 1994; Bryant 1994; de Queiroz 1996; Sereno 1999; Benton 2000; Bryant and Cantino 2002).

The node-based structural definition is clarified in terms of the point of delineation of two or more taxa from a common ancestor (de Queiroz and Gauthier 1992; Sereno 1999). Any node-based definition must use taxa that are at least inclusive and well nested within the clade to avoid relocation and internal inconsistency resulting in the creation of impossible clades (de Queiroz and Gauthier 1990; Schander and Thollesson 1995; Sereno 1999; Bryant and Cantino 2002). The use of names of multiple subordinate taxa in the node-based definition is only an issue in terms of stability if the taxa used in the definition are poorly supported (Sereno 1999; Bryant and Cantino 2002). All taxa that are basal need not be included. However, the definition needs to comprise enough basal taxa to avoid a more reduced inclusive clade than was originally intended. This use of designated phylogenetic context (Bryant and Cantino 2002) is a means of maximising stability within a node-based definition. Cantino et al. (1997) outlined recommendations in the definition in order to maximise stability. First, there must be a level of ‘substantial evidence’. Without this, there would be confusion through proliferation of phylogenetic synonyms.

Second, a taxon whose membership is questionable should be avoided. Third, Sereno (1999) argued that the number of inclusive taxa used in the definition is dependent on whether the clade content is well supported and nested. The use of well-supported and nested taxa increases the clade stability, even as taxa are internally redistributed.

The stem-based structure for naming clades is based on the closer relationship between an ancestral taxon and its descendants than to more distant taxa (de Queiroz and Gauthier 1992; Sereno 1999). The stem-based definition in phylogenetic nomenclature is suited to revisions that have a lack of prior tree resolution (de Queiroz and Gauthier 1990; Sereno 1999; Bryant and Cantino 2002). The use of stem-based nomenclature also allows future division of all levels of taxa, and free movement within, or out of, a particular clade, which in turn eliminates the restrictions that the assignment of apomorphy and node-based definitions create. Dyke (2002) suggested that the movement of a taxon would cause greater inclusion than the definition intended if the taxon that is used in the definition is involved in the movement. However, in his example of theropod dinosaurs, the principle concerns were of synonymic duplication as resolution increased. This is an issue for stem-based definitions only if ‘proper’ formulation of the principle definition from the start is lacking. Therefore, Dyke (2002) failed to recognise stability and unambiguous interpretation as having priority. It is only when priority is given to stability and clarity that the problem of proliferation of unnecessary definitions can be overcome, a concern to those who would oppose phylogenetic stem-based definitions (Dyke 2002). The stem-based definition grants higher significance to terminals, avoids ranking into unnecessary Linnaean categories, gives priority to clades irrespective of characters and the need for inclusiveness, and is determined principally by historical phylogeny (Härlin 1999).

The apomorphy-based definition of a clade is based on the synapomorphy of the first ancestor in which it arose and includes all its descendants (de Queiroz and Gauthier 1992; Sereno 1999). The use of apomorphy-based definitions in phylogenetic nomenclature is a major area of contention (Bryant 1994; Schander and Thollesson 1995; Pleijel 1999; Sereno 1999; Bryant and Cantino 2002). The apomorphy-based structure seeks to directly tie the actual empirical evidence to the recognition of taxa (Pleijel 1999). However, it is a fundamental concept to the study of taxonomic biology, with the focus on historicity rather than morphology, that makes apomorphy-based definitions principally non-evolutionary (de Queiroz and Gautier 1992). Bryant (1994) argued for the avoidance of apomorphy-based definitions. The restriction that this definition imposes upon the tree structure, and patterns that are absent in node and stem-based definitions, is the major fallibility in this descriptive approach. Apomorphy-based definitions are fundamentally flawed because they rely on homoplasy to allow cladistic discernment, with the actions of evolutionary processes that cause the loss of primary apomorphs, and levels of continued congruence with other apomorphs of near taxa makes ancestral states problematic to identify with certainty. While Bryant and Cantino (2002) rightly point out that apomorphs do have a role in phylogenetic nomenclature, their use should be incorporated into either node or stem-based definitions as a means of providing added stability.

5.2 Bryant and Clade Definitions

A crown taxon differs from other taxon formulations by its definition being restricted to living taxa that have an immediate extinct outgroup (Sereno 1999). While it is possible to describe a crown taxon or clade with a stem-based definition, the inadvertent use of a node-based definition is the form most widely encountered within the nomenclature (de Queiroz and Gauthier 1992; Rowe and Gauthier 1992; Wyss and Meng 1996). The use of crown clades is common in much of the taxonomy, but this does not necessarily improve taxonomic clarity or stability unless it is accompanied by a structured definition (Lee 1996). The aim must be for the taxonomist to obtain maximum stability, and the definition of a crown clade must be determined by the state of resolution of the basal dichotomy (Sereno 1999). The use of a crown clade as a mode of definition does not preclude the recognition of ancestral taxa within it, only that these taxa are not used in the formulation of the definition. Bryant (1996) argued for eight conventions that facilitate effective phylogenetic taxonomic definitions of clades:

> *Phylogenetic definitions should name clades identified through phylogenetic analysis.*

There needs to be an explicit phylogenetic context and pattern to the naming of a clade (de Queiroz and Gauthier 1994). Clades need to have a basis in evolutionary fact that supports their erection. It is unnecessary to generate ranks within a hierarchy that are "space fillers" and do not contribute to the evolutionary contextualisation of the nomenclature.

> *Phylogenetic definitions should have standardised formats.*

There needs to be a standardised format in the naming of taxa. The use of a stem or node-based definition is the individual concern for the taxonomist and is dependent on the level of resolution of the clade under consideration (Sereno 1999). A clade that has a high level of internal resolution is more suited to a node-based definition, and is independent of outgroup relations, compared to a clade that has a low level of internal resolution, which is more suited to a stem-based definition.

> *Typification of taxa is an optional heuristic device for standardising hierarchical relationships among clades with particular taxon names.*

It is not necessary to include a terminal taxon in the definition at every level of the hierarchy, with higher order taxonomic ranks being sufficient if inclusivity is codified (Cantino et al. 1997). While the use of types is redundant in phylogenetic taxonomy, as the diagnosis fulfils the role of grounding the rank in the real world, types may assist with the standardising of hierarchical relationships and in defining the most inclusive taxa (de Queiroz and Gauthier 1992; Sundberg and Pleijel 1994; Bryant 1996). Bryant (1994) argued that, for a definition to achieve accuracy, there needs to be an explicit reference to a single common ancestor in the wording. Bryant (1994) also argued that providing an ancestral basis upon which a clade is grounded needs to be with the inclusion of "most recent", which has significant implications for the clade structure that is chosen. A clade with a poorly resolved basal relationship is best defined by a stem-based definition because the reference upon which it is founded is based on outgroups, which by definition implicitly creates the ancient ancestor. Another ambiguity in wording is created when the definition of a crown clade is dependent on the current non-extinction of members, where future extinctions would change the clade definition (Lucas 1992). This problem can be avoided if the terms 'extant' and 'living' are not used in the definition (Bryant 1994, 1996). This allows evolution of the definition and retains stability in meaning while losing extant taxa to extinction. Tautology also causes a level of ambiguity in the wording of cladistic definitions (Bryant 1996).

Emendation of phylogenetic definitions is necessary in particular instances but should preserve the association between taxon names and clades.

The need for emendation of cladistic names is often required when there is confusion in the wording of the definition and where there is a lack of clarity in meaning, or appropriateness of the taxa that are included (Bryant 1996). This is particularly relevant as the suffixes used under the codes for nomenclature that are attached to a name may not truly reflect the organisational position when contextualised with evolutionary evidence. There are no rules governing the use of prefixes, but the inclusion of “Neo+ type taxon” is advantageous to the recognition that a crown clade has been defined.

Crown clades should have “widely known taxon names”.

Where possible, existing taxonomic crown clade names should be retained in order to maintain stability. The current state of taxonomy often reflects the underlying phylogenetic understanding, albeit tied to ranks that obscure this. Therefore, a revision may involve a review and possible rejection of rules of priority in the ordering of ranks in nomenclature to save this taxonomy (Rowe 1998; de Queiroz and Gauthier 1992; Anderson 2002). This can be achieved if names are crown clades (Bryant 1996). The issue of implied ranking based on the Linnaean suffix means that the suffix should be amended to reflect the nature of the definition (convention 8 *vide infra*). Cantino et al. (1997) argued that current suffixes utilised by existing taxonomy could be maintained to avoid unnecessary changes and make the shift to a phylogenetic system more acceptable. In addition, taxonomists familiar with a particular taxon would still be able to recognise the cladistic group that is implied, irrespective of the suffix.

Given several “widely known taxon names” that could be used for a crown clade, the one at the lowest rank in the Linnean hierarchy should often be chosen.

If more than one name is available within the Linnaean hierarchical system, then the lowest rank should be applied. This would leave the higher ranks available for use for more inclusive clades (Bryant 1996).

Stem-based taxon names could be formed from the name of the appropriate less inclusive node-based taxon and an appropriate suffix.

The use of a suffix should be used to indicate whether the definition is based on the node, apomorph, or stem structure. De Queiroz and Gauthier (1992) suggested *-gens* or *-genea*, and Bryant (1996) suggested *-morpha* or *-formia*. However, recent revisions make the use of these suffixes somewhat problematic due to an inconsistent application to one level of rank as internal clade structures change (Bryant 1996). Furthermore, the conflation of stem and node names, with shifts in stem structure, may obscure the evolutionary meaning that each different approach to formulating a definition brings. In the present work, stems are formulated in order of nomenclatural position under the ICZN (1999).

Taxon names should have recommended usages.

Bryant (1996) argued that there may be a limitation in the use of names in particular contexts, and this may reflect the level of meaning intended at the time by the taxonomist formulating the definition. That is, there may be a need to restrict the inclusivity of a definition as the understanding of the phylogeny expands and more taxa are brought into a particular cladogram.

5.3 Methodology for Discerning Phylogeny

Pure cladistics searches are the most parsimonious hierarchical arrangements based on character scoring of terminal taxa that do not include evolutionary considerations, nor the geographical distribution of the characters used (Davis and Nixon 1992). Thus, cladistical hierarchy is purely an epistemological axiom that is without an explanatory causal hypothesis (Brower 2000). In contrast, phylogenetics is a form of cladistics that seeks to reconstruct relationships that are dependent on the distribution of characters (Davis and Nixon 1992). In order to achieve a sound basis for the reconstruction of relationships, species must be treated as separate terminals (Yeates 1995). In creating terminals, the taxonomist is then able to either intuitively deduce ground plan character states of the higher clades, or choose exemplars that represent real species, both of which have the same goal of providing the basis for coding (Yeates 1995). The discovery of islands of individuals within multiple most parsimonious trees enables the determination of these exemplars (Maddison 1991). Definitions should only be applied to clades after considered analysis and a sound basis for need has been established, particularly with reference to the delineation of islands out of a greater diverse organism character set (Brochu and Samrall 2001). This need is systematically subjective and may be argued on the basis of phylogenetic support, phenotypic distinctiveness, ecological significance, economic importance or some other argument made by the taxonomist (Forey 2002). However, it is a phylogenetic principle that the formation of the definition of higher taxa has stability and that there is unambiguous interpretation of what taxa are to be included and excluded. That is, uses of the name in association with a particular keystone taxon, represented by a type, must have priority (de Queiroz and Gauthier 1990).

5.4 Summary

In this chapter, I outlined the processes for the discernment of higher taxa, and explored the three forms of definitions used to define clades: stem, node, or apomorphy. The choice of form of definition is dependent on the level of resolution with the clade, which gives the highest level of stability to the nomenclature and, therefore, must be based on the most robust understanding of the internal content and relationships of the clade being defined. The eight conventions of Bryant (1996) outline the rationales that guide the taxonomist in selecting appropriate clades within a phylogeny to define them within the nomenclature.

Chapter 6 Material

Maxwell SJ, Rymer TL (2022) Population Structure of *Canarium* (*Canarium*) *urceus* (Mollusca, Strombidae) from Nha Trang, Vietnam. *Strombus*, 28(1-2), 1-5.

Maxwell SJ, Todd, S.J. Rymer TL (2022) Population structure and morphology of *Canarium* (*Canarium*) *incisum* (Wood, 1828) and *Canarium* (*Canarium*) *esculentum* (Maxwell, Rymer, Congdon and Dekkers 2020) (Mollusca: Neostromboidae: Strombidae) from the Philippines with preliminary notes on aperture colouration based on DArTseq Data. *Acta Zoologica* 124, 1-7.

6.1 Material Held in Collections

The sample material used in this thesis is divided into two sets of information: A) the archival material, which is held by myself; and B) material examined that is held in public and private collections. In the archival collection, the location of the sample and from whom the material was procured is noted, as well as the date (month/year) that the sample was collected, if known. Information retained from private and institutional specimens included: A) the name, town and country of the collection the specimen is held in, and its collection reference number, if applicable; and B) the location that the sample was collected from. Collection material was listed under each taxon that it pertained to.

6.2 Regions Available for Sampling

The "urceus" complex is restriced to the Indo-Australian Archipelago, and this includes the Malayan Peninsula, the flooded area of the Sunda landmass, south-western Indonesia, the Philippines and Okinawa Islands to Eastern Papua New Guinea, forming the central Indo-West Pacific, and also extends into the northwestern Australia (Hoeksema 2007; Spalding et al. 2007; Kulbicki et al. 2013; Gaboriau et al. 2018). There has been a plethora of publications that have sought to define the regions within the Indo-Australian Archipelago realm based on the phylogenetic history of a diverse set of marine organisms (Santini and Winterbottom 2002; Spalding et al. 2007; Carpenter et al. 2011; Kulbicki et al. 2013; Veron et al. 2015; Borsa et al. 2016; Yang et al. 2016; Wainwright et al. 2018b; Petuch and Berschauer 2020). From a synthesis of these papers, distinct provinces are evident, although these divisions may not hold for all organisms. They do, however, reflect a region between which there are significant differences in the composition of their biodiversity. This thesis applies the biogeographical nomenclature of Petuch and Berschauer (2020), which is based on the endemacy of Mollusca.

The Anadmanian Subprovince is isolated from the broader realm by the Malaysian Peninsula to the east, the delta of the Irawaddy River in Burma and the Andaman Island to the west, and separates the ecotone of the Malacca Straits (Santini and Winterbottom 2002; Spalding et al. 2007; Carpenter et al. 2011; Borsa et al. 2016; Kulbicki et al. 2013; Petuch and Berschauer 2020). This region has been linked to the Indian Ocean realm due to similarities between it and taxa found in the African and southern Indian regions (Spalding et al. 2007). However, this region is also distinct from the Indian Ocean realm due to the similarity of taxa with the Pacific Ocean (Yang et al. 2016), making it a region of unique significant overlap (Kulbicki et al. 2013). Furthermore, during the last interglacial maximum, this region remained relatively stable; this has held for the currents for the region, past and present (Carpenter et al. 2011; Levy and Kochzius 2016).

The Indo-Malyan Province contains the Philippines to the Sulu and Molucca Seas, East Timor, the Makassar Strait, the Java Sea, and the western Banda Sea, bounded by the Weber Line (Spalding et al. 2007; Carpenter et al. 2011). This region has remained relatively stable during the interglacial fluctuations, comprising the region generally considered Wallacea. The currents have remained relatively consistent during periods of sea level fluctuations (Carpenter et al. 2011; Levy and Kochzius 2016).

Within the Indo-Malaysian Province, an area between the Weber and Lydekker biogeographical lines in the eastern Banda Sea. This area contains a small set of islands with unique biodiversity quite distinct from the neighbouring Philippine-Indonesian and Western Australian provinces (Santini and Winterbottom 2002; Spalding et al. 2007; Borsa et al. 2016; Yang et al. 2016). This small area, the Malukuan Infraprovince, did not undergo drying during the interglacial shifts in sea level that gave rise to the greater Sahul landmass (Petuch and Berschauer 2020). This area is also unique in its circulatory currents, where it is not subjected to Indonesian flow through (Carpenter et al. 2011; Levy and Kochzius 2016).

The Meanesian Subprovince takes in the Bismarck Archipelago and the north coast of New Guinea (Spalding et al. 2007; Borsa et al. 2016; Petuch and Berschauer 2020). This region had a stable current flow during interglacial periods, and the land mass remains relatively unchanged with fluctuations of sea level (Carpenter et al. 2011; Levy and Kochzius 2016).

In order to encapsulate the known range of "urceus" and its close associates, the Northwest Australian and Southwest Pacific regions had to be added. Similarly, the broader northeastern Pacific, which includes Guam, Palau and the island chains of Japan had to be included because these regions also contain sporadic occurrences of "urceus" (Figure 6; SMC).

6.3 Locality Validation

Where material was obtained from local fishermen or resident dealers, the reliability of the data was regarded as falling within the general region of operation and the capability of the fishermen. Material was typically supplied with the market locality rather than the actual collection location. Archival material obtained from dealers or collectors was classified into two sets: A) specimens obtained by the dealer directly from the collecting source (providenced); and B) specimens that were acquired from a third party (non-providenced). All non-providenced material was considered carefully and used with caution when expanding known ranges of forms and varieties of a species. Data from private and institutional specimens were similar, and were viewed in the context of the assessment of reliability with self and local, both seen as providenced, and third-party material, seen as non-providenced.

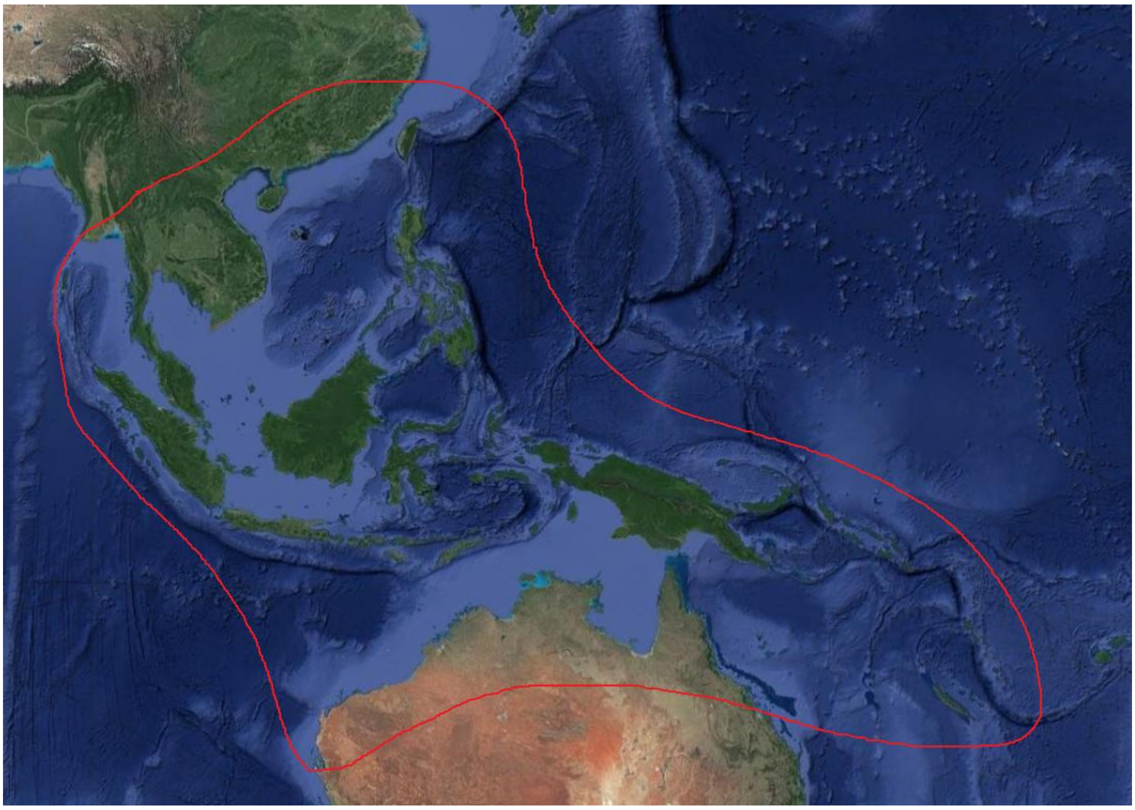


Figure 6: The region targeted for sampling in this project that encapsulate the known populations of organisms attributed to the *Canarium urceum* complex.

6.4 Assessing Samples

Assessing samples involved the determination of how the sample was derived and its nature: sorting, sexing, preserved specimen or empty shells. Understanding sorting enabled an informed judgement to be made on the level of randomness of a sample. Sorting was classified in four ways: A) self-collected by the researcher (sound); B) a random sample of mixed *Strombidae* species (mixed); C) a random sample of “urceus” (random); or D) a sample selected for a particular trait, such as uniformity in size (trait).

Sound and mixed species samples were optimal as they were not been artificially selected and were more representative of the overall population structure and phenotypes, not having undergone selection bias. Random and trait samples had experienced a level of quality selectivity by the vendor providing the specimens, with selection against juveniles, dead, or damaged specimens. In terms of size distribution, this is not an issue for random samples as phenotypic selection will not affect distribution. Trait samples on the other hand may have strong bias in size selectivity. Notwithstanding this, when samples were obtained from a second-hand source, it was assumed that the exceptionally large shells would have been removed as these specimens are often sold to specialist dealers and collectors at a premium.

Wet sample animals were removed from their shells, and the following information was documented for each specimen: total axial length; colouration of the aperture; and sex (presence of a verge indicated a male, while presence of an oviduct indicated a female); presence or absence of pseudohermaphroditism - masculinised females are readily distinguished from males and normal females by a deformed and vestigial verge (Reed 1995; see Ruaza 2019 for illustrations of sexual organs and pseudohermaphroditism). The masculinised female verge is muscular, may be multi-lobed, and may contain superficial channels with ciliated epithelia (Reed 1993b). Shells were catalogued into the Stephen Maxwell Collection (SMC) for future reference.

6.5 Discussion

Here, I provided the regions targeted for sampling and how the samples from those regions were assessed. All examined material in collections was listed under the distribution records for each species. Locations were assessed for validity and population structure, which is presented in later chapters in this thesis.

Chapter 7 Methods

Dekkers AM, **Maxwell** SJ (2020) An Examination of the Relationships Between Extant *Dolomena* Wenz, 1940, *Doxander* Wenz, 1940, *Mirabilistrombus* Kronenberg, 1998, *Neodilatilabrum* Dekkers, 2008 and *Labiostrombus* Oostingh, 1925 (Stromboidea: Neostromboidae: Strombidae). *The Festivus* 52(1), 39-59.

Liverani V, Dekkers AM, **Maxwell** SJ (2021) Resolving phylogenetic and classical nomenclature: A Revision of *Canarium* Schumacher, 1817 (Mollusca, Neostromboidae, Strombidae). *The Festivus* 53(1), 26-43.

Maxwell SJ, Dekkers AM, Rymer TL, Congdon BC (2020) Towards Resolving the American and West African Strombidae (Mollusca: Gastropoda: Neostromboidae) Using Integrated Taxonomy. *The Festivus* 52(1), 3-38.

7.1 Taxonomic Processes

There are major issues facing the review of any complex group of taxa. The treatment of existing taxonomy, the ordering of precedence, and the assessment of validity are challenges faced in any systematic review. This is often because early authors principally based their nomenclature on observable differences in illustrations (Linné 1758; Gmelin 1791; Röding 1798), which lacked the proper descriptive power that could help with the identification of the species. These works often referred to hand processed textural illustrations from earlier pictorial works, and this led to considerable variation in the interpretation of those illustrations in the finished product between authors (Linné 1758; Gmelin 1791; Röding 1798). This illustrative differences can cause confusion when the species being dealt with has many morphological variations, or is close to another species in form, or the actual specimen that was illustrated or described is unclear. Notwithstanding these issues, these (sometimes) enigmatic early descriptions are taxonomically valid under the applicable ICZN rules. The primary consideration as to whether a species has been deemed to be described is dependent on the level of consistency in the hand drawn illustration. An early description can only be resolved if the illustration and descriptions enable a clear species to be distinguished from the others, and that a clear indication of the location of the population under consideration is given. The primary considerations ought to be whether or not there is a supporting type specimen, whether the overall series of illustrations shows the characters that are unique to what is now considered one species, and whether the illustrations have variations that are exhibited in more than one currently accepted species, which could lead to confusion of the author's original intention.These obscurities affect the determination of the true identity and complicate the revision of historically described taxa. There is a requirement for an individual interpretation to be made by the reviewing taxonomist.

This type revision involved two primary steps. The first step comprised obtaining images of the type material held in two Linnaean collections linked to *C. urceus*: Uppsala University Museum of Evolution Zoology Section no. 685, MLU, no. 288 and no. 1225 a-e; and the Linnaean Society of London box LSL. 440, Dance label: P-Z 0010875. The second step involved a complete examination of each of the iconotypes listed under "urceus" in the *Systema Naturae* editions (Linné 1758, 1764, 1767; Gmelin 1791), as well as the translation and examination of the descriptive text that accompanied these references. The type specimens and iconotypes were then identified and classified, with the species level identification based on the current accepted taxonomy (Abbott 1960, WoRMS: www.marinespecies.org). After this identification process, the holotype was identified from the Uppsala University Museum of Evolution Zoology (Abbott 1960). Once identified, the type was compared to a series of "urceus" specimens from across its known range. The type locality was then corrected to the region where the phenotype represented a form consistent with the type morphology (maxwell et al.

7.2 Morphological Characters

For the morphological character analysis, all recognised members of *Neostrombini* (see

Chapter 10), which included the *Canarium* (after Abbott 1960), were included. This encompassed those that have subsequently been moved into new genera, such as *Tridentarius* and *Terestrombus.* A total of 34 taxa were selected based on the classification of Abbott (1960) and the species included in that work or described later, but within the subgenus *Canarium* (Table 1), and their derivatives. The (sub)genus *Canarium* of Abbott (1960) was at the time of this study regarded as sitting at the rank of genus (MolluscaBase 2020). The names used in Table 1 have been updated to reflect *post-hoc* taxonomic shifts.

Fourteen characteristics (Figure 7) were chosen that represent unique aspects of shell morphology for the discrimination of species morphological relationships (Liverani et al. 2021) and the coding is based on the type and examples from the type location (Table 1). Atypical examples of all species are known and have been omitted for character clarity. Characteristics were grouped into five categories: 1) shape of the shell (characteristics A-C); 2) form of the labrum (characteristics D-F); 3) form of the columella (characteristics G-I); 4) inner aperture (characteristics J); and 5) morphology of the shell (characteristics K-N). Characteristics and coding used to determine the species relationships were:

A) Form of shell: fusiform (1); orbicular (2); eliptic-rhomboid (3);
B) Teleoconch height (ventral): ~1/5 height of shell (1); ~1/4 height of shell (2); ~1/3 height of shell (3);
C) Shell thickness: fragile (1); solid (2);
D) Cross section of the labrum: spathulate (1); cunicate (2); falcate (3); acuminate (4);
E) Cross section of the labrum with fine rim ridge: absent (1); located centrally (2); located on the inner edge (3); forming outer edge of the labrum (4);

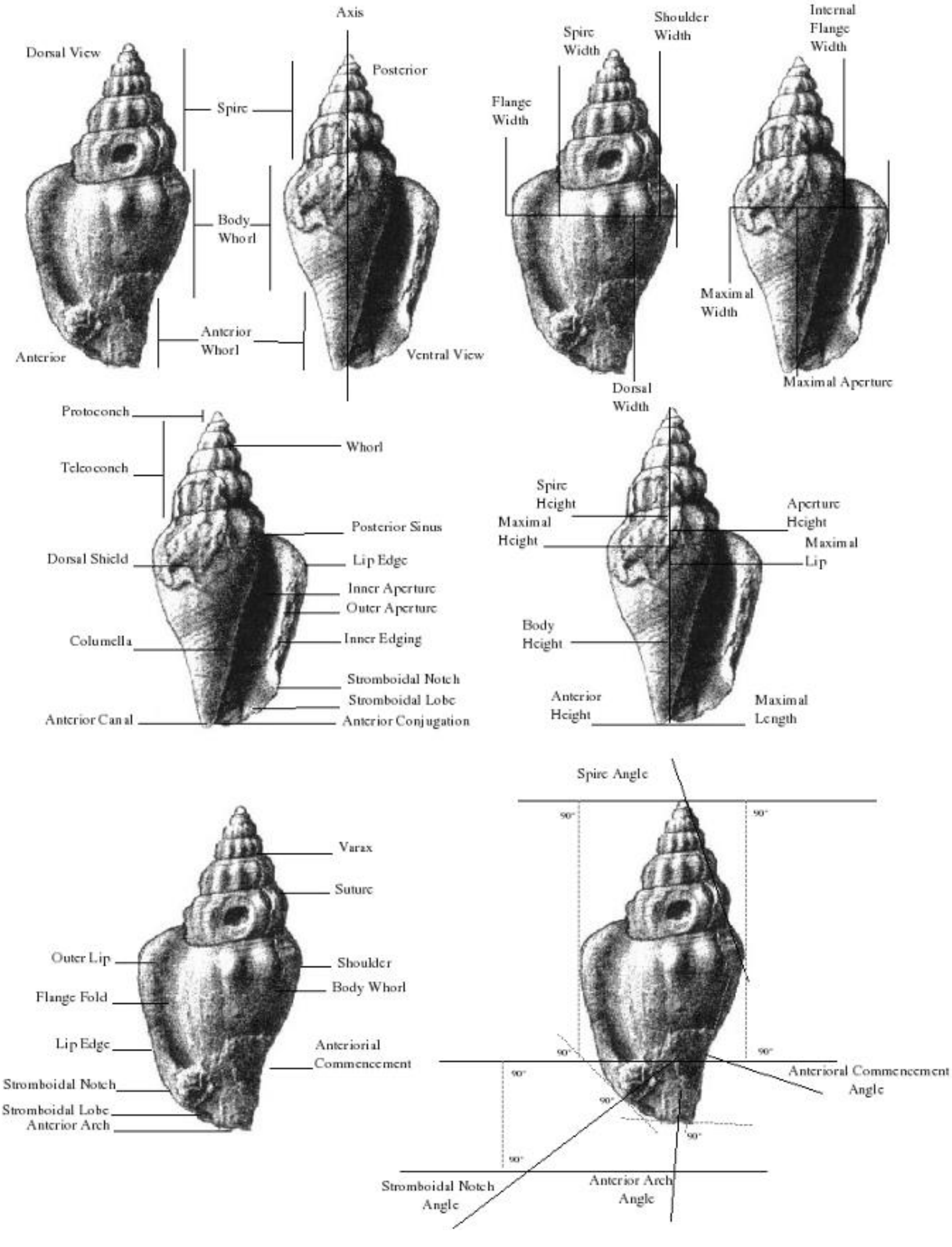


Figure 7: The shell characteristics used in the descriptions contained in this thesis.

Table 1: Coded characteristics used to determine morphological relationships and discern members of the *Canarium* complex from sister clades.

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N
afrobellatus	3	1	1	3	1	1	3	4	1	1	1	1	1	1
anatellum	3	1	2	1	2	1	1	1	3	3	2	1	3	3
andamanense	3	2	2	1	2	1	1	1	3	3	2	1	3	3
betuleti	3	1	2	1	3	1	1	2	3	3	1	1	2	2
daveyi	3	2	2	1	2	1	1	1	3	3	2	1	3	3
darwinensis	3	2	2	1	2	1	1	1	3	2	2	1	3	3
dentatus	3	1	2	3	1	2	1	1	3	3	2	1	2	2
depauperatus	3	1	2	3	1	1	1	1	3	1	1	1	2	2
elegans	3	3	2	3	4	1	1	2	4	3	2	2	3	3
erythrinum	3	2	2	3	4	1	1	2	4	3	2	2	3	3
esculentum	3	2	2	1	2	1	1	3	3	3	2	1	1	1
fragilis	3	1	1	3	1	1	3	1	1	3	1	1	1	1
fusiformis	1	2	2	2	1	1	2	1	4	2	1	1	1	1
geelvinkbaaienses	3	2	2	3	2	1	1	1	3	3	2	1	3	3
hellii	2	2	2	4	4	1	1	1	2	2	2	2	3	3
incisum	3	1	2	1	2	1	1	1	3	3	1/2	1	3	3
klineorum	3	2	2	1	3	1	1	2	3	3	3	1	3	3
labiatum	3	2	2	1	2	1	1	1	2	3	2	3	3	3
maculatus	3	1	2	3	1	1	1	1	3	1	1	1	2	2
manintveldi	3	1	2	1	2	1	1	1	3	3	2	1	3	3
microurceus	3	1	2	1	3	1	1	2	2	2	1	1	2	2
mutabile	3	1	2	1	3	1	1	1	2	2	1	1	2	2
nipponium	3	2	2	1	2	1	1	2	3	3	2	1	3	3
ochroglottis	3	2	2	1	3	1	1	2	3	3	2	1	2	2
olydium	3	2	2	1	2	1	1	1	2	3	2	3	3	3
orrae	3	2	2	1	2	1	1	1	3	3	2	3	3	3
ostergaardi	3	1	2	1	3	1	1	2	3	2	1	1	2	1
radians	3	2	3	3	4	1	2	3	2	3	2	2	3	3
rapanuensis	3	1	2	3	1	1	1	1	3	1	1	1	2	2
rugosum	3	2	2	3	4	1	1	1	4	1	2	2	3	3
scalariformis	3	2	2	4	4	1	1	1	2	2	2	2	3	3
terebellatus	3	1	1	3	1	1	3	4	1	2	1	1	1	1
urceus	3	2	2	1	2	1	1	3	3	3	3	1	3	3
wilsoni	3	1	2	1	3	1	1	1	3	3	2	1	2	2
youngorum	3	2	2	3	2	1	1	1	3	3	2	1	3	3

F) Labrum with teeth: absent (1); present (2);

G) Columellar callus: well-formed along the length of the aperture (1); diminished posteriorly (2); diminished (3);

H) Columella colouration: single colour (1); axially bicoloured (2); variably flushed with colour (3); diminished columella (4);

I) Columella liration: absent (1); completely lirate (2); anteriorly and posteriorly lirate only (3); variable and specimen dependant (4);

J) Aperture colouration: white (1); colouration only where lirate (2); coloured (3);

K) Ventral body whorl shoulder sculpture: smooth (1); nodules, which may form shoulder plications – these may be diminished (2) or strongly knobbed (3);

L) Central ventral body whorl: smooth (1); axially ribbed (2); variable (3);

M) Mid-teleoconch sculpture: smooth (1); tuberculated, which may be axially compressed and elongated (2) or axially plicated (3); and

N) Sculpture of penultimate whorl: smooth (1); tuberculated, which may be axially compressed and elongated (2) or axially plicated (3).

The MEGA X (Kumar et al. 2018) software was used to determine morphologically based clusters of species. The use of software developed for molecular analyses of character states was tested and validated in previous studies with congruence when comparing new outputs with prior studies (Dekkers and Maxwell 2020a; Maxwell et al. 2020a; Liverani et al. 2021). Trees were generated using Maximum Likelihood with a neutral evolutionary neutrality. Character states were transcribed and coded (1 = A, 2 = G, 3 = C, 4 = T). Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor Markov 4-state model (Jukes and Cantor 1969). All trees generated were tested using 50 bootstrap replications, which is reflective of the data matrix size.

7.3 Taxonomic Presentation

The higher taxonomy derived here meets the requirements of the PhyloCode (2019) and the ICZN (1999). This includes a stylised version of the published phylogeny on which the clades are based, highlighting the clades that contain "urceus". These clades are presented with: a) the synonymy of the clade, outlining its historical use and names that have been relegated under it; b) the unique registration number that identifies the clade within the RegNum, the database for the PhyloCode (2019); c) the definition, which provides information on the phylogenetic position of the clade in terms of the taxa contained within it and the taxa in its sister clades; d) the reference phylogeny on which the definition is based; e) the composition of the clade, which lists a selection of taxa that are contained within the clade, as well as the clade outgroups; f) the diagnostic apomorphies and/or the original description that enables the morphological characteristics of the members of the clade to be identified; and g) the clade type. The rank of subgenus is not defined under the PhyloCode (2019), and is presented with the synonymy, description and type only. In order to complete the definitions, it was nessesary to first define the outgroups (Maxwell. et al 2019b; Maxwell 2021a, 2021b; Maxwell and Rymer 2021).

Species are presented in alphabetical order and corrected names have been applied throughout this thesis to reflect the taxonomy presented for ease of understanding. The species level taxa are presented in accordance with the ICZN (1999) by: a) the synonymy of the species in order of literary occurrence, and then data order for the subsequent mention of that synonymised name; b) the type information of the species; c) the type location of the species; d) the original description and, where appropriate, a supplementary description is provided to give further taxonomic clarity; and e) the distribution of the species, which is listed in two sections, first the literary recorded data, and second the data from the examined material.

7.4 Morphometric Analysis

Morphometric image libraries were generated in tpsUtil 1.81 (Rohlf 2015) and landmark mark placement (Figure 8) and scaling conducted using tpsDig2 2.31 (Rohlf 2015). Analyses were carried out using MorphoJ 1.07a (Klingenberg 2011). A Procrustes fit for the images was undertaken and a covariance matrix generated. A principal component analysis (PCA) was performed, and the two components with the highest eigenvalues were used to form the graphical axes. The MorphoJ Procrustes Centroid ANOVA to differences in shape was undertaken to test the statistical significance of the difference in traits or species. Specific information is contained within the text where the analyses are presented.

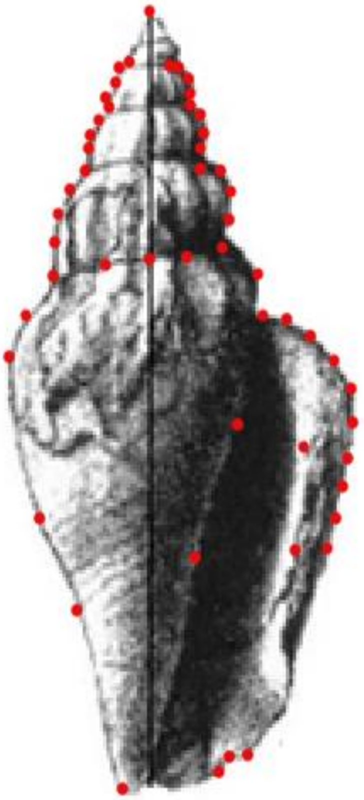


Figure 8: The shell morphometric landmarks used in analsysis of shell form.

7.5 Genetic Analysis

DNA extraction, library preparation, array-based sequencing and in silico genotyping of single nucleotide polymorphisms (SNPs) were conducted by Diversity Arrays Technology (DArT), Canberra, at a depth of 2.5 million reads. This service, and the data it produces, is known as 'DArTseq'. The following data filtering criteria were sequentially applied: reproducibility ≥ 90%; all secondaries were removed; average read depth ≥ 10; individual call rate ≥ 50%; locus call rate = 100%. After filtering, 5,361 SNP loci with no missing data remained. Specific information is contained in the text where the analyses are presented. Genetic variance across the sample was visualised using Pearson Principal Component Analysis (PCA) using the *R package dartR* (Gruber *et al.* 2018), which simplifies multidimensional data along ordination axes (Pearson 1901; Jolliffe 2003). Population groupings were inferred from Discriminant Analysis of Principal Components (DAPC) using the R packages *SambaR v.1.08* (Jong et al. 2020) and *adegenet v2.1.5* (Jombart 2008). The optimal number of clusers (K) is repsested as the minimum values of the BIC and K plot curve. DPAC also indicates the number number of migrants based on inferred genetic clusters. The positions of black apertured individuals among the taxa were also examined, given historical taxonomic arguments that this phenotype is unique to a single species (eg. Abbott 1960).

7.6 Sample Statistical Analyses

For population samples (n > 20), statistical analyses were conducted using SPSS Statistics v 28 (IBM). For each sex, shell summary statistics were generated, and the mean and standard errors for each sex were presented to statistically demonstrate the presence or absence of sexual dimorphism (wet samples). An independent-sample t-test was conducted to determine if there were significant differences in the size of each sex. The proportion of males was tested against a hypothesised proportion of 0.5 using an exact binominal test to determine if a sex ratio bias was present. Aperture colour ratios were calculated as a percentage of the total sample. Pseudohermaphroditism was scored as present or absent. No summary statistics were carried out for samples where n < 20

7.7 Summary

Here, I outlined the taxonomic process used to recircumscribe “urceus”, and presented the morphological characteristics used to distinguish that species from others in *Neostrombini*. The morphometric and genetic methodologies that were used throughout this study were also presented. The components for the presentation of clades and species were outlined. Both of these are structured to comply with the PhyloCode (2019) and ICZN (1999) for higher taxonomy, and the ICZN (1999) for the species level presentations.

Chapter 8 Intra-specific Morphological Variability

Maxwell SJ, Rymer TL (2022) Population Structure of *Canarium* (*Canarium*) *urceus* (Mollusca, Strombidae) from Nha Trang, Vietnam. *Strombus*, 28(1-2), 1-5.

Maxwell SJ, Rymer TL, Congdon BC (2022) A theoretical composite model for population sex-specific shell size dynamics in Strombidae (Gastropoda, Neostromboidae). *Journal of Natural History* 55(41-42), 2661-2672.

Maxwell SJ, Todd, S.J. Rymer TL (2022) Population structure and morphology of *Canarium* (*Canarium*) *incisum* (Wood, 1828) and *Canarium* (*Canarium*) *esculentum* (Maxwell, Rymer, Congdon and Dekkers 2020) (Mollusca: Neostromboidae: Strombidae) from the Philippines with preliminary notes on aperture colouration based on DArTseq Data. *Acta Zoologica* 124, 1-7.

Maxwell SJ, Watt J, Rymer TL, Congdon BC (2021) A checklist of near-shore Strombidae (Mollusca, Gastropoda, Neostromboidae) on Green Island, Queensland. *Biogeographia – The Journal of Integrative Biogeography* 36, a004.

8.1 Preserved Samples (n> 20) Summary Statistics

Canarium (*Canarium*) *incisum* [providenced, random, unsexed]: Corong Corong Beach, El Nido, Philippines (11.35 N, 119.46 E; Total: n = 81; Females: n = 33; Males: n = 48). The mean size of females was 41.91 mm (± 0.73 SE) in contrast to males, which had a mean size of 35.10 mm (± 0.60 SE). This difference in size, biased towards larger females, was significant ($t_{2,79} = -7.21$, $p < 0.001$). The number of females collected was smaller than the number of males (1:1.45), although this difference was not statistically significant ($p = 0.120$; $\alpha = 0.95$). While most (92.6 %) of the sample exhibited typical aperture colouration of shades of orange, 7.4 % showed atypical colouration with a black aperture (Black Aperture Shells: Females: n = 3 (9 % of females); Males: n = 3 (6.3 % of males)).

Canarium (*Canarium*) *incisum* [providence, random, unsexed]: Madura Island (7.21 S, 113.55 E; Total: n = 114; Females: n = 54; Males: n = 60). The mean size of females was 46.72 mm (± 0.56 SE) in contrast to males, which had a mean size of 44.05 mm (± 0.87 SE). This difference in size, biased towards larger females, was significant ($t_{2,112}$ = - 4.21, $p < 0.001$). More males were collected than females (1:0.9), but this difference was not statistically significant ($p = 0.640$; $\alpha = 0.95$). The aperture colouration of the sample was predominantly of shades of orange (68.4 %); however, 31.6 % showed atypical colouration with a black aperture (Black Aperture Shells: Females: n = 13 (24.1 % of females); Males: n = 23 (38.3 % of males)).

Canarium (*Canarium*) *incisum* [providenced, random, unsexed]: Sakala Island (6.93 S, 116.23 E; Total: n = 359; Females: n = 164; Males: n = 195). The mean size of females was 41.48 mm (± 0.23 SE) in contrast to males, which had a mean size of 34.70 mm (± 0.22 SE). This difference in size, biased towards larger females, was significant ($t_{2,357}$ = - 21.02, $p < 0.001$). More males were collected than females (1:0.84), but this difference was not statistically significant ($p = 0.056$; $\alpha = 0.95$). The aperture colouration of the sample was predominantly of shades of orange to red (80.8 %), although 19.2 % showed atypical colouration with a black aperture (Black Aperture Shells: Females: n = 34 (20.7 % of females); Males: n = 35 (17.9% of males)).

Canarium (*Canarium*) *esculentum* [non-providenced, random, unsexed]: Olango Island, Philippines (10.01 N, 124.09 E; Total: n = 73; Females: n = 40; Males: n = 33). The mean size of females was 54.77 mm (± 0.65 SE) in contrast to males, which had a mean size of 49.74 mm (± 0.62 SE). This difference in size, biased towards larger females, was significant ($t_{2,77}$ = - 5.27, $p < 0.001$). The number of males collected was smaller than the number of females (1:1.21), although this difference was not statistically significant ($p = 0.483$; $\alpha = 0.95$). The sample exhibited an equal percentage of coloured and black apertures, with the aperture colouration of shades of white being 49.9 %, and the aperture colouration of black being 50.1 % (Black Aperture Shells: Females: n = 22 (55 % of females); Males: n = 15 (45.5 % of males)).

Canarium (*Canarium*) *urceus* [providence, random, unsexed]: Khánh Hòa Province, Vietnam (12°11′ N, 109°14′ E, Total: n = 37; Females: n = 22; Males: n = 15; Dead: n = 5). Females were significantly larger than males ($t_{2,35} = 3.14$, $p = 0.003$; females = 40.83 ± 0.51 mm, males = 38.12 ± 0.73 mm). More females were collected than males (1:0.68), but this difference was not statistically significant ($p = 0.176$; $\alpha = 0.95$). All individuals in the sample presented a black aperture.

While pseudohermaphroditism is known from *C.* (*C.*) *esculentum* (Ruaza 2019), I found no evidence for this in any of the animals from any of the populations I examined. There are four possibilities for this (Maxwell *et al.* 2020a): first, the causal agent tribtyktin (TBT) was not in concentrations high enough to negatively affect these organisms in any population; second, the sample was too small to observe this characteristic; third, the phenotype is not naturally present in any of these populations; and fourth, penis-bearing females are misinterpreted as males.

8.2 Size Variability

Patterns of sexual dimorphism in gastropods are as diverse as the phylogeny itself, and are reflected in all aspects of life history, from body size, shell morphology and the relative weight of internal organs, to population-specific sex ratios (de Maintenon 2004; Alyakrinskaya 2008). In general, this variation is attributed to the phylogenetic history of these organisms via the effects that size has on fecundity and sexual selection. However, these existing evolutionary models fail to explain localised, periodic fluctuations in population-specific sex-size ratios that are regularly observed in these animals at relatively small spatial scales. To explain these phenomina, the influence of localised factors also needs to be considered, including the importance of environmental growth regulators, such as food availability, predation rates and patterns of gene flow.

In order to fully understand the regulation of sexual size dimorphism in gastropods at local and regional scales, it is necessary to include all potential factors of influence in a single model. However, current models of sexual size dimorphism fail to combine phylogenetic history with localised ecological factors that influence body size. Such factors have the potential to explain periodic and localised fluctuations in dimorphism. Here, for the first time, I modelled twelve factors to explain sexual dimorphism in gastropod molluscs. In all, this updated model includes sex-specific fecundity, sexual selection and competition, ecological determinates, and gene flow, with each factor being considered from the perspective of both sexes.

8.2.1 Fecundity selection

Fecundity selection offers a causal explanation for the evolution of sexual size dimorphism in gastropods because of the allometric benefits of larger female body size. Larger females have increased ovarian size, resulting in increased fecundity (Wiedemeyer 1998; Shawl and Davies 2004). The quantity of eggs spawned in a single spawning is not necessarily related to the size of the female, but this varies among populations (Robertson 1959; Randall 1964; Bradshaw-Hawkins and Sander 1981; Wiedemeyer 1998; Brito Manzano et al. 1999; Gómez et al. 2007); however, the number of spawnings per female, per season, is affected by body size, with larger females being more fecund, producing greater numbers of egg masses, and therefore having a higher overall annual reproductive output (Wiedemeyer 1998; Shawl and Davies 2004). Therefore, in general, large females are expected to have higher annual fecundity than small females (Katoh 1989; Son and

Hughes 2000). This would indicate that there is a fecundity-driven evolutionary directional force up-regulating the size of females, with significant impacts for models seeking to explain sexual dimorphism.

On the other hand, male fecundity, in terms of ability to spawn, is not constrained by body size, but is rather constrained by access to females. Therefore, there is unlikely to be selection for increased male body size beyond the minimum size needed for maturity unless there is direct male-male competition for access to females, where larger males have an advantage. However, there may be selection for males to reach sexual maturity earlier at considerably smaller body size than females so as to maximise access to females (Appeldoorn 1988; Cob et al. 2008; Tamburi and Martín 2008). Furthermore, the number of females in an aggregation within a population is often larger than males, limiting male competition for access to females (Maxwell et al. 2017, 2020). This differential fecundity selection between males and females would likely lead to consistant patterns of sexual size dimorphism within and between populations.

8.2.2 Sexual Selection and Competition

There is limited evidence in some gastropod taxa for male-male competition, where larger males have a competitive advantage (Zahradnik et al. 2008). This occurs primarily in carnivorous gastropods, where males attempt to dominate access to female reproductive organs after mating. In these species, males tend to be similar in size to females (Alyakrinskaya 2008), thus providing some support for the importance of such competitive interactions.

Given the nature of gregarious mating in the Strombidae, and that males will seek out virgin females irrespective of body size, it is unlikely that females influence male mate choice as males are not inhibited in copulation by this open mating system (Brownell

1977; Catterall and Poiner 1983; Tewfik et al. 1998). Furthermore, there is no evidence of internal female sperm selectivity (Simone 2005). Once mating has occurred, females can store sperm; as such, *post hoc* fertilisation may result from a number of male progenitors (Catterall and Poiner 1983). For example, it is not uncommon to find more than one male *Conomurex luhuanus* (Linné, 1758) attempting to copulate with one female (Catterall and Poiner 1983). Multiple males have also been observed stimultaneously copulating with a single female in other Strombidae, particularly *Euprotomus aratrum* (Röding, 1798), *Ministrombus variablis* (Swainson,1820), *Canarium labiatum* (Röding, 1798) and *Dolomena hickeyi* (Willan, 2000). This polygamous mating invariably leads to significant gene flow within populations. Therefore, in terms of explaining sexual dimorphism in species with larger females, sexual selection for larger males is likely to be a minor regulating evolutionary force, while female mate choice is likely to be inconsequential.

Sexual selection, where males actively seek out larger females, may also result in selection for increasingly larger females (Zahradnik et al. 2008). While the phenomenon of male selection for larger females has not been studied in Strombidae, it is often observed in other gastropods, such as *Littorina* (Zahradnik et al. 2008). However, while males preferentially choosing large females would have a positive effect on female size as a consequence of selection, the random mating of males with smaller females, which has also been seen in *Littorina*, would mediate this effect within the overall population (Zahradnik et al. 2008).

In herbivorous Strombidae, males are smaller than females. However, larger males are still able to push smaller males aside simply because of greater body size. There are rare examples of inter-male conflict in mating behaviour in normally gregarious herbivorous gastropods. For example, in some populations of *Strombus alatus* Gmelin, 1791 and

Strombus pugilis Linné, 1758, females are often found mating with one male, and this male then defends the female from other males, preventing them from spawning (Bradshaw-Hawkins and Sander 1981; Gillette and Shawl 2006). However, such behaviour is highly dependent on the population density and sex ratio, only occurring under laboratory conditions in populations with a limited number of individuals (Gillette and Shawl 2006). In large, female-dominated aggregations of Strombidae, it would be impossible for such protective behaviour to be effective through the weight of male competitors (Catterall and Poiner 1983). While intra-specific competition appears to limit the benefits of small male size through ease of displacement, the smaller size does correspond to faster development and increasing mating potential for smaller males prior to the maturation of larger males, particularity as spawning in the Strombidae, while seasonally variable, occurs throughout the year. This means that smaller males are likely to fertilise initial spawning events prior to the maturation of larger males (Brownell 1977; Cardenas et al. 2005; Irie and Morimoto 2008). Therefore, in general, there are two intra-specific forces acting on the size of males relevant to the modelling of sexual size dimorphism: one force driving an increase in size through intra-sexual competition, and a second opposing selective force for smaller males, driven by the benefits of rapid maturity and consequential maximisation of reproductive potential.

8.2.3 Ecological determinants of sexual size dimorphism

Non-phylogenetic factors that affect the expression of sexual dimorphism may be ecological (Aldana Aranda et al. 1989; Aldana-Aranda and Suárez 1998; Brito Manzano et al. 1998, 2000). They include phenomena that affect growth rates and impact post-settlement development, such as food availability, regional water temperature and intra-population competition for food (McKillup and McKillup 1997; Barroso et al. 2005;

Preston and Roberts 2007; Yokoyama and Amaral 2011). Evidence from increasing size distributions of *Gibberulus dekkersi* Maxwell, Hernandez Duran, Rowell and Rymer, 2021 harvested in the Palau Islands indicates compliance with Copes's rule, where animals evolve larger body sizes through time to maximise fecundity and increase the exploitation of resources (Blanckenhorn 2000; Giovas et al. 2010). Importantly, neither harvesting nor environmental factors provide an explanation for the up-shift in size, with populations increasing in both width and length from 3000 BP to today (Giovas et al. 2010). However, in smaller organisms, each sex may have particular selection pressures acting to drive divergent size distributions, suggesting that genetic and ecological determinants affect the size of animals at maturity (Blanckenhorn 2000; Roy et al. 2001)

How the organism responds to changes in the environment can have a significant impact on the temporal expression of sexually dimorphic characteristics. For example, variations in food availability may result in fluctuating asymmetry between the sexes (McKillup and McKillup 1997; Mutlu 2004; Yang and Zhang 2011). Similarly, differences in post-settlement growth between populations of the same species affect the size at maturity of each sex, thus leading to sex-specific differences in mean body sizes among populations (Abbott, 1960; Estebenet et al. 2006). Therefore, the innate variability in size at maturity between populations highlights the need to treat the mean sizes of each geographical population independently when undertaking morphometric analyses.

Importantly, in these gastropods, size at maturity is not significantly regulated by predation. The greatest predatory influence on the survivability of gastropods occurs during the veliger ontological stage (Weidmeyer 1998; Stoner et al. 1998; Preston and Roberts 2007), which occurs pre-settlement while the veligers are still planktonic.

8.2.4 Gene Flow

Veliger planktonic dispersal and the subsequent exchange of organisms between disparate populations acts to genetically connect populations, restricting the potential for genetic drift, or natural/sexual selection, to generate different patterns of dimorphism between populations (Delgado et al. 2006; Paris et al. 2006; Aldana-Aranda and Perez-Perez 2007). For example, the veligers of *Aliger gigas* (Linné, 1758) can travel hundreds of kilometres on currents in the western Caribbean, with the recruits replenishing populations in other regions (Delgado et al. 2006; Paris et al. 2006; Aldana-Aranda and Perez-Perez 2007). Therefore, the time spent in veliger dispersal has an important role in maintaining diversity within populations that may have historically arisen from a small recruitment base (Pérez-Enriquez et al. 2011). This external recruitment mediates the extent of overall regional population size divergence. In terms of modelling sexual dimorphism, this acts to genetically connect populations, and is an explanatory cause for non-divergent intra-population dimorphic means (Delgado et al. 2006; Paris et al. 2006; Aldana-Aranda and Perez-Perez 2007). The new model, therefore, needs to also consider that an adult population may be derived from multi-vectorial external post-settlement recruitment.

8.2.5 The Model

If we consider both the phylogenetic history of the species and the localised effects acting on the specific population, the key inter-and intra-populational factors that should be considered in modelling evolutionary factors regulating sexual size dimorphism in Strombidae are:

1. the gene flow between populations as a consequence of the veliger life-stage, which provides a genetic connection across benthically isolated regional

populations, limiting genetic drift and selection (Delgado et al. 2006; Paris et al. 2006; Aldana-Aranda and Perez-Perez 2007; Pérez-Enriquez et al. 2011);

2. the environmental constraints that affect the development and growth of the animal (which is reflected in the ecophenotypic plasticity in shell morphology) and differences in the mean size of the shell between populations that share gene flow (Aldana Aranda et al. 1989; Aldana-Aranda and Suárez 1998; Brito Manzano et al. 1998, 2000);
3. the population sex ratio that favours females, which limits the effects of male-male competition, generating only a small selectional force in favour of larger male size (Abbott 1949; Wiedemeyer 1998; Mutlu 2004; Yusa 2007; Maxwell et al. 2017, 2020);
4. the clustering habits of Strombidae, and the ability of females to store sperm, limits the potential for effective male competition (Catterall and Poiner 1983);
5. no evidence for female selectivity in mate choice;
6. time to maturity in males, where smaller males have a reduced time to sexual maturity, which enables primary access to females and provides a selectional force favouring smaller males (Appeldoorn 1988; Cob et al. 2008). The time taken to mature affects the reproductive potential, and larger males take longer to achieve sexual maturity (Irie and Morimoto 2008);
7. males seek out larger females as primary targets for mating. However, the impact of this selectional pressure is reduced as males also prefer virgin females (Brownell 1977; Tewfik et al. 1998; Zahradnik et al. 2008);
8. predation occurs primarily during the veliger life-stage and is not considered a major selection factor for inter-population or sex-specific size differences in the

Strombidae (Weidmeyer 1998; Stoner et al. 1998; Preston and Roberts 2007; McIntyre et al. 2006);

9. no intra-population resource access pressures generate sexual dimorphism within a population in Strombidae. The animals are phytophagous raspers living in gregarious populations (Abbott 1960; Catterall and Poiner 1983);
10. sexually dimorphic differences in soft-part morphology are a consequence of allometric physiological differences among sexes or, in rare cases where there appears to be no physiological explanation, a consequence of fluctuating asymmetry (Colton 1905; Mutlu 2004; Simone 2005);
11. in gastropods, larger females, have higher reproductive success (Shawl and Davies 2004; Cardenas et al. 2005); and
12. Cope's Rule in terms of small animals, which states that taxa evolve larger body sizes through time to maximise reproductive potential and heighten the exploitation of resources where carrying capacity is not a signifcat regulator of population size (Blanckenhorn 2000).

Using two overlapping normal distribution curves to reflect the sexual size dimorphism in Strombidae, the directional effect of each factor on each sex is indicated (Figure 9). It is expected that sexual size dimorphism will differ between populations primarily as a consequence of the environmental constraints that regulate the development and growth of the animals in each population (Figure 9). Conversely, the relative ratio between the sexes is expected to remain constant if populations are subjected to the same environmental conditions (Figure 9). The mean size of populations that have strong gene flow between them would be expected to remain statistically similar (Figure 9). The regulating factors described here are similar to those found in all gastropods that have a pelagic life stage, are herbivorous and have a sex bias towards females. These componets of this new model can, therefore, explain and be applied to a wider range of sexually dimorphic organisms, aiding in our ability to explain evolutionary factors involved in regulating sexual dimorphism.

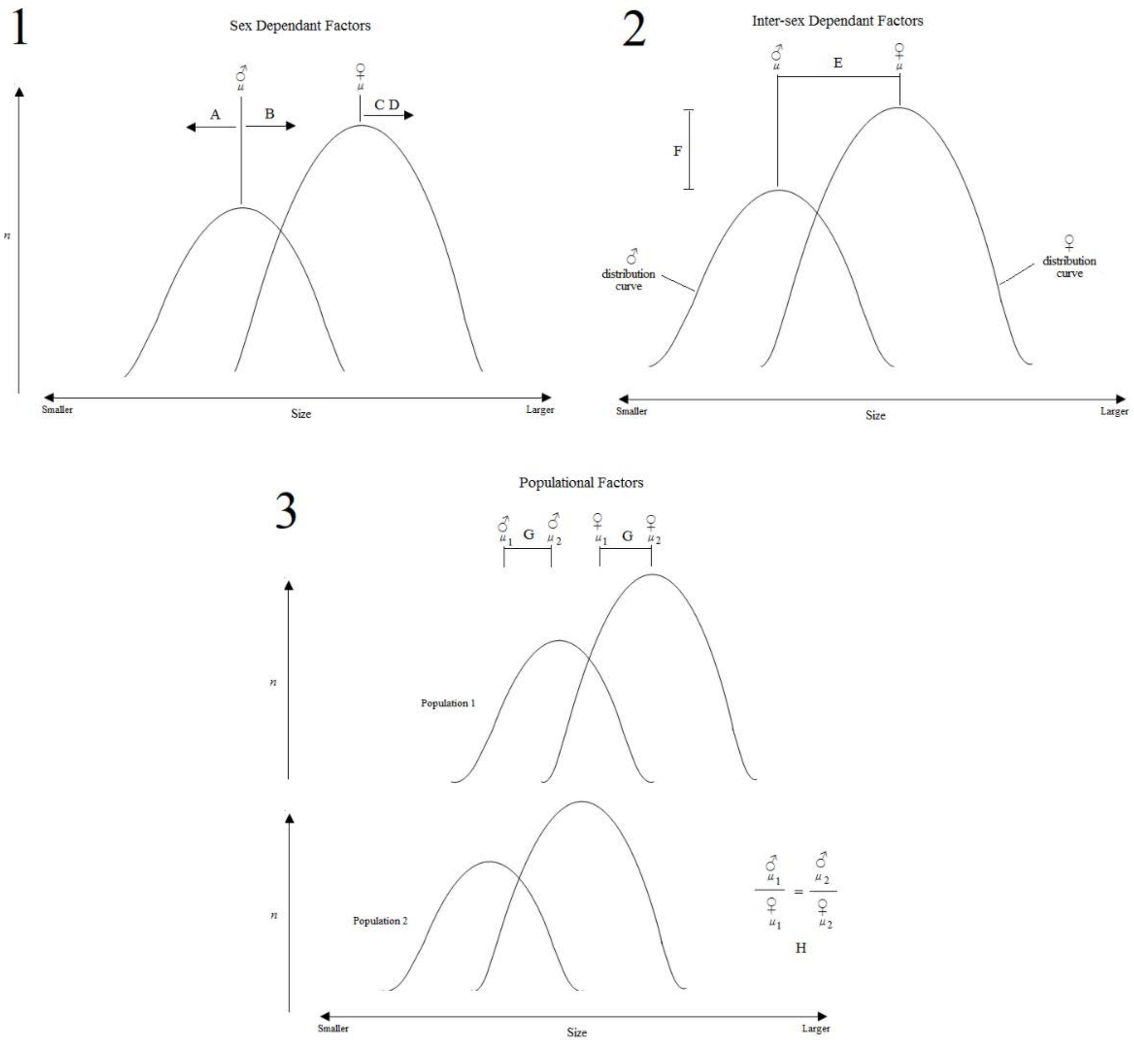


Figure 9: Modelling male and females population distribution curves showing the mean size (μ) of each sex and the (1) Sex dependant factors: A) time to maturity; B) intra-male competition; C) female-specific sexual selection; D) fecundity; (2) Inter-sex dependant factors: E) time to maturity; F) sex bias towards larger numbers of females; and (3) Populational factors: G) environmental conditions; and H) universal size regulators that affect the size ratio between females and males (Maxwell et al. 2022).

Modelling the dynamics that regulate size is critical to understanding the evolutionary potential of an organism through time. Once the factors that regulate size are modelled, the effects of environmental or other population dynamics on size can be inferred. In this approach to modelling size, I incorporate the localised ecological factors that regulate population size in conjunction with theories of sexual dimorphism. This composite modelling has not previously been undertaken in gastropods, where the early developmental life-history is highly ecophenotypically dependent and has a significant regulating effect on growth rates and size at maturity of animals at the population level (Aldana Aranda et al. 1989; Aldana-Aranda and Suárez 1998; Brito Manzano et al. 1998, 2000). Furthermore, modelling the effects of veliger developmental stage indicates that it is unlikely that the differences in mean sizes of populations with dimorphic sexes is related to genetic isolation. This lack of isolation results from the natural transmission of larvae between populations, which results in recruitment outside of the spawning population (Yokoyama and Amaral 2011).

Modelling sexual dimorphism is useful for understanding the evolutionary development of the Strombidae. However, there are two limitations when working with Strombidae. Firstly, there are underlying reproductive mechanisms favouring larger females that remain unexplained; and secondly, the behavioural ecology of male-male competition has yet to be fully explored. Understanding the mechanisms that regulate sexual dimorphism aids in the discrimination of taxa, and aids understanding of the innate variability within populations. This has a particular impact on the differentiation of closely related fossil taxa. Notwithstanding the evolutionary pressures for the sexes to diverge, there is a trend in mean sizes of each sex to change proportionally with a shift in the population mean. This indicates that the growth rate of both sexes may be regulated by environmental factors and, because the model argues that fluctuations in the sex means occur, there must be an underlying population genetic correlation regulating for the length of a shell that limits the sex-mean size divergence potential. This model accounts for previously unexplaind field observations of intra- and inter-specific divergence in shell morphology, such as localised population variation through time, open mating systems and the effects of time to maturity on fecundity.

8.3 Shape Variability

In stromboidians, there is considerable plasticity in form between and within species populations. Understanding the variability of form within a population is important as considerable evidence for phenotypic plasticity along environmental gradients leading to variability in adult shell morphology in many species exists (Vasconcelos et al. 2020). This phenotypic plasticity has been linked to the Baldwin effect, where localised adaptation can lead to speciation as novel phenotypic expressions generate selection pressures that can change evolutionary direction (Robinson and Dukas 1999; Van Bocxlaer et al. 2020). Morphological plasticity can have effects on the identification of organisms and can, therefore, also have implications on taxonomic practice (Rassam et al. 2021). In relation to the “urceus’ complex, variability in shape is explored in terms of the sexes and variability between populations.

8.3.1 Sex Dimorphic Shape Variability

In this study, morphometric analysis of two populations showed statistically different shell shapes between males and females of *C. incisum* from El Nido, Philippines (Centroid ANOVA: $F_{1,46} = 2.21$, $p < 0.001$; Figure 10A) and *C. esculentum* from Olango Island, Philippines (Centroid ANOVA: $F_{1,66} = 57.63$, $p < 0.001$; Figure 10B). The overlap in the morphometrics of both sexes in each of the species that were examined makes the determination of sex based on shell characteristics problematic.

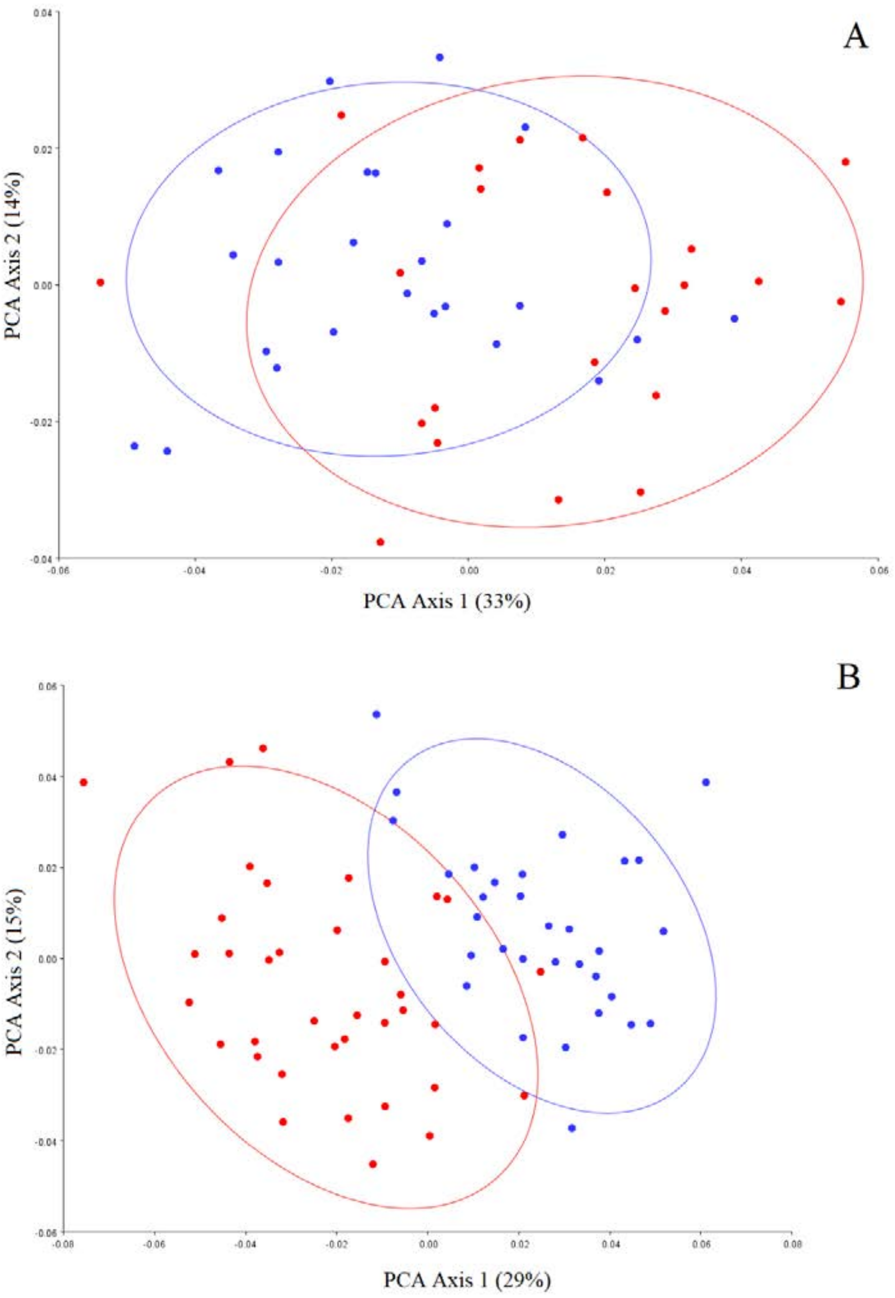


Figure 10: The two most explanatory principal components of a principal components analysis (PCA) of morphometrics showing the distribution of specimens based on sex across species: A) *Canarium incisum* (Wood, 1828) from Kangean Islands (n = 47); B) *Canarium esculentum* Maxwell, Rymer, Congdon and Dekkers, 2020b from Olango, Philippines (n = 67). Males are shown with blue dots and females with red dots and 0.90 confidence ellipses based on aperture colouration.

Notwithstanding the overlap in shape variability, in *C. incisum*, the spires of females tend to be wider and larger in relation to the body whorl than males, the point of inflection of the columella is approximately mid-length the aperture in females and tends to be more anteriorly placed in males. Males also look stouter than females, which tend to look more elongated; however, there is no difference in nodulation in the observed population. In *C. esculentum*, females tend to have a body whorl that is broader and has higher and wider spires than males, which gives males an elongated appearance rather than the more fusiform nature of the female shells.

Sexual dimorphism in Stromboideans thus is not limited to size, with several morphological characters noted as potentially being different. Colton (1905) found sexual differentiation in *Strombus alatus* Gmelin, 1791, with the angle of the columella to the shell length being slightly larger in females (40 º) than males (37.4 º). Females of *Lambis lambis* (Linné, 1758) typically have spines that curve upward, while males tend to have spines that are on the dorsal plane (Abbott 1961; Abbott and Dance 1982; Ueno 1997; Maxwell et al. 2021b). This dimorphism is also noted in the lip thickness size reached in *Aliger gigas* (Linné, 1758) from Colombia, with females having a lip thickness of 3.0 mm in contrast to males, which have a thickness of 2.4 mm (Avila-Poveda and Baqueiro-Cárdenas 2006).

8.4 Colour Variability

The margin of the mantle is the area responsible for primary shell formation and colouration. While the entire mantle is capable of shell production, and thickens the shell as the animal grows, it is only the edge that possesses the ability to provide colouration (Cooke 1885). Colouration has been shown to be under genetic control (Mann and Jackson 2014; Lemer et al. 2015); however, it is also strongly influenced epigenetically by environmental factors including food, substrate, water quality and temperature, which all affect the biochemistry of the organism (Underwood and Creese 1976; Graham 1985; Köhler et al. 2021). These influences have impacts on the non-directional changes in phenotypic expression within the bounds of the organism state (Köhler et al. 2021).

Within the ‘urceus” complex, I have now explored the differences between species in their propensity for shell colour expression.

8.4.1 Aperture Colour Variability

There is significant variability in aperture colouration, particularly in relation to the occurrence of black or dark staining of the aperture, which has led to taxonomic confusion. *Canarium urceus* is known for its black coloured aperture in all specimens (Maxwell and Rymer 2022). However, within *C. incisum* and *C. esculentum* there are two known aperture colour morphs, their normal colouration, and also a form where there are varying degrees of black colouring in the aperture. This black coloured apertured form has been called *Strombus ustulatum* Schumacher, 1817 by some authors and has been used as one of the charateristics to aggregate the “urceus” complex (Abbott 1960). This black coloured aperture colour dimorphism is also shared with *Canarium* (*Elegantum*) *radians* (Duclos, 1844), hinting that its use taxonomically to distinguish species is limited.

Using DaRTseq data, I found no evidence that the black coloured aperture trait is associated with genetic structuring in *C. incisum* from El Nido, Philippines and *C. esculentum* from Olango Island, Philippines (Figure 11). Black aperture individuals were scattered along both PCA1 and PCA2. The two *C. incisum* shells sampled with black coloured apertures were close to each other in genetic distance and, together with a third orange apertured individual, formed a cluster that was distinct from the other three individuals of this species.

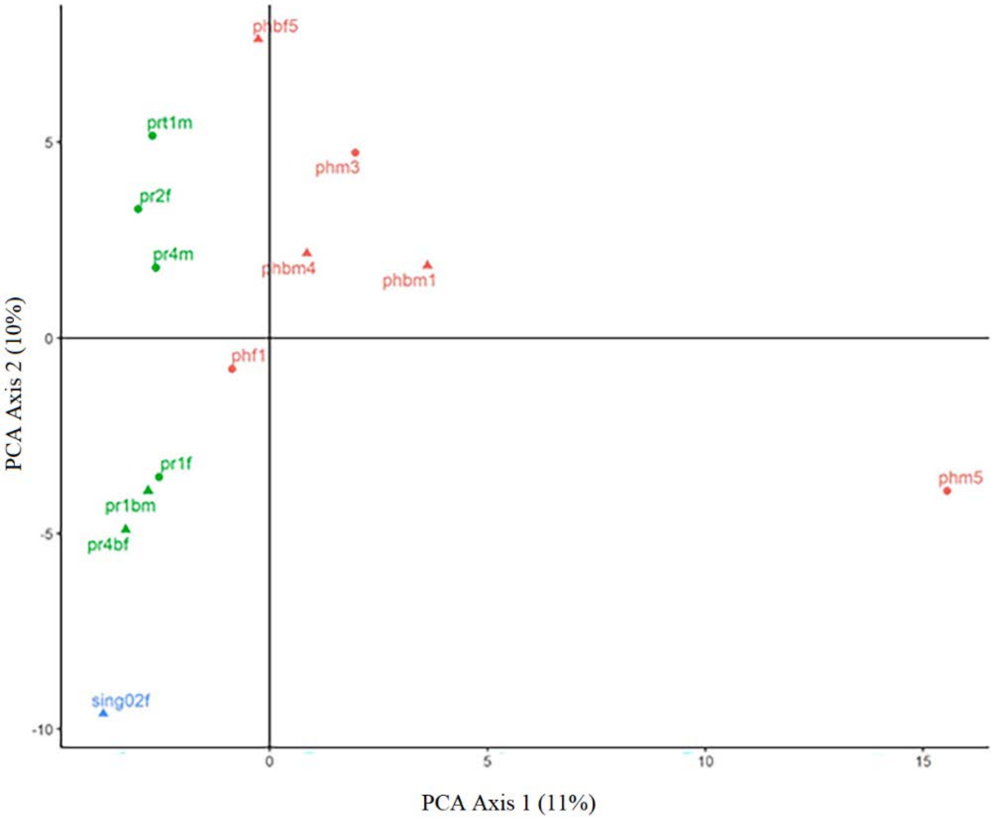


Figure 11: The two most explanatory principal components of a PCA analysis of SNP genotypes, showing distribution of specimens with a black aperture across species: seven *Canarium esculentum* Maxwell, Rymer, Congdon and Dekkers, 2020b (male: n = 4; female: n = 3), of which three specimens had a black aperture (male: n = 2; female: n = 1) (pink – 'ph') from Olango, Philippines; six *Canarium incisum* (Wood, 1828) (male: n = 3; female: n = 3), of which two were black aperture morphs (male: n = 1; female: n = 1)(green – 'pr'), from El Nido, Philippines; and *Canarium urceus* (Linné, 1758) (blue – 'sing') from Singapore. Individuals with a black aperture are indicated with triangles, and males (m) and females (f) noted in the labelling. One *C. esculentum* female from Olango was removed due to poor sample sequencing quality (Maxwell et al. 2022b).

Morphometric analysis showed no evidence that the black aperture trait is associated with species association within *C. incisum* from the Kangean Islands, Indonesia (Centroid ANOVA: $F_{1,46} = 0.11$, $p = 0.737$; Figure 12A) and *C. esculentum* from Olango Island, Philippines (Centroid ANOVA: $F_{1,66} = 0.48$, $p = 0.491$; Figure 12B). This cluster was closer to black apertured *C.* (*C.*) *urceus* along PCA2. The clustering of black apertured *C. incisum* individuals closer to *C. urceus,* a species in which this trait is universal, may indicate historic hybridisation between these species leading to introgression of the black aperture trait into *C. incisum.*

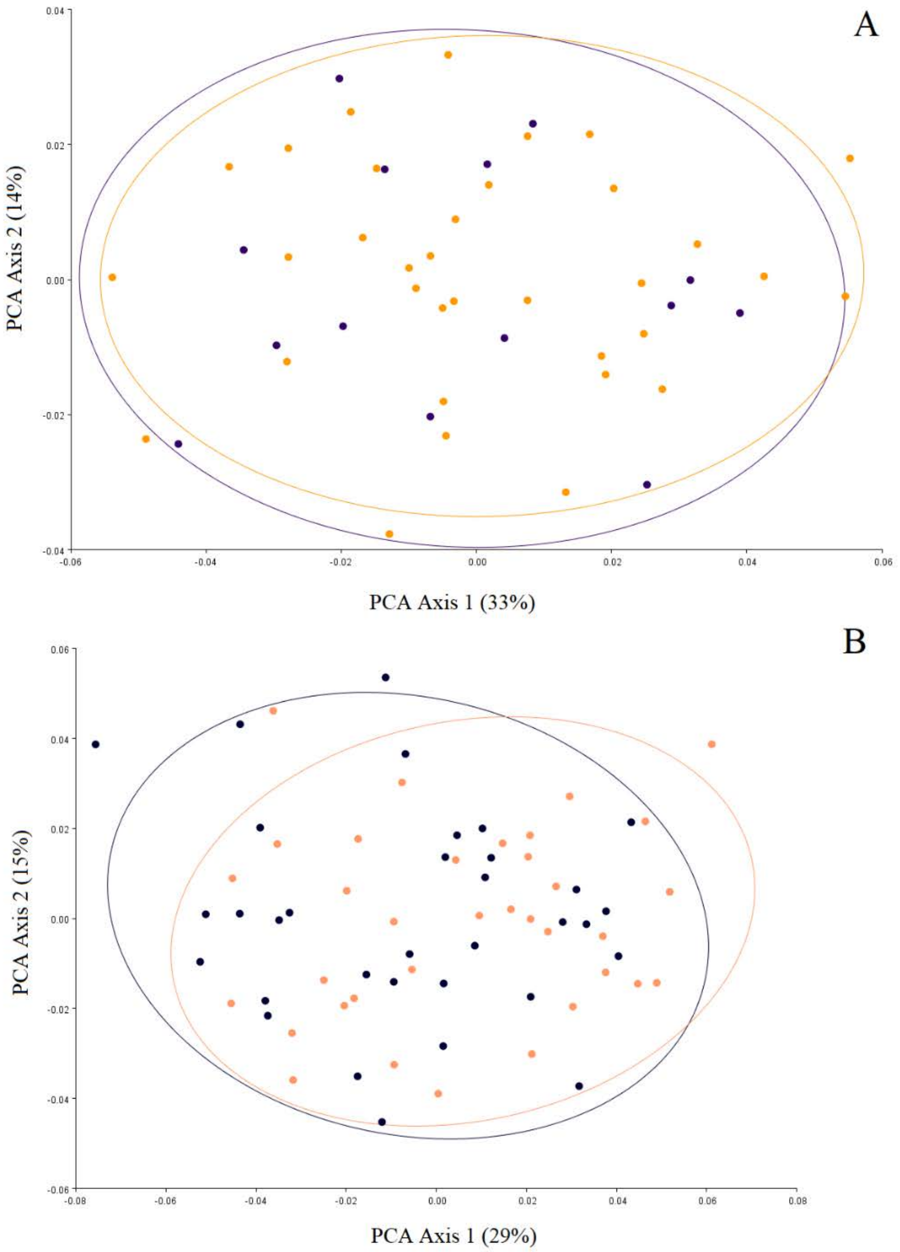


Figure 12: The two most explanatory principal components of a principal components analysis (PCA) of morphometrics showing distribution of specimens with a black coloured aperture across species: A) *Canarium incisum* (Wood, 1828) from Kangean Islands (n = 47); B) *Canarium esculentum* Maxwell, Rymer, Congdon and Dekkers, 2020b from Olango, Philippines (n = 67). Individuals with a black coloured aperture are shown with black dots and the non-black apertured specimens with orange dots and 0.90 confidence ellipses based on aperture colouration.

The staining of the aperture, which may occur in some species under some environmental conditions, is not a plausible explanation for black apertured specimens in “urceus” because of the shared habitat of the non-black apertured section of the sample (Willians 2017). If an environmental factor were at play to cause this colouration, it should have affected the population equally. Nor is the black acperture likely a consequence of sexual selection, with gastropods having limited colour vision (Williams 2017). Black pigmentation has been linked to specific genes, such as eumelanin, which suggests that there may be a strong genetic factor regulating its expression within the population (Willians et al. 2016). The expression of colour is also sensitive to environmental factors, and this may affect regional ratios of colours in some species (Zheng et al. 2013). Therefore, the black coloured aperture is a recurrent morphological theme that can be explained in four ways: first, there is a lag between the time of genetic divergence and evidence of this split in the morphology of organisms (Baum 2008); second, within a population, there are enough carriers of a mutation that drift and selection maintain allelic frequency without leading to either extinction or fixation (Baum 2008); third, there is enough genetic inflow from populations outside the particular bioregion that would enable recurrent introduction within a population of a particular morphological trait to sustain its ongoing recurrence; or fourth, there are environmental factors that regulate that phenotypes expression (Delgado et al. 2006; Paris et al. 2006, 2008; Zheng et al. 2013). There is a high degree of hybridisation within the stromboidean complex and, given the ability for veligers to travel hundreds of kilometres, coupled with a year-round spawning habit, this makes the potential for introgression of traits high (Delgado et al. 2006; Paris et al. 2006, 2008; Aldana-Aranda and Perez-Perez 2007; Maxwell et al. 2019b).

8.5 Summary

The variability within the “urcues” complex can be explained in terms of sexual dimoprhism in size and morphological variation. Patterns of sexual dimorphism are an artefact of all aspects of the evolutionary history and localised impacts on organisms. I describe a new model that hypothesizes that sexual selection and competition, environmental constraints and gene flow between different populations, in conjunction with fecundity, regulate the expression of sexual size divergence within a population, and between different populations of the same taxon. The growth and size at maturity of an organism can be explained by a combination of life-history traits. Sexual dimorphism in size results from these traits having differing effects on each sex. Consequently, understanding the regulatory factors that govern sexual size dimorphism provides insights into the evolutionary trade-offs and adaptability of organisms to mitigate the effects of environmental change, such as changes in larval development time and size at maturity.

While the shape of males and females differs, the determination of sex based on any characteristics is problematic due to morphological overlap. Similarly, the colouration of the aperture is not a sound variable to use for taxonomic discrimination, with some species having highly variable aperture colouration, which may be locally affected by evironmental conditions. Where it exists in populations, individuals with black apertures cannot be differentiated from other members of the population by genetics or morphometrics. The black colouration of the aperture is thus a phenotype shared by many stromboidians, and should not be used as means of determining species in isolation of other shell characteristics.

Chapter 9 Biogeography

There are many biogeographic factors that regulate the distribution of marine organisms with a veliger life stage within the Indo-Australian Archipelago, Northern Western Australian Coast and the Central and Southern Pacific. In particular, glacial cycles, land dispersal barriers, ocean current mediated dispersal and environmental barriers will be explored. These biogeographic influences are discussed *inferius* in terms of how they may affect radiation patterns, possibly mediating reticulation, and reduce the impact of genetic drift and secondary contact between populations. Notwithstanding, there is a level of biological interplay between different bioregions and this affects the distribution and morphology of the organisms that are contained within these geographical zones. To understand broader radiation provinces that have affected speciation processes that has given rise to diversity within the provinces, it is necessary to examine those speciation processes in the context of the region as a whole.

I herein define the provinces within the Indian Tropical Region and Northern Australian Tropical Region based on the distribution of the "urceus" complex. Each of these provinces contains regions that have acted as refugia during periods of maximum glaciation, facilitating a wide variety of speciation processes leading to the realm becoming a global hotspot for biodiversity as these refugia are cyclically linked and then divided by changes in sea level.

I also explore the biogeographical current and historical factors that affect the dispersal of this group of marine molluscs with a veliger life stage. The chapter focuses on glacial cycles and land barriers, major ocean currents, and environmental barriers and how these may have affected gene flow between members of the "urceus" complex. The current distributions of members of this complex are discussed with the context of refugia during interglacial periods, and how these periodic blockages and reconnections that have occurred with sea level changes have given rise to the diversity of the "urceus" complex.

9.1 Glacial Cycles and Land Dispersal Barriers

Inter-glacial cycles are a driving factor in shaping coastlines and oceans through periodic and cyclical changes in sea levels (Figure 13). These changing sea levels formed land barriers and stepping stones for marine species micro-evolution that are often overlooked as structural factors in the current evolution of marine organisms (Macieira et al. 2015; Stigall 2018). During the last inter-glacial maximum, most of the current Indo-Australian Archipelago marine species were restricted, with limited connectivity due to land barriers (Figure 14). It is important to recognise that, during the last inter-glacial period, most of the South China Sea, Indonesia and the seas around Malaysia and Thailand were part of the greater Sunda landmass, and that all marine species arrived there after the current inundation.

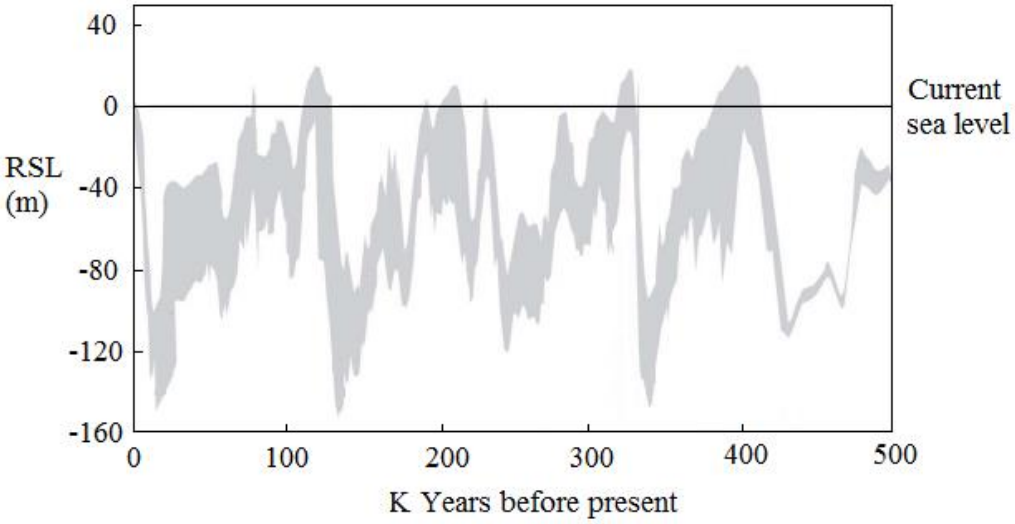


Figure 13: Sea level heights for the last half million years (after Rabineau et al. 2006).

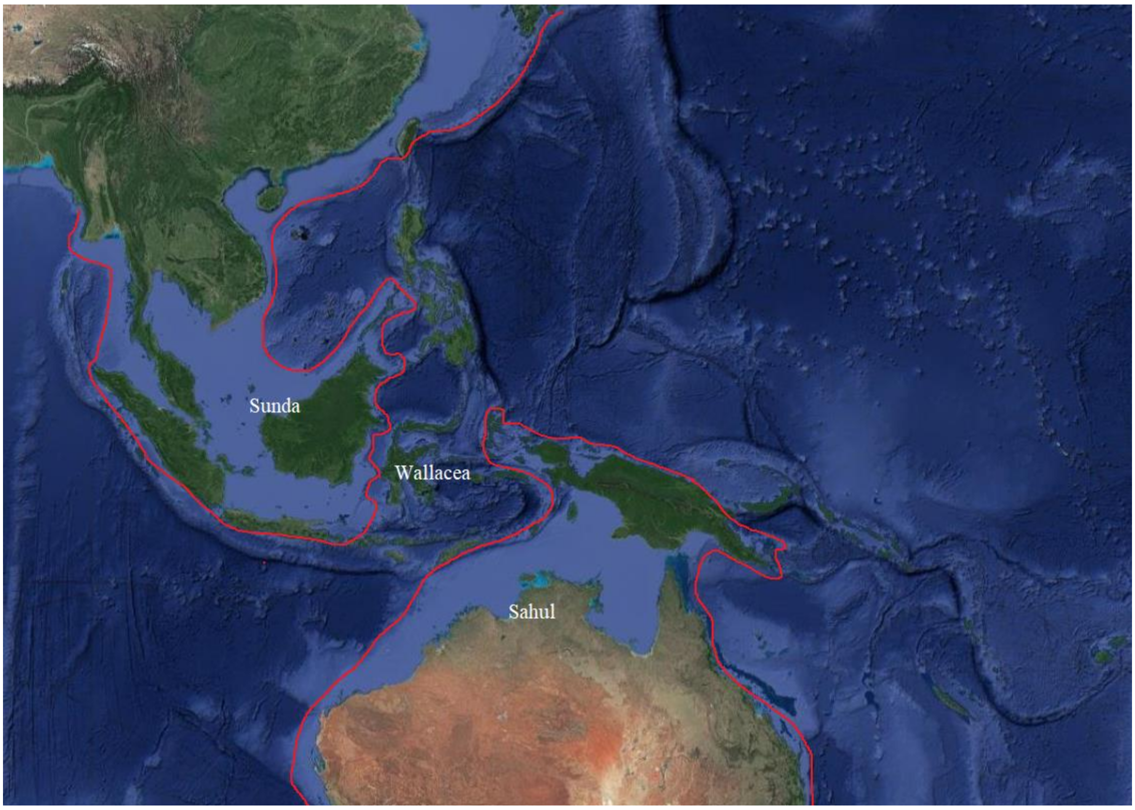


Figure 14: The approximate continental boundaries of the Sunda and Sahul continents during the last inter-glacial maximum based on depth, and the central region of island chains known as Wallacea.

The last inter-glacial maximum that occurred 20,000 BP provides a geological point of reference from which to understand speciation processes that gave rise to the current distribution of many marine organisms (Yang et al. 2016). Areas of repeated inundation and drying generated niches for re-colonisation by displaced taxa as varying benthic habitats changed as the coastline moved across differing substrates (Ma et al. 2017). This habitat variability increased the resilience of the organisms, as well as their fitness, and provided the opportunity for continuous selection, resulting in localised parapatric speciation events.

The Western Australian coast has also retreated since the post-glacial maximum, and this has had a great significance for species that are primarily coastal and intertidal niche specialists that need to migrate rapidly to keep pace with shifting coastlines (Yang et al. 2016). Changes in sea level had an impact on Northern Australia, drying the Gulf of

Carpentaria. The seas of the western Indo-Australian Archipelago were more impacted. They either completely dried, as with the current Java Sea, or became predominantly land locked, as with the Sulu Sea. In contrast to the horizontally shifting shorelines of the Indo-Australian Archipelago, changing sea levels may not have impacted the distribution of south-western Pacific species, primarily as these are chains of islands that are volcanic or coral atolls with fringing reefs that are depth dependant. The tops of the coral atolls correlate with sea-level and, therefore, species undergo a process of vertical displacement rather than large scale regional dislocation due to the effects of drying (Darwin 1842).

Therefore, depending on the region, the post-glacial maximum has varying degrees of significance on the potential radiation of marine species in terms of rapid re-colonisation of newly submerged lands, the need to follow retreating coastlines, the breakdown of barriers leading to reticulation, and changing sea-level impacts on distribution and recruitment in remote atolls and island chains.

9.2 Ocean Current Mediated Dispersal

The recent inter-glacial maxima did not disrupt the major surface oceanic currents in the open water, but they did affect how these major currents feed through the central Indo-West Pacific (Figure 15). In particular, the Wallacea region experienced increasing flow rates as the Indonesian flow-through was diverted through that region. Similarly, there are significant eddies that cause regions of potential biodiversity hotspots, particularly the Mindanao and Halmahera eddies and those in Tomini Bay, which were not affected by the inter-glacial fluctuations in sea level (Carpenter et al. 2011; Borsa et al. 2016; Levy and Kochzius 2016; Miller et al. 2016).

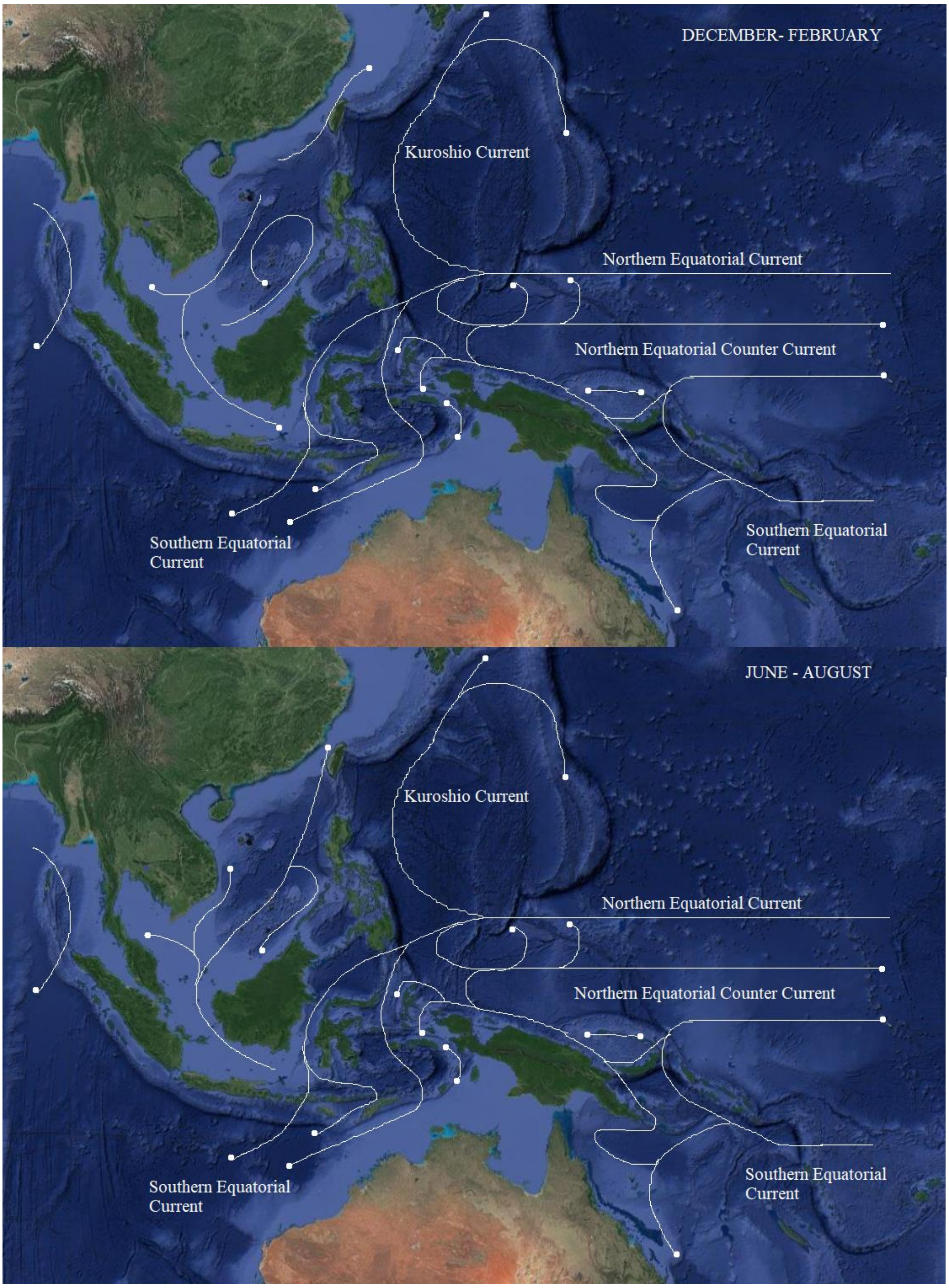


Figure 15: (A) The major flow direction of the Indo-Australian Archipelago currents (white lines) showing direction of flow (white circles), and showing the currents that change direction seasonally (Carpenter et al. 2011; Levy and Kochzius 2016; Additional Data – https://earth.nullschool.net).

During the last inter-glacial maximum, the South China Sea was enclosed and flowed out into the Sulu Sea, generating directional genetic drift (Yang et al. 2016). There are two feeder currents into the South China Sea: direction of inflows from the Northern Equatorial Current as it sweeps the northern coast (Carpenter et al. 2011), and a secondary inflow from the Northern Equatorial Current along the west coast of the Philippines, which joins the South China Sea Current to flush into the Sulu Sea. Modern taxa of the South China Sea demonstrate shared genetic material and, given the little shift in currents during the inter-glacial fluctuations in that region, this reticulation mitigates the potential for genetic divergence, leading to congruence in the form of many taxa (Dorman et al. 2016; Huang et al. 2018). Similarly, the flooding of the Sunda landmass from the South China Sea has led to incursions of mainland coastal taxa into Malaysia, Singapore and northern Boneo (Kakioka et al. 2018).

The central Philippines has remained relatively stable, with many regional currents dominating the archipelago and leading to a centre of regional maximum diversity (de Vantier and Turak 2017; Yang et al. 2016). While the archipelago may be subjected to a number of inflows from the western Pacific currents and the South China Sea, the outflow is through the Sulu Sea. The Sulu Sea, and associated western Philippine islands, remained relatively enclosed during the inter-glacial maximum. Regardless, the inflows into Indonesia remained relatively stable, with changes in sea level leading to a high degree of shared taxa (Carpenter et al. 2011; de Vantier and Turak 2017).

Western Indonesian Throughflow currents did not flow through the eastern Banda Sea (Levy and Kochzius, 2016; Wainwright et al. 2018b). This provides a region with limited potential for dispersal, which may lead to localised speciation (Borsa et al. 2016; Levy and Kochzius 2016). Similarly, during the last inter-glacial, the Sahul landmass blocked the Southern Equatorial Current passing through the Gulf of Carpentaria causing it to deviate to the north. This affected the North Australian Coastal Current, disrupting the northern flow. Evidence indicates that the Gulf of Carpentaria acts as a current mediated distributional blockage prohibiting the incursion of most taxa from east to west (Veron et al. 2015; Yang et al. 2016; de Vantier and Turak 2017). However, the effects of local environmental barriers that effect gene flow are not always clear in all taxa (Maxwell et al. 2019b; Puckridge et al. 2019).

The Andaman Sea remains removed from the main Indo-Australian Archipelago, with its currents dominated by the Bay of Bengal and the Malaysian landmass. During inter-glacial maxima, the west coast of Malaysia and Thailand marine fauna, while restricted, remained relatively stable in terms of oceanic currents and inflows, leading to the formation of distinct regional taxonomic diversity (Veron et al. 2015; Borsa et al. 2016; de Vantier and Turak 2017).

9.3 Environmental Dispersal Barriers

Walters (2011) argued that there was a level of competitive interaction between closely related species that occurred with the breaking of the sea barriers, which facilitated and maintained phylogeographical disjunctions that were once mediated by physical barriers. Furthermore, shifting sea levels also created ecological barriers, with changes in localised environmental conditions due to freshwater inflows, changing sea temperatures and variations in salinity, all of which shaped the patterns of diversity (Gaither et al. 2002; Crandall et al. 2008; Figure 16).

9.4 Disperal Biology

The reason for the development of the pelagic period in the stromboidean life cycle has not been linked primarily to distribution, but rather transportation of the veliger to a more suitable habitat on which to settle (Newell 1964; Paris et al. 2008). Veligers of stromboideans are phototaxic, directing movement towards a light source (Delgado et al.

2006; Cob et al. 2009). Veligers are typically found in the upper five metres of the water column and not below the pycnocline indicating that the veligers are able to control their position in the water column, which means that the upper-level currents dominate dispersal patterns (Chaplin and Sandt, 1992; Stoner and Smith 1998). However, wind direction may play a significant role in the horizontal dispersal of larvae (Stoner and Smith 1998). Specific locations may act as areas of supply of larval recruits that have been dispersed on currents, and the supply of veligers from these sites is critical to the replenishment of populations in other regions (Stoner et al. 1996; Delgado et al. 2006; Paris et al. 2006; Aldana-Aranda and Perez-Perez 2007; Paris et al. 2008). The reliance on currents and other hydrodynamic factors for stromboidean dispersal means that meta-populations may recruit from outside neighbouring populations, and this can lead to significant genetic diversity between juxtaposed meta-populations, or leave some

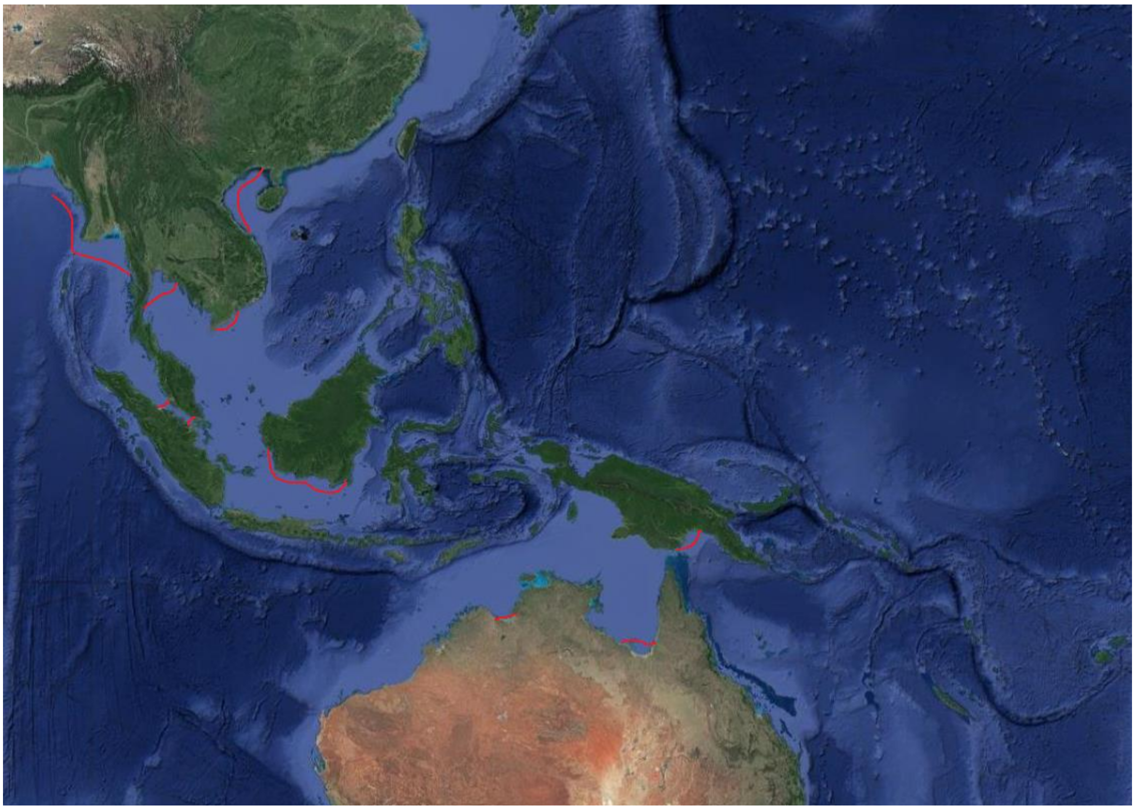


Figure 16: Possible ecological barriers to marine organism dispersal in the Indo-Australian Archipelago, with land-bounded regions demonstrated to have regular low salinity levels (< 30%) or estuarine drainage (after oeksema 2007) indicted by enclosed red spaces.

populations declining where outside recruitment is not occurring (Delgado et al. 2006; Paris et al. 2006).

Population genetics of stromboideans is dominated by the currents, and genetic diversity increases with larger geographical distances (Pérez-Enriquez et al. 2011). Due to the distance travelled, the time spent in veliger dispersion plays an important role in maintaining diversity in small isolated populations that may have historically arisen from a small recruitment base. It is these populations with limited numbers that are most at risk of over exploitation and need replenishment from other more distant populations (Pérez-Enriquez et al. 2011). Furthermore, it is expected that species with a high potential for disperial will show limited drift effects and a higher level of genetic diversity than those species with limited gene exchange (Riquet et al. 2017). The veligers of stromboideans may remain in the water column for up to 4 weeks, meaning they can travel over 1000 km on currents, and this has implications for understanding distribution and radiation patterns (Brito Manzano et al. 1999; Brito Manzano and Aldana Aranda 2004; Aldana-Aranda and Perez-Perez 2007; Truelove et al. 2017).

9.5 Distributions and Regions

The distribution of each species contained within the “urceus” complex is based on the records contained in the systematic part. This indicates that there are three realms that contain the target complex: 1) the entirety of the West Pacific Tropical Region, which Indonesia to Fiji, and the Japonic Province (Hoeksema 2007; Spalding et al. 2007; Kulbicki et al. 2013; Gaboriau et al. 2018; Petuch and Berschauer 2020); 2) the North Australian Tropical Region, with a focus on the Damperian bioregion contained within it (Wilson 2013); and 3) the Indian Tropical Region, particlaurly the Andamanian Subprovince (Petuch and Berschauer 2020; Figure 17). Outside these areas, sporadic occurrences are known, such as *C. manintveldi* Dekkers and Maxwell, 2020 from Lord Howe Island and Queensland and *C. orrae* from Port Moresby, Papua New Guinea. Such occurrences are discussed *inferius*.

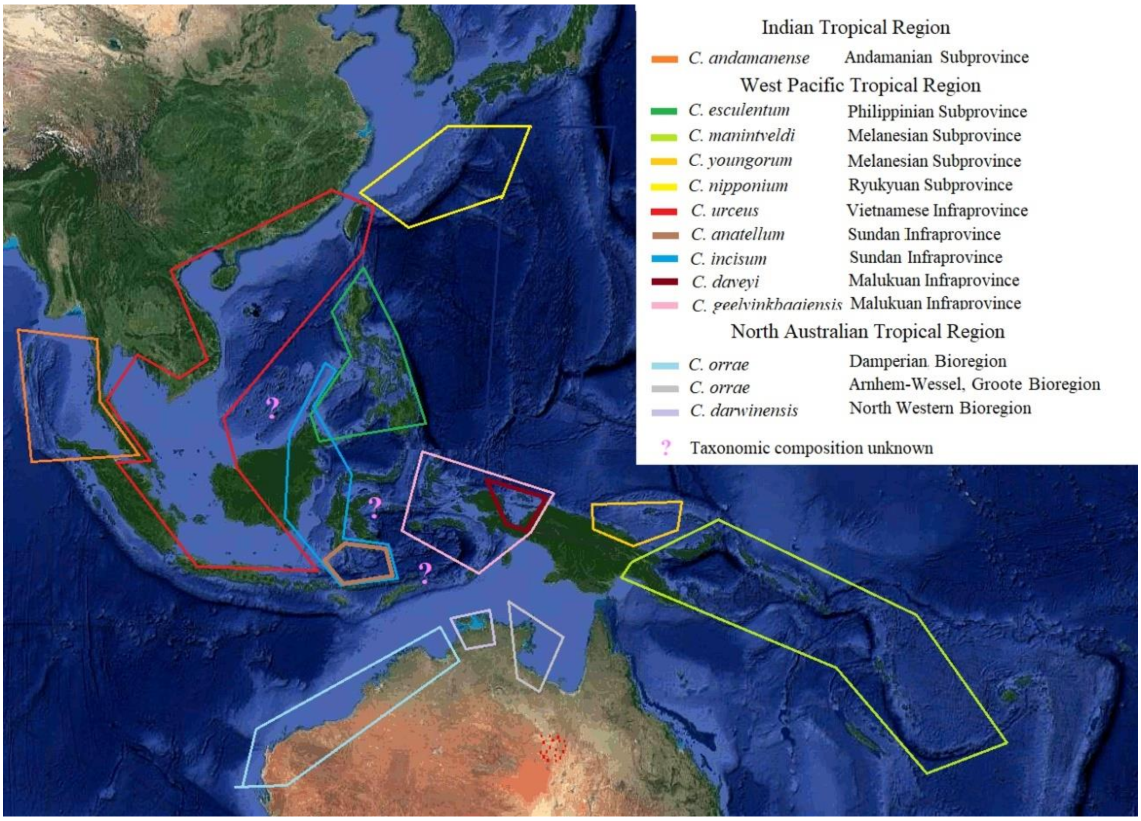


Figure 17: The colour-coded distribution of species within the “urceus” complex showing biogeographic regions. Areas where sampling is limited, or the taxonomic status of “urceus” in that region is unknown are indicated with a question mark (?).

9.5.1 Indian Tropical Region

Within the Indian Tropical Region the Andamanian Subprovince is defined by by the Malaysian Peninsula to the east, the delta of the Irawaddy River in Burma and the Andaman Islands to the west, and separated the ecotone of the Malacca Straits (Santini and Winterbottom 2002; Spalding et al. 2007; Carpenter et al. 2011; Borsa et al. 2016; Kulbicki et al. 2013; Figure 17). This subprovice has been linked to the Indian Tropical Region due to similarities between it and taxa found in Africa and the southern Indian regions (Spalding et al 2007). However, this region is also distinct from the Indian Ocean realm due to the similarity of taxa with the Pacific Ocean (Yang et al 2016) making it a region of unique significant overlap (Kulbicki et al. 2013). Furthermore, during the last Interglacial maxima this region remained relatively stable; this has held for the currents for the region past and present (Carpenter et al. 2011; Levy and Kochzius 2016).

Canarium andamanense is the only member of the complex to reside in this area. This species is relatively stable in form, but variable in colour (Dekkers et al. 2022). The Andaman Sea offered a sink for this species during glacial periods, and during the interglacial periods there was a circular current that had the potential to maintain gene flow between populations on the west Thailand coast and Andaman Island chain. The distribution of this species remains relatively stable during and between interglacial periods. The north and south of the Andaman Sea is bound by areas of high freshwater intake and turbidity, making the areas unsuitable for this species to establish long terms colonies. Veliger drift is dominated by north-south currents that flow along the coast of Thailand and through the Andaman Islands, while there may be some contact with other *Canarium* species via southern veliger movement, particularly with the most northerly populations of *C. urceus* in the southern Straits of Malacca (Figure 18).

9.5.2 West Pacific Tropical Region

The West Pacific Tropical Region, or Indo-West Pacific, is the centre of an increased gradient of taxonomic diversity (Matias and Riginos 2018). This realm includes the Eastern Malayan Peninsula, the flooded area of the Sunda landmass, south-western Indonesia, the Philippines and Okinawa Islands down the Mariana Island chain to Eastern Papua New Guinea, forming the geographical region of the central Indo-West Pacific, colloquially known as the Coral Triangle (Hoeksema 2007; Spalding et al. 2007; Kulbicki et al. 2013; Gaboriau et al. 2018).

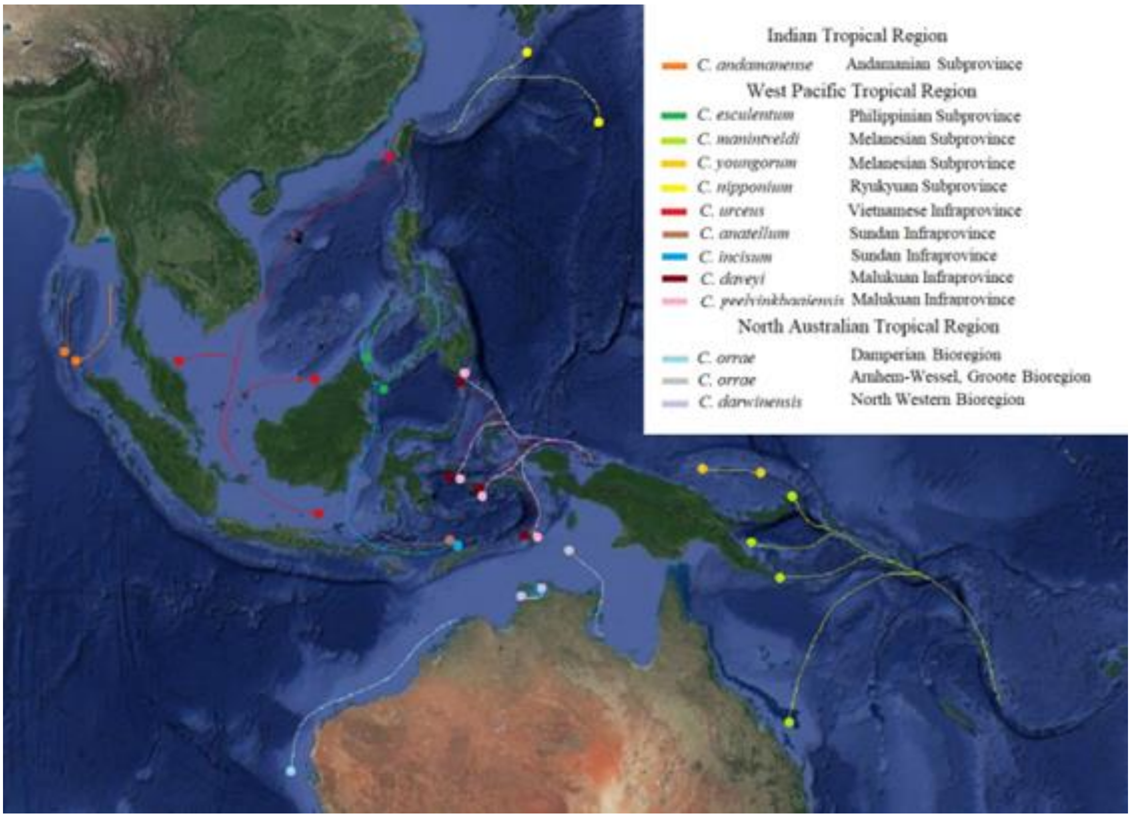


Figure 18: Direction of principle veliger drift patterns based on currents and ecological barriers, illustrated by species and bioregion.

An alternative definition of the West Pacific Tropical Region is limited to Wallacea, the Philippines, and northern and eastern Papua New Guinea, an area indicative of the last inter-glacial refugia, but this is considered too restrictive (Huang et al. 2017). A broader definition, which defines the Indo-West Pacific to encapsulate the Indian subcontinent and islands of the central Pacific, is generally considered too broad and biogeographically encapsulating (Briggs and Bowen 2012).

Indonesian Subprovince – Vietnamese Infraprovince

The Vietnamese Infraprovince ranges from the islands north of Taiwan along the Asian continental coast, including the islands within the South China Sea and the flooded Sunda region east of the Malaysian Peninsula down to western Indonesia and the western coast of Borneo (Borsa et al. 2016; Veron et al. 2015; Yang et al. 2016; Petuch and Berschauer

2020; Figure 17). This province incorporates the last interglacial refugia of the South China Sea and the regions that species from that refugia colonised after the flooding of Sunda. The currents within this region tend to be enclosed in terms of their potential to distribute taxa, and there are many smaller bioregions that reflect this limited ability to draw taxonomic influences from the wider realm to which the species belongs (Spalding et al. 2007; Carpenter et al. 2011; Yang et al. 2016).

The eastern South China Sea is home to *C. urceus*, a species that is stable in terms of general morphology and limited in its colour variability, with all specimens exhibiting some level of black aperture colouration (Maxwell et al. 2020b). During the interglacial period, this species colonised west into the South China Sea to Singapore and the west coasts of Borneo carried by the western South China Sea Throughflow (Susanto and Song 2015). When there are low sea levels during glacial periods, the species retreats into the South China Sea, and the eastern coast of Vietnam in particular. Veliger movement is driven by seasonaly shifting surface currents in the western South China Sea; during December through to February there is north to south directional currents, which contrasts June to August, when the currents are south to north (Figure 18). There are rare examples in the Kangean Islands of this species, indicating probable ingression through the Java Sea via Singapore (Susanto and Song 2015; SMC). However, while the currents of the regions are seasonal, there is no evidence of *C. andamanense* making it to Singapore (SMC). The east coast of Palawan, and north-eastern Borneo, have populations of *Canarium insicum*, indicating that there is historical gene flow between it and the eastern populations of *Canarium urceus* (Maxwell et al. 2022b).

Indonesian Subprovince – Sundan Infraprovince

The Sundan Infraprovince contains the region from the west coast of Palawan and northern and eastern Borneo, the area west of the Huxley modified Wallace Line down to the eastern Java Sea, and west to the Flores Sea (Petuch and Berschauer 2020; Figure 17). The coastlines of this subprovince are not significantly affected by coastline shifts, which remain in place and do not migrate with eustatic sea level changes. The area is affected strongly by the Indonesian Throughflow and has an inflow via western coastal currents of the Sulu and Celebes Seas (Carpenter et al. 2011; Levy and Kochzius 2016).

There are two species that come from this region, *C. anatellum* and *C. incisum,* both of which are congruent in range in the eastern Java Sea (Maxwell et al. 2020c). *C. anatellum* is restricted to the eastern Java Sea and Lesser Sunda Islands, while *C. incisum* is more widely distributed from north-western Palawan down into the Flores Sea (Maxwell et al. 2020c). The veligers of *C. incisum* from Palawan are directly dispersed based on season: with December to February, south to north currents carry veligers into the central south China Sea and back to southern Palawan nd northern Borneo; from June to August, the currents are reversed, and there is a north to south movement of veligers, which may then be carried down into the Sulawsei Sea by the eastern South China Sea Throughflow where it joins the Indonesian Throughflow into the Makassar Strait (Susanto and Song 2015; Figure 18). During interglacial periods, the Indonesian Throughflow continues, and *C. incisum* remains in the same geographical locations. Both *C. incisum* and *C. anatellum* are highly variable and differentiation is problematic at times, which may be indicative of long-term reticulation between the two species based on propensity of stromboideans to hybridise (Maxwell et al. 2019a).

Indonesian Subprovince – Malukuan Infraprovince

The Malukuan Infraprovince incorporates an area east of Sulawesi in the eastern Banda Sea to northern West Papua (Petuch and Berschauer 2020; Figrure 17). This province demarcates a small set of islands with unique biodiversity quite distinct from that of the neighbouring Philippiinian and Sundan subprovinces and the North Australian Tropical Region (Santini and Winterbottom 2002; Spalding et al. 2007; Borsa et al. 2016; Yang et al. 2016; Maxwell et al. 2019b; Petuch and Berschauer 2020). This small area did not undergo drying during the interglacial shifts in sea level that gave rise to the greater Sahul landmass. This area is also unique in its circulatory currents, where it is influenced by the Indonesian Throughflow (Carpenter et al. 2011; Levy and Kochzius 2016).

While West Papua is home to *C. daveyi* and *C. geelvinkbaaiense*, little is known of the taxonomic composition of eastern Wallacea (Dekkers and Maxwell 2020b). *Canarium daveyi* is know from that region and these often have some characteristics in terms of overall shape of the more northern and restricted *C. esculentum*. Veliger movement is dominated by the direction of currents, traveling cyclically in the Banda Sea, coupled with the north westerly southern currents associated with the Indonesian Throughflow in the Halmhera and Maluki regions, which accounts for this species in the island chains of the eastern Banda Sea (Susanto and Song 2015; Figure 18; SMC). The western movement of the Indonesian Throughflow into the Sulawesi Sea means that there is propensity for these species to arrive in the southern Philippines and far eastern Coast of Borneo (Susanto and Song 2015; Figure 18; SMC). Given that both these species are congruent and also known from relatively small numbers, albeit with morphological distinctiveness and consistency in form, the may represent the extremes of a morphological cline. The long-term stability in distribution, with little effect of sea level glacial oscillations on the distributions, means that it is only after more material comes to hand that greater resolution of this region’s species can be settled.

Philippinian Subprovince

The Philippinian Subprovince ranges from the Philippines, incorporating those island chains of the Sulu Sea and the northern Celebes Sea (Spalding et al. 2007; Carpenter et al. 2011; Petuch and Berchauer 2020; Figure 17). This region has remained relatively stable during interglacial fluctuations, comprising the region generally considered to be northern Wallacea. The currents have remained relatively consistent during periods of sea level fluctuations (Carpenter et al. 2011; Levy and Kochzius 2016). This subprovince contains one member of the "urceus' complex.

The endemic *C. esculentum* is highly variable in colour but relatively stable in form (Maxwell et al. 2020c). It is most prolific in the central regions of the Philippines centred on the Cebu and Bohol Island groups. This species is relatively unaffected by interglacial fluctuations as the populations are bound to the fringing reefs of islands. The ocean currents that circulate within and through the southern Philippines join into the Indonesian Throughflow, and this has the propensity to carry *C. esculentum* veligers south into Indonesia, and to the east coast of Borneo and the Kangean Island chain in particular (Susanto and Song 2015; Figure 18). This Philippinian Subprovince also receives veliger inflows from the Pacific, and there is limited recruitment of both *C. daveyi* and *C. geelvinkbaaiense* into this region (SMC), although there is no evidence of either having established a population.

Melanesian Subprovince

The Melanesian Subprovince takes in the Bismarck Archipelago and the north coast of New Guinea down into Fiji and the Solomon Islands (Spalding et al. 2007; Borsa et al. 2016; Petuch and Berchauer 2020; Figure 17). This region has a stable current flow during interglacial periods, and the landmass remains relatively unchanged with fluctuations of sea level (Carpenter et al. 2011; Levy and Kochzius 2016). While there is a broad understanding of the macro-evolution and radiation of Indo-Australian Archipelago taxa (Liu et al. 2014; Tornabene et al. 2016), little is known of the micro-evolutionary impacts of inter-glacial cycles on speciation. Understanding speciation at the micro-scale in the central Indo-West Pacific involves understandaing the repeated drying/flooding events limiting absolute vicariance in marine species, where contact is regulated by glacial cycles. These periodic disentanglements and subsequent confluxes of species would indicate that allopatric, peripatric and parapatric speciation all might have contributed to the divergence of taxa (Campbell et al. 2018). The Melanesian Subprovince is dominated by atolls and islands, and marine species are relatively unaffected by disruptions to distribution via changes in sea levels through time. The currents are also relatively stable during interglacial periods, with the Southern Equatorial Current, and Southern Equatorial Counter Current dominating the east of the zone, while localised currents with stable directional flows occur within the island chains (McGregor et al. 2008).

Canarium manintveldi is a widely distributed species among the islands and reefs of the south Pacific. The high shouldered white apertured form with its distinctive blue hue is dominant in Vanuatu, Lord Howe Island, and Mooloolabah on the Queensland Coast (SMC) and is dispersed by the East Australian Currents (McGregor et al. 2008). The more northern populations in Papua New Guinea, and Rabaul in particular, lose the strong shoulder and become less patterned, tending to take a uniform hue (pers. obs., SMC). Individuals at the extreme ends of the range have remarkable distinctness in form, but these differences are suggested to be clinal in form, reflecting directional veliger flows from south to north following the direction of the New Guinea Coastal Undercurrent and across to the Australian Coast (McGregor et al. 2008; Figure 17).

Canarium youngorum is currently suggested to be restricted to the northern regions of this Subprovince, predominantly Manus Island and the north eastern areas of Papua New Guinea. This is a rare species in collections, and little is known of its complete range and morphological variability. The currents of this region are highly localised, and populations of *C. youngorum* are dominated by the New Guinea Coastal Current, which oscillates along the northern coast of the main island, limiting the poteinial for veliger dispersal (McGregor et al. 2008; Figure 18).

Japonic Province - Ryukyuan Subprovince

The Ryukyuan Subprovince encompasses the islands of the Amami and Okinawan group and is known for its high levels of molluscan endemism (Petuch and Berchauer 2020; Figure 17). The dominant current is the Kuroshio Current that runs south to north, with a counter current turning and covering the Ogasawara Islands (Figure 18). Consisting of islands and atolls, the coast line in this region does not significantly move with changes in sea level, nor are the currents that flow through the region affected by sea level oscillations.

The sole member of the "urceus" found here, *C. nipponium*, is contained within the Ryukyuan Subprovince, and veliger movement is directional south to north with the Kuroshio Current. Part of this current breaks off and connects this population with the more isolated island populations in the Ogasawara Islands, which then feeds into the Marianas (Figure 17).

9.5.3 North Australian Tropical Region

The North Australian Tropical Region ranges from Shark Bay in Western Australia north to the Gulf of Carpentaria (Wilson 2013; Petuch and Berschauer 2020; Figure 17). The North Australian Tropical Region is divided into several distinctive mesoscale biogeographical Bioregions (Thackway and Cresswell 1998).

The Damperian, Arnhem-Wessel, Groote Bioregions

The Damperian biogreion ranges from Shark Bay in Western Australia north to along the Kimberley coast Bioregions (Thackway and Cresswell 1998; Figure 17). Also included because of its similar taxa, the western Northern Territory, in the Arnhem-Wessel Bioregion, is relatively unexplored in terms of its biodiversity; reefs tend to the eastern border regions with the Groote Biogeographical Bioregion, and there are sporadic records of *Canarium* from that region (per sobs., ALA 2021). These regions have well developed localised fringing coral reefs and extensive seagrass beds separated by narrow fringing mangrove stands (Thackway and Cresswell 1998).

Canarium orrae is a coastal species that is found throughout the Damperian, Arnhen-Wessel and Groote Bioregions (Figure 17). This species followed the shore line with the shifting sea levels during periodic glacial and interglacial fluctuations. It is constant in form, with no significant variability between populations across the range. The veliger movement in the Damperian Bioregion is dominated by a coastal north to south current, while the Arnhen-Wessel and Groote Bioregions have a current that sweeps past, south to north, along the east coast of the Gulf of Carpentaria into the eastern Arafura Sea (Figure 18).

The North Western Bioregion

The North Western Bioregion contains the Van Diemen Gulf and area surrounding Darwin. The area is characterised by diverse tropical environments including large estuarine drainage systems, mangrove flats, localised intermittent fringing reefs and rocky headlands (Thackway and Cresswell 1998; Figure 17).

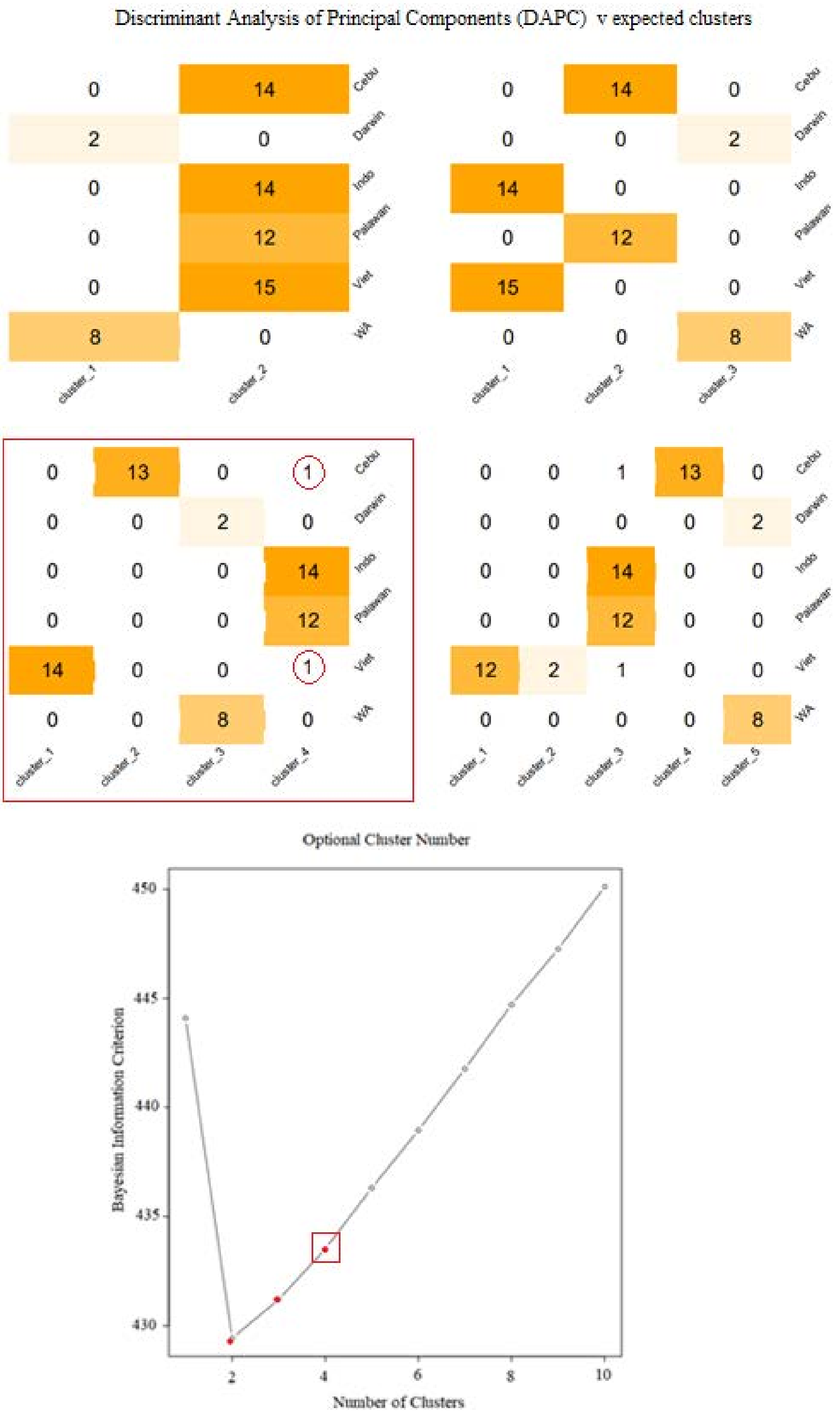
Canarium darwinensis is unique to the North Western Bioregion and is highly stable in both colour and form. This species is relatively young, and may be an ecomorph of *C.*

orrae, recently splitting from that lineage. Veliger movement for this population is regulated by localised currents in the Darwin region, and there is little inflow from outside, leading to a drift in morphology (Figure 18).

9.6 Diversification and Genetic Evidence

The genetic results indicate that there are two optimal complexes buried within the “urceus” group, each of which represents differing regions (Figure 19). The first comprises Australian organisms from Northern Australia, while the second contains those of the central Indo-Pacific. The Bayesian Information Criterion (BIC) and cross-entropy values for K = 2 were only slightly lower than K = 3 and 4. Cluster 4 in this study is considered optimal as it reflects the current state of taxonomy with species, with potential migrants showing in both Cebu and Vietnam populations. Cluster 5 is rejected as optimal as it starts to see the breakdown internally of known populations. As the set is forced into greater numbers of clusters, the allelic dropout between these two groups means the results are likely overwhelmed by missing values as the cluster number is increased; notwithstanding, forcing rarer alleles into the analysis resolves more recent divergences, and this evidence shows that all populations are genetically distinct (K = 6).

The structure plot (Figure 20) shows the two optimal clusters; these represent two ancestral groups contained within the “urceus” complex (K = 2). Genetically, the Cebu and Palawan populations share greater similarity than those organisms from Vietnam (K = 3), with Indonesian organisms showing an ancestral link with both the Philippines (Cebu and Palawan) and Vietnam (K = 3).



	cluster_1	cluster_2
Cebu	0	14
Darwin	2	0
Indo	0	14
Palawan	0	12
Viet	0	15
WA	8	0

	cluster_1	cluster_2	cluster_3
Cebu	0	14	0
Darwin	0	0	2
Indo	14	0	0
Palawan	0	12	0
Viet	15	0	0
WA	0	0	8

	cluster_1	cluster_2	cluster_3	cluster_4
Cebu	0	13	0	①
Darwin	0	0	2	0
Indo	0	0	0	14
Palawan	0	0	0	12
Viet	14	0	0	①
WA	0	0	8	0

	cluster_1	cluster_2	cluster_3	cluster_4	cluster_5
Cebu	0	0	1	13	0
Darwin	0	0	0	0	2
Indo	0	0	14	0	0
Palawan	0	0	12	0	0
Viet	12	2	1	0	0
WA	0	0	0	0	8

Figure 19: Discriminant Analysis of Principal Components (DAPC) and Bayesian Information Criterion against the number of potential clusters indicates that there are two optimal species clusters, those from Australia and a second from the central Indo-Pacific. This indicates that genetically there are two to four optimal clusters of organisms, with all circumscribed species resolving with 4 clusters. Potential migrants are indicated with circles.

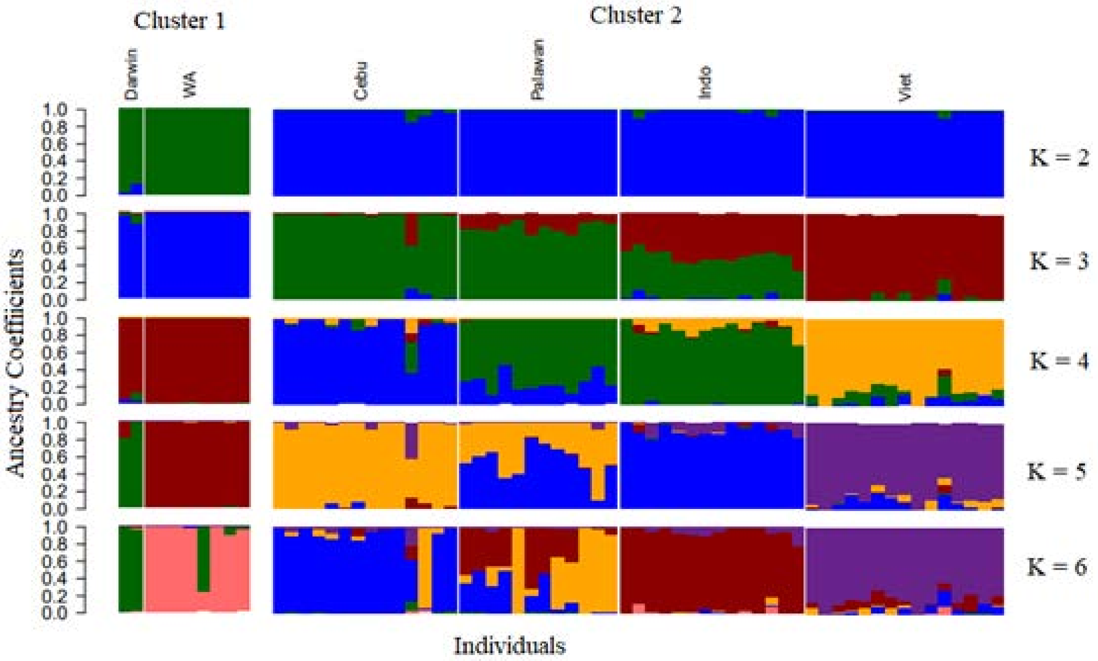


Figure 20: The LEA least-squares estimates of ancestry or structure plot of the "urceus" complex showing the genetic relationships between populations, as more similarity is included. The ancestral relationships can be seen, as well as showing that each population has recently diverged and is genetically distinct. At K = 4, 5 we see the species contained in this thesis are genetically distinguished (note colours are independent in each row).

The optimal clustering based on taxonomy (K = 4) shows the genetic similarities between Palawan and Indonesia have become more pronounced, with the Indonesian population showing introgression from Vietnam, and the Palawan population indicating inflows from Cebu. The structure plot K= 5 - 6 indicates that the Palawan population is drawing genetic material from both Cebu and Vietnam. It is only with the inclusion of more alleles, reducing the drop out, that the Darwin and Australian populations resolve.

These patterns in gene flow mirror the previously proposed veliger distribution and currents earlier in this chapter, and the distinctiveness of all populations indicates that they are not from a single centre of origin, but rather arise out of multiple centres with genetic distinctiveness, in this case Cebu, Vietnam and Northern Australia, with Palawan and Indonesia appearing to be centres of accumulation based on shared ancestry.

9.7 Indo-Australian Archipelago Radiation Theories

There are four primary hypotheses used to explain the observed distributional patterns of taxa: 1) The centre of survival theory were species retreat to refugia during glacial maxima; 2) The centre of overlap theory with different widespread populations coming together; 3) The centre of origin theory, where species radiate out from central refugia; and 4) The centre of accumulation theory, which offers a coalescent model were smaller isolated populations, all derived form a larger population once riven by ecological and environmental factors, come together.

9.7.1 Centre of Survival

The centre of survival theory agues that species retreat into refugia during glacial periods. This in turn generates regions where there is limited gene flow between isolated populations, there is a high potential for regional genetic drift to facilitate the divergence of taxa. However, the potential of this divergence between isolated populations is highly taxon specific, and reflects each organism's potential to successfully disperse and reticulate with other populations (Drew and Barber 2012). The migration rates in the central Indo-Australian Archipelago are often high enough to hold the homogeny of a species across a large range with many remote populations (Dohna et al. 2015). Current phylogenetic processes in some form have been tied to an ongoing process of reticulating cryptic species derived in the Pliocene (Cheng and Sha 2017; Titus 2018). One of the major vectors for sympatric speciation is hybridisation as new phylogenies are spontaneously thrown up amid existing species complexes (Maxwell et al. 2019a). Within the Indo-West Pacific during peak glaciation events, the taxa of the South China Sea and Philippines-Wallacea are demonstrated to have a level of genetic isolation due to land barriers, enabling sympatric speciation to occur (Ravago-Gotanco et al. 2018).

9.7.2 Centre of Overlap Theory: Post Tethian Breakdown

The breakdown and subsequent changes in the circum-global oceanic currents with the closure of the Tethys led to the dissolution of ancestral species distribution. This disruption led to widespread allopatric speciation (Santini and Winterbottom 2002). Under this model, it is hypothetically possible to track the ancestral character states from east to west within now divergent populations (Santini and Winterbottom 2002). Therefore, each region would, through drift, have an independent evolutionary trajectory, with only periodic influence from neighbouring regions.

The centre of overlap theory argues that the rapid rise in sea levels led to niche expansion into areas that had been isolated from each other by geographical barriers, with recruitment occurring from the western Indian Ocean and eastern Pacific Ocean (Ma et al. 2017). This overlap and accumulation has not affected the ongoing regional speciation processes in areas that act as reservoirs for species during the last glaciation (Tornabene et al. 2016; Ukuwela et al. 2016). This theory is supposes by the presence of sister taxa, one in the Indian Ocean and another in the Pacific Ocean, that have divergent lineages but with an overlapping of distributions occurring on the flooded Sunda landmass (Ma et al. 2017).

9.7.3 Centre of Origin

The centre of origin theory suggests that speciation occurs in a central area of high diversity, and these species then radiate out as changes in sea level occur. These new populations then become isolated and evolve independently to the main source population (Fransen 2007; Ma et al. 2017). The species richness of the Indo-Australian Archipelago is the consequence of radiation out from a central area of high diversity, centred on the Philippines and eastern Indonesia. These regions act as sinks for marine species that have retreated during the continental drying of the inter-glacial events. This model is supported by the number of endemics within the central region that, as yet, have not radiated (Ma et al. 2017; Gaboriau et al. 2018).

Centre of origin speciation is the consequence of random colonisation of neighbouring archipelagos from a central source (Hickerson and Meyer 2008). These isolated populations undergo genetic drift which, through time, leads to divergence from the ancestral taxa and may provide the source for genetic novelties in the genome of the ancestral taxa through reticulation (Fernandez-Silva et al. 2015).

9.7.4 Centre of Accumulation

This process of speciation occurs in organisms on the edges of the Indo-Australian Archipelago area and, as a result of convergent dispersal, there are regions of accumulated high diversity as barriers break down and reform over relatively short geological time scales (Hoeksema 2007; Ma et al. 2017; Simmonds et al. 2018). The centre of accumulation theory is illustrated with sister taxa that have a high degree of diversity between the extremes of the range, leading to a conflux of this diversity in the middle of the range (Ma et al. 2017).

9.8 Summary

The Indo-Australian Archipelago realm was formed with the closure of the Tethys Sea and subsequent tectonic activity associated with conditional drift. These geological forces, coupled with fluctuating sea levels, have made the Indo-Australian Archipelago a region of great diversity driven by a variety of speciation processes. More importantly, these geological forces have created provinces, which have maximised the potential for biodiversity throughout the realm as a whole.

Four models may explain speciation within the Indo-Australian Archipelago. First, the centre of survival theory is based on soft vicariance and sympatric speciation in regions where there is limited gene flow between isolated populations. Second, the centre of overlap theory, or post-Tethian breakdown, is based on allopatric speciation where broader circum-global oceanic currents have been disrupted, leading to large scale speciation as populations with large distribution become divided. Third, the centre of origin theory, which is a peripatric conception of speciation, where speciation occurs in a central area of high diversity and these species then radiate out as changes in sea level occur, later becoming isolated. Fourth, the centre of accumulation theory, which is post-parapatric in that speciation occurs at the edges of the realm and new species migrate into the centre resulting in pockets of high biodiversity.

Within the urceus, each set of taxa has undergone a variety of diversification processes across its range, and therefore it would not be unexpected that a group of related organisms would need more than one speciation model to explain the observable diversity. There is no single explanation for the observable distribution patterns, meaning that broad conclusions for radiation patterns that explain a general set of organisms with shared life history traits is not possible (Crandall et al. 2019). The “urceus” have undergone periodic interactions with sister taxa as they radiate out during interglacial periods and their associated sea level rises.

Chapter 10 Systematics

Dekkers AM, Dekker H, **Maxwell** SJ (2022) Studies in *Canarium urceus* (Linné, 1758) Part 6*:* a new *Canarium* species from the Andaman Sea (Gastropoda: Neostrombidae: Strombidae). *The Festivus* 54(1), 29-35.

Dekkers AM, **Maxwell** SJ (2020) Studies in *Canarium urceus* (Linnaeus, 1758) Part 3: new species from the western Pacific (Gastropoda: Neostromboidae: Strombidae). *The Festivus* 52(4), 345-358.

Liverani V, Dekkers AM, **Maxwell** SJ (2021) Resolving phylogenetic and classical nomenclature: A Revision of *Canarium* Schumacher, 1817 (Mollusca, Neostromboidae, Strombidae). *The Festivus* 53(1), 26-43.

Maxwell SJ (2021) Recognising and defining new crown clades in Stromboidea Rafinesque, 1815. *Bulletin of the Russian Far East Malacological Society* 25(1/2), 9-16.

Maxwell SJ (2021) Registration of Neostromboidae Clades in the RegNum of the PhyloCode and errata. *The Festivus* 53(3), 193-209.

Maxwell SJ, Dekkers AM (2021) Studies in *Canarium urceus* (Linné, 1758) Part 5: a new species from the northern Pacific Ocean (Gastropoda: Neostromboidae: Strombidae). *The Festivus* 53(4), 282-287.

Maxwell SJ, Dekkers AM (2021) Studies in *Canarium urceus* (Linné, 1758) Part 4: *Canarium* (*Canarium*) *orrae* (Abbott, 1960) (Gastropoda: Neostromboidae: Strombidae) and a new species from the Northern Territory, Australia. *The Festivus* 53(4), 270-281.

Maxwell SJ, Rymer TL (2021) Are the ICZN and PhyloCode that incompatible? A summary of the shifts in Stromboidean taxonomy and the definition of two new subfamilies in Stromboidae (Mollusca, Neostromboidae). *The Festivus* 53(1), 44-51.

Maxwell SJ, Rymer TL, Congdon BC, Dekkers AM (2020) Studies in *Canarium urceus* (Linné, 1758) Part 2: *Strombus anatellus* Duclos, 1844, *Strombus crassilabrum* Anton, 1839, *Strombus incisus* Wood, 1828 and *Strombus ustulatus* form *laevis* Dodge, 1946 (Neostromboidae: Strombidae). *The Festivus* 52(4), 335-344.

Maxwell SJ, Rymer TL, Dekkers AM (2020) *Canarium urceus* (Linné, 1758) Studies Part 1: The recircumscription of *Strombus urceus* Linné, 1758 (Neostromboidae: Strombidae). *The Festivus* 52(2), 113-127.

Here, I seek to resolve the taxonomic conundrum that is *Strombus urceus* Linné, 1758 (= *Canarium urceus* (Linné, 1758)) through identifying the type and explicitly defining a range for that phenotype by first principles. I have brought together the physical type material and lectotypes to provide a sound resolution to the taxonomical enigma of what Linné (1758, 1764, 1767) intended when describing “urceus”, and have reviewed its synonymy in the context of modern systematic understanding. The classification is hypothesised to epifamily based on the literature. Five RegNum registered clades are outlined, and the rank of sub-genus is presented, but this rank is not defined under the PhyloCode (2019). Twelve species are presented in alphabetical order. No organisms in this study were classified as subspecies, indicating that they are all morphologically distinct from one another.

10.1 Taxonomy

Phylum	*Mollusca* Linné, 1758
Class	*Gastropoda* Cuvier, 1795
Subclass	*Caenogastropoda* Cuvier, 1797
Order	*Sorbeoconcha* Ponder and Lindberg, 1987
Suborder	*Strombacea* Rafinesque, 1815
Superfamily	*Stromboidea* Rafinesque, 1815

Neostromboidae

Maxwell, Dekkers, Rymer and Congdon, 2019 [Maxwell, 2021]

(Figure 21)

Synonymy.

2019 *Neostromboidea* Maxwell, Dekkers, Rymer and Congdon, p. 3, fig. 2.

2019 *Neostromboidae* Maxwell, Dekkers, Rymer and Congdon – Maxwell 2019 (corrigenda). Maxwell and Rymer 2021, p. 46. Maxwell 2021a, p. 12, fig. 1.

RegNum Registration Number. 565.

Definition. The total clade of the largest crown clade containing *Strombus pugilis* Linné, 1758, *Terebellum terebellum* (Linné, 1758) and *Tibia fusus* (Linné, 1758) but not *Struthiolaria papulosa* (Martyn, 1784) or *Aporrhais pespelecani* (Linné, 1758).

Composition. The clade contains members of three families, *Strombidae* (see Maxwell and Rymer (2021) for content), *Rostellariidae*, and *Seraphsidae*. It excludes *Struthiolariidae* and *Aporrhaidae*.

Diagnostic Apomorphies (Original Description). “The animal possesses eyes on the end of the peduncles. The cephalic tentacle is also located on the peduncle towards the distal end. The radula has a central rachidian tooth with three lateral teeth either side. The foot is laterally compressed, with a defined propodium and a metapodium. The shell form changes upon maturation with the development of an outer lip structure” (Maxwell et al. 2019b, p. 3).

Type Genus. *Strombus* Linné, 1758 (Type *Strombus pugilis* Linné, 1758).

Reference Phylogeny. Figure 2A in Maxwell et al. (2019b).

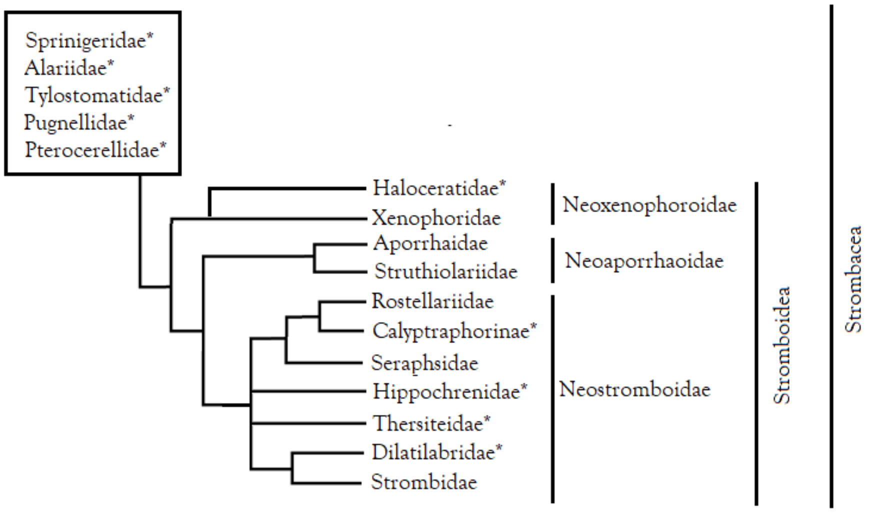


Figure 21: The defined clades within *Strombacea* showing the position and internal content of *Neostromboidae* (Maxwell 2021a, fig.1).

Strombidae

Rafinesque, 1815 [Maxwell, 2021]

(Figure 22)

Synonymy.

1815 *Strombidae* Rafinesque, p. 145. Maxwell et al. 2020b, p. 115. Maxwell and Rymer 2021, p. 46.

RegNum Registration Number. 566.

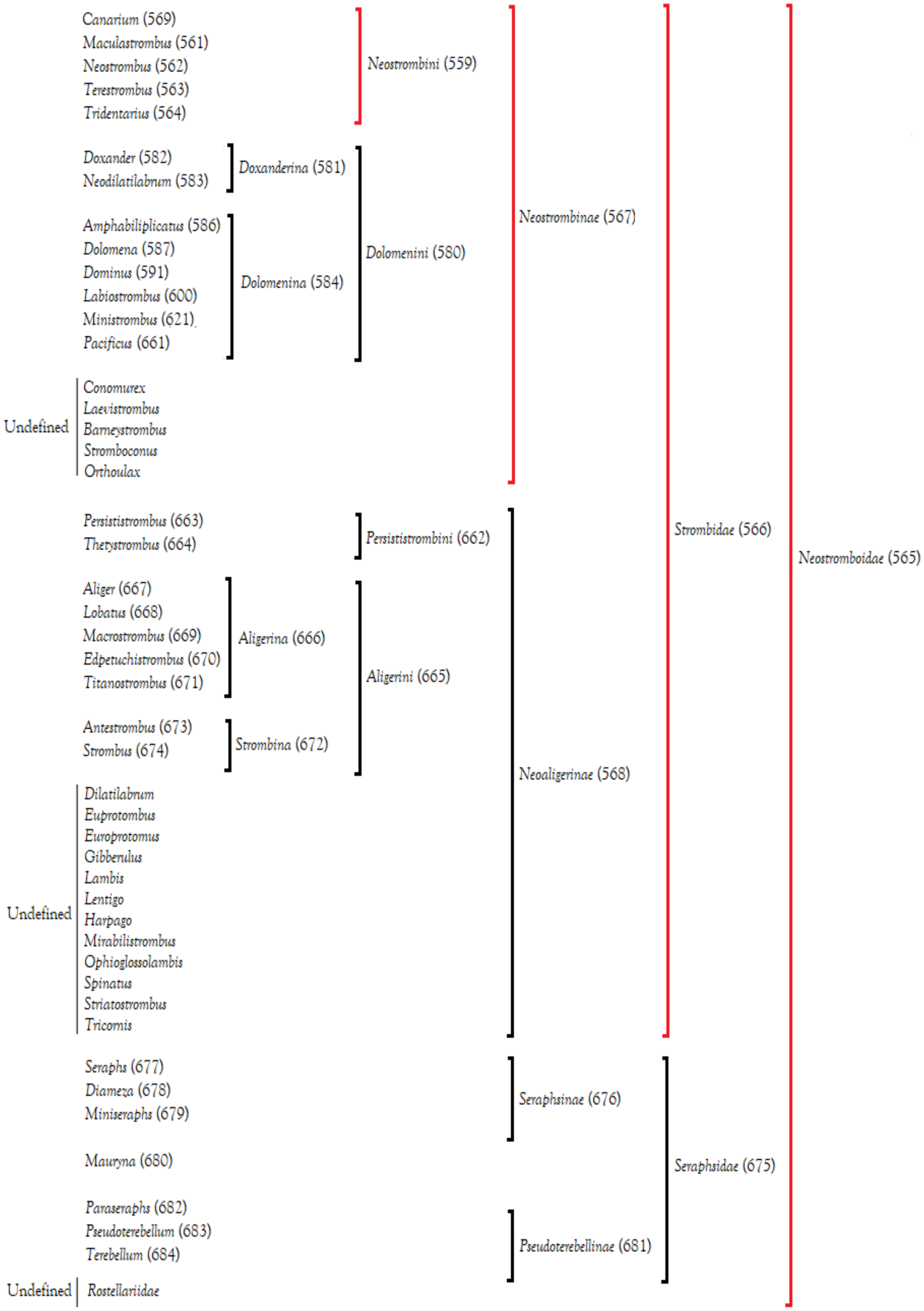


Figure 22: The defined clades within *Neostromboidae* with RegNum numbers shown in brackets after each taxon name. The *Canarium* lineage is highlighted in red (Maxwell 2021b, fig.1).

Definition. The maximum clade consisting of *Aliger gallus* (Linné, 1758) and *Canarium urceus* (Linné, 1758) and all species that share a more recent common ancestor with them than with *Terebellum terebellum* (Linné, 1758) or *Tibia fusus* (Linné, 1758).

Reference Phylogeny. Figure 1 in Maxwell and Rymer (2021).

Composition. The clade containing the two subfamilies *Neostrombinae* (see Maxwell and Rymer (2021) for content) and *Neoaligerinae* (see Maxwell and Rymer (2021) for content). It excludes the *Rostellariidae* and *Seraphsidae*.

Diagnostic Apomorphies. Shell with a body whorl that is longer than the combined teleoconch, stromboidal notch well formed, and body whorls sculpture may vary significantly from that of the teleoconch (Abbott 1960; Walls 1980; Bandel 2007; Maxwell et al. 2019; Maxwell and Rymer 2021; Maxwell and Rymer, 2021, p. 46).

Original Description. "2. S. F. *Strombia*. Les Strombiens. Bord de la base ou bouche, dilaté en aile latérale. G. 15. *Strombus* L. 14. *Pterocera* Lam. 17. *Rostellaria* Lam." (Rafinesque, 1815, p. 145).

Type Genus. *Strombus* Linné, 1758 (Type *Strombus pugilis* Linné, 1758).

Neostrombinae

Maxwell and Rymer, 2021 [Maxwell, 2021]

(Figure 22)

Synonymy.

2021 *Neostrombinae* Maxwell and Rymer, p. 47.

RegNum Registration Number. 567.

Definition. The maximum clade consisting of *Dolomena pulchellus* (Reeve, 1851) *Conomurex luhuanus* (Linné, 1758), *Laevistrombus canarium* (Linné, 1758), and

Neostrombus fusiformis (Sowerby II, 1842) and all species that share a more recent common ancestor with them than with *Aliger gallus* (Linné, 1758), *Euprotomus aurisdiane* (Linné, 1758), *Lambis lambis* (Linné, 1758), *Gibberulus gibberulus* (Linné, 1758) or *Persististrombus granulatus* (Swainson, 1822).

Reference Phylogeny. Figure 3 in Maxwell and Rymer (2021).

Composition. The clade containing the two tribes *Neostrombini* (see Liverani et al. (2021) for content) and *Dolomini* (see Dekkers and Maxwell (2020a) for content), and also other genera such as *Conomurex* (see Abbott (1960) for content) and *Laevistrombus* (see Maxwell et al. (2019a) for content). It excludes *Neoaligerinae* (see Maxwell et al. (2020a) for content).

Diagnostic Apomorphies. "There is a basal peg on the radula first lateral tooth. The shells are small to medium in size. The posterior canal is straight and extended. Dorsum of the body whorl often smooth or with limited shoulder ornamentation" (Maxwell and Rymer 2021, p. 47).

Original Description. "The shells are small to medium in size. The posterior canal is straight and extended. There is a basal peg on the first lateral teeth. Dorsum of the body whorl often smooth or with limited shoulder ornamentation" (Maxwell and Rymer 2021, p. 47).

Type Genus. *Neostrombus* Liverani, Dekkers and Maxwell, 2021 (Type: *Strombus fusiformis* Sowerby II, 1842). The original erroneous designation of *Canarium* (Maxwell and Rymer 2020) was corrected in Maxwell (2021).

Neostrombini

Liverani, Dekkers and Maxwell, 2021 [Maxwell, 2021]

(Figure 23)

Synonymy.

2021 *Neostrombini* Liverani, Dekkers and Maxwell, p. 28.

RegNum Registration Number. 559.

Definition. The maximum clade consisting of *Dolomena pulchellus* (Reeve, 1851), *Conomurex luhuanus* (Linné, 1758), *Laevistrombus canarium* (Linné, 1758), and *Neostrombus fusiformis* (Sowerby II, 1842) and all species that share a more recent common ancestor with them than with *Aliger gallus* (Linné, 1758), *Euprotomus aurisdiane* (Linné, 1758), *Lambis lambis* (Linné, 1758), *Gibberulus gibberulus* (Linné, 1758) or *Persististrombus granulatus* (Swainson, 1822).

Reference Phylogeny. Figure 3 in Maxwell and Rymer (2021).

Composition. The clade containing the two tribes *Neostrombini* (see Liverani et al. (2021) for content) and *Dolomini* (see Dekkers and Maxwell (2020a) for content), and also other genera such as *Conomurex* (see Abbott (1960) for content) and *Laevistrombus* (see Maxwell et al. (2019a) for content). It excludes *Neoaligerinae* (see Maxwell et al. (2020a) for content).

Diagnostic Apomorphies. “There is a basal peg on the radula first lateral tooth. The shells are small to medium in size. The posterior canal is straight and extended. Dorsum of the body whorl often smooth or with limited shoulder ornamentation” (Maxwell and Rymer, 2021, p. 47).

Original Description. “Shells small with a narrow aperture that is posteriorly constricted forming a narrow sinus with the body whorl. The radula has a central tooth with five cusps the central being the largest, and lateral teeth with a basal peg” (Liverani et al. 2021,

p. 28).

Type Genus. *Neostrombus* Liverani, Dekkers and Maxwell, 2021 (Type: *Strombus fusiformis* Sowerby II, 1842).

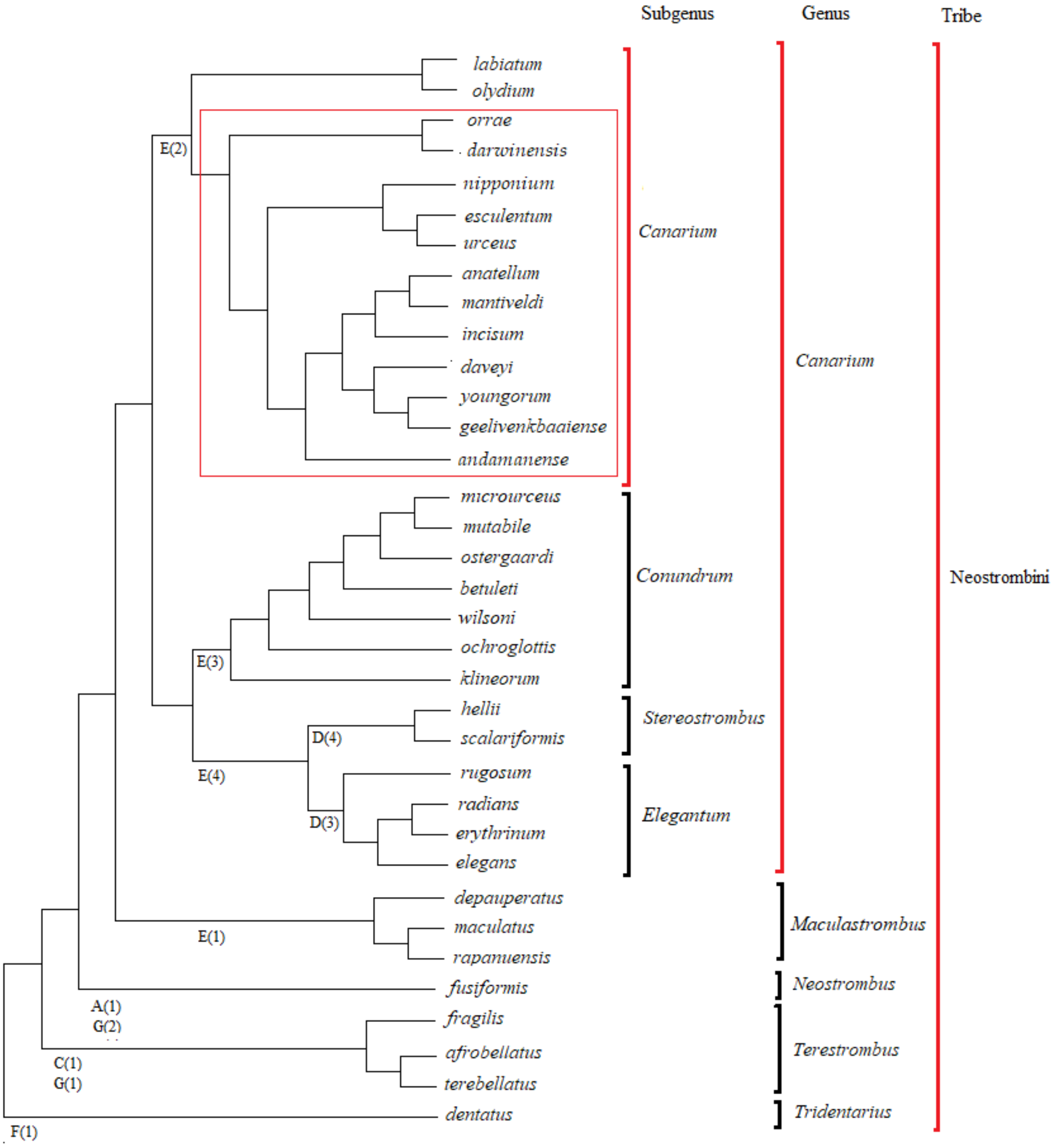


Figure 23: *Neostrombini* showing morphological relationships of taxa based on character analysis using MEGA X (Kumar et al. 2018) software, with important defining character states inserted and the *Canarium urceus* complex boxed.

Canarium

Schumacher, 1817 [Maxwell, 2021]

(Figure 23)

Synonymy.

1817 *Canarium* Schumacher, p. 219. Maxwell et al. 2020b, p. 115. Liverani et al. 2021, p. 29.

RegNum Registration Number. 569.

Definition. The maximum clade consisting of *Canarium urceus* (Linné, 1758) and all species that share a more recent common ancestor with them than with *Tridentatarius dentatus* (Linné, 1758), *Terestrombus fragilis* (Röding,1798), *Maculastrombus maculatus* (Sowerby II, 1842) or *Neostrombus fusiformis* (Sowerby II, 1842).

Reference Phylogeny. Figure 1 in Liverani et al. (2021).

Composition. This clade belongs to the Neostrombini (see Liverani et al. (2021) for content) and contains *Canarium* (see Liverani et al. (2021) for content). It does not include members of the *Maculastrombus*, *Neostrombus*, *Terestrombus* and *Tridentarius* (see Liverani et al. (2021) for content on all four genera).

Diagnostic Apomorphies. Small solid shells with an elliptic-rhomboid form and a variable height of teleoconch, and a cross section of the labrum that is thickened with a fine ridge (Liverani et al. 2021, p. 29).

Original Description. "Testa suboblonga; spira subelongata, acutiuscula. Apertura linearis, postice integerrima, coarctata; rostrum breve subadscendens, subrecurvum; canalis apertus; labium externum acutum, in dorso marginatum, antice lobo semilunari inter sinum sigmoideum et truncaturam obliquam, postice integerrimum, interne substriatum; labium internum callosum, adnatum, columellaque tortilli antice substriatum" (Schumacher 1817, p. 219).

Type Species. *Canarium ustulatum* Schumacher, 1817 (= *Strombus urceus* Linné, 1758).

***Canarium* (*Canarium*)**

Schumacher, 1817

(Figure 23)

Synonymy.

1817 *Canarium* Schumacher, p. 219 (Type: *Canarium ustulatum* Schumacher, 1817 = *Strombus urceus* Linné, 1758). Liverani et al. 2021, p. 29.

1840 *Strombidea* Swainson, p. 138 (Type: *Strombus urceus* Linné, 1758).

1888 *Conarium* Jousseaume, p. 174 (Type: *Strombus mutabilis* Swainson, 1821).

1960 *Conorium* "Jousseaume" Abbott, p. 63 (Printing error for *Conarium* Jousseaume, 1888).

Description. "Shell small and robust. Columella well defined. Outer lip not flared, but typically thickened, with no spines or protuberances. Stromboidal notch well developed. Aperture finely lirate in most taxa. Spire ribbed, although this may be reduced or rudimentary. Apex of spire acute. Shoulder of body whorl typically with knobs. Typically, there is a high degree of variability in colour and form within the genus. Rachadian tooth with five cusps, middle largest, laterals with basal peg. Operculum with numerous well-developed serrations" (Maxwell et al. 2020, pp. 115-116).

Discussion. The name "urceus" appears in the Linné (1758) *Systema Naturae* as no. 440 with a description that consists of three clauses: *S. testæ labro attenuato retuso brevi striato* [The shell lip diminished, recurved with short striations], *ventre spiraque plicato-nodosis* [the spire and ventral body whorl plicated and nodulated], *apertura bilabiata inerni* [aperture with two lips and no armature (translations SM)]. The first clause describes the general shape: a shell that does not have the expanded outer-lip, is recurved and the outer lip lirate. This characteristic is shared by many species in the genus *Canarium*, particularly *C. radians*, *C. labiatum*, *C. mutabile* and. *C. urceus*. However, it is only with *C. urceus* that we find the lirations short and diminished. The second clause implies a plicate and nodulated spire and body whorl. There are three members of *Canarium* that fit into this description: *C. radians*, *C. labiatum* and. *C. urceus*. The third clause seeks to separate this species from the similar *Tridentarius dentatus*, which shares similar features used to describe "urceus" but has distinct serrations on the outer lip lacking in *C. urceus*. Furthermore, added to this description are three lectotype citations. First, "Rumph. Mus. t. 37, f. T", or Rumphius (1705) *Thesaurus Imaginum Piscium Testaceorum; Conchearum; Conchylia, et Mineralia*, plate 37, figure T, an image of *C. labiatum*. The second reference is to "Pet. Gaz. t. 98, f. 19" refers to Petiver (1711) *Gazophylacii Nature et Artis*, plate 98, figure 19, which I have not been able to locate on the plate as the figure numbers do not extend past figure 18. However, figure 14c is *C. labiatum*, and similar to the Rumphius illustration cited. Furthermore, the other strombids illustrated are not members of the clade *Canarium* but rather fall within *Doxander*, *Laeviostrombus*, and *Conomurex*. The third citation that Linné provides is "Gualt. Test. t. 32, f. G", or Gualtieri (1742) *Index Testarum Conchyliorum*, Plate 32, figure G, which is *Ministrombus minimus* (Linné, 1771).

The definition provided by Linné (1764) in the *Museum Ludovicae Ulricae* provides a greater description of the taxon than contained in the *Systema Naturae* 10th edition (Linné 1758). While citing and repeating the same description as found in the *Systema Naturae* 10th edition, Linné (1767) further adds to the description in four sections: *TESTA facie & habitu antecedentium quatour; dorso nodis 3 s. 4, compressis* [Shell ventral face similar in ornamentation to earlier coiling; dorsal knobs three or four and compressed] ; *SPIRA testa brevior, plicato-subnodosa* [Shell spire short, with plications that have a small nodule] ; *LABIUM exterus dorso elevatum, transverse striatum – internius reflexum and adnatum* [The outerlip is raised from the dorsum, with transverse striations – innerlip reflexed and blubiform]; and *FAUX utrinque striata* [Aperture sides striated]. This additional description clearly indicates a shell with three or four dorsal knobs and a ventral body whorl that is similar to the spire, both characteristics that are indicative of *C. labiatum*. Two illustrative references were provided. These two, Rumphius (1705, 1711) and Gualtieri (1742), are the same offered in the *Systema Naturae* 10th edition (Linné 1758). However, the *Museum Ludovicae Ulricae* omits the Petiver (1711) *Gazophylactium Nature et Artis* reference found in the *Systema Naturae* 10th edition (Linné 1758). From the additional description and refined reference list, it can be deduced that Linné had *C. labiatum* as the most probable taxon intended when writing this description and matched the series of specimens in Uppsala University Museum of Evolution Zoology Section (no. 1225a-e) 1767 *Strombus urceus* Linné, *Systema Naturae* 12th edition, p. 1212, no. 512. The name "urceus" appears in the Linné (1767) *Systema Naturae* as no. 512, with the same description provided in the 10th edition (Linné 1758). Linné (1767) also provides an additional reference to the "M.L.U. p. 624, n. 288", the *Museum Ludovicae Ulricae* (Linné 1764). The *Museum Ludovicae Ulricae* includes a more expanded descriptive text of "urceus" than is contained in this repeated 10th edition text (Linné 1758, 1764). Petiver (1711) *Gazophylactium Nature et Artis* is again reinstated after an absence in the *Museum Ludovicae Ulricae* (Linné 1764). As well as the three references provided in 1758, a further five more illustrative examples are cited and all drawn from "Seb. Mus. 3" or Seba (1758) *Locupletissimi Rerum Naturalium Thesauri*, III. Two representatives are drawn from plate 60, figs. 28 and 29. The Seba (1758) figure 28 is an example of *C. klineorum* (Abbott, 1960) while figure 29 is *C. labiatum*. A further three more illustrations are drawn from Seba (1758): plate 62, figures

41, 45 and 47, all of which illustrate examples of *C. labiatum*.

The name "urceus" appears in the Gmelin (1791) *Systema Naturae* as no. 29, with same description provided in the 10th edition (Linné 1758). However, Gmelin (1791) extensively expands the list of references and highlights eight forms, while the main textual references contain a mixture of *C. labiatum*, *C. urceus* and *C. mutabile*. Gmelin (1791) in recognising these eight forms highlights the growing awareness of morphological differences within the growing "urceus" aggregation. More importantly, the forms represent two species for the most part *C. mutabilie* and *C. labiatum* indicating a move to isolate what is now *C. urceus* as the species intended as species no. 29 of Gmelin (1791). There are three groups within the Gmelin (1791) *C. urceus*: the first forms that contain a mixed species composition form α which contains both *C. mutabile and C. urceus*; second forms β, δ and η illustrate *C. mutabile*; and the third forms γ, ε, ζ and ϑ which show representations of *C. labiatum*.

Alata canarium muricatum Martini, (1777) is an image has the overall shape, shell colouration shell, and aperture associated with *C. urcues* from the continental Asian coast. The accompanying text to this illustration contained a mixture of references that include *C. urceus*, *C. mutabile* and *C. labiatum*.

Born (1778) erred in citing "Linn. S. N. 312" (= *Cypraea moneta* Linné, 1758). The references that Born (1778) used, and Linné (1758,1767) overlooked, were in part incorporated into Gmelin (1791). These references are an aggregation of many now established species, including: *C. klineorum*, *C urceus*, *C. labiatum* and *C. mutabile* following the synonymy of Linné (1758, 1767).

Röding (1798) provided four lectotypes drawn from Martini's (1777): the first, pl. 78, f. 803 (= *C. urceus*); the second, pl. 78, f. 806 which is the dorsal view of *C. labiatum*; and figures 804-805 were used to define Röding's (1798) sp. 23 *Lambis labiata* (= *C.*

labiatum).

Link (1807) listed Gmelin (1791) species no. 3518 (= *C. urceus*) and followed Röding's (1798) taxonomy with the use of the genus *Lambis*. However, Link (1807) cited Martini pl. 78, fig. 805 (= *C. labiatum*), which was used by Röding as material in his description of *C. labiatum*. Link (1807) also described *L. reticulata* Link, 1807 and provided Martini pl. 77, fig. 806 (= *C. labiatum*).

Schumacher (1817) cites two references to support his species: "Martin. 3. pag. 98 Tab.78. fig. 803.805". Figure 803 is the *C. urceus ustulatum* of modern authors (Abbott 1960), while 805 is considered *C. labiatum* and was one of Röding's (1798) types for that species. Schumacher (1817) recognised that description and references to "urceus' of Linné (1758) were best suited to *C. labiatum*, and that therefore, what is considered *C. urceus* was invalid. Through time, *C. urceus ustulatum* has grown to be associated with specimens of "urceus" with a black aperture due to the use of the Maritini fig. 803 reference (Schumacher 1817).

Canarium* (*Canarium*) *urceus

(Linné, 1758)

(Plate 11)

Synonymy.

1758 *Strombus urceus* Linné, p. 745, no. 440. Linné 1764, p. 624, no. 288. Born 1778, p. 281. Gmelin, 1791, p. 3518, no. 29. Reeve 1851, pl. 11, spc. 24c. Reeve 1860, p. 94. Hanley 1860, p. 74. Abbott and Dance 1982, p. 77. De Bruyne 2003, pp. 91 - 92. Maxwell et al. 2020b, p. 116, figs. 1, 3 and 4. Dekkers and Maxwell 2020b, fig. 5F.

= *Strombus var. urceus* Kiener, 1843, p. 60, pl. 30, fig. 3.

= *Strombus* (*Strombidea*) *urceus* Chenu 1859, p. 257, fig. 1606.

= *Strombus* (*Canarium*) *urceus* Tryon 1885, p. 118, pl. 6, fig. 65. Bandel 2007, p. 150, fig. 19A. Liverani et al. 2021, p. 30, fig. 2.

= *Lambis urceus* Röding, 1798, p. 63, no 807. *Lambis urceus* Link 1807, p. 108.

1777 *Alata canarium muricatum* Martini, p. 98, pl. 78, fig. 803.

= *Strombus* (*Canarium*) *muricatus* Horst and Schepman 1908, p. 218. Adam and Leloup 1938, p. 114. Watson 1885, p. 417. Wagner and Abbott 1978, p. 09-655. Adam and Leloup 1938, p. 114. Abbott 1960, p. 65.

= *Strombus muricatus* Beets 1950, p. 244. *Strombus muricatus* Walls 1980, p. 189.

1817 *Canarium ustulatum* Schumacher, p. 219.

= *Strombus urceus* form *ustulatus* Abbott 1960, pl. 20 fig. 29.

1844 *Strombus dentatus* Duclos in Chenu, pl. 4, figs. 8 and 9. (non Linné, 1758: [the original description of *dentatus* still valid]).

Type. Holotype – *Strombus urceus*, Uppsala University Museum of Evolution Zoology Section, Sweden (UZM) no. 685 (Linné 1767, *Museum S:æ R:æ M:tis Luovicæ Ulricæ*, n. 288), selected by Abbott (1960, p. 66) based on image no. 300 on the Microfiche of that collection. The holotype is slightly juvenile which is reflected in the development and colouration of the aperture when Linné described the species in 1758, but it was not until the Linné redescription in 1764 that a reference was made to specimens in his working material. The "urceus" type material is contained in two Linnaean collections: the Linnaean Collection of the Linnaean Society of London (LSC), and the Linnaean collection held in the UZM. In total there are three lots attributed to "urceus": UZM – *Strombus urceus* no. 685, donated by Gustav IV (MLU, Linné 1767: No. 288, which

Plate 1

Canarium (Canarium) urceus
(Linné, 1758)
Ubin, Singapore (48.2 mm)
(Stephen Maxwell Collection no. U1.003)

reflects the modern understanding of *C. urceus*; UZM – *S. urceus*; no. 1225, donated by Gustav IV/Karl XIII, is a mixture of both *C. labiatum* (Röding, 1798) and *C. erythrinum*; and LSC – *S. urceus*, box LSL. 440, Dance label: P-Z 0010875 contains a single shell (= *C. mutabile*).

Type Locality. Designated as Cebu Island, Philippines by Abbott (1960, p. 66) is rejected and the type locality is re-designated as Singapore (Maxwell et al. 2020b). This re-designation of the type to Singapore reflects the shells of the more eastern population to which the type specimen more closely resembles and is in congruence with the distribution given by Gmelin (1791) (Maxwell et al. 2020b).

Original Description. “S. testæ labro attenuato retuso brevi striato ventre spiraque plicato-nodosis apertura bilabiata inerni” (Linné 1758, p. 745).

Supplementary Description. “The shell is elongated and fusiform and may appear biconic. The spire and body whorl have a distinctive rounded nodulated shoulder that may become acute towards the anterior of the shell as the nodulation becomes finer, more acute and denser. The anterior canal is often well formed and acute in nature, being slightly reflected dorsally. The posterior of the body whorl is stained, and this staining continues to the dorsum where it remains along the outerlip marginal fold and onto the dorsal whorl proper. The spire is always nodulated, with the knobs varying from acute in some populations to more rounded and less pronounced in others. The aperture is margined in all cases with dark staining. The inner aperture with dark lirations over a rosy white base colour. The columella is midnight black, sometimes with some traces of deep plum that flush the posterior. The lirations of the columella while present, are indistinct” (Maxwell et al. 2020b, p. 119).

Distribution. Literary Records – *China* (Abbott 1960); Hong Kong Rocky Harbour, Tai

She Wan (Abbott 1960). *Thailand* Bandon Bight (Abbott 1960); Koh Chang (Abbott 1960); Bangbert Bay (Abbott 1960); Hualpa Island (Abbott 1960); Koh Samet (Abbott 1960); Koh Samui (Abbott 1960); Koh Tao (Abbott 1960). *Singapore* (Chim et al., 2009); Tanah Merah Besar (Abbott 1960). *Malaysia* Pankor Laut (Johnson, 1964); Jesselton North Borneo (Saul 1962); Merambong Shoal, Johor Straits (Cob et al. 2009). Material Examined – *Singapore* Tanah Merah (1 x TMC); Changi Beach (2 x SMC). *Pulau Islands* Ubin (2 x SMC). *Malaysia* Tioman Island (1 x SMC), Rawa Island (3 x SMC). *Thailand* South of Pan Phé (4 x SMC). Vietnam Khánh Hòa Province (SMC x 27); Nha Trang (SMC x 263).

Canarium* (*Canarium*) *anatellum

(Duclos, 1844)

(Plate 1)

Synonymy.

1844 *Strombus anatellus* Duclos, pl. 4, figs. 11 and 12, pl. 21, figs. 8 and 9. Tryon 1885, p. 118. Adam and Leloup 1938, p. 113. Dodge 1956, p. 285. Abbott 1960, pp. 65 and 66. Cernohorsky 1972, p. 74. Wagner and Abbott 1978, p. 09-652. Walls 1980, p. 188.

= *Canarium anatellum* Maxwell et al. 2020c, pp. 336 and 337, figs. 1 and 2. Dekkers and Maxwell 2020b, fig. 5D.

= *Canarium* (*Canarium*) *anatellum* Liverani et al. 2021, p. 30, fig. 2.

Type. Syntypes – Muséum National d'Histoire Naturelle, Paris (France), Molluscs (IM) MNHN-IM-2000-32467.

Type Locality. Kangean Islands, Indonesia (Maxwell et al. 2020c).

Original Description. "Duclos (1844) provided no original description, with the name being introduced on plate 4, figures 11 and 12, and plate 21, figures 8 and 9, based on the

Plate 2

Canarium (Canarium) anatellum
(Duclos, 1844)
Singaraja, Indonesia (27 mm)
(Stephen Maxwell Collection no. 19b.008ds)

Chenu (1859) plate sets (Sherborn and Smith 1911). The combination of illustration and binominal name is considered valid at the time of publication (ICZN 1999)" (Maxwell et al. 2020c, p. 336).

Description. "This ovate species has both a uniformly red-orange toned columella and outer lip. The shell is solid and smooth. The body whorl has axially aligned knobs on the shoulder. The columella is always smooth and, inside the labrum, it is red-orange with mostly dark coloured lirae entering deep inside the aperture; the last 4-5 mm towards the rim loses the brown colour. The outside colour is variable, with brown, green, cream, tan, yellow, orange, etc., and is mostly mottled. The anterior canal is almost always tipped with black within and on the outside. The whorls are rounded, with a weakly angled shoulder. The spire whorls have up to 17 axial shoulder knobs, which may be weak or obsolete. The base of the shell has 8 – 10 incised lines giving rise to flat cords. The aperture is elongated with a small but sharp posterior canal just ending under the shoulder" (Maxwell et al. 2020c, p. 33).

Distribution. Literary Records – *Indonesia* Kangean Islands (Maxwell et al. 2020c).

Canarium* (*Canarium*) *andamanense

Dekkers, Dekker and Maxwell, 2022

(Plate 2)

Synonymy.

2022 *Canarium* (*Canarium*) *andamanense* Dekkers, Dekker and Maxwell, p. 31, figs. 2A-H.

Type. Holotype – Naturalis Biodiversity Center, Leiden, The Netherlands, RMNH.MOL.511430.

Type Locality. Phuket, Thailand (Dekkers et al. 2022).

Plate 3

Canarium (Canarium) andamanense
Dekkers, Dekker and Maxwell, 2022
Campbell Bay, Great Nicobar Island (44 mm)
(Stephen Maxwell Collection no. 19i.001b)

Original Description. “The shell is rather large, solid, and sturdy shells for the genus. The size is typically between 30 - 60 mm. Spire roughly 1/3 of total height. The shell form is cone-like, with a body whorl bearing strong knobs on the shoulder, usually 3 dorsally, 4 shallower ones ventrally (which are the prolongation of the small knobs on the shoulder of the earlier whorls) and one in between them. The spire with 8 whorls with some minor varices. The apex is sharp and pointed. The body whorl is covered with many very narrow spiral lines giving the shell a silky look, with several stronger lines separated by a regular distance, whiter and a bit more raised. Spiral lines becoming courser and flattish towards the anterior, about 12-14 in total. The aperture is pinched at the posterior end forming a shallow channel and with a wide bulge on the shoulder. The labrum straight and not protruding, the last part to the rim has a faint orange to whitish colour. The columella smooth, except for the posterior end which has some 4 lirae and the anterior part which bears up to around 10 small lirae, all in the same colour as the columella itself. Columella dark yellow to bright orange. Interior of the labrum the same colour as the columella, bearing numerous thin lirae entering the deeper aperture. The lirae are simple, not forked, and becoming dark brown to black after about 4-5 mm, roughly for about 10 mm into the shell interior. At the anterior end, the anterior channel, the colour becomes solid black. Basic colour dirty white, with random patches of light brown, greyish-blueish and greenish colour on the body whorl. A solid yellow form is known with a white interior” (Dekkers et al. 2022).

Distribution. Literary Records – *Indonesia* north-western Sumatra, mapped only (Abbott 1960). *Thailand* Phuket (Dekkers et al. 2022); Ban Khao Thong Tai, Krabi (Dekkers et al. 2022); Noppharat Thara Beach, Krabi (Dekkers et al. 2022); Ban Ko Kwang, Krabi (Dekkers et al. 2022); Ko Sire, Ban Laem Tukkae, Ko Phuket, Phuket Bay (Dekkers et al. 2022); Ban Ko Kwang on sandflats with coral growth, rocks and mangroves (Dekkers et al. 2022); Ko Lanta, Beached (Dekkers et al. 2022); Ao Nang Beach, Krabi (Dekkers et al. 2022); near Krabi (Dekkers et al. 2022). Material Examined – *India* Campbell Bay, Great Nicobar Island (SMC x 3).

Canarium* (*Canarium*) *darwinensis

Maxwell and Dekkers, 2021

(Plate 3)

Synonymy.

1960 *Strombus* (*Canarium*) *urceus orrae* Abbott, pl. 20, fig. 28. (non Abbott, 1960: [the original description of *orrae* still valid]).

1980 *Strombus* (*Canarium*) *urceus incisus* Walls, p. 107. (non Walls, 1980: [the original description of *incisus* still valid]).

1987 *Strombus* (*Canarium*) *urceus* Short and Potter, p. 34, pl. 16, fig. 10. (non Linné, 1758: [the original description of *urcues* still valid]).

2021 *Canarium* (*Canarium*) *darwinensis* Maxwell and Dekkers, p. 273, figs. 4, 5a-d.

Type. Holotype – Queensland Museum, QM MO 85658.

Type Locality. Lee Point, Darwin (Maxwell and Dekkers 2021a).

Original Description. “The shell is strongly bitriangulate with the body whorl being much wider than the final whorl of the spire. The teleoconch is low and the plications are fine, triangulate and regular, not forming distinct nodules at the shoulder. The posterior of the outer lip is square and thickened, causing a strong contraction of the aperture. The outer lip protrudes forming a strong callused knob, the mid outer lip is thickened and the stromboid sinus is narrow, with a large flange give the impression of a ‘U” shape between the posterior callus and the sinus; the columella is always white and the inner aperture

Plate 4

Canarium (Canarium) darwinensis
Maxwell and Dekkers, 2021
Lee Point, Darwin (40 mm)
(Stephen Maxwell Collection no. 20a.001)

has sparse brown lirae. The ventral body whorl is not axially plicated, and the rounded angulate shoulder has knobs that are blunt, becoming stronger dorsally. Ventral body whorl colouration is typically restricted to the lower third of the body whorl, this colour being a brown stain. The outer lip typically joins at or just below the shoulder" (Maxwell and Dekkers 2021a, p. 272).

Distribution. Literary Records – *Northern Territory* Darwin (Maxwell and Dekkers 2021); Shell Island, Darwin (Abbott 1960); East Point, Darwin (Abbott 1960); Port Darwin, Darwin (Abbott 1960); Quail Island, 35 miles west of Darwin, (Abbott 1960); Nightcliff Point, Darwin (Abbott 1960); Casuarina, Darwin (Maxwell and Dekkers 2021a); Lee Point, Darwin (Maxwell and Dekkers 2021a). Institutional Records – *Northern Territory* Gunn Point Beach, Darwin (NMV F151986); Tree Point, Darwin (QM MO46855); Shoal Bay, Darwin (NMV F233793); Port Darwin, Darwin (NMV F28765); Vesteys Beach, Darwin (QM MO28495). Material Examined – *Northern Territory* Darwin (VC x 5; YC x 1); Lee Point, Darwin (SMC x 81; VC x 1); Dripstone Cliffs, Darwin (SMC x 7); One Arm Point (VC x 2); Timor Sea (VC x 3); Vesteys Beach, Darwin (SMC x 2).

Canarium* (*Canarium*) *daveyi

Dekkers and Maxwell, 2020

(Plate 4)

Synonymy.

2020 *Canarium daveyi* Dekkers and Maxwell, p. 346, fig. 1 and 5H.

= *Canarium* (*Canarium*) *daveyi* Dekkers and Maxwell – Liverani et al. 2021, p. 30, fig. 2.

Type. Holotype – Naturalis Biodiversity Center, Leiden, The Netherlands, RMNH

Plate 5

Canarium (Canarium) daveyi
Dekkers and Maxwell, 2020
Geelvink Bay, Indonesia (28 mm)
(Dekkers Collection no. STR3583e)

MOL.112282a.

Type Locality. Paulau Auri, ca. 1 mile NE off Palau Rumwakon, Geelvink Bay, Indonesia (Dekkers and Maxwell 2020b).

Original Description. “Slender and rather small for the *C. urceus* complex: average height 26.6 – 32.5 mm (types). The shell is lightweight, shiny and thin walled. Spire whorls consist of two protoconch whorls, which are coloured white to mostly purple glassy, and five more whorls with many axials. Earlier whorls with thinner axial ribs and some varices. Body whorl dorsally rather smooth, with the exception of axially aligned knobs on the shoulder, axial growth lines and spiral ridges that run along the anterior canal, becoming obsolete towards the shoulder. The axial ribbing continues on the ventral side of the shell, as the spiral ribbing towards the anterior end. Spire whorls with a ramp towards the shoulder. Penultimate whorl runs back to the shell below the shoulder. The rather straight and narrow wing has a strong ridge just before the end of it, only dorsally. Aperture wide, with a well-defined columellar callus that is sharply cut and raised a bit, attached to the ventral side of the body whorl with a gutter. Smooth columella in the middle and both ends bear strong white lirae. Place of attachment below the shoulder. Inside of the outer lip with visible white spiral lirae. Outer lip thickened and white. Strombid notch very shallow, almost obsolete. Colour of the shell of three vague bands of orange-brown on a white background, the one at the anterior end broadest and the one under the suture smallest. These bands show through at the aperture. The white bands end in four white spots on the outside part of the labrum and a broad one at the anterior end. The anterior channel ends in a black spot” (Dekkers and Maxwell 2020b, p. 348).

Distribution. Literary Records – *Indonesia* Seroei, Japen Island (Dekkers and Maxwell 2020b); Coral coast near Hollandia (Dekkers and Maxwell 2020b); Dohreh-baai (Dekkers and Maxwell 2020b); Wandammen Bay, Wasior, Geelvink Bay (Dekkers and Maxwell

2020b); Serui, Japen Island (Dekkers and Maxwell 2020b). Material Examined – *Indonesia* southside of the Japen Island, Geelvink Bay (SMC x 1).

Canarium* (*Canarium*) *esculentum

Maxwell, Rymer, Congdon and Dekkers, 2020

(Plate 5)

Synonymy.

1946 *Strombus ustulatus* form *laevis* Dodge, p. 3, figs. 1 and 5 (not *Strombus laevis* Perry, 1811 (= *Euprotomus bulla* Röding, 1798 (Abbott 1960)).

2020 *Canarium esculentum* Maxwell, Rymer, Congdon and Dekkers, p. 336 and 337, figs. 4 and 5. Dekkers and Maxwell 2020b, fig. 5I.

= *Canarium* (*Canarium*) *esculentum* Maxwell, Rymer, Congdon and Dekkers – Liverani et al. 2021, p. 30, fig. 2.

Type. Holotype – American Museum of Natural History No. 12927 as the holotype of *Strombus ustulatus* form *laevis* Dodge, 1946, p. 3. figs. 1 and 5.

Type Locality. Olango Island, Philippines (Maxwell et al. 2020c). Dodge (1946) gave no locality for his specimen.

Original Description. “I here propose for the extremely smooth form of *ustulatus* the name form *laevis*” (Dodge 1946, p. 3).

Supplementary Description. “This species has both a uniformly white toned columella and rather slender fusiform to ovate appearance. The shell is medium sized, solid, smooth and relatively broad. Larger shells tend to be more slender. The body whorl has axially aligned knobs on the shoulder. The early whorls with mostly white varices, and a blueish black protoconch. The white columella is predominantly white, and is always smooth in the mid part; the posterior has ca. 10 lirae; and the anterior part 5-6 lirae. Inside labrum

Plate 6

Canarium (Canarium) esculentum
Maxwell, Rymer, Congdon, Dekkers, 2020
Cebu Island, Philippines (51 mm)
(Stephen Maxwell Collection no. 19a.001)

is yellowish-orange, with mostly dark coloured lirae entering deep in the aperture, the last 3-4 mm towards the rim has a pure white colour. Outside colour is variable with brown, green, cream, tan, yellow, orange, lilac, purple, etc., uniformly or mottled. The end of the anterior canal is almost always tipped with black within and on the outside. The body whorl is rounded, earlier whorls with a sharp angled shoulder diminishing in acuteness with growth. The penultimate whorls with 12-14 axial knobs at the shoulder which may be obsolete. The base of the shell has 10 – 12 incised lines that gradually become less strong; the remainder of the body whorl covered with very thin spiral lines. The aperture is elongated with a small but sharp posterior canal just ending under the shoulder. The labrum is rather straight and not very much thickened" (Maxwell et al. 2020c, p. 339).

Distribution. Literary Records – *Philippines* Olango Island (Maxwell et al. 2020c). Material Examined – *Philippines* Batag Island, Samar (SMC x 15); Cebu Island (SMC x 115); Culion Island (SMC x 2); Cuzo Island (SMC x 1); Diplong, Mindanao (SMC x 439); Mactan (SMC x 6); Negros Island (SMC x 8); Olango Island (SMC x 121); Surigao, Mindanao (SMC x 38).

Canarium* (*Canarium*) *geelvinkbaaiensis

Dekkers and Maxwell, 2020

(Plate 6)

Synonymy.

1960 *Strombus (Canarium) urceus* 'Geelvink Bay form' Abbott, p. 64, pl. 41, fig. 3. Dutch New Guinea. (non Linné, 1758: [the original description of *urcues* still valid]).

2020 *Canarium geelvinkbaaiensis* Dekkers and Maxwell, p. 349, fig. 2 and 5H.

= *Canarium* (*Canarium*) *geelvinkbaaiensis* Dekkers and Maxwell – Liverani

Plate 7

Canarium (Canarium) geelvvinbaaiensis
Dekkers and Maxwell, 2020
Manokwari, Indonesia (25 mm)
(RHNH MOL.179571b)

et al. 2021, p. 30, fig. 2.

Type. Holotype – Naturalis Biodiversity Center, Leiden, The Netherlands, RMNH MOL.179571a.

Type Locality. Manokwari, Western Papua, Indonesia (Dekkers and Maxwell 2020b).

Original Description. "Slender and rather small shells for the *C. urceus* complex, height between 21.2 – 29.5 mm (types), but mostly around 27-28 mm. The shell is lightweight and has thin shell walls, shiny. Spire whorls consist of about three protoconch whorls, mostly brown-purple and glassy, and 4-5 more whorls with many axials. Earlier whorls with thinner axial ribs and sometimes old varices. Body whorl dorsally rather smooth with the exception of axially aligned knobs on the shoulder, and ca. 10 stronger spiral ridges that run along the anterior canal; the remainder of the body whorl bears many very thin spiral lines that become obsolete around and above the shoulder. No visible axial growth lines. The axial knobs dorsally are preceded on the ventral side of the shell, just towards the aperture in the paratypes 2-7 and in the holotype and paratype 1 the ventral side is smooth. It is preceded on the penultimate whorl with about 20-21 finely raised knobs that form the axial ribbing in that whorl, and form a corona on the shoulder. This is preceded on the earlier whorls, becoming more and more tiny. Spire whorls with a smooth ramp from the simple suture towards the shoulder; after the coronation on the shoulder the shell becoming smaller, giving a sharp edge shoulder. Penultimate whorl runs back to the shell below the shoulder. The rather straight and narrow wing has a strong ridge of about 2.5-3 mm just before the end of it, only dorsally and not internally reinforced. Aperture narrow, with a well-defined columellar callus that is sharply cut and raised a bit, attached to the ventral side of the body whorl with a gutter. Smooth columella for the naked eye, but some tiny lirae near the small posterior sinus. Place of attachment below the shoulder of the penultimate whorl. Inside of the outer lip with many clearly visible, but thin, white spiral lirae, that become brown after about 4 mm. Outer lip white. Strombid notch very shallow, about 1 mm deep and 4 mm wide. Colour of the shell dirty white with 2 greenish bands. Old shells dirty white with purple hue dorsally and two vague bands of orange-brown that start mid dorsally and end before the reinforced lip; the one at the anterior end broadest and darkest and the one there under the longest and the lightest of colour. These bands show through at the aperture. The anterior part of the shell toward the anterior channel with a dark brown to black band that is broadest at the ventral side of the shell' (Dekkers and Maxwell 2020b, p. 350).

Distribution. Literary records – *Indonesia* 1/2 mile south of Ambai, Japen Island (Dekkers and Maxwell 2020b); Doreh Baai (Dekkers and Maxwell 2020b); coast near Sara Wandori, West of Serui, Japen Island (Dekkers and Maxwell 2020b); Beach of Sorong (Dekkers and Maxwell 2020b); Near Seroei Leg. D. Smits, ex coll. J. van der Land (Dekkers and Maxwell 2020b); Manokwari (Dekkers and Maxwell 2020b); Bay of Seroei, Japen Island (Dekkers and Maxwell 2020b); Palau Roon, Geelvink Bay (Dekkers and Maxwell 2020b); Serui, Japen Island (Dekkers and Maxwell 2020b); Wandammen Bay, Wasior, Geelvink Bay (Dekkers and Maxwell 2020b); Serui Bay (Dekkers and Maxwell 2020). Material Examined – *Indonesia* Manokwari (1 x SMC).

Canarium* (*Canarium*) *incisum

(Wood, 1828)

(Plate 7)

Synonymy.

1828 *Strombus incisus* Wood, p. 14, pl. 4, fig. 12a (no locality). Abbott 1960, p. 65 “Quadrate form”.

= *Strombus urceus incisus* Man in ‘t Veld 1988, p. 7, fig. 2 only (b/w drawing

Plate 8

Canarium (Canarium) incisum
(Wood, 1828)
Singaraja, Indonesia (35 mm)
(Stephen Maxwell Collection no. 19d.007da)

from Wood).

= *Canarium incisum* Maxwell et al. 2020c, p. 340, figs. 6 and 7. Dekkers and Maxwell 2020b, fig. 5B.

= *Canarium* (*Canarium*) *incisum* Liverani et al. 2021, p. 30, fig. 2.

Type. Holotype – *Strombus incisus* Wood, 1828, p. 14, pl. 4, fig. 12. The illustration of Wood's incisus in the "Supplement to the Index Testaceologicus or A Catalog of Shells, British and Foreign" is selected as the type (Abbott 1960).

Type Locality. Labuan Bujo, Benonko Beach, Flores, Indonesia, based on the collecting data of Hans Post (shells now in coll. AMD and Hans Post). Wood (1828) gave no locality data. The selection of the type locality by Man in 'T Veld (1988, p. 8) is in error: there was confusion of the species of Wood (1928) (Maxwell et al. 2020c).

Original Description. No original description. The combination of illustration (Wood 1828, pl. 4, fig. 12) and binominal name (Wood 1828, p. 14) was valid at the time of publication (ICZN 1999).

Supplementary Description. This bi-pyramidal species has both a uniformly red/orange toned columella and rather high-shouldered outer lip. The shell is around 40-45 mm in length, solid, smooth, relatively broad. The body whorl is variable ranging from smooth to axially aligned knobs on the shoulder. The aperture is elongated, with a small but sharp posterior canal just ending under the shoulder. The columella is always smooth in the mid part: the posterior and anterior with lirae. The inside labrum is the same colour as the columella with mostly dark coloured lirae entering deep in the aperture. Outside colour variable with brown, green, cream, tan, yellow, orange, etc., mostly mottled with a dull white-greyish colour as the base colour. The anterior canal is almost always tipped with black within and on the outside. The body whorl has an angled shoulder, which may have axial knobs, with the largest being at the edge of the left dorsal shield and right ventral body whorl. Base of the shell has 8 – 10 incised lines giving rise to flat cords.

Distribution. Literary Records – *Indonesia* Labuan Bujo, Benonko Beach, Flores (Maxwell et al. 2020c). Material Examined – *Indonesia* Madura Island (SMC x 114); Raas Island (SMC x 38); Sakala Island (SMC x 621); Singaraga, West Bali (SMC x 544). *Philippines* Corong Corong, El Nido (SMC x 81).

Canarium* (*Canarium*) *manintveldi

Dekkers and Maxwell, 2020

(Plate 8)

Synonymy.

Strombus (Canarium) incisus Abbott 1960, p. 64, pl. 41, fig. 4 'Quadrate form'. (non Wood, 1828: [the original description of *incisus* still valid]).

= 'a form close to *incisum*' – Romagna Manojo 1980, pl. 1, fig. 9 (no locality). (non Wood, 1828: [the original description of *incisus* still valid]).

= *Strombus* (*Canarium*) *urceus incisus* Wood – Man in 't Veld 1988, p. 6 – 10. Cernohorsky 1972, p. 74, pl. 20, fig. 2. Walls 1980, pp. 107-108. Kreipl et al. 1999, pp. 12 and 40, pl. 76. (non Wood, 1828: [the original description of *incisus* still valid]).

Strombus urceus Hinton 1972, p. 10, pl. 5, fig. 15.

= *Strombus urceus urceus* Linné – Hinton 1978, p. 11, no. 14. (non Linné, 1758: [the original description of *urcues* still valid]).

2020 *Canarium manintveldi* Dekkers and Maxwell, p. 352, figs. 3 and 5E.

= *Canarium* (*Canarium*) *manintveldi* Dekkers and Maxwell – Liverani et al. 2021, p. 30, fig. 2.

Type. Holotype – Zoölogisch Museum Amsterdam, housed in the Naturalis Biodiversity

Plate 9

Canarium (Canarium) manintveldi
Dekkers and Maxwell, 2020
Irirka Islands, Vanuatu (19.1 mm)
(Stephen Maxwell Collection no. 21.001a)

Center, Leiden, The Netherlands, ZMA.MOLL.187523a.

Type Locality. Malapoa, Islands, Vanuatu (Dekkers and Maxwell 2020b).

Original Description. “Shells small in size for the *C. urceus* complex, height between 20–28 mm (types), but mostly around 20 mm in the Solomons Islands and Vanuatu and becoming larger (27–29 mm) in the southern range. The shell is sturdy and the body whorl is almost smooth and shiny. The width of the shell is variable, from relatively slender to broad at the shoulder. Spire whorls consist of about three protoconch whorls, regularly becoming larger. Dirty white to brown-purple, and 4–5 more whorls with many axials. Earlier whorls with tiny axial ribs and old varices. Body whorl dorsally rather smooth for the naked eye but on close inspection with ca. 6 slightly stronger spiral ridges that run along the anterior canal, and the remainder of the body whorl with many very thin spiral lines that become obsolete around and above the shoulder. No visible axial growth lines. Body whorl with a central knob on the shoulder; the axial knob dorsally is proceeded towards and on the ventral side of the shell, just towards the aperture. It is succeeded on the penultimate whorl with about 13-20 finely raised knobs that form the axial ribbing in that whorl, and form a corona on the shoulder. This is proceeded on the earlier whorls, becoming more and more tiny. Spire whorls with a smooth ramp from the simple suture towards the shoulder; after the coronation on the shoulder the shell is becoming smaller giving a sharp edge shoulder. The earliest whorls are straighter. Penultimate whorl runs back to the shell well above the shoulder, even surpassing the suture. The rather straight and narrow wing has a strong ridge of about 2.0–2.5 mm just before the end of it, only dorsally and not internally reinforced. Aperture very narrow, with a well-defined columellar callus that is sharply cut and raised a bit, attached to the ventral side of the body whorl with a deep gutter. Smooth columella for the naked eye, but some tiny lirae near the small posterior sinus. The aperture callus is bulbous at the posterior end where it is raised above the suture; it is so thick that the posterior channel is often very shallow. First 1 mm of the inside of the outer lip smooth, then with many thin white spiral lirae on a white to brownish background inside the aperture. Outer lip white. Strombid notch very shallow, about 1 mm deep and 3-4 mm wide. Colour of the shell dirty white with more or less purplish hue dorsally and very vague broad bands of blueish-brown that start dorsally and (as the ventral side is dirty white) end before the reinforced lip. Towards the lip they can fuse into a broad axial band. Sometimes these bands do show through at the inside of the aperture. The anterior part of the shell toward the anterior channel with a dark brown to black band that is broadest at the ventral side of the shell, but the last 1 mm is often white" (Dekkers and Maxwell 2020b, p. 352-353).

Distribution. Literary Records – *Papua New Guinea* North coast, Madang (Dekkers and Maxwell 2020b). *Vanuatu* (Dekkers and Maxwell 2020b); Crab Bay, Malekula (Dekkers and Maxwell 2020b); Malapoa, Vila (Dekkers and Maxwell 2020b). Material Examined – *Australia* Lord Howe Island (SMC x 1). *Solomon Islands* Kakabona (SMC x 1); Uoei Island (SMC x 1). *Vanuatu* Irirka Islands (SMC x 2).

Canarium* (*Canarium*) *nipponium

Maxwell and Dekkers, 2021

(Plate 9)

Synonymy.

1936 *Strombus ustulatus* Hirase, pl. 86, fig. 11. Hirase 1954, pl. 86, fig. 11. (non Schumacher, 1817 = *Strombus urceus* Linné, 1758).

= *Strombus ustulatum* Kira, 1959, p. 35, pl. 15, fig. 4.

2021 *Strombus* (*Canarium*) *nipponium* Maxwell and Dekkers, p. 283, fig. 1.

Type. Holotype – Muséum National d'Histoire Naturelle, Paris (France), Molluscs (IM)

Plate 10

Canarium (Canarium) nipponium
Maxwell and Dekkers, 2021
Hahajima Retto, Ogasawara Islands (43 mm)
(Stephen Maxwell Collection no. 19g.001)

MNHN-IM-2000-35893.

Type Locality. Ryukyu, Japan (Maxwell and Dekkers 2021b).

Original Description. “The shell is heavy and solid. The shape is ovate to fusiform with an extended anterior sinus (broken in holotype) that is not dorsally exposed. The stromboid sinus is acute and axially angled in the direction of shell growth, and has a thin protruding flange that is quadrate and typically dark stained with black to brown both externally and internally. The ventral shoulder has reduced blunt knobs that continue to the dorsum with three well defined blunt shoulder knobs, and one greatly reduced knob prior to the formation of the outer lip. There are fine axial incised lines on the lower third of the body whorl both dorsally and ventrally. Early teleoconch whorls are rounded and smooth, with a distinctive subsutural ramp. Later whorls become more angulate at the shoulder, developing axially elongated shoulder knobs, with fine well-spaced spiral incised lines that do not extend to the body whorl. The spire often has a purplish tint. The aperture is lanceolate, being restricted at the posterior end, white, with very thin brownish lines entering the aperture on the inside of the lip. The columella is well formed and uniform along the aperture, having a yellowish hue. The other lip is thickened and somewhat quadrate posteriorly, joining at the shoulder of the body whorl, becoming thinner and sharp-edged anteriorly” (Maxwell and Dekkers 2021b, p. 283).

Distribution. Literary Records – *Japan* Ryūkyū (Hirase 1936, 1954); Yaka Beach, Ishikawa (Abbott 1960). *Palau* Palau Lagoon (Maxwell and Dekkers 2021b). Material Examined – *Japan* Hahajima, Ogasawara Islands, Japan (SMC x 1); Ryūkyū (SMC x 1).

Canarium* (*Canarium*) *orrae

(Abbott, 1960)

(Plate 10)

Synonymy.

1960 *Strombus* (*Canarium*) *urceus orrae* Abbott, p. 66, pl. 41, fig. 5. Wilson and Gillett 1971, p. 40, p. 18, figs. 2a-b. Wilson and Gillett 1974, p. 40, pl. 18, figs. 2a-b. Wilson and Gillett 1979, p. 73, pl. 14, figs. 2a-b. Coleman 1975, p. 90. Walls 1980, p. 109, fig. 110. Kreipl et al. 1999, pp. 12 and 40, pl. 77.

= *Strombus orrae* Dekkers and Maxwell 2020b, fig. 5.

= *Strombus* (*Canarium*) *orrae* Abbott – Liverani et al. 2021, p. 30, fig. 2. Maxwell and Dekkers 2021, p. 272, figs. 2,3 and 5 e-o.

Strombus urceus Wilson 1993, p. 156, pl. 21, figs. 5 a-c. (non Linné, 1758: [the original description of *urcues* still valid]).

Type. Holotype – Academy of Natural Sciences of Philadelphia, USA, no. 247756.

Type Locality. Augustus Island, Western Australia (Abbott 1960).

Original Description. “This new subspecies is characterised and distinguished from the southwest Pacific typical *urceus* by its heavier, more quadrate, less coloured shell, its stronger and fewer nodules and its shorter siphonal canal. Its penultimate whorl bears 7-11 knobs (instead of as many as 10 to 16 in typical *urceus*). The top of the outer lip is square and thickened; the columella is always white and the inner aperture with sparse brown lirae. Body whorl with 7 to 9 nine nodules at the shoulder, the first one of two at the shoulder being large, swollen and prominent. The young show a narrow, broken spiral band of brownish black on the body whorl. Nuclear whorls 2.5, translucent yellowish and glossy” (Abbott 1960, p. 66).

Plate 11

Canarium (Canarium) orrae
(Abbott, 1960)
King Sound, Western Australia (36 mm)
(Stephen Maxwell Collection no. 20.001a)

Distribution. Literary Records – *Western Australia* Augustus Island (Abbott 1960); Broome (Abbott 1960; Maxwell and Dekkers 2021a); Cape Leveque (Abbott 1960; Maxwell and Dekkers 2021a); Dampier (Maxwell and Dekkers 2021a); Dampier Archipelago (Slack-Smith and Bryce 2004); East Moore Island, Balla Balla (Maxwell and Dekkers 2021a); Gantheaume Point, Broome (Abbott 1960); La Grange Bay (Abbott 1960); Middle Mangrove Island, Onslow (Maxwell and Dekkers 2021a). *Northern Territory* Bickerton Island (Abbott 1960); Bing Bong (Maxwell and Dekkers 2021a). *Northern Territory* Groot Eylandt (Abbott 1960); Hardy Island (Maxwell and Dekkers 2021a). *Indonesia* – North Coast of Sumbawa (Maxwell and Dekkers 2021a). *Papua New Guinea* Port Moresby (Maxwell and Dekkers 2021a). *Institutional Records – Western Australia* 22 km South of Exmouth (NMV F152000); 80 mile Beach south end, Cape Keraudren (F233792); Adele Island (WAM S46615, S46635); Augustus Island, Bonaparte Archipelago (NMV F28768); Back Beach, Dampier (NMV F233795; QM MO83450); Barred Creek (NMV F28786); Black Ledge area, Broome (QM MO83449); Brecknock Island, Bonaparte Archipelago (WAM S46618, S46619); Broome (NMV F28949, F233790; WAM S46588; QM DM11576073); Bundgei Reef (NMV F151685); Cambridge Gulf (F28875); Camden Sound (WAM S46599); Cape Leveque (AM 77745; QM MO67999; NMV F233800, F28763); Cassini Island, Bonaparte Archipelago (WAM S46591, S46592); Cleaverville, Dampier (NMV F152005; F233717); Cockatoo Island, Buccaneer Archipelago (NMV F19849; WAM S46598, S46633); Corneille Island, Bonaparte Archipelago (WAM S46594); Coronation Island, Bonaparte Archipelago (WAM S46617); East Monalivet Island (WAM S46602); Finucane Island (NMV F151687); Jones Island (WAM S46828l QM MO56772); Karratha (NMV F233716); Lesueur Island (WAM S46601); Long Island, Buccaneer Archipelago (WAM S46614); Montgomery Reef (WAM S46646); One Arm Point (NMV F233719); Pender Bay (NMV

F28779); Scorpion Island, Sir Graham Moore Islands (S46596); Sunday Island, Buccaneer Archipelago (WAM S46631, S46590); Troughton Island (WAM S46616); Turtle Bay (NMV F233798); Yampi Sound, Buccaneer Archipelago (NVM F28784). *Northern Territory* Groote Eylandt Island (QM MO38297, MO38332). *Material Examined – Western Australia* Augereau Island (VC x 2); Back Beach, Dampier (VC x 5); Broome (SMC x 46); Bundeyi Beach (SMC x 3); Cassini Island (SMC x 1; VC x 4); Dixon Island, Wickham (VC x 4); East Moore Island, Balla Balla (VC x 5); Exmouth (SMC x 1; VC x 2; YC x 1); Forty Mile Beach (SMC x 8; VC x 6); Intercourse Island, Dampier (SMC x 12; YC x 1); King Sound (SMC x 2; YC x 1); Monkey Mia, Shark Bay (BC x 4); Onslow (SMC x 6; VC x 8); Port Smith, Broome (VC x 4); Pretty Pool, Port Hedland (SMC x 7; VC x 9); Roebuck Bay (VC x 10); Walcott Inlet, Kimberley (SMC x 4; VC x 2); *Northern Territory* Drimmie Head, Gove (BC x 4); Wallaby Beach, Gove (BC x 8); Wessel Island (SMC x 1).

Canarium* (*Canarium*) *youngorum

Dekkers and Maxwell, 2020

(Plate 12)

Synonymy.

2020 *Canarium youngorum* Dekkers and Maxwell, p. 354, figs. 4 and 5A.

= *Canarium* (*Canarium*) *youngorum* Dekkers and Maxwell – Liverani et al. 2021, p. 30, fig. 2.

Type. Holotype – Queensland Museum, QM MO.85756.

Type Locality. Manus Island, Papua New Guinea (Dekkers and Maxwell 2020b).

Original Description. “The fusiform shells are medium sized for the *C. urceus* complex; height between 35 – 40 mm (types). The shell is thin with a uniformly thickened outer

Plate 12

Canarium (Canarium) youngorum
Dekkers and Maxwell, 2020
Manus Island, Papua New Guinea (36 mm)
(Stephen Maxwell Collection no. 19f.001)

lip. The spire is approximately one third to one quarter the length of the shell. The protoconch is smooth consisting of one or two whorls. The first spiral whorls are convex smooth with a subsutural chord (paratype 1), that may be indistinct in some specimens due to wear (holotype), and without varices. Varices appearing only on the third and fourth whorls, typically with three per whorl. Later spire without the earlier subsutural chord that forms into a short subsutural ramp, becoming moderately angulated at the shoulder. The shoulder of latter whorls with distinctive and regular small axial folds that reach the suture of the proceeding whorl. The folds tend to be skewed spirally forward as they descend the whorl. There is an absence of spiral sculpture to the spire. The ventral body whorl with the same uniform axial folds that do not extend below the top one third of the whorl, these may be diminished in some specimens. The dorsal body whorl folds have diminished in number, becoming axially elongated knobs which do not extend much past the mid-dorsum. The edge of the outerlip is dorsally stepped and thickened in contrast to the smooth shell. The stromboid notch is moderately shallow but well formed. The spiral striae on the lower third body whorl reduce in width towards the anterior. The columella is uniform in thickness, with a few faint, but distinct, lirae at the anterior and posterior ends. Both the columella and outerlip share the same uniform colouration, typically red. The columella and outerlip join below the shoulder of the body whorl, forming two sides of a shallow sinus. The inner aperture with many fine raised lirae that move more toward the edge of the outer lip anteriorly, and which become darkly stained over a plain interior base colour. The colour and pattern of the shell is small fine white tents on a tan shell giving the appearance of axially formed maculations. The colour of the inner aperture can be seen through some specimens, giving the appearance of a dark hue to the area preceding the outer lip. The lower third of the body whorl may contain a dark stain in some examples, being a continuation and deepening of the colour of the inner aperture" (Dekkers and Maxwell 2020b, pp. 354-355).

Distribution. Currently *C. youngorum* is only known from the far north eastern islands of Papua New Guinea; however, it is expected that this range will be expanded as further explorations of museum records are undertaken. Literary Records – *Papua New Guinea* Manus Island (Dekkers and Maxwell 2020b). *Material Examined – Papua New Guinea* Rabaul (SMC x 1; VC x1).

10.2 Paleontological Notes

The genus *Canarium* arose during the Miocene, with the subgenus *Canarium* (*Canarium*) arising in the Pliocene/Pleistocene of Indonesia. The early species from the Pliocene and Miocene belong to the subgenus *Conundrum* and *Maculastrombus* and are discussed *inferius*. The purported *Strombus* (*Canarium*) *urceus* (in Ladd 1972) from Vanuatu is not that species and represents an early example of *Canarium* (*Elegantum*) complex.

Within the Naturalis Leiden collection from the Pliocene/Pleistocene of Nias Island, North Sumatra Province, Indonesia, are specimens labelled *Strombus plicatus* Lamarck and *Strombus (Canarium) plicatus* Lamarck var. *ustulatus* Schumacher and these are members of the *Canarium* (*Canarium*) with great affinity to *C. incisum* and *C. manintveldi* with their biconic shells, thickened outer lip, fine nodulated angulated spires and well-formed columella. More work is needed on this material, and it is highly probable that there are undescribed species contained within it.

Canarium (*Conundrum*) *unifasciatum* (Martin, 1884) (Miocene, Yogyakarta, Java, Indonesia) is an early member of *Conundrum* and has many affinities to modern species in that subgenus, particularly within *Canarium* (*Conundrum*) *mutabile* (Swainson, 1821) with its lirate columella and ovate form; however, it lacks the subsutural cord of that species. While the shell is not dissimilar to members of the *Maculastrombus*, the form of the outer lip, with a distinctive labial ridge, and the strong sculpture of the columella rules out placement within that genus.

Canarium (*Maculastrombus*) *spolongense* (Martin, 1916) (Lower Miocene, Gunung Spolong, Yogyakarta, Java, Indonesia) has a strong affinity to modern *Terestrombus* being elongated and fusiform in shape with a thin not thickened labium and lacking a fine labial ridge. However, there is a well-formed columella, and this, along with the lack of labial ridge and a lack of spiral sculpture, are characters typical of *Maculastrombus*.

Canarium (*Conundrum*) *gendinganesis* (Martin, 1899) (Pliocene Sondé Village, Madiun, Java Island, Indonesia) is the earliest member of the *Canarium* that provides a common ancestor between *Canarium* (*Canarium*) and *Canarium* (*Conundrum*). In this species the labial marginal ridge is located inward, a character typical of *Conundrum*, as is the fusiform shape and form of the spire, which is typical for the genus in modern taxa, and also being smooth with a distinctive subsutural cord. The more fusiform shape is an indicator of this species' connection with *Neostrombus,* as is the form and sculpture of the aperture which tends smooth.

Canarium (*Conundrum*) *bawenauruensis* (Wissema, 1947) (Pliocene/Pleistocene, Bawonauru, Nalawo Valley, Nias Island, Indonesia) is one of the more recent members of the *Conundrum*. In this species the spire is reduced in height and with the nodulation that is typical to *C. mutabile*.

10.3 Summary

This chapter presented the morphologically and biogeographically based taxonomy and higher relationships of the *Neostrombini*, a clade that incorporates *Maculastombus, Neostrombus*, *Terestrombus* and *Tridentarius* as separate clades to *Canarium*. *Canarium* was divided into four subgenera, of which the twelve species previously known as “urceus”, and its two sister taxa, were confirmed to be related and placed within *Canarium* (*Canarium*), a genus that arose in the Pliocene/ Pliestocene.

Chapter 11 Conclusion

This thesis addressed the three key themes:

Theme 1: Did Abbott (1960) over-synonymise in his revision? I demonstrated that Abbott (1960) over synonymised in his revision. With consideration to biogeography and speciation processes, I have argued that: 1) a more extensive set of species hypotheses can best explain the regional morphotypic diversity within the "urceus" complex; and 2) Abbott's (1960) model of a single "urceus" species should be rejected.

Theme 2: Can classical taxonomy contribute to the formulation and construction of sound phylogenies? I demonstrated that the use of classical taxonomic practice is acceptable as means of constructing sound phylogenies, the structure within which clades can be defined and described. Comparing phylogenetic analyses with morphological similarity analyses on the same set of organisms did resolve some unanswered questions; for example, in relation to a colour synapomorphy that had perplexed taxonomists, I found that the black aperture is not a sound taxonomic marker for species delimitation. Using these classical methods also allowed me to present a model for the resolution of the subgenus.

Theme 3: If there are two alternative species hypotheses for a set of organisms, can biogeographic analyses indicate the most robust hypothesis to integrate into the nomenclature, with the observed speciation process used as a causal argument? The robustness of a species hypothesis is strengthened with an understanding of the life history and biogeography of the organism. In this thesis, I demonstrated that biogeographic evidence differentiated species into defined bioregions, and that there was the potential for overlap and gene flow between populations based on larval dispersal, which again supports the hypothesis of multiple species and rejects the Abbott (1960) model of a single "urceus" species.

While there are process theories that explain speciation, both at the scale of realm and also, to some degree, at the scale of province, these cannot explain all the nuances found in the distribution and species richness of all taxonomic groups. Essentialistic pluralism allows this nuanced approach to the use of evidence to be used in species identification. This thesis has resolved much of the taxonomic status of the clades to which *Canarium urceus* belongs, and has explored and postulated on the radiation and speciation processes that gave rise to the organisms under consideration, those that fall within the genus *Canarium*. These organisims were examined individually within the framework of known radiation theories, biogeographical barriers, and then geographically contextualised with the use of identified provinces. It is only through examination of the lower taxonomic ranks that a true understanding of radiation and diversification within the greater realm of Indo-Australian Archipelago can be achieved with a level of robustness.

Finally, this thesis postulates that the "urceus" complex is a result of post-Tethys breakdown of a once universal species in the Indonesian Archipelago, which then speciated during peak cyclic glacial periods in refugia. From these refugia, species undergo periodic interactions with sister taxa as they radiate out during interglacial periods and their associated sea level rises. Therefore, twelve species herein are considered to have arisen from multiple isolated centres of origin, having diversified from a common Indonesian ancestor. While, the phylocode does not require the application of the ICZN. The ICZN is applied here for universality of acceptance only, not out of necessity.

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