Convergent evolution of life habit and shell shape in scallops (Bivalvia: Pectinidae) with a description of a new genus

by

Alvin Alejandrino

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Program of Study Committee:
Jeanne M. Serb, Major Professor
Dean C. Adams
Dennis Lavrov
Nicole Valenzuela
Kevin J. Roe

Iowa State University

Ames, Iowa

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DEDICATION

To my brother, Edward Andrew Haffner (May 19, 1986 – December 26, 2011). You showed me that family and happiness are the most important things in life. I miss and love you.

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ABSTRACT

Phenotypic convergence is a fascinating evolutionary pattern. Many taxa evolve remarkable similarities, often due to similar selection pressures, which suggest that there may be a limited number of solutions to a particular ecological challenge. However, some phenotypes are only superficially similar. For example, convergent evolution may occur at one phenotypic level such as behavior, but other components (morphology) of the same phenotype exhibit divergence. In other words, the solutions might be the same, but how taxa approach the problem could be very different. This then suggests that there may be multiple phenotypic optima that can tackle similar ecological challenges.

In this dissertation, I investigate the evolutionary patterns of life habits and shell shapes in scallops and how these phenotypic traits contribute to biological diversity. I found many scallop species have converged in life habit, but only a few lineages converged in shell shape. Rather, shell shape variation tends to be greater in species with less specific life habit requirements. However, scallop species with the gliding life habit have lesser shell shape variation. Interestingly, gliding can be performed by two distinct shell shapes, indicating that only some components of shell shape are important for the life habit, and others are free to vary. This research indicates that there is likely greater diversity in form, despite phenotypic similarities in function.

CHAPTER 1: GENERAL INTRODUCTION

Overview

Repeated phenotypic traits in unrelated taxa are a common evolutionary phenomenon. From the streamlined bodies of sharks and tunas to the powered flight achieved by birds and bats, repeated traits have evolved independently in different lineages as a result of similar selection pressures (McFall-Ngai 1990, Givnish et al. 2005, Revell et al. 2007, Ellingson et al. 2014). Contrary to the diversification pattern of evolution where there is an *a priori* expectation of increasing morphological variation over time, repeated phenotypic patterns suggests that there may be a limited number of solutions to any single environmental challenge (Donley et al. 2004, Givnish et al. 2005). As a result, repeated patterns tend to indicate evolutionary outcomes are somewhat predictable (Morris 2006). Thus, fundamental research in evolutionary biology examines the ubiquity of repeated patterns and the predictability of phenotypic trait evolution.

Repeated evolutionary patterns of phenotypic traits can be identified as convergent or parallel evolution. While there are a number of ways these two terms have been applied (Haas and Simpson 1946, Arendt and Reznick 2008), I will follow the definition by Wiens *et al*. (2003), where convergent evolution is the independent origin of similar traits from dissimilar ancestral traits and parallel evolution is the independent origin of similar traits from similar ancestral traits. The use of ancestral traits is a means of directional comparison, along branches of a phylogeny. Similarly, I use the term “trajectory” to mean the transition of a trait along a branch, independent of the pattern.

This dissertation examines repeated evolutionary patterns of phenotypic traits in scallops (Mollusca: Bivalvia: Pectinidae). Specifically, I investigate the evolution of life habits, the shell shapes associated with these life habits, and how these phenotypic traits may contribute to scallop morphological and taxonomic diversity. Similar life habits are exhibited by multiple scallop species, but it is unknown whether these traits are shared by groups of taxa originating from a common ancestor or whether they have independent origins. To investigate this, I reconstruct the scallop phylogeny to map the life habit of extant species, which are then used to reconstruct the life habits of the ancestors. The resulting patterns will be compared to determine which life habit has evolved multiple times, and a comparison of trait change between ancestors and their descendants will determine the evolutionary trajectory of the life habits so that I can distinguish between or parallel evolution. Stanley (1970) proposed that life habits of bivalves might constrain the shell shapes they exhibit. To test the diversity of shell shapes exhibited by scallops with the same life habit, I have quantified the shell shapes of extant species. If, as Stanley proposed, shell shapes are closely associated with life habits, I predict that shell shapes will have evolved in similar evolutionary trajectories as the associated life habits. Lastly, I investigate how repeated evolution of shell shapes may have led to the underestimation of the taxonomic diversity of scallops. In this introductory chapter, I provide the background and the necessity to conduct the dissertation research project.

Scallop Life Habits

Scallops are a large family of marine bivalves with approximately 300 species (Waller 2006). They are found in many marine environments from the polar to the tropical regions, from intertidal to deep sea, and on many different types of substrates like rock, vegetation, or mud

(Stanley 1972, Waller 1984, Raines and Poppe 2006). Scallops exhibit a great diversity of life habits e.g., byssal attaching, nestling, cementing, free-living, recessing, and gliding (Stanley 1970). In scallops, these life habits are primarily defined by two factors: the animal's position to the substrate and its mode of attachment or locomotion (Stanley 1970). Below, I describe each life habit and how they are characterized by these factors.

Byssal attaching is the most common life habit of scallops, as it is exhibited by approximately 66% of extant species as adults (Stanley 1972). Byssal attaching is identified by the production of protein threads (byssus) for epifaunal substrate attachment (Brand 2006). This attachment is temporary, as scallops can release their byssus and swim to another substrate (Stanley 1970, 1972). As juveniles, all scallop species are able to produce byssus (Hamilton and Koch 1996, Brand 2006), but as adults some species permanently lose this ability and have made use of other attachment methods or forego attachment (Minchin 2003, Brand 2006).

Two life habits, nestling and cementing, are relatively rare in scallops. Nestling is an infaunal byssal attachment where juveniles attach themselves to live corals or sponges, and during ontogenetic growth of the biotic substrate, the scallop becomes permanently embedded (Yonge 1967, Kleemann 1990, Dijkstra 1991, 1998, Kleemann 2001). The uniqueness of this life habit warrants its own category, separate from epifaunal byssal attachment. Cementing, in contrast, is the permanent epifaunal attachment through secretion of shell material directly onto hard substrate (Stanley 1970, Waller 1996, Minchin 2003).

Some scallop species have no form of attachment as adults, and instead sit on or dig into soft sand or mud substrate. The free-living life habit is when the scallop rests on the surface of soft substrate (epifaunal) (Stanley 1970, Minchin 2003, Brand 2006), while recessing scallops excavate a cavity or actively burrow within a substrate (Stanley 1970, Minchin 1992, Minchin

2003, Brand 2006). Once in the substrate, recessing species repeatedly adduct or “clap” their valves to deposit sediment onto themselves in an attempt to conceal their presence (Baird 1958, Sakurai and Seto 2000). This life habit is considered semi-infaunal substrate positioning.

The last life habit category of scallops is gliding, which is defined as the ability of a scallop to propel itself, ventral-side first, by forcing water through the anterior and posterior dorsal margin while the valves are closed (Minchin 2003, Brand 2006). This provides a near-horizontal trajectory above the substratum, resulting in a distance traveled greater than five meters per effort. At rest, gliding scallops are epifaunal and have no attachment to the substrate. The biomechanics of gliding has been of great interest to many researchers as this mode of locomotion is not accomplished by other bivalves (Caddy 1968, Gould 1971, Morton 1980, Joll 1989, Dadswell and Weihs 1990, Hayami 1991, Cheng et al. 1996, Cheng and DeMont 1996, Ansell et al. 1998, Denny and Miller 2006, Wilkens 2006, Guderley and Tremblay 2013).

Shell Shape Diversity

Stanley’s (1970) seminal work on life habits and shell shape provided the foundation for understanding bivalve morphological diversity. In scallops, byssal attaching species tend to be greater in height (along the dorsovental axis) than length (along the anterior-posterior axis), and have left valves that are more convex than right valves (Minchin 2003). In addition, they have unequal auricles or “ears,” with the anterior auricle elongated, which is said to inhibit overturning (Stanley 1970, 1972). Both nestling and cementing species also have shells that are greater in height than in length, but nestling species have reduced auricles (Yonge 1967) and cementing species have auricles and valves that are highly irregular in shape, and are influenced by the topology of the substrate to which they are attached (Stanley 1970, Minchin 2003). Free-living species tend to be equal in shell height and length, have equal convexity of the left and right valves (Minchin 2003), and the auricles are equal in shape (Stanley 1970). In contrast, recessing species tend to have lengths greater than heights, and the left valves are either flat or concave while the right valves are convex (Stanley 1970). The convexity of the right valves in recessing species are said to lower the center of gravity below the surface of the substrate that contributes to the semi-infaunal positioning (Minchin 2003). Finally, gliding species tend to have equal shell height and length, giving a circular outline to the shell. In addition, the left and right valves of these shells are equally convex with reduced auricles compared to other scallops (Stanley 1970). In addition to shell attributes of height, length, and convexity, scallops have varying degrees of external ribbing (Minchin 2003). Most gliding species lack external ribbing while byssal attaching species have a wide variation in number of external ribbing, and some even have small scales that protrude from the surfaces of the ribs (Raines and Poppe 2006).

Stanley (1970) identified an association between life habits and shell shapes. Given that life habits will have different biomechanical requirements, the associated shell shapes may have greater or lesser shell shape variation (morphological disparity) depending on the environment. For example, the lack of attachment and specific locomotion requirements of free-living species may allow them to have greater diversity in shapes to possess external ribs and scales. In contrast, elongated anterior auricles may be important for successful byssal attachment. It is then expected that byssal attaching species will have shells with asymmetric auricles. Shape limitations may be especially true for species with the gliding life habit. As mentioned above, most gliding species have smooth, slightly convex valves and reduced auricles, which many authors suggest as necessary to maximize lift and reduce drag during gliding (Gould 1971, Morton 1980, Joll 1989, Dadswell and Weihs 1990, Ansell et al. 1998). If true, then reduced shape variation may have independently evolved in scallops multiple times.

Purpose and Significance

Scallops are an excellent group to study patterns of phenotypic trait evolution because they are species rich, exhibit many life habits, and have a wide variety of qualitative shell shapes. Due to the lack of a scallop phylogenetic hypothesis with dense taxonomic sampling, it has not been possible to test the evolutionary patterns of these traits. As a consequence, we do not have a foundation to investigate the evolutionary processes involved in generating phenotypic and species diversity in scallops. Therefore, this study seeks to provide evidence for the prevalence of repeated phenotypes and the predictability of trait evolution. Invertebrates make up the majority of animal groups and are rarely represented in assessing general trends in evolution, which may provide other alternatives to evolutionary processes.

Dissertation Organization

In the following chapters, I investigate the evolutionary patterns of scallop phenotypic traits and how they contribute to their diversity. In Chapter 2, I examine the repeatability of life habits in scallops. First, I developed a historical framework by reconstructing the scallop phylogeny using four molecular markers to develop phylogenetic hypotheses for relationships within the family. Using this phylogeny, I maped the life habit characters exhibited by each species and reconstructed the life habit characters at the ancestral nodes to determine the evolutionary trajectory of the life habits. In Chapter 3, I tested whether there is convergence in shell shape in the gliding species, which may be limited by the requirements of the life habit. I examined the patterns of shape evolution by quantifying scallop shells using three-dimensional, landmark-based geometric morphometrics. Non-shape attributes such as size was removed to focus solely on shape to statistically compare variation in the shells between life habit groups. I then reconstructed ancestral shells to compare ancestor and descendant shapes to identify convergent patterns. Based on the results from the previous chapters, in Chapter 4 I describe a new genus of scallop, previously masked by convergence that had been identified using the phylogeny, life habit, and shell shape. Finally, in Chapter 5, I summarize the overall conclusions and explore future research that can be conducted using the results of this study.

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CHAPTER 2. CONVERGENT AND PARALLEL EVOLUTION IN LIFE HABIT OF THE SCALLOPS (BIVALVIA: PECTINIDAE)

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ALVIN ALEJANDRINO[1], LOUISE PUSLEDNIK[1,2], AND JEANNE M. SERB[1,3]

[1]*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames IA, 50011*

[2]*Institute for Conservation Biology and Environmental Management, School of Biological Sciences, University of Wollongong, New South Wales, Australia 2519*

[3]*Corresponding author*

Email addresses:

AA: aalejand@iastate.edu

LP: louisep@uow.edu.au

JMS: serb@iastate.edu

Running Head: Evolutionary Convergence and Parallelism in Scallops

Abstract

Background

We employed a phylogenetic framework to identify patterns of life habit evolution in the marine bivalve family Pectinidae. Specifically, we examined the number of independent origins of each life habit and distinguished between convergent and parallel trajectories of life habit evolution using ancestral state estimation. We also investigated whether ancestral character states influence the frequency or type of evolutionary trajectories.

Results

We determined that temporary attachment to substrata by byssal threads is the most likely ancestral condition for the Pectinidae, with subsequent transitions to the five remaining habit types. Nearly all transitions between life habit classes were repeated in our phylogeny and the majority of these transitions were the result of parallel evolution from byssate ancestors. Convergent evolution also occurred within the Pectinidae and produced two additional gliding clades and two recessing lineages. Furthermore, our analysis indicates that the byssal attaching gave rise to significantly more of the transitions than any other life habit and that the cementing and nestling classes are only represented as evolutionary outcomes in our phylogeny, never as progenitor states.

Conclusions

Collectively, our results illustrate that both the evolutionary processes of convergence and parallelism generated repeated life habit states in the scallops. Bias in the types of habit transitions observed may indicate constraints due to physical or ontogenetic limitations of particular phenotypes.

Introduction

When two species occupy comparable trophic niches, similar phenotypes can be generated via analogous evolutionary responses [1-4]. As a consequence, repeated phenotypes have long been treated as evidence for adaptation at the macroevolutionary scale [5-9]. Two important patterns in iterative morphological evolution are convergence and parallelism, which can be distinguished by examining the phenotypic trajectories along a phylogeny [10]. Evolutionary convergence is implicated when two or more lineages with different ancestral phenotypes independently evolve along different trajectories towards the same adaptive phenotype; whereas, evolutionary parallelism is revealed when independent lineages with comparable ancestral morphologies evolve towards a new, but similar, phenotype. Importantly, the application of a phylogenetic approach to discern between convergence and parallelism alleviates some of the operational difficulties of separating these two concepts, thereby allowing a meaningful, quantitative way of assessing repeated evolutionary patterns (for reviews of this highly contested issue see: [11-13]).

The best known studies examining repetitive evolutionary patterns include morphological, ecological, and behavioral traits in all major vertebrate lineages (e.g., fishes: [3, 14]; amphibians: [15]; reptiles: [16, 17]; birds: [18, 19]; mammals: [20]). To a lesser extent, similar work has been done in invertebrate groups, specifically arthropods. For example, convergent or parallel evolution has been identified in replicated shifts of host use in insects [21, 22], web construction in arachnids [8], larval morphology and antipredator behavior in aquatic insects [23], and adult morphology in barnacles [24]. Outside of arthropods, few studies using invertebrates explicitly test for convergence and parallelism (but see gastropods: [25, 26]; bivalves: [27]). Indeed, if the patterns seen in vertebrates are representative, it suggests that repetitive patterns of phenotypic evolution should be far more prevalent across the animal kingdom than is currently recognized, as vertebrates comprise only about 5 percent of all animal diversity.

Here we use scallops as a non-arthropod invertebrate model to study convergence and parallelism. Scallop species comprise a large family (Pectinidae) of 264 recognized species and are found globally in a wide range of marine habitats from the intertidal zone to depths of 7000 meters (m) [28, 29]. Scallops exhibit a diverse set of life habits that are related to the animal's ecological requirements and behavioral attributes [30] and are organized into six categories based on the methods and permanence of attachment to a substrate, locomotive ability, and spatial relationship to a substrate (epifaunal versus semi-infaunal; see Table 1). Species are categorized by the life habit displayed during adulthood and membership to a life habit class typically precludes the display of other habits. Recent work by Smith and Jackson [31] has demonstrated the evolutionary importance of pectinid life habit by linking environmental factors to the diversification or decline of lineages.

In this paper, we employ a phylogenetic framework to examine the evolution of species-specific life habit categories in the scallops. We have generated the most comprehensive multigene phylogeny of the Pectinidae to date in order to determine the number of independent origins of each life habit class. We then distinguished between convergent and parallel trajectories of life mode evolution by applying a phylogenetically-based approach [10] to answer the following questions: How repetitive is the evolution of life mode in the scallops? When a life habit has multiple origins, are these lineages the result of convergent evolution or parallel evolution? Are particular transitions between life habit classes more likely than others? Our results demonstrate that five of the six life habit types exhibited by scallops have evolved multiple times. We identified 17 repeated transitions between life habit classes within the Pectinidae that were the result of both parallel and convergent evolution. Interestingly, despite repeated evolutionary transitions, we found that not all life habit classes function as progenitor states in the scallops.

Methods

Phylogenetic analysis

We examined 81 species, representing 31% of extant taxa from the Pectinidae. Taxonomic classification follows that of Dijkstra [28] and Waller [29]. Eleven species from three closely allied families, Propeamussiidae, Limidae, and Spondylidae, were included as outgroup taxa based on the results from [32]. All specimens were preserved in 95% ethanol and were provided by either museum collections or colleagues. When possible, DNA was extracted from two or more individuals per species as a test for congruent placement in the phylogenetic analyses.

Previously, nuclear Histone H3 and mitochondrial 12S rRNA and 16S rRNA gene fragments were amplified for 39 taxa by Puslednik and Serb [32]. Here, we build on their three-gene dataset by adding 53 more species and a nuclear gene region, 28S rRNA. Primer sequences for 12S rRNA, 16S rRNA, and Histone H3 and PCR and sequencing conditions are described in Puslednik and Serb [32]. We designed new primers for the 28S rRNA region for this study (sc28S_70F: 5’-CAGCACCGAATCCCTCAGCCTTG-3’, sc28S_950R: 5’-TCTGGCTTCGTCCTACTCAAGCATAG-3’, 28S_Limoida_121F: 5’-TCAGACGAGATTACCCGCTGAATTTAAGC-3’). When the PCR optimization steps failed to amplify a significant amount of product (<20ng/µl) or a single product, we cloned the PCR products following manufactures instructions (TOPO Cloning Kit, Invitrogen). Sequencing was carried out in an ABI 3730 Capillary Electrophoresis Genetic Analyzer at the Iowa State University DNA Sequencing Facility. All sequences are deposited in Genbank (accession numbers: HM485575-HM485578, HM535651-HM535659, HM540080-HM540106, HM561991-HM562003, HM600733-HM600765, HM622672-HM622722, HM630371-HM630556; see also additional file 1: Table1). Sequences were aligned using CLUSTAL W [33] with a gap-opening penalty of 10.00 and a gap-extending penalty of 0.20 in Geneious Pro [34]. Due to ambiguous alignment, a 169 base pair (bp) hypervariable region in the 16S rRNA gene fragment was excluded from phylogenetic analyses.

Aligned sequences (2438 bp) were partitioned according to locus, and codon position for the protein-coding gene Histone H3. For each partition, an appropriate nucleotide substitution model was selected on the basis of the hierchical Likelihood Ratio Test (hLRT) and the Akaike Information Criterion (AIC) using ModelTest 3.7 [35]. Both tests agreed on the GTR+G model for the 12S rRNA partition and the GTR+G + I model for 16S rRNA, 28S rRNA, and Histone H3 partitions. All partitions were analyzed simultaneously as a mixed model Bayesian analysis in MrBayes 3.1.2 [36]. We used the Metropolis Coupled Markov Chain Monte Carlo method with one cold and three hot chains for 5 million generations, sampling every 100th generation for three simulations. The number of generations required to attain stationarity was estimated when the standard deviation of split frequencies fell below 0.01. All trees prior to stationarity were discarded as burn-in and the remaining trees were used to compute a majority-rule consensus topology, branch lengths, and posterior probabilities (PP). Maximum Likelihood (ML) was executed in PhyML 3.0 [37] using the GTR+G + I model. The ML analyses consisted of 1000 replicates and clade support was assessed with 100 bootstrap (BP) pseudoreplicates.

Life habit classes

Scallops exhibit a diversity of species-specific life habits that range from permanent attachment to or within a substrate to mobile species able to swim continuously over long distances in a single effort. We divided behaviors exhibited by sexually mature individuals into six categories. Byssal-attachers retain the ability to produce a temporary protein fastening, the byssus, into adulthood. Nestling species also attach with a byssus, but differ in that the scallop eventually becomes permanently confined within a cavity of living corals or sponges [38]. Other scallop species are cementers that permanently fasten onto hard substrates through the secretion of new shell material. In contrast, free-living pectinids rarely attach as adults and many species are unable to secrete a byssus once the shell takes on the adult morphology. Whereas free-living species passively occupy a position on or partially covered in soft or sandy substrates, recessers actively construct a saucer-shaped depression in the substrate in which the animal resides so that the upper (left) valve is level or just below the sediment surface [39, 40]. The most mobile life habit class is gliding. Although all non-permanently attached species have the ability to swim for short distances (<1 m) to escape predators [39] or to move between desirable habitats [41], few species can swim greater than 5 m in a single swimming effort before the animal sinks passively to the substrate [39]. Gliding (5 - 30 m/effort) is distinguished from a common swimming response by the presence of a level swimming phase, where the animal is able to maintain a near horizontal trajectory above the substrate [42-44]. The level swimming phase also contains a glide component, where the animal is propelled forward while the valves are held closed [44-46]. Neither a level swimming phase nor a glide component is present in short distance swimming [44, 47, 48], making gliding a unique life habit state among scallop species.

Analysis of the life habit evolution

Life habit data for extant species of Pectinidae and outgroup taxa were assembled via a review of the literature and supplemented with the personal observations of collectors. Species from outgroup families Propeamussiidae and Limidae are treated as byssal attachers. Waller [49] speculated that the typical habit of the Propeamussidae is to actively secrete a byssus based on the presence of a byssal notch in the adult. Species of the Limidae have been directly observed to byssally attach or build nests made of byssus threads [50, 51]. In scallops, classifying life habit involves distinguishing between active versus passive actions of an adult organism. So while most species are able to attach with a byssus for a period of time as juveniles or swim short distances as an escape response, these activities do not determine the life habit of the adult animal. Thus, species were placed into life habit classes based on active and prominent responses of the adult animal to its environment. For example, some species are primarily epifaunal, but are passively buried in soft substrates due to the accumulation of sediment. However, since these species do not actively bury, they are treated as free-living and not recessing species. Life habit assignment for each species is given in additional file 2: Table2. Life habits were organized into six states and a character matrix was constructed using standard categorical data (0, unknown behavior; 1, cementing; 2, byssal attaching; 3, free-living; 4, recessing; 5, gliding; and 6, nestling). Brief definitions of life habits are provided in Table 1.

We then reconstructed ancestral states on the Bayesian topology using parsimony and likelihood reconstruction methods in Mesquite 2.6 [52]. Changes between states were unordered. The one parameter Markov k-state (Mk1) model was applied in the likelihood analysis and assumes a single rate for all character state transitions [53]. Likelihood-ratio tests of respective nodes determined the best estimate of the state. Differences in log-likelihoods larger than 2.0

rejected the higher negative log-likelihood value, while values less than 2.0 were treated as ambiguous character-state reconstructions.

Finally, to test the null hypothesis that transitions between life habit states (permanent attachment, byssal attaching, free-living, recessing, and gliding) are equally likely to come from any of the five states, we used a Chi-square test to compare the number of the observed to the expected transitions. The test follows an asymptotic chi-squared distribution with four degrees of freedom.

Results

Of the six life habits examined, byssal attaching is the most common state and is represented by 42 species (52%). Of the remaining species, 21 (25%) are free-living, 10 (12%) species recess, and eight (9%) species glide. In our sample, we included one of the two extant species that exhibit nestling (*Pedum spondyloideum*) and two of the five extant species that cement to a substrate (*Crassadoma gigantea* and *Talochlamys pusio* [= *Chlamys distorta*]). These proportions of non-byssate life habit categories in our taxonomic sample are similar to their representation across the family (free-living = 16.3%; recessing = 12.1%; gliding = 3%; nestling = 0.75%; cementing = 1.9%), where 66% of species byssally attach (data not shown). Phylogenetic relationships among these species were congruent in both BI (Fig. 1) and ML (additional file 3) topologies except for the placement of three lineages: the *Scaeochlamys livida* + *Mimachlamys townsendi* clade, the basal clade of the non-*Delectopecten* scallops, and the *Nodipecten subnodosus* lineage. Of these, only the placement of *N. subnodosus* alters the ancestral state estimation (see below).

To investigate the number of independent origins of life habit categories, we reconstructed ancestral states assuming a Markov model of character evolution with a single parameter to describe the rate of change on the BI topology (Fig. 1). For the species analyzed here, ML estimations of ancestral states (pie charts in Fig. 1) identify a minimum of 17 transitions between life habit classes (Table 2). These transitions include two origins of recessing, seven origins of the free-living condition, four separate lineages of gliding, and three occurrences of permanent (non-byssal) attachment through either cementation or enclosure within living corals. Byssal attachment was the most likely ancestral state of the Pectinidae and originates a second time in the phylogeny from a free-living ancestor in the *Leptopecten* lineage (Fig. 1). Gliding occurs in three genera: *Amusium* (4 species in the genus), *Adamussium* (monotypic genus) and *Placopecten* (monotypic genus). Our analysis included three of the four currently recognized species in *Amusium* (= "*Amusium*") genus. Because *Amusium* did not form a monophyletic clade in either BI or ML topologies, these species represent three separate origins of gliding (Fig.1; additional file 3). The fourth origin of gliding includes the monotypic genera *Adamussium* and *Placopecten*.

We then examined the number of convergent versus parallel evolutionary events that lead to a particular life habit using phylogenetically-based definitions of convergence and parallelism [10]. Of the 17 life habit transitions, the majority (12; 70%) originated from byssate ancestors and was cases of parallel evolution. Nearly all transitions are repeated at least twice in the phylogeny (Table 2; Fig. 1). Six of the seven origins of the free-living state were parallel trajectories arising from byssal attaching ancestors. Likewise, the cementing life habit in *Crassadoma gigantea* and *Talochlamys pusio* lineages arose in parallel from byssal attaching ancestors. The gliding life habit arose in four independent lineages along both parallel and convergent trajectories. “*Amusium*” *papyraceum* and *Amusium pleuronectes* arose in parallel from recessing ancestors, while the “*A.*” *balloti* + “*A.*” *japonicum* clade and *Adamussium* + (*Pseudamussium* + *Placopecten*) clade arose in parallel from byssal attaching ancestors. The recessing life habits of the *Euvola* + *Pecten* clade and the *Patinopecten* + *Mizuhopecten* clade are convergent and are derived from a free-living ancestor and a byssal attaching ancestor, respectively. Last, nestling of *Pedum spondyloideum* is a unique life habit in our phylogeny and originated from a byssal attaching ancestor. Ancestral state estimation is congruent when using the ML topology (additional file 3), with one exception. The placement of *Nodipecten subnodosus* as the sister taxon to *E. chazaliei* in the ML topology creates a unique transition from the recessing condition to a free-living state not observed on the BI topology (data not shown).

Last, we examined whether transitions between life habit states were evolutionarily constrained. Without constraint, we would expect that each state would be equally likely to give rise to any of the other state. However, the byssal attaching gave rise to significantly more of these transitions, while the other states appear to be nearly fixed once they arise ($X^2 = 37.003$; d.f. = 5; $p < 0.001$). Even when we combined the nestling and cementing categories as “permanent attachers” to reduce the number of categories with a low number of observations, the byssal life habit is still significantly more likely to be the evolutionary progenitor of all other states ($X^2 = 27.999$; d.f. = 4; $p < 0.001$).

Discussion

While patterns of convergence and parallelism are well-documented in vertebrate groups [3, 10, 14-16, 18-20], less is known about such patterns in non-vertebrates. Our study represents a major contribution to understanding repeated patterns of evolution in a non-model invertebrate group, the Pectinidae. The complex evolutionary history of scallops involves multiple origins of life habit phenotypes, with five of the six life habits evolving at least twice during the diversification of the family. Byssal attachment was not only the most common life habit in scallops, but was the ancestral condition to significantly more of the habit transitions than any other category. Interestingly, gliding independently evolved at least four times through both convergent and parallel evolution implying that there is strong positive selection for this life habit. Thus the patterns revealed in this study, a limited number of possible evolutionary transitions and the evolution of repeated phenotypes correspond closely to what is expected for phenotypes under strong selection and functional constraint [54-56].

Byssal attachment and the subsequent loss of the byssal apparatus may have had a profound effect on the evolution and phenotypic diversification of the Pectinidae. All pectinid species have a byssate stage to secure the post-larval scallop to a substrate while metamorphosing into its adult form, and the majority of scallop species (5:1) retain this early ontogenetic condition into sexual maturity [49]. Our results indicate that byssal attaching is the most common life habit in extant scallop species and byssal attachers gave rise to significantly more life habit classes than any other state. Furthermore, we observed that particular transitions between states are unidirectional, while other transitions never occur. For example, cementing only occurs as a derived state. In contrast, the other life habit classes, byssal attaching, free-living, recessing, and to a lesser extent gliding, are both ancestral states and transitional outcomes. This bias in the types of observed life habit transitions may indicate a restriction in possible evolutionary outcomes for certain states due to the degree or complexity of physiological changes needed to transition from one life habit to another.

One possible constraint on the lability of a given life habit state may be the degree of morphological specialization of the shell. If shell morphology can restrict life habit transitions, we would expect the greatest number of transitions to occur between classes with most similar shell shapes (i.e. the smallest phenotypic distance). Qualitatively, byssal attachers and free-living species possess the most similar shell shapes, and we detected the greatest number of transitions (six) between these two classes. Additionally, both byssal attaching and free-living habits are epifaunal, allowing a simple transition from temporary attachment to non-attachment on a substrate - no specializations in habitat use required. Other life habit classes are associated with a dramatic change in shell morphology and/or specialized habitat use (e.g., from epifaunal to semi-epifaunal). For instance, distantly-related gliding species (*A. pleuronectes* and "*A.*" *balloti*, Fig. 1) share a similar lightweight, smooth, symmetrical shell. This convergent morphology [27] may restrict the ability of gliders to transition into a different state. Likewise, permanently attached species that cement to a substrate also may possess specific physiological traits that may prohibit life habit transitions.

Based on these observations, it would appear that some life habit classes are evolutionary dead ends. To examine this hypothesis it is important to consider whether all life habit classes have had sufficient time to serve as progenitor states. It may be that because lineages exhibiting byssal attaching are the most ancestral and widespread in the Pectinidae, sufficient time has passed to allow opportunities to generate other life habits, whereas "younger" lineages from the Miocene, such as those exhibiting gliding [29, 57], may not have not had enough time to diversify. The cementing life habit seems to support of the hypothesis that some states are "dead ends." This state is old (Jurassic) and appears to have been more common during the Jurassic and Early Cretaceous periods than at present [58]. This suggests that although there may have been ample opportunities for the cementing life habit to function as a progenitor state, these lineages either were unable to transition to another life habit or went extinct before a transition.

Our ancestral state reconstruction analysis identified the minimum number of transitions on the tree, but due to incomplete taxonomic sampling, our analysis may not have detected all life habit transitions. However, the majority (58%) of the life habit transitions discussed in this study occur in clades that were most densely sampled (see dashed boxes in Fig. 1). So far, the phylogenetic relationships within these clades generally follow the currently accepted taxonomic classification of scallops. In the remaining clades where taxonomic sampling is less complete, the majority of the unsampled taxa belong to the tribes Chlamydini (75 species) and Mimachlamydini (25 species). While the genera within these tribes largely are nonmonophyletic in our analyses, an increase in sampling may alter some phylogenetic relationships. However, since the majority of these taxa are byssate [29] it is unlikely that the addition of these species will alter the main conclusions of this work.

Conclusions

Our study suggests that scallops have iteratively evolved similar life habit types. Previous authors have hypothesized that morphological evolution in the Pectinidae is highly repetitive, with particular shell forms representing putative adaptations to specific living habits [29, 30, 59]. Our results support this hypothesis, but the role of shell morphology needs to be further studied. Because life habit and shell morphology are closely linked [30, 60], a formal test of the association between life habit and shell forms relative to pectinid ecology is needed. Recently, Serb et al. [27] identified substantial convergence of shell morphology in a subset of gliding scallop species, which suggests that iterative morphological evolution may be more prevalent in the family than previously thought. Further investigations into the convergence of shell morphology and life habit could provide insight into what compensatory changes in morphology are required to allow transitions between life habits.

Authors' Contributions

AA, LP, and JMS conceived the study. AA (23%), LP (66%) and JMS (11%) collected data and all authors were involved in the analyses. AA, LP and JMS wrote the paper. All authors have read and approved the manuscript.

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Table 2.1 - Descriptions of life habit classes in the Pectinidae. Species-specific classes are the predominant life habit exhibited by sexually mature individuals listed from least to most active. An asterisk indicates multiple life habits are exhibited within the genus.

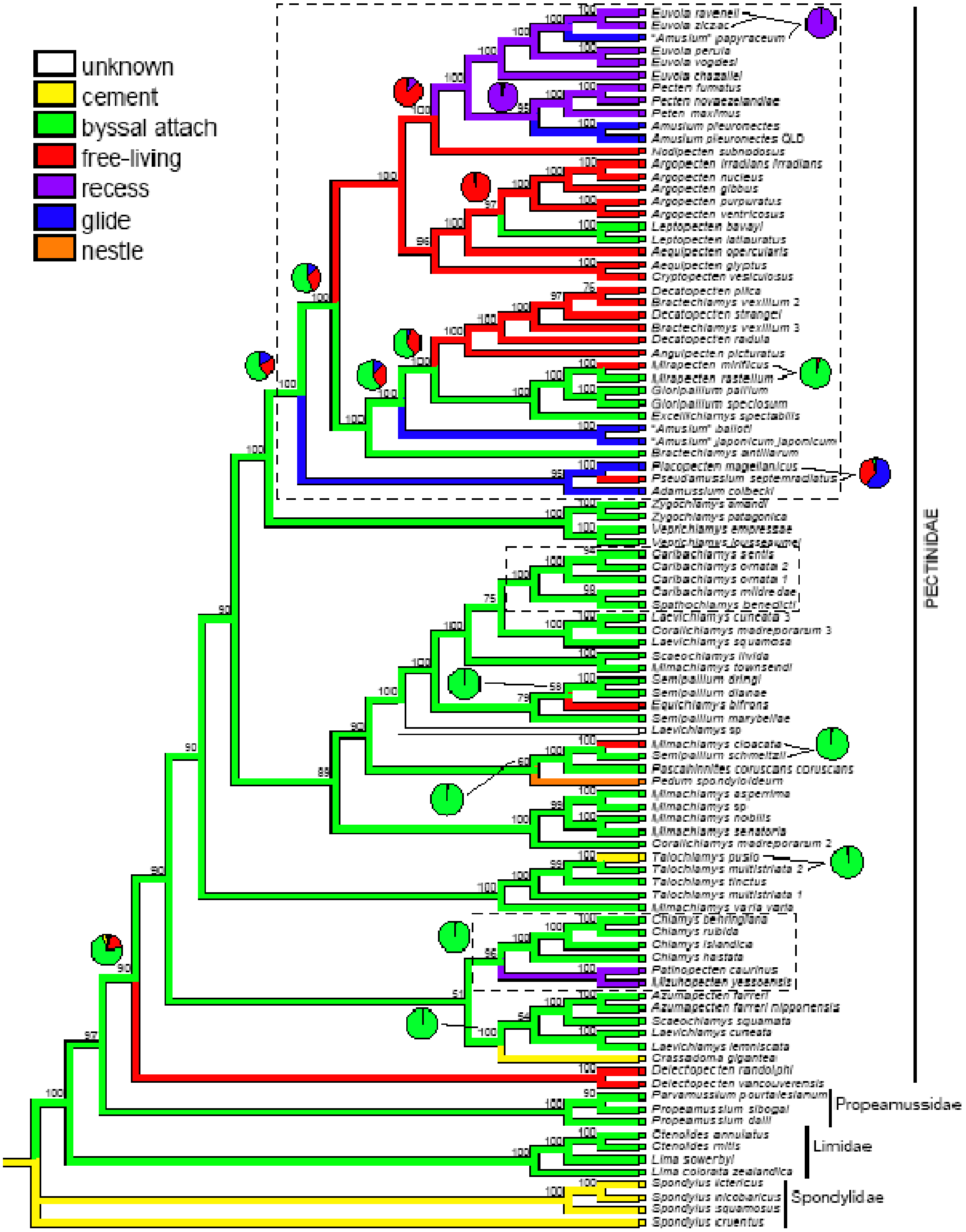
Life habit	**Description**	**Genera included in study**	**References**
Nestle	Settle and byssally attach to living *Porites* corals; coral grows around and permanently contains scallop	*Pedum*	[38, 61]
Cement	Permanently attaches to hard or heavy substratum as new shell is generated	*Crassadoma*, *Talochlamys**	[62]
Byssal attach	Temporarily attaches to a substratum by byssus threads; can release and reorient	*Azumapecten*, *Brachtechlamys**, *Caribachlamys*, *Chlamys*, *Coralichlamys*, *Cyclopecten*, *Excellichlamys*, *Gloripallium*, *Laevichlamys*, *Leptopecten*, *Mimachlamys**, *Pascahinnites*, *Scaeochlamys*, *Semipallium*, *Spathochlamys*, *Talochlamys**, *Veprichlamys*, *Zygochlamys*	[39]
Recess	Excavates cavity in soft sediment; full/ partial concealment	*Euvola*, *Mizuhopecten*, *Pecten*, *Patinopecten*	[39, 40]
Free-living	Rests above soft sediment or hard substratum	*Aequipecten*, *Anguipecten*, *Annachlamys*, *Argopecten*, *Brachtechlamys**, *Cryptopecten*, *Decatopecten*, *Delectopecten*, *Equichlamys*, *Mimachlamys**, *Mirapecten*, *Nodipecten*, *Pseudamussium*	[39]
Gliding	Able to swim > 5 m/effort; includes a level swimming phase with a glide component	*Adamussium*, *Amusium*, *“Amusium,” Placopecten*	[44-46]

Table 2.2 - Transitions between life habit states determined from ancestral state reconstruction on the Bayesian topology.

Behavioral transition	**Number of observed**
Recessing to permanent attachment	0
Recessing to byssal attachment	0
Recessing to free-living	0
Recessing to gliding	2
Permanent attachment* to byssal attachment	0
Permanent attachment to free-living	0
Permanent attachment to recessing	0
Permanent attachment to gliding	0
Byssal attachment to permanent attachment	3 (2 cementing; 1 nestling)
Byssal attachment to free-living	6
Byssal attachment to recessing	1
Byssal attachment to gliding	2
Free-living to permanent attachment	0
Free-living to byssal attachment	1
Free-living to recessing	1
Free-living to gliding	0
Gliding to permanent attachment	0
Gliding to byssal attachment	0
Gliding to recessing	0
Gliding to free-living	1
Total number of transitions	**17**

*Cementing and nestling are grouped together under permanent attachment.

Figure 2.1 - Bayesian Inference majority-rule consensus topology. Posterior probability support values (>50) above respective nodes. Branch colors represent MP reconstruction of life habit and pie charts represent their relative probabilities from ML reconstructions. If probability of ML reconstruction equals 1.0, no pie chart is given. ML ancestral state reconstructions are used to illustrate the 17 life habit transitions described in the text. Dashed boxed represent densest taxonomic sampling.



Supplementary Material 2.1 – Genbank accession numbers

		Genbank Accession Numbers of Gene Sequences			
ID Number	**Locality**	**12S rRNA**	**16S rRNA**	**Histone 3**	**28S rRNA**
amandi E1	Panama	HM485575	HM485576	HM485577	HM485578
amandi E2	Panama	HM535651	HM535652	HM535653	HM535654
AMNH 298075_1	unknown	EU379406	EU379460	EU379514	HM630528
antillarum	unknown	HM535656	HM535657	HM535658	HM535659
asperrima 1	Hobart, Tasmania, Australia	HM540080	HM540081	HM540082	HM540083
asperrima 3	Hobart, Tasmania, Australia	HM540084	HM540085	HM540086	HM540087
balloti 1	Bundaberg, Queensland, Australia	HM540088	HM540089	HM540090	HM540091
balloti 2	Bundaberg, Queensland, Australia	EU379379	EU379433	EU379488	HM540092
balloti 3	Bundaberg, Queensland, Australia	EU379380	EU379434	EU379489	HM540093
balloti 4	Bundaberg, Queensland, Australia	HM540094	HM540095	HM540096	HM540097
balloti 5	Bundaberg, Queensland, Australia	HM540098	HM540099	HM540100	HM540101
behringiana	Alaska, USA	FJ263632	FJ263641	FJ263661	FJ263650
bifrons 1	Tasmania, Australia	HM561991	HM561992	HM561993	HM561994
bifrons 2	Tasmania, Australia	HM561995	HM561996	HM561997	HM561998
caurinus	Alaska, USA	FJ263633	FJ26642	FJ263662	FJ263651

chazaliei	Gulfo de Los Mosquitos, Panama	EU379382	EU379436	EU379490	HM561999
*colbecki**	Terra Nova Bay, Antarctica	EU379383	EU379437	EU379491	FJ263652
cruentus HPC	Tateyama City, Chiba, Japan	HM600761	HM600754	HM600734	HM600747
cuneata	Tateyama City, Chiba, Japan	HM622702	HM622703	HM622704	HM622705
farreri 1	Aquaculture Facility in Qindao, China	HM622677	HM622678	HM622679	HM622680
farreri 2	Aquaculture Facility in Qindao, China	HM622681	HM622682	HM622683	HM622684
fumatus 1	Hobart, Tasmania, Australia	HM622689	HM622690	HM622691	HM622692
fumatus 2	Hobart, Tasmania, Australia	HM622693	HM622694	HM622695	HM622696
gibbus 2	Harrington Sound, Bermuda	EU379388	EU379442	EU379496	HM622697
gibbus 3	Harrington Sound, Bermuda	EU379389	EU379443	EU379497	HM622698
gigantea	Santa Barbara, California, USA	FJ263635	FJ263644	FJ263664	FJ263654
hastata	San Juan Island, Washington, USA	FJ263639	FJ263648	FJ263667	FJ263658
HPC 556	Kyonan-cho, Chiba, Japan	HM622710	HM622711	HM622712	HM622713
HPC 663	Hitachi City, Ibaraki, Japan	HM630488	HM630489	HM630490	HM630491
HPC 735	Kasasa-cho, Kagoshima, Japan	HM600762	HM600755	HM600735	HM600748
HPC 771	Bonotsu City (Minanisatsuma), Kagoshima, Japan	HM630483	HM630484	HM630485	HM630486
HPC 1578	Miura City, Kanagawa, Japan	HM622673	HM622674	HM622675	HM622676
irradians	Gulf Marine Specimens Laboratory, USA	EU379392	EU379446	EU379500	HM622700
islandica	Quebec, Canada	FJ263637	FJ263646	FJ263666	FJ263656
japonicum	Oyano Island, Kumamoto, Japan	HM622706	HM622707	HM622708	HM622709

Laevichlamys	Japan	HM630469	HM630470	HM630471	HM630472
latiauratus	Goleta Pier, Santa Barbara, California, USA	EU379393	EU379447	EU379501	HM622714
lemniscata 1	Tateyama City, Chiba, Japan	HM622715	HM622716	HM622717	HM622718
lemniscata 2	Tateyama City, Chiba, Japan	HM622719	HM622720	HM622721	HM622722
magellanicus	Georges Bank, USA	FJ263638	FJ263647	EU379506	FJ263657
maximus 1	Millport, Scotland	EU379400	EU379454	EU379508	HM630545
multistriata 1	Gallicia, Spain	EU379403	EU379457	EU379511	HM630539
multistriata 2	Gallicia, Spain	HM630535	HM630536	HM630537	HM630538
nipponensis	Kitaibaraki City, Ibaraki, Japan	HM622685	HM622686	HM622687	HM622688
nobilis	Kami-amakusa, Kumamoto, Japan	HM630531	HM630532	HM630533	HM630534
novaezeland 2	Mercury Cove, Great Mercury Island, New Zealand	EU379404	EU379458	EU379512	HM630530
novaezeland 3	Mercury Cove, Great Mercury Island, New Zealand	EU379405	EU379459	EU379513	HM630529
opercularis 1	Millport, Scotland	EU379408	EU379462	EU379516	HM630527
opercularis 2	Millport, Scotland	EU379409	EU379463	EU379517	HM630526
ornata 1	Collao, Puerto Rico, USA	HM630379	HM630380	HM630381	HM630382
ornata 2	Collao, Puerto Rico, USA	HM630375	HM630376	HM630377	HM630378
papyraceum 1	Gulf of Mexico, USA	HM630371	HM630372	HM630373	HM630374
patagonica J3	Chile	EU379412	EU379466	EU379520	HM630524
patagonica J6	Chile	HM630520	HM630521	HM630522	HM630523
perulus 1	Panama	EU379413	EU379467	EU379521	HM630515

perulus 2	Panama	EU379414	EU379468	EU379522	HM630514
pleuronectes 1	Rayong Province, Thailand	EU379415	EU379469	EU379523	HM630508
pleuronectes 3	Rayong Province, Thailand	HM630504	HM630505	HM630506	HM630507
pleuro QLD1	Queensland, Australia	HM630500	HM630501	HM630502	HM630503
pleuro QLD2	Queensland, Australia	HM630496	HM630497	HM630498	HM630499
plica	Tateyama, Chiba, Japan	HM630435	HM630436	HM630437	HM630438
purpuratus H3	Tongoy Bay, Chile	EU379417	EU379471	EU379525	HM630495
pusio 1	Gallicia, Spain	HM600764	HM600757	HM600737	HM600750
pusio 2	Gallicia, Spain	HM600765	HM600758	HM600738	HM600751
rubida	San Juan Island, Washington, USA	FJ263636	FJ263645	FJ263665	FJ263655
senatoria 1	Gulf of Thailand, Thailand	HM630479	HM630480	HM630481	HM630482
septem 2	Millport, Scotland	EU379420	EU379474	EU379528	FJ263659
septem 3	Millport, Scotland	EU379421	EU379475	EU379529	HM630477
squamata	Tateyama City, Chiba, Japan	HM630444	HM630445	HM630446	HM630447
subnodosus 9P	Panama	EU379427	EU379481	EU379535	HM630434
subnodosus 3M	Baja California, Mexico	HM630430	HM630431	HM630432	HM630433
UF280376	Sulawsi Island, Indonesia	not seq'd	HM630492	HM630493	HM630494
UF281663	Phuket, Thailand	HM630391	HM630392	HM630393	HM630394
UF282407	Guam, USA	EU379422	EU379476	EU379530	HM630456
UF282416	Guam, USA	HM630461	HM630462	HM630463	HM630464

UF286387	Oman	HM600763	HM600756	HM600736	HM600749
UF287521	Guam, USA	EU379399	EU379453	EU379507	HM630546
UF288930	Guam, USA	HM630510	HM630511	HM630512	HM630513
UF289624	Panama	HM630541	HM630542	HM630543	HM630544
UF289879	Monroe County, Florida, USA	EU379416	EU379470	EU379524	HM600740
UF292105	Viti Levu Island, Fiji	EU379410	EU379464	EU379518	HM630525
UF292110	Viti Levu Island, Fiji	HM630465	HM630466	HM630467	HM630468
UF292821	West Masirah, Oman	HM630422	HM630423	HM630424	HM630425
UF295809	Saipan Island, Mariana Islands	EU379401	EU379455	EU379509	HM630540
UF296052	Viti Levu Island, Fiji	EU379396	EU379450	EU379504	HM630548
UF296350	Cocos-Keeling Island, Australia	EU379384	EU379438	EU379492	HM600739
UF296996	Western Australia, Australia	HM630439	HM630440	HM630441	HM630442
UF297000	Tanzania	HM630473	HM630474	HM630475	HM630476
UF309990	Taiwan	HM562000	HM562001	HM562002	HM562003
UF310406	Milne Bay, Papua New Guinea	EU379429	EU379483	EU379537	HM622701
UF313444	Philippines	HM630395	HM630396	HM630397	HM630398
UF313459	Philippines	GU953232	GU953234	GU953233	HM630478
UF322180	Bismark Archipelago, Papua New Guinea	EU379385	EU379439	EU379493	HM535655
UF322550	West of New Briton, Papua New Guinea	EU379424	EU379478	EU379532	HM600743
UF323764	Florida Straits, Florida, USA	EU379411	EU379465	EU379519	HM600741

UF323809	Bismark Archipelago, Papua New Guinea	EU379397	EU379451	EU379505	HM630547
UF329089	Port Elizabeth, South Africa	HM630426	HM630427	HM630428	HM630429
UF332786	North Cape, New Zealand	HM600760	HM600753	HM600733	HM600746
UF343587	Stingray Shoals, Mariana Islands	HM630452	HM630453	HM630454	HM630455
UF348872	Sullivan's Patches, Papua New Guinea	HM630448	HM630449	HM630450	HM630451
UF351155	Florida, USA	EU379391	EU379445	EU379499	HM622699
UF351301	Florida, USA	EU379419	EU379473	EU379527	HM630487
UF351954	Okinawa, Japan	EU379426	EU379480	EU379534	HM630443
UF352373	Ie Island, Okinawa, Japan	EU379387	EU379441	EU379495	HM622672
UF352374	Okinawa, Japan	HM630457	HM630458	HM630459	HM630460
UF352388	Okinawa, Japan	HM630553	HM630554	HM630555	HM630556
UF367478	Florida Keys, Florida, USA	EU379386	EU379440	EU379494	HM600745
UF367487	Florida Keys, Florida, USA	EU379423	EU379477	EU379531	HM600742
UF367882	Muscat, Qurm, Oman	HM630549	HM630550	HM630551	HM630552
UF368676	Shefa Province, Vanuatu	EU379425	EU379479	EU379533	HM600744
UF369432	Fiji	HM540103	HM540104	HM540105	HM540106
UF371263	Gulf of Panama, Panama	HM630516	HM630517	HM630518	HM630519
UF371875	East of Naos, Panama	EU379381	EU379435	EU379487	HM540102
vancouv*	USA	HM630418	HM630420	HM630416	HM630417
varia varia 1	Gallicia, Spain	EU379428	EU379482	EU379536	HM630415

varia varia 2	Gallicia, Spain	HM630411	HM630412	HM630413	HM630414
ventricosus 1	Bahia Magdalena, Baja California Sur, Mexico	HM630407	HM630408	HM630409	HM630410
vesiculosus 1	Miura City, Kanagawa, Japan	HM630403	HM630404	HM630405	HM630406
vesiculosus 2	Miura City, Kanagawa, Japan	HM630399	HM630400	HM630401	HM630402
vogdesi 1	Bahia Magdalena, Baja California Sur, Mexico	HM630387	HM630388	HM630389	HM630390
yessoensis 1	Mutsu Bay, Aomori, Japan	FJ263640	FJ263649	FJ263668	FJ263660
yessoensis 2	Mutsu Bay, Aomori Japan	HM630383	HM630384	HM630385	HM630386
ziczac 1	Harrington Sound, Bermuda	EU379430	EU379484	EU379538	HM630509

Supplementary Material 2.2 – Life habit assignment

Species	**Life Habit**	**ID Number***
Family Pectinidae		
Subfamily Camptopectinae		
Delectopecten randolphi Dall, 1897	free-living (T. Haga, Trawled, fine sand and mud bottom)	HPC 663
Delectopecten vancouverensis (Whiteaves, 1893)	byssal attach [1]	vancouv
Subfamily Chlamydinae		
Tribe Adamussiini		
Adamussium colbecki (Smith, 1902)	glide [2, 3]	*colbecki*
Tribe Chlamydini		
Azumapecten farreri farreri (Jones & Preston, 1904)	byssal attach [4, 5] "Zhikong Scallop"	*farreri* 1 *farreri* 2
Azmapecten farreri nipponensis (Kuroda, 1932)	byssal attach (T. Haga, attached to oyster shell, lower intertidal zone)	nipponensis
Chlamys behringiana (Middendorff, 1849)	byssal attach (inferred from shell morphology)	*behringiana*
Chlamys hastata (Sowerby II, 1842)	byssal attach [4]	*hastata*
Chlamys islandica (Müller, 1776)	byssal attach [3, 4, 6]	*islandica*
Chlamys rubida (Hinds, 1845)	byssal attach [4]	*rubida*
Coralichlamys madreporarum (Sowerby II, 1842)	byssal attach [7]	UF296052 UF323809
Equichlamys bifrons (Lamarck, 1819)	free-living [4, 8]	*bifrons* 1 *bifrons* 2
Laevichlamys cuneata (Reeve, 1853)	byssal attach [9], (T. Haga, gravel bottom attached, gillnet)	UF310406 *cuneata*
Laevichlamys lemniscata (Reeve, 1853)	byssal attach (T. Haga, gravel bottom attached, gillnet)	*lemniscata* 1 *lemniscata* 2
Laevichlamys sp.	byssal attach (T. Haga, gravel bottom attached, gillnet)	*Laevichlamys*

Laevichlamys squamosa (Gmelin, 1791)	byssal attach [9]	UF351954
Pascahinnites coruscans coruscans (Hinds, 1845)	byssal attach [9]	UF296350
Pedum spondyloideum (Gmelin, 1791)	nestle [7]	UF343587 UF348872
Scaeochlamys livida (Lamark, 1819)	byssal attach [10]	UF367882
Scaeochlamys squamata (Gmelin, 1791)	byssal attach (T. Haga, gravel bottom attached, gillnet)	*squamata*
Semipallium dianae (Crandall, 1979)	byssal attach [10]	UF352388
Semipallium dringi (Reeve, 1853)	byssal attach [11]	UF352373
Semipallium marybellae Raines, 1996	byssal attach (inferred from shell morphology)	UF287521
Semipallium schmeltzii Dunker *in* Küster & Kobelt, 1888	byssal attach (T. Haga & Y. Kano, attached to stone underside)	HPC 771
Talochlamys multistriata (Poli, 1795)	byssal attach [12]	*multistriata* 1 *multistriata* 2
Talochlamys pusio (Linnaeus, 1758)	cement [3, 12]	*pusio* 1 *pusio* 2
Talochlamys tinctus (Reeve, 1853)	byssal attach (inferred from shell morphology)	UF329089
Veprichlamys empressae Kuroda, Habe & Oyama, 1971	byssal attach (T. Haga, attached to a stone, dredged)	HPC 1578
Veprichlamys jousseaumei (Bavayi, 1904)	byssal attach (T. Haga, attached to sunken wood on mud bottom)	HPC 556
Zygochlamys amandi (Hertlein, 1935)	byssal attach (inferred from shell morphology)	*amandi* E1 *amandi* E2
Zygochlamys patagonica (King & Broderip, 1832)	byssal attach [4]	*patagonica* J3 *patagonica* J6

Tribe Crassadomini

Caribachlamys mildredae (Bayer, 1941)	byssal attach [12]	UF289624
Caribachlamys ornata (Lamarck, 1819)	byssal attach [12]	*ornata* 1 *ornata* 2
Caribachlamys sentis (Reeve, 1853)	byssal attach [12]	UF313459
Crassadoma gigantea (Gray, 1825)	cement [4, 13]	*gigantea*

Tribe Fortipectinini

Mizuhopecten yessoensis (Jay, 1857)	recess [2-4]	*yessoensis* 1

		yessoensis 2
Patinopecten caurinus (Gould, 1850)	recess [4, 14]	*caurinus*
Tribe Mimachlamydini		
Mimachlamys asperrima (Lamarck, 1819)	byssal attach [3, 4, 8]	*asperrima* 1 *asperrima* 3
Mimachlamys cloacata (Reeve, 1853)	free-living [10]	UF309990
Mimachlamys nobilis Reeve, 1852	byssal attach [4], (T. Haga, lower intertidal zone, attached to pebble)	*nobilis*
Mimachlamys senatoria Gmelin, 1791	byssal attach [4, 7]	*senatoria* 1
Mimachlamys sp.	byssal attach (inferred from shell morphology)	UF297000
Mimachlamys townsendi (Sowerby III, 1895)	byssal attach [15]	UF292821
Mimachlamys varia *varia* (Linnaeus, 1758)	byssal attach [3, 4]	*varia varia* 1 *varia varia* 2
Spathochlamys benedicti (Verrill & Bush in Verrill, 1897)	byssal attach [12]	UF369432
Tribe Palliolini		
Placopecten magellanicus (Gmelin, 1791)	glide [3]	*magellanicus*
Pseudamussium septemradiatus Müller, 1776	free-living [16]	septem 2 septem 3
Subfamily Pectininae		
Tribe Decatopectinini		
Anguipecten picturatus Dijkstra, 1995	free-living (inferred from shell morphology)	UF288930
Bractechlamys antillarum (Récluz, 1853)	byssal attach [17]	*antillarum*
Bractechlamys vexillum (Reeve, 1853)	free-living [11]	UF313444 UF281663
Decatopecten plica (Linnaeus, 1758)	free-living [7]	*plica*
Decatopecten radula radula (Linnaeus, 1758)	free-living [10]	UF280376
Decatopecten strangei (Reeve, 1852)	free-living (inferred from shell morphology)	UF296996
Excellichlamys spectabilis (Reeve, 1853)	byssal attach [7, 9]	UF282416 UF352374
Gloripallium pallium (Linnaeus, 1758)	byssal attach [7]	UF292105

Gloripallium speciosum (Reeve, 1853)	byssal attach [10]	UF292110
Mirapecten mirificus (Reeve, 1853)	free-living [11]	UF295809
Mirapecten rastellum (Lamarck, 1819)	byssal attach [7]	UF282407
Nodipecten subnodosus (Sowerby I, 1835)	free-living (Dr. Ana M. Ibarra, personal communication)	*subnodosus* 9P *subnodosus* 3M
Tribe Pectinini		
Aequipecten glyptus (Verrill, 1882)	free-living (inferred from shell morphology)	UF351155
Aequipecten opercularis (Linnaeus, 1758)	free-living [3, 4]	*opercularis* 1 *opercularis* 2
"*Amusium*" *balloti* (Bernardi, 1861)	glide [3, 18]	*balloti* 1 *balloti* 2 *balloti* 3 *balloti* 4 *balloti* 5
"*Amusium*" *japonicum japonicum* (Gmelin, 1791)	glide [4], (N. Deguchi, sandy bottom, gillnet)	*japonicum*
"*Amusium*" *papyraceum*	glide [4]	*papyraceum* 1
Amusium pleuronectes (Linnaeus, 1758)	glide [3, 4, 19]	*pleuronectes* 1 *pleuronectes* 3 pleuro QLD1 pleuro QLD2
Argopecten gibbus (Linnaeus, 1758)	free-living [3, 4]	*gibbus* 2 *gibbus* 3
Argopecten irradians irradians (Lamarck, 1819)	free-living [3, 4, 20]	*irradians*
Argopecten nucleus (Born, 1778)	free-living [4]	AMNH 298075_1
Argopecten purpuratus (Lamarck, 1819)	free-living [4, 21]	*purpuratus* H3
Argopecten ventricosus (Sowerby II, 1842)	free-living [4]	*ventricosus* 1
Cryptopecten vesiculosus (Dunker, 1877)	free-living [15], (C. Kobayashi, gravel bottom, dredged)	*vesiculosus* 1 *vesiculosus* 2
Euvola chazaliei (Dautzenberg, 1900)	recess (inferred from shell morphology)	*chazaliei*
Euvola perula (Olsson, 1961)	recess (inferred from shell morphology)	UF371263 *perula* 1

		perula 2
Euvola raveneli (Dall, 1898)	recess (inferred from shell morphology)	UF351301
Euvola vogdesi (Arnold, 1906)	recess [4]	*vogdesi* 1
Euvola ziczac (Linnaeus, 1758)	recess [4, 22]	*ziczac* 1
Leptopecten bavayi (Dautzenberg, 1900)	byssal attach [17]	UF371875
Leptopecten latiauratus (Conrad, 1837)	byssal attach [23]	*latiauratus*
Pecten fumatus Reeve, 1852	recess [3, 4]	*fumatus* 1
		fumatus 2
Pecten maximus (Linnaeus, 1758)	recess [3, 4]	*maximus* 1
Pecten novaezelandiae Reeve, 1852	recess [3, 4]	novaezeland 2
		novaezeland 3

OUTGROUPS

Family Limidae

Ctenoides annulatus (Lamarck, 1819)	byssal attach [24]	UF322180
Ctenoides mitis (Lamarck, 1807)	byssal attach [24]	UF367478
Lima colorata zealandica Sowerby, 1876	byssal attach [24]	UF332786
Lima sowerbyi Deshayes, 1863	byssal attach [24]	UF286387

Family Propeamussidae

Parvamussium pourtalesianum (Dall, 1886)	byssal attach [15]	UF323764
Propeamussium dalli (Smith, 1885)	byssal attach [15]	UF289879
Propeamussium sibogai (Dautzenberg & Bavay, 1904)	byssal attach [15], (T. Haga, sandy-muddy bottom, shrimp trawl)	HPC 735

Family Spondylidae

Spondylus cruentus Lischke, 1868	cement (T. Haga, gravel bottom, sessile on a mud rock, gillnet)	*cruentus* HPC
Spondylus ictericus Reeve, 1856	cement [25]	UF367487
Spondylus nicobaricus Schreibers, 1793	cement [26]	UF322550
Spondylus squamosus Schreibers, 1793	cement [26]	UF368676

*UF, Florida Museum of Natural History (University of Florida, Gainesville); HPC, field collection number for Takuma Haga.

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Supplementary Material 2.3 – Phylogram of the Maximum Likelihood analysis. Bootstrap support values (>50%) above respective nodes. The Pectinidae are demarcated by a grey box. Each hatch mark on outgroup branches indicates a reduction of branch length by 1 scale bar (0.3)

CHAPTER 3. DIVERGENT CONVERGENCE: MULTIPLE SHELL SHAPE OPTIMA FOR GLIDING SCALLOPS (BIVALVIA: PECTINIDAE)

JEANNE M. SERB[1*], ALVIN ALEJANDRINO[1], AND DEAN C. ADAMS[1,2]

[1]*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames IA, 50011*

[2]*Department of Statistics, Iowa State University, Ames IA, 50011*

[*]*Corresponding author email: serb@iastate.edu*

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Abstract

Form and function comprise two hierarchical levels of phenotypic traits that have been understood to evolve in a coordinated fashion to provide an adaptive advantage for organisms. In light of recent studies, selection can act independently on both levels such that a given function is linked to multiple forms. Here we test the hypothesis that gliding scallops have converged to the same quantitative shell shape due to life habit requirements. We found that there is a strong phylogenetic signal in the evolution of shell shape in scallops, which suggests ancestral shell shapes greatly influence descendant shell shapes. Despite this, we found that there are two distinct shapes linked to the gliding life habit, which can be differentiated by the degree of shell curvature. Phylogenetically-informed tests show that the gliding shape has both convergent and divergent patterns, illustrating the importance of studying evolutionary patterns at multiple phenotypic levels to understand biodiversity.

Introduction

One common pattern observed in evolutionary biology is the morphological resemblance among species inhabiting similar environments at different geographic locations. This evolutionary convergence occurs when environmental factors exert strong selection pressures on different species, generating similar phenotypic responses (Losos 1992, Losos et al. 1998, Rüber et al. 1999, Rüber and Adams 2001, Melville et al. 2006, Stayton 2006). Thus, patterns of morphological similarity provide strong evidence of a link between the selective forces shaping trait evolution and the evolutionary responses to those forces (Pagel 1994, Schluter 2000, Blackledge and Gillespie 2004, Harmon et al. 2005). Convergent evolution may imply that there are a limited number of biological solutions available to organisms (Givnish et al. 2005, Revell et al. 2007, Ellingson et al. 2014). To identify patterns of convergence, measurements of morphology, fitness (or performance data), and a phylogeny are needed to assess whether similar traits arose independently or via a common ancestor (Kaster and Berger 1977, Arnold 1983).

In bivalve mollusks, qualitatively similar shell shapes repeatedly occur (Kauffman 1969, Stanley 1970, 1972). Stanley (1970) hypothesized that convergent evolution is a frequent occurrence in bivalves because shell shapes may be limited by the requirements of their life habits. Life habits relate to the animal’s position to the substrate (i.e., epifaunal, semi-infaunal, or infaunal), mode of locomotion or attachment, and feeding mechanism (Stanley 1970). Predation has also been suggested to play a role in shell shape (Carter 1968), but Stanley (1970) considered the effect is small. Of the various bivalve families, scallops (Pectinidae) are particularly amendable to test for repeated evolution of shell shape as many species in the family display similar life habits (Alejandrino et al. 2011).

Scallops comprise approximately 300 species found in many marine habitats (Waller 2006). Scallop diversification has been attributed to the evolution of a comb-like ctenolium, which is a row of small spines at the dorso-anterior end of the right valve (Waller 1984). The ctenolium separate byssus threads over a greater surface area, allowing the scallop better resistance to being overturned when attached to a substrate (Stanley 1972, Waller 1984). As a result, scallops have diversified in life habits with epifaunal and semi-epifaunal substrate position (Stanley 1972). Of the six life habits exhibited by scallops, gliding is the most studied for its biomechanic properties (Morton 1980, Joll 1989, Dadswell and Weihs 1990, Hayami 1991, Cheng et al. 1996, Cheng and DeMont 1996, Ansell et al. 1998, Denny and Miller 2006, Guderley and Tremblay 2013) (Table 1). Gliding is characterized by propulsion of water at the anterior and posterior dorsal margins while the valves are closed. This provides a near-horizontal trajectory above the substratum, resulting in a distance traveled greater than five meters per effort.

Gliding has provided scallops with an adaptive advantage (Yonge 1936, Thayer 1972, Manuel and Dadswell 1993), but it is only performed by a few species (Caddy 1968, Morton 1980, Joll 1989, Hayami 1991, Ansell et al. 1998). Collectively, these scallop species have shells that are discoid in shape and lack prominent external shell sculptures. Alejandrino *et al*. (2011) identified at least four independent origins of gliding across the scallop family. Subsequently, the shell shape of two of these lineages was quantified by Serb *et al*. (2011) where it was discovered that two gliding species from two disparate lineages have converged in shell shape. One question that remains to be answered is whether all known lineages of gliding scallops have quantitatively similar shell shapes. Herein, we test the hypothesis that the four independent lineages of gliding scallops have converged on the same shell shape. For this study we have increased the taxonomic and shell sampling from previous studies to include all four gliding species as well as 38 other scallop species exhibiting other life habits. We tested the prediction that all four lineages of gliding scallops will have the same shell shape. If supported, it will provide insight on whether there are few morphological solutions to the gliding life habit.

Methods

Specimen selection and morphological characterization

A total of 591 specimens from 49 species were used in this study. Specimens were obtained from various museum collections (Appendix 1) and were selected to represent a wide range of taxa displaying four of the life habit groups exhibited by the Pectinidae. From each specimen, shell morphology was quantified using geometric morphometric methods (Bookstein 1991, Mitteroecker and Gunz 2009, Adams et al. 2013). These methods utilize the locations of landmark coordinates as the basis of shell shape quantification. First we obtained high-resolution scans of the left valves of each individual using a NextEngine 3D surface scanner. From these scans we then digitized the locations of five homologous anatomical locations following Serb *et al*. (2011): 1: ventroposterior auricle, 2: dorsoposterior auricle, 3: umbo, 4: dorsoanterior auricle, 5: ventroanterior auricle (Figure 2). Next, eleven semilandmarks were placed equidistantly along the ventral edge of the valve between the anterior and posterior auricles. Finally, we used an automated procedure to place 496 equally spaced semilandmarks on the surface of each scan to characterize its general surface structure (see Gunz et al. 2005, Serb et al. 2011). For this we produced a template mesh on a single specimen, and used the thin-plate spline to warp this template to the surface of a second specimen. The common set of fixed points and edge landmarks between the template and the specimen were used as the basis of this warping. Then, the remaining template points were matched to the specimen scan and the surface points nearest to those in the template were treated as surface semilandmarks for that specimen.

To obtain a set of shape variables for each specimen we aligned the 591 landmark configurations using a generalized Procrustes analysis (GPA: Rohlf and Slice 1990). Procrustes superimposition removes differences in specimen position, orientation, and scale, and aligns all specimens to a common coordinate system. During this analysis the semilandmarks were permitted to slide along their tangent directions using the Procrustes distance criterion. The aligned specimens were then projected orthogonally to tangent space to obtain a set of shape variables (Procrustes tangent coordinates: (Rohlf 1999)) for use in all subsequent analyses. Specimen digitizing and GPA were performed in R 3.02 (R Development Core (Team 2014)) using the package geomorph ((Adams and Otárola-Castillo 2013, Adams et al. 2014)).

Statistical Analyses

To investigate patterns of shell shape variation we performed a combination of standard and phylogenetic comparative analyses. First we used Procrustes ANOVA (Goodall 1991) to compare shell shape among life habit groups. This approach was utilized rather than a parametric MANOVA, because the number of variables (1536) greatly exceeded the number of specimens (591), thereby rendering the computations of test statistics from MANOVA singular. Next we performed pairwise comparisons between life habit groups using the Euclidean distances among group means. With this approach, the observed values were statistically evaluated using permutation, where individuals were randomly assigned to groups and the distances recalculated and compared to the observed patterns of shape divergence (see e.g., (Adams and Collyer 2009, Collyer and Adams 2013)). Patterns of shape variation within and among life habit groups were also visualized in morphospace using a principal components analysis (PCA). Finally, we assessed differences in levels of variation within life habit groups using disparity tests (Stayton 2006); see also (Zelditch et al. 2012). Here, Procrustes variance was estimated for each life habit group separately, and these measures were statistically compared to one another using permutation tests. All statistical analyses were performed in R 3.02 (R Development Core (Team 2014)) using the package geomorph (Adams and Otárola-Castillo 2013, Adams et al. 2014).

To evaluate morphological trends in a phylogenetic context, we performed several phylogenetic comparative analyses, using a multi-gene molecular phylogeny containing 81 species of Pectinidae (Alejandrino et al. 2011). First, we obtained a time-calibrated phylogeny using nine fossil calibration points (Table 2) and the relaxed molecular clock approach as implemented Beast 1.8 (Drummond and Rambaut 2007). Next the mean shell shape was estimated for each species and the morphological dataset was matched to the phylogeny, resulting in 42 species found in the two datasets. Both the phylogeny and the morphological data matrix were then pruned such that they contained the unique set of 42 taxa. With this dataset we evaluated the degree of phylogenetic signal in shell shape, using a multivariate generalization of the Kappa statistic (Adams 2014). Finally, phylogenetic patterns of shell shape evolution were examined using a phylomorphospace approach (sensu (Sidlauskas 2008)), where the extant taxa and the phylogeny were projected into morphospace, and evolutionary changes in shape were visualized along the first two axes of this space using principal components analysis. Analyses were performed in R 3.02 (R Development Core (Team 2014)) using the package geomorph (Adams and Otárola-Castillo 2013, Adams et al. 2014) and routines written by DCA.

Results

We found significant differences in shell shape across life habit groups using Procrustes ANOVA (MANOVA, $F = 168.23$, $P < 0.0001$, $R^2 = 0.462$), and pairwise comparisons revealed that all life habit groups were morphologically distinct from one another (Table 3a). A principal components analysis confirmed these findings, illustrating that the life habit groups formed distinct clusters in morphospace (Figure 3). Interestingly, individuals from the glider life habit group occupied two distinct regions of morphospace. This implied that two sub-clusters of subtle, yet distinct shell shapes are exhibited by species that utilize this behavior. Further, gliding species appeared to display less variation in shell shape when compared to the other life habits. Indeed, comparisons of morphological disparity between groups demonstrated that the two glider morphotypes had roughly 30% of the variation observed in the other life habit groups, indicating a significant reduction in shell shape variation among individuals in this life habit (Table 3b).

When phylogeny was taken into consideration, shell shape displayed significant phylogenetic signal ($K_{mult} = 0.142$; $P = 0.036$). This implied some degree of correspondence between morphological differentiation and phylogenetic relatedness, such that closely related species tended to be more similar in shell shape. Nevertheless, other phylogenetic patterns in shell shape evolution were also evident when viewed in phylomorphospace (Figure 4). For instance, two clear clusters of gliding species were observed in phylomorphospace, consistent with patterns observed in the specimen-level analysis (Figure 4). One of these clusters (the ‘A’ morphotype) was comprised of four species derived from two distinct phylogenetic lineages (*Y. ballotti* & *Y. japonicum*; *A. pleuronectes* & *E. papyraceum*). Importantly, this morphotype displayed strong evidence of evolutionary convergence, as the shell morphologies of the extant species were much more similar to one another than were the shell morphologies of their hypothesized ancestors (Figure 4). In contrast the ‘B’ gliding morphotype was comprised of two closely related species (*P. magellanicus* & *Ad. colbecki*). However, the phylogenetic lineage of these species also contained two species in the ‘A’ morphotype (*Y. ballotti* & *Y. japonicum*). Thus, phenotypic evolution of shell shape in this lineage exhibited divergence of extant morphologies towards the two gliding morphologies. Taken together, these patterns imply that evolutionarily, extant scallops have arrived at their gliding morphologies through both convergent and divergent shifts in shell shape through time.

Discussion

Morphological resemblance among species indicates similar responses to particular selection pressures. Testing for these convergent morphologies is an important area of study in evolutionary biology because they provide the foundation to begin teasing apart factors that may be responsible for the similarities. The gliding life habit in scallops is exceptionally rare within the family and among bivalves, that similarities in shell shape could provide clues about the selection factors responsible. In this study, we quantified scallop shells using three-dimensional, landmark-based geometric morphometrics to compare shell shape similarity of gliding scallops in a phylogenetic context and to examine evolutionary patterns of convergence within the family. We found that gliding scallops have converged in shell shape, with decreased shape variation compared to other life habit groups and ancestral shapes. Curiously, we also found two distinct, divergent gliding morphotypes that evolved from similar ancestral shapes. Here, we discuss the general patterns and the importance of morphological variation and evolution.

The pattern of shell shape morphospace occupation in this study reveals morphological differences, especially among gliding scallop species. The addition of taxa, particularly the recessing species, shows a different pattern from the study by Serb et al. (2011), where recessing scallops occupy the positive end of the first principal component axis that is not occupied by species with other life habits (Figure 3). The main shape that differentiates recessing species is that their left valves are either concave or flat. Thus, the first principal component axis corresponds to the degree of shell curvature. More importantly, the two gliding morphotypes (‘A’ and ‘B’) can be differentiated along this axis, revealing that shell curvature differs between these two groups. This result then shows morphological convergence for some gliding scallops (species with each respective morphotype), but not between morphotypes.

The phenotypic differences observed between ‘A’ and ‘B’ morphotypes may indicate that the two groups display gliding performance differences. Unfortunately, researchers that studied the performance of gliding scallops of either morphotype over the years examined many different hydrodynamic aspects and few of the data can be compiled or accurately compared (Caddy 1968, Morton 1980, Joll 1989, Hayami 1991, Ansell et al. 1998). It is important to consider other differences between the two morphotypes beyond shape, including muscle composition (Gould 1971, Thayer 1972) and shell density (Pennington and Currey 1984) that may influence gliding performance. Interestingly, species with gliding morphotype ‘A’ inhabit tropical waters of the Indo-Pacific or Atlantic Ocean while species with gliding morphotype ‘B’ occupy either the temperate-cold Atlantic or the Antarctic Ocean. Denny & Miller (2006) found the protein structure (resilium) that counters muscle contraction in the Antarctic species performs better in cold water compared to one of the Indo-Pacific species. Therefore, an essential future study would be a comparative test of the hydrodynamic performances of species from both morphotypes, accounting for other morphological and habitat differences.

Our results also reveal shell shape similarities between the gliding morphotypes, which may be more important in hydrodynamics than shell curvature. Both gliding morphotypes show a pattern of convergence, occupying the positive second principal component axis with little overlap with the other life habit groups. The main difference between gliding species and the species of other life habit groups is that they have reduced auricles. In combination with large dorsal gaps, auricle reduction may be important in propulsion (Minchin 2003), allowing greater maneuverability. Shell modifications that appear to improve hydrodynamic performance have been identified other mollusks with external shells. For example, Monnet *et al*. (2011) identified the parallel evolution of a lid covering the region where shell coiling originates (umbilicus) in two disparate lineages of ammonoid cephalopods. Quantifying and comparing the variation in dorsal gaps with auricle reductions among scallop species may shed light on their importance to gliding performance. This will require quantification of the right valves, as left and right valves are not symmetric for all scallop species due to life habit requirements.

The phylogenetic tests of this study further support evolutionary convergence of morphology in gliding scallop species. However, this is only evident for some species, as other gliding scallops have diverged in shell shape. These findings are similar to studies of other organisms where there are multiple solutions to a common problem (Alfaro et al. 2005, Wainwright 2007), which could indicate a decoupling between the morphological and functional traits (Alfaro et al. 2004), such that functional diversity may not predict morphological diversity (Revell et al. 2007, Wainwright 2007). Although disparate taxa may experience similar selective pressures for a functional trait, morphological responses may be different due to constraints including phylogenetic, developmental/construction, and other factors of the environment. Therefore, it is important to explicitly investigate evolutionary patterns at respective biological levels. Lastly, our study's use of an invertebrate group provides some support for the generality of form and function decoupling, leading to diversification.

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Table 3.1 - Scallop behavioral life habit categories.

Life Habit	Description	Species included in this study
Cement	Permanent attachment of the right valve by direct secretion of shell material onto hard or heavy substratum (Waller 1996)	
Nestling	Permanent attachment within the crevices of corals (Yonge 1967, Dijkstra 1991, Kleeman 2001)	
Byssal attaching	Temporary attachment by byssus threads onto substratum allowing reorientation (Stanley 1972, Brand 2006)	*Antillipecten antillarum* (Récluz, 1853), *Mimachlamys asperrima* (Lamarck, 1819), *Chlamys behringiana* (Valh & Clausen 1980), *Spathochlamys benedicti* (Verrill & Bush in Verrill, 1897), *Pascahinnites coruscans* (Hinds, 1845), *Juxtamusium coudeini* (Bavay, 1903), *Mimachlamys crassicostata* (Sowerby II, 1842), *Laevichlamys cuneata* (Reeve, 1853), *Zygochlamys delicatula* (Hutton, 1873), *Semipallium dringi* (Reeve, 1853), *Chlamys islandica* (Müller, 1776), *Veprichlamys jousseaumei* (Bavay, 1904), *Leptopecten latiauratus* (Conrad, 1837), *Coralichlamys madreporarum* (Sowerby II, 1842), *Cryptopecten nux* (Reeve, 1853), *Gloripallium pallium* (Linnaeus, 1758), *Zygochlamys phalara* Roth, 1985, *Caribachlamys sentis* (Waller, 1993), *Gloripallium speciosum* (Reeve, 1853), *Excellichlamys spectabilis* (Reeve, 1853), *Laevichlamys squamosa* (Gmelin, 1791), *Swiftopecten swiftii* (Bernardi, 1858), *Delectopecten vancouverensis* (Whiteaves, 1893)
Recessing	Excavating or burrowing into soft sediment providing partial or complete concealment (Baird 1958, Minchin 1992, Sakurai and Seto 2000, Brand 2006)	*Pecten fumatus* Reeve, 1852, *Pecten maximus* (Linnaeus, 1758), *Euvola perula* (Olsson, 1961), *Euvola raveneli* (Dall, 1898), *Euvola vogdesi* (Arnold, 1906), *Euvola ziczac* (Linnaeus, 1758)

Table 3.1 (Continued)

Free-living	Rests above soft or hard substratum (Stanley 1970)	*Equichlamys bifrons* (Lamarck, 1819), *Mimachlamys cloacata* (Reeve, 1853), *Aequipecten glyptus* (Verrill, 1882), *Argopecten irradians*, *Argopecten nucleus* (Born, 1778), *Aequipecten opercularis* (Linnaeus, 1758), *Decatopecten plica* (Linnaeus, 1758), *Argopecten purpuratus* (Clark 1965), *Decatopecten radula* (Linnaeus,1758), *Serratovola rubicunda* (Récluz in Chenu, 1843), *Pecten septemradiatus* Müller, 1776, *Decatopecten strangei* (Reeve, 1852), *Argopecten ventricosus* (Sowerby II, 1842), *Bractechlamys vexillum* (Reeve, 1853)
Gliding	Able to swim >5 meter per effort (Cheng et al. 1996, Brand 2006)	*Adamussium colbecki* (Smith, 1902), *Ylistrum japonicum* (Gmelin, 1791), *Placopecten magellanicus* (Gmelin, 1791), *Euvola papyraceum* (Gabb, 1873), *Amusium pleuronectes* (Morton, 1980), *Ylistrum balloti* (Joll 1989)

Table 3.2 - Fossil calibration points used in this study. Fossils placements were to the stem nodes of their respective taxonomic group.

Node	Mean Age (MYA)	Age standard deviation (MA)
Pecten-Euvola subclade	20.27	17.73
Euvola	18.22	15.68
S. benedicti	3.07	0.53
Caribachlamys	2.703	0.897
Pectinidae	241.35	11.35
Propeamussiidae	173.85	73.35
Argopecten	12.785	10.245
Aequipecten	84.125	60.875
Cryptopecten	11.515	11.515

Table 3.3 - Statistical evaluation of shell shape. A) Pairwise comparisons of group means based on Euclidean distances (below diagonal) with significance levels (above diagonal) based on 9999 permutations (significant in bold). B) Disparity measures for each life habit group based on Procrustes variance (gliders represented by their two clusters found in PCA). Significance levels comparing disparity between groups are based on 9999 permutations (significant in bold).

	Pairwise comparisons of species means using Euclidean distance			
	Byssal attachers	Free-living	Gliders	Recessors
Byssal attachers	-	**0.0001**	**0.0001**	**0.0001**
Free-living	0.2735	-	**0.0001**	**0.0001**
Gliders	0.5377	0.0567	-	**0.0001**
Recessors	0.1195	0.1339	0.1000	-

	Procrustes variance for life habit groups				
	Byssal attachers	Free-living	Gliders-A	Gliders-B	Recessors
	1.824×10^{-3}	2.567×10^{-3}	4.179×10^{-4}	7.584×10^{-3}	2.048×10^{-3}

	Probability values for pairwise comparisons of disparity using Procrustes variance				
	Byssal attachers	Free-living	Gliders-A	Gliders-B	Recessors
Byssal attachers	-	0.0808	**0.0023**	0.0597	0.7149
Free-living		-	**0.0001**	**0.0022**	0.4252
Gliders-A			-	0.5783	**0.0116**
Gliders-B				-	0.0744
Recessors					

Figure 3.1 - Phylogenetic relationships among species of Pectinidae used in this study. Topological relationships are from (Alejandrino *et al*. 2011). Time calibration based on nine node groups (see Methods for description and Table 2).

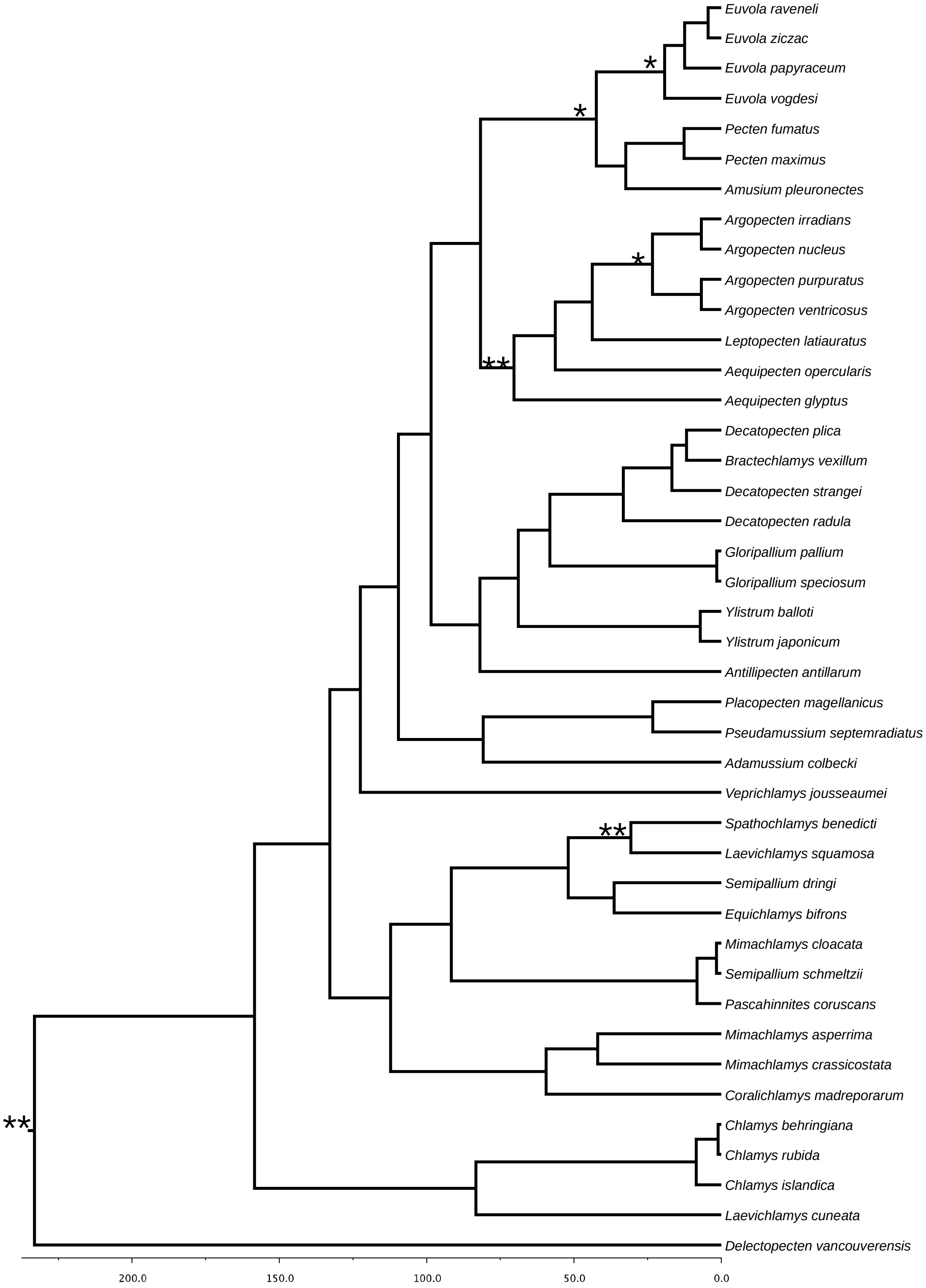


Figure 3.2 - Three-dimensional scan of the left valve of a scallop, with the position of landmarks and semilandmarks indicated. Surface semilandmarks are shown in gray, landmarks along the boundary edge are shown in black, and fixed points are numbered (see text for description).

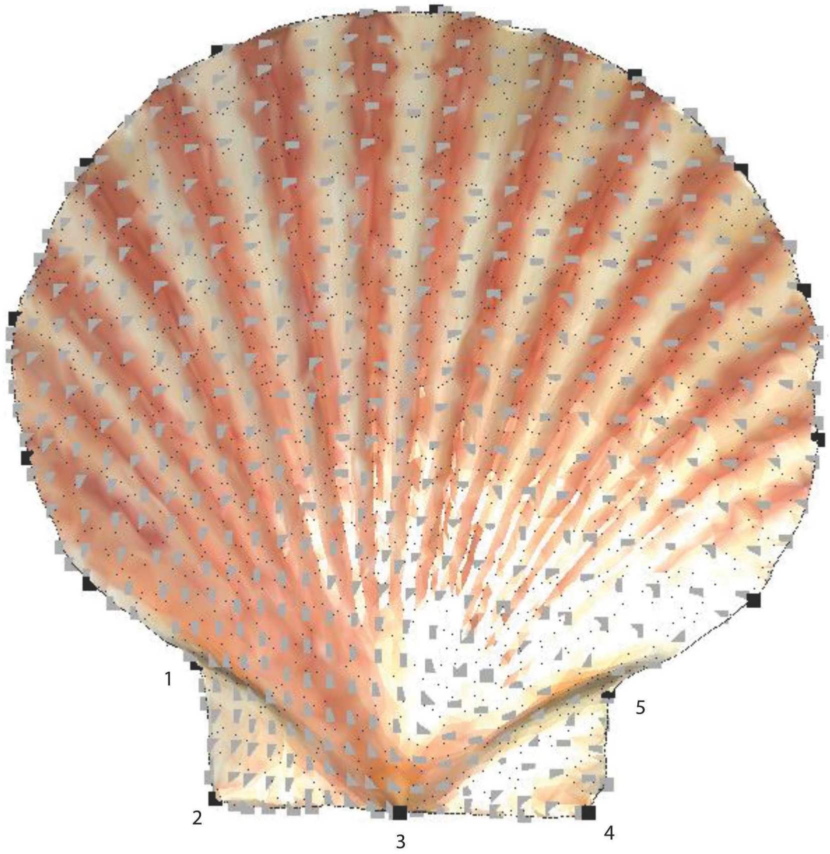


Figure 3.3 - Principal components plot of shell shape based on 591 specimens. The first two axes explain 72.3% of the total shape variation (PC1 = 60%; PC2 = 12.3%). Specimens are colored by the life habit group to which they belong (black = byssal attachers, red = free-living, green = gliding, blue = recessors).

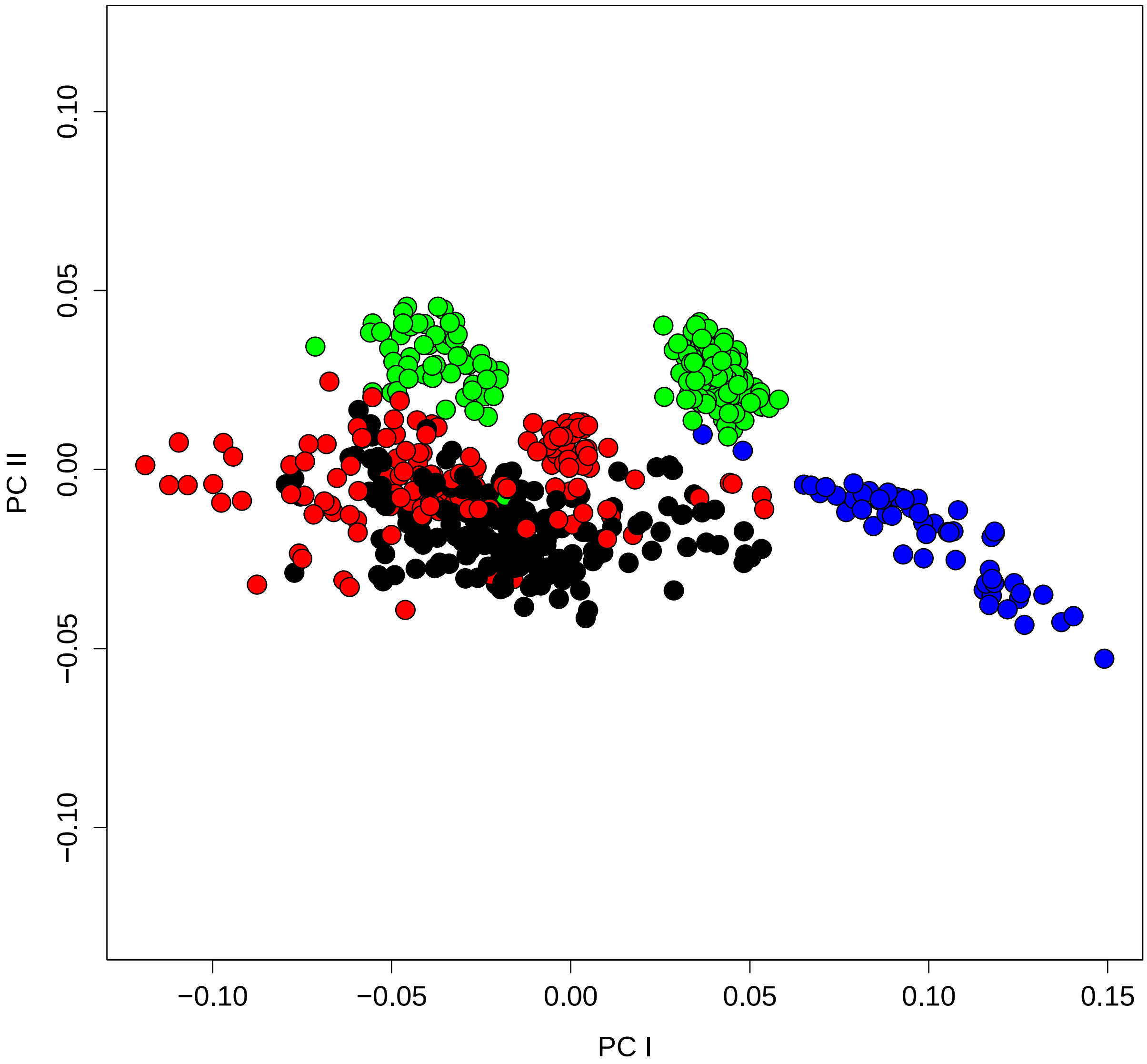
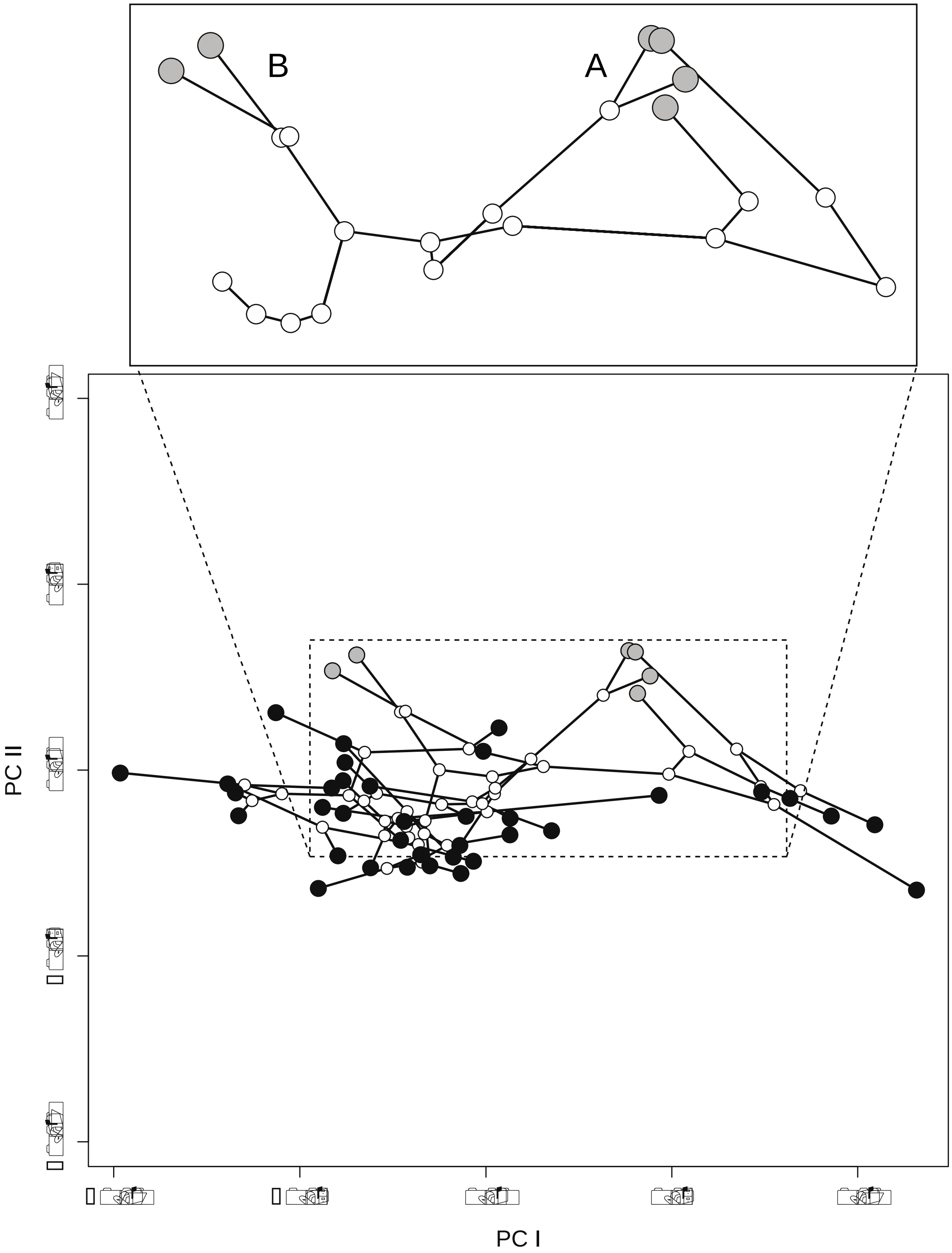


Figure 3.4 - Phylomorphospace plot visualizing the first two axes of morphospace of scallops, with the phylogeny superimposed. Black dots represent extant species, gray dots signify extant gliding species, and white dots represent hypothesized ancestors found from ancestral state reconstruction. The inset shows an enlargement of the region in morphospace containing gliding species, displaying the two glider morphotypes (A and B). Only those phylogenetic branches containing gliding species and their ancestors are shown.



Supplementary Material 3.1 - Museums from which specimens were obtained. The left valves of individuals from both in-house and museum collections: American Museum of Natural History (AMNH), New York City, New York, United States; Bernice Pauahi Bishop Museum (BPBM), Honolulu, Hawai'i, United States; California Academy of Sciences (CAS), San Francisco, California, United States; Delaware Museum of Natural History (DMNH), Wilmington, Delaware, United States; Field Museum of Natural History (FMNH), Chicago, Illinois, United States; Florida Museum of Natural History (FLMNH), Gainesville, Florida, United States; Iowa State University (ISU), Ames, Iowa, United States; Museum of Comparative Zoology Harvard University (MCZH), Cambridge, Massachusetts, United States; Muséum National d'Historie Naturelle, Paris, France (MNHN); Natural History Museum of Los Angeles County (LACM), Los Angeles, California, United States; North Carolina Museum of Natural Sciences (NCMNS), Raleigh, North Carolina, United States; United States National Museum, Smithsonian Institution (USNM), Washington, D. C., United States; Western Australian Museum (WAM), Perth, Australia; and Yale Peabody Museum (YPM), New Haven, Connecticut, United States.

Species (*N*)	**Collection ID**	**Locality**
Adamussium colbecki (38)	USNM 522464	Marguerite Bay, Antarctica
	USNM 522467	Horseshoe Island, Antarctica
	USNM 1024098-1024100, USNM 1024201-1024202	Victoria Land, Antarctica
	USNM 1024126	Adelie Cove, Antarctica
	USNM 1024128, USNM 1024139	Icaro Cove, Antarctica
Aequipecten glyptus (5)	FMNH 57045	Gulf of Mexico
	FMNH 71114-B, FMNH 71114-C, FMNH 77954	Port Isabel, Texas, United States
	FMNH 227444	Florida Keys, Florida, United States
Aequipecten opercularis (6)	FMNH 69059	Palma, Majorca, Spain, Sta. TD-69059
	FMNH 149185	England, Sta. FMNH149185
	FMNH 149185B	England
	FMNH 160770	Venice, Italy, Sta. FMNH160770
	FMNH 325802	France, Sta. ML-325802
Amusium pleuronectes (28)	USNM 254931	Borneo Island, Malaysia

	USNM 810892	La Union, Luzon, Philippines
	USNM 1236642	Ban Phe, Rayong Province, Thailand
Antillipecten antillarum (7)	FLMNH 378319	Cape Florida, Florida, United States
	LACM 177784	West Indies, West Atlantic
	USNM 764816	Bear Cut, Miami, Florida, United States
Argopecten irradians (27)	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Argopecten nucleus (10)	LACM 60922, LACM 167681, LACM 177781	Florida
Argopecten purpuratus (12)	FLMNH 337447	Paracas Bay, Peru
Argopecten ventricosus (5)	LACM 23174	La Paz, Mexico
	LACM 177782	Mission Bay, San Diego, California, United States
	LACM 177783	Santa Ana jetty, California, United States
Bractechlamys vexillum (7)	LACM 34137, LACM 53735, LACM 86066	Zamboanga, Zamboanga del Sur Province, Mindanao Island, Philippines
	LACM 53927	Amboina, Maluku Islands, Indonesia
	LACM 177778	Jolo, Jolo Island, Sulu Archipelago, Sulu Province, Philippines
Caribachlamys sentis (28)	FLMNH 374737	Biscayne Bay, Florida, United States
Chlamys behringiana (20)	USNM 1236650	Monti Bay, Yakutat, Alaska, United States
Chlamys islandica (8)	LACM 167521, LACM 177789, YPM 7448	Newfoundland, Canada

	LACM 167522, LACM 177788, LACM 177790	Iceland
	LACM 118060	Massachusetts, United States
Coralichlamys madreporarum (7)	LACM 167529	Java, Indonesia
	MNHN -----	Tulear, Madagascar
Cryptopecten nux (5)	MNHN 1266	Eiao Island, Marquesas Islands, French Polynesia
	MNHN -----	Hiva Oa Island, Marquesas Islands, French Polynesia
Decatopecten plica (8)	LACM 53930	Maqueda Bay, Samar, Philippines
	LACM 113495	Ryukyu Shoto, Okinawa, Japan
	LACM 167737	Sri Lanka, Indian Ocean
	LACM 177770	Fukura, Awaji-shima, Hyogo, Honshu, Japan
	LACM 177771	Taiwan
	LACM 177775	Kii-suido, Honshu, Japan
Decatopecten radula (5)	LACM 53966	Zamboanga, Zamboanga del Sur, Mindanao, Philippines
Decatopecten strangei (5)	LACM 22102	Hervey Bay, Queensland, Australia
	LACM 28417	Keppel Bay, Queensland, Australia
	LACM 177776	Urangan, Queensland, Australia
	LACM 177777	Perth, Western Australia, Australia
Delectopecten vancouverensis (7)	LACM 1964-65.8	Cape Foulweather, Oregon, United States
Equichlamys bifrons (7)	ISU bifr01-bifr04	Hobart, Tasmania, Australia

	LACM 167614	South Australia, Australia
	LACM 167618	Tasmania, Australia
	LACM 177794	D'Entrecasteaux Channel, Tasmania, Australia
Euvola papyraceum (25)	ISU papy01-papy25	Gulf of Mexico
Euvola perula (7)	FLMNH 0033, FLMNH 175399, FLMNH 344458, FLMNH 352802, FLMNH 412161	Panama
Euvola raveneli (6)	LACM 25708	Lee County, Florida, United States
	LACM 69308	Brevard County, Florida, United States
	LACM 112475, LACM 114335	San Juan, Puerto Rico
Euvola vogdesi (11)	LACM 1937-120.2	San Luis Island, Gulf of California, Mexico
	LACM 1960-5.11	Loreto, Gulf of California, Mexico
	LACM 167473	Gulf of California, Mexico
	LACM 176403	La Paz, Gulf of California, Mexico
Euvola ziczac (13)	FMNH 183573	Key West, Florida, United States
	LACM 114368	Margarita Island, Venezuela
	LACM 176405	Bermuda
Excellichlamys spectabilis (17)	LACM 63-132	Talaga Cove, Bataan Province, Luzon Island, Philippines
	LACM 71-198	east of Suva, Viti Levu Group, Fiji

	LACM 71-205	Yanu-yanu-i-loma Island, Great Astrolabe Reef, Kadavu Group, Fiji
	LACM 78-61.7	west of Kia village, Santa Isabel Island, Solomon Islands
	LACM 86-233	Kolotahi Bay, Vava'u Island, Vava'u Group, Tonga
	LACM 87-176	south of Beagle Island, Marau Sound, Guadalcanal Island, Solomon Islands
	LACM 88-290	northwest tip of Coron Island, Coron Bay, Busuanga Island, Palawan Province, Philippines
	LACM 53571	Kii-suido, Honshu, Japan
	LACM 60904	Ya-shima, Yamaguchi Prefecture, Honshu, Japan
	LACM 60909	Mauritius
	LACM 86031	Baler, Quezon Province, Luzon Island, Philippines
	LACM 117745	Sunuba, Okinawa-jima, Okinawa Prefecture, Japan
	LACM 167646	Japan
Gloripallium pallium (8)	FMNH 13847, FMNH 82376	Japan
	FMNH 82379	Loo-Choo Islands, Japan
	FMNH 88822	Puerto Galera, Philippines
	FMNH 149182D	Maluku Islands, Indonesia
	FMNH 183866	Carolina Island, Palau
	FMNH 309702	Punta Engana, Cebu, Philippines
	FMNH 325810	-----

Gloripallium speciosum (8)	LACM 78-99	Horseshoe South, 1km west of Onna Village, Okinawa-jima, Okinawa, Japan
	LACM 86-162	Pelangi & Putri Islets, Palau-Palau Seribu Islands, off Java, Indonesia
	LACM 86-218	south side Nuku Island, west of Kapa Island, southwest of Vava'u Island, Vava'u Group, Tonga
	LACM 88-56	south side Bunaken and Siladen Islets, off Menado, Sulawesi, Indonesia
	LACM 88-63	off Ajer (Gili Air) and Meno Islets, Lombok, Indonesia
	LACM 90-6	north side Hardy Reef, northeast of Whitsunday Islands, Great Barrier Reef, Queensland, Australia
	LACM 117748	Serigaki, Okinawa-jima, Okinawa, Japan
	LACM 177769	Philippines
Juxtamusium coudeini (5)	MNHN DE11	Nouméa, New Caledonia
	MNHN 713	Canala, New Caledonia
	MNHN 892	Pouebo, New Caledonia
Laevichlamys cuneata (8)	LACM 177796	Kii-suido, Wakayama Prefecture, Honshu, Japan
	MNHN -----	Japan
Laevichlamys squamosa (8)	CAS 63086, CAS 63088, CAS 63091	Oshima, Japan
	MNHN 12, MNHN 57	New Caledonia
Leptopecten latiauratus (5)	BPBM 196931	Santa Barbara, California, United States

	CAS 089510	San Diego Bay, California, United States
	NCMNS 20625	Alamitos Bay, California, United States
Mimachlamys asperrima (5)	LACM 177804	D'Entrecasteaux Channel, Tasmania, Australia
Mimachlamys cloacata (7)	MNHN 1002, MNHN 1299	New Caledonia
	USNM 764127, USNM 764129, USNM 764131, USNM 764133	Japan
Mimachlamys crassicostata (10)	FMNH 44304	Tosa Bay, Japan
	FMNH 151907	Japan
Pascahinnites coruscans (5)	FMNH 13247	-----
	FMNH -----	-----
Pecten fumatus (13)	ISU fuma03-fuma05, LACM 60895	Hobart, Australia
	LACM 22038, LACM 53835, LACM 167438	Tasmania, Australia
	LACM 28424	Albany, Australia
	LACM 28443	Port Lincoln, Australia
	LACM 53617	Eden, Australia
	LACM 53638	Portland, Australia
	LACM 114040	Wallaroo, Australia
	LACM 176402	Australia
Pecten maximus (5)	LACM 28153	Quiberon, France
	LACM 103489	Cherbourg, France
	LACM 112233	Brest, France
	LACM 167452	Bantry Bay, Ireland
	LACM 167454	Bristol Channel, Great Britain

Placopecten magellanicus (24)	ISU mage01-mage24	New Bedford, Massachusetts, United States
Pseudamussium septemradiatus (30)	USNM 62645	Loch Fyne, Scotland
Semipallium dringi (23)	MCZH 93565, MCZH 317354-317355, 317359	Broome, Australia
	MNHN Stn1300	west of Koumac, New Caledonia (20°35.6S, 164°15.2E)
	MNHN StnCP1387	south of Rovodrau Bay, Viti Levu, Fiji (18°18.5S, 178°04.7E
	MNHN StnDw09	northwest of Beqa Island, Fiji (18°21.4S, 178°06.3E)
	MNHN StnDW12	northeast of Beqa Island, Fiji (18°21.4S, 178°09.6E)
Serratovola rubicunda (5)	MNHN StCH205	Makassar Strait, Indonesia (01°08S, 117°18E)
Spathochlamys benedicti (5)	DMNH 105890	southwest John's Pass, Florida, United States
	DMNH 105890 (532)	southwest John's Pass, Florida, United States
	FMNH 164384	Sta. S-164384, Gulf of Mexico
	FMNH 325814	Port St. Joe, Florida, United States
Swiftopecten swiftii (7)	CAS 63	Japan
	DMNH 9599, DMNH 013718, DMNH 63290	Hokkaido, Japan
	DMNH 63282	Nemoro, Hokkaido, Japan
	DMNH 155991	off South Hokkaido, Japan
Veprichlamys jousseaumei (5)	MNHN CP143	Philippines

Ylistrum balloti (32)	WAM 33076.2-33076.4, WAM 33077.1-33077.2, WAM 33077.4	Rottnest Island, Western Australia, Australia
	WAM 33078.2-33078.4, WAM 33079.2-33079.4, WAM 33080.3-33080.4	South Denham Sound, Shark Bay, Western Australia, Australia
	WAM 33081.2-33081.3, WAM 33082.2-33082.4	North West Peron, Shark Bay, Australia
	WAM 33083.3-33083.4	Houtman Abrolhos Islands, Australia
	WAM 33084.2-33084.4	Doubtful Islands, Albany, Western Australia, Australia
	WAM 33085.2-33085.4	Quoin Head, Fitzgerald River National Park, Western Australia, Australia
	WAM 33086	Hassell Beach, Bald Island, Western Australia, Australia
	WAM 33087.2-33087.3, WAM 33088.2-33088.3	Point Ann, Western Australia, Australia
Ylistrum japonicum (20)	USNM 023947, USNM 304217, USNM 763645, USNM 818253	Honshu Island, Japan
	USNM 229068-229070, USNM 343967, USNM 753705	Kyushu Island, Japan
	USNM 333959	Fuzhou, China
Zygochlamys delicatula (5)	AMNH 257649	Stewart Island, New Zealand, Pacific Ocean
	AMNH 275131	Macquarie Island, Tasmania, Australia, Pacific Ocean
	AMNH 275132	Timaru, South Island, New Zealand, Pacific Ocean
	AMNH 306022	Snares Island, New Zealand
	MCZH 166387	South Island, New Zealand

Zygochlamys phalara (10)	FLMNH 338623	Juan Fernandez Island, Chile

CHAPTER 4. SHELL SHAPE CONVERGENCE MASKS BIOLOGICAL DIVERSITY IN GLIDING SCALLOPS: DESCRIPTION OF *YLISTRUM* N. GEN. (PECTINIDAE) FROM THE INDO-PACIFIC OCEAN

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GLENÉ MYNHARDT[1*], ALVIN ALEJANDRINO[1*], LOUISE PUSLEDNIK[1], JOEZEN CORRALES[1,2], AND JEANNE M. SERB[1]

[1]*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa, USA*
[2]*Department of Biology, University of San Carlos, Cebu City, Philippines*

* authors contributed equally to this work

NEW SCALLOP GENUS *YLISTRUM*

(Received 9 June 2013; accepted 14 March 2014)

Correspondence: J. M. Serb; email: serb@iastate.edu

Abstract

The scallop genus *Amusium* Röding, 1798 is one of few genera of Pectinidae that includes taxa capable of long-distance swimming or gliding. Membership of the genus has been defined primarily by shell shape, and it currently includes only three species: the type species *A. pleuronectes* (Linnaeus, 1758), *A. balloti* (Bernardi, 1861) and *A. japonicum* (Gmelin, 1791). In this study, we use molecular data and aspects of shell morphology to resolve the systematics of the genus. Phylogenetic reconstruction of Pectinidae using nuclear and mitochondrial DNA sequence from four genes supports a polyphyletic *Amusium*. Differences in internal ribbing pattern provide morphological evidence for the recognition of the two clades identified in our phylogenetic analyses. In contrast, quantification of shell shape through geometric morphometric methods indicates that shape is a convergent phenotype and is not informative in terms of distinguishing between the two gliding lineages. Based on these results, we describe *Ylistrum*, n. gen, which includes two species previously assigned to *Amusium*. We provide characters that separate the now monotypic *Amusium* from the two species, *Ylistrum balloti*, n. comb. and *Y. japonicum*, n. comb.

Introduction

Bivalve molluscs are a diverse group of invertebrates, consisting of approximately 30,000 species worldwide (Bieler & Mikkelsen, 2006). These animals have evolved a broad range of morphological and behavioral characteristics that make them an attractive model for studying patterns and processes of evolution. Perhaps the most interesting facet of bivalve evolution involves the often tight association between morphology and ecological niche (Stanley, 1970, 1972). As a result, unrelated taxa that occupy similar habitats often converge on a distinct suite of morphological characters (Trueman, Brand & Davis, 1966; Stanley, 1970, 1981, 1988; Watters, 1994) and a similar behavioral habit (Stanley, 1970).

Scallops (Pectinidae) exemplify the association between morphology and ecological niche. All non-permanently attached scallop species have the ability to swim to escape predators (Himmelman, Guderley & Duncan, 2009) or seek favorable habitat (Buddenbrock & Moller-Racke, 1953; Hamilton & Koch, 1996), but the distance travelled is short, usually less than 1 m between lifting from and settling back onto a substrate (Brand, 2006). In contrast, a small number of scallop species can glide. Gliding is a type of swimming behaviour that includes: (1) a great distance travelled per swimming effort (5–30 m per effort; Brand, 2006); (2) the presence of a level swimming phase, where the animal is able to maintain a near-horizontal trajectory above the substrate (Morton, 1980; Joll, 1989; Ansell, Cattaneo-Vietti & Chiantore, 1998) and (3) a glide component, where the animal is propelled forward while the valves are held closed (Manuel & Dadswell, 1993; Cheng *et al.*, 1996; Ansell *et al.*, 1998). Neither a level swimming phase nor a glide component is present in the more common short-distance swimming scallops (Marsh, Olson & Guzik, 1992; Ansell *et al.*, 1998; Donovan *et al.*, 2002). Gliding has evolved at least four times in Pectinidae (Alejandrino, Puslednik & Serb, 2011), as represented by *Amusium*

Röding, 1789; *Euvola* Dall, 1898; *Adamussium* Thiele, 1934; and *Placopecten* Gmelin, 1791. In each of these evolutionary instances, gliding species have shell shape that is qualitatively similar (Stanley, 1970; Hayami, 1991; Millward & Whyte, 1992), suggesting that gliding scallops have converged on a single morphological solution to a common ecological problem. As a consequence, the highly similar conchological characteristics of gliders may mask biological diversity.

The gliding genus *Amusium* currently includes three species, namely *A. balloti* (Bernardi, 1861), *A. japonicum* (Gmelin, 1791) and *A. pleuronectes* (Linnaeus, 1758) (Raines & Poppe, 2006; Dijkstra, 2013). All three species possess a disc-like shape and smooth outer surface of the shell (Fig. 1). Coloration aside, the most variable conchological feature among the three species is the development of linear structures that radiate from the umbo to the margin on the valve's interior, to which we apply the general term 'internal ribs', but which have also been called 'carinae' (Waller, 1991) or 'lirae' (Dijkstra, 1988) by others. The number and pattern of internal ribs have been used to distinguish the type species, *A. pleuronectes*, from other members of the genus (e.g., Habe, 1964; Raines & Poppe, 2006).

In this study, we show that a combination of molecular markers and morphological characters support the recognition of a new genus of gliding scallop, distinct from *Amusium*. First, we test the polyphyly of the genus *Amusium* (Alejandrino *et al.*, 2011) by generating a molecular phylogeny with greater geographic sampling of *Amusium sensu lato*. Second, we use 16S ribosomal RNA gene sequences to determine whether the amount of sequence variation of these two lineages is greater between than within a clade. Finally, we examine shell shape and internal rib patterning to determine whether these morphological characters can be used to separate reliably these two molecularly defined lineages. We demonstrate that the number of internal ribs is a reliable character to distinguish between the now monotypic *Amusium* and a new genus, *Ylistrum* n. gen. We reclassify '*A.*' *balloti* and '*A.*' *japonicum* as species of *Ylistrum*.

Materials

Institutional abbreviations

DMNH, Delaware Museum of Natural History, Wilmington, Delaware, USA
FLMNH, Florida Museum of Natural History, Gainesville, Florida, USA
LACM, Natural History Museum of Los Angeles, Los Angeles, California, USA
LSL, Linnean Society of London, London, UK
MNHN, Muséum National d'Histoire Naturelle, Paris, France
MSNP, Museo di Storia Naturale, Università di Pisa, Pisa, Italy
USNM, National Museum of Natural History, Washington D.C., USA
WAM, Western Australian Museum, Perth, Australia
YPM, Yale Peabody Museum, New Haven, Connecticut, USA

Phylogenetic analysis

We examined 81 species, representing 31% of the extant taxa of Pectinidae. Taxonomic classification follows that of Dijkstra (2013) and Waller (1991). Eleven species from three closely allied families, Propeamussiidae, Limidae and Spondylidae, were included as outgroup taxa based on the results from Puslednik & Serb (2008) and Alejandrino *et al.* (2011). All specimens were preserved in 95% ethanol and were provided by either museum collections or colleagues (Supplementary material: Appendix A). When possible, DNA was extracted from two or more individuals per species as a test for congruent placement in the phylogenetic analyses.

We added to the dataset of Alejandrino *et al.* (2011), increasing the geographic sampling of *Amusium s. l.* by 22 more specimens (*A. pleuronectes*: northern Australia, Andaman Sea of Thailand, China and Philippines; '*A.*' *balloti*: New Caledonia and multiple Western Australian locations; Fig. 2). Primer sequences (12S rRNA, 16S rRNA and histone H3), polymerase chain reaction (PCR), and sequencing conditions were described by Puslednik & Serb (2008). Parameters used for PCR and sequencing of the 28S rRNA gene portion were described by Alejandrino *et al.* (2011). When the PCR optimization steps failed to amplify a sufficient amount of product (< 20ng/μl) or a single product, we cloned the PCR products following manufacturer's instructions (TOPO TA Cloning Kit with pCR2.1-TOPO, Invitrogen).

Sequencing was carried out in an ABI 3730 Capillary Electrophoresis Genetic Analyzer at the Iowa State University DNA Sequencing Facility. DNA sequences generated during this study are deposited in Genbank (accession numbers: KC879113 – KC879138; see also Supplementary material: Appendix A). Sequences were aligned using CLUSTAL W (Thompson, Higgins & Gibson, 1994) with a gap-opening penalty of 10.00 and a gap-extending penalty of 0.20 in Geneious Pro v. 5.6.4 (Drummond *et al.*, 2011). Ambiguous alignment of the 16S rRNA gene sequences was identified using the GBlocks Server (Castresana, 2000; Talavera & Castresana, 2007) with parameters that allow for smaller final blocks, gap positions within final blocks and less strict flanking positions. This region was not included in phylogenetic analysis. The remaining aligned sequences (2,259 bp) were partitioned by locus; the protein-coding gene histone H3 was further partitioned by codon position. For each partition, an appropriate nucleotide substitution model was selected using the Akaike Information Criterion (AIC) in MrModeltest v. 2.3 (Nylander, 2004). The GTR+G model was selected for the 12S rRNA partition and the GTR+G+I model was the best fit for the remaining three gene regions. The multi-gene sequence alignment was analysed using Bayesian Inference (BI), where model parameters were unlinked between data partitions, in MrBayes v. 3.1.2 (Huelsenbeck & Ronquist, 2001). We used the Metropolis Coupled Markov Chain Monte Carlo method with one cold and three hot chains for 25,000,000 generations, sampling every 100th generation for three simulations. We discarded the first 62,500 trees as burn-in and the remaining trees were used to compute a majority-rule consensus topology, branch lengths and posterior probabilities (PP).

To test the current hypothesis that *Amusium* is a clade, we ran a second BI analysis with the same priors as described above. In this analysis, we constrained all *Amusium* and '*Amusium*' taxa as a monophyletic group, but did not impose a requirement of a completely resolved topology. We used the Shimodaira-Hasegawa Test (Shimodaira & Hasegawa, 1999; Goldman *et al.*, 2000) in PAUP* v. 4.0b10 (Swofford, 2002) to compare topologies. To estimate genetic differences among individuals of *Amusium sensu lato*, we calculated p-distances among pairs of DNA sequences (Geneious Pro v. 5.6.4). Genetic distances are based on the 16S rRNA gene fragment as it was the only dataset common to publically available *Amusium s. l.* and museum specimens used in our study. Because p-distance does not correct for multiple substitutions at homologous nucleotide positions or account for differences in evolutionary rates among sites, it is a relatively conservative estimate of genetic distance.

Statistical evaluation of shell ribbing variation

Internal and external features of both left and right valves were examined (Fig. 1). Due to the customary use of internal ribbing in *Amusium* species identification, we counted internal ribs for *A. pleuronectes* (*n* = 42), '*A.*' *balloti* (*n* = 40), and '*A.*' *japonicum* (*n* = 11). A t-test was used to examine pairwise differences in mean rib counts between *A. pleuronectes* vs. '*A.*' *japonicum*, '*A.*' *balloti* vs. *A. pleuronectes*, and '*A.*' *balloti* vs. '*A.*' *japonicum*. We also noted whether ribs were paired on each valve, a feature typically observed in *Amusium s. l.* (Waller, 1991; Supplementary material: Appendix B).

In order to demonstrate that ribbing counts are unaffected by size of the scallop, we calculated mean rib counts for smaller specimens (shell height < 80 mm, *n* = 22) and larger specimens (shell height ≥ 80mm, *n* = 18) of '*A.*' *balloti* (Supplementary material: Appendix B). These analyses were not performed for *A. pleuronectes* and '*A.*' *japonicum* due to a lack of samples from the different size categories.

Geometric morphometrics

To determine the reliability of shell shape in separating *Amusium* and '*Amusium*,' we used geometric morphometrics to quantify and statistically evaluate shell shapes. We selected a total of nine species, three species representing each of three life habits (gliding, byssally attaching and free-living) exhibited by scallops (Alejandrino *et al.*, 2011). For each life habit, we examined three species, two of which were congeneric to account for morphological similarity due to shared evolutionary history (Felsenstein, 1985). All three species of *Amusium s. l.* were examined: *A. pleuronectes* (*n* = 18), '*A.*' *japonicum* (*n* = 20), and '*A.*' *balloti* (*n* = 32). Species representing the byssally attaching life habit included: *Caribachlamys sentis* (Reeve, 1853) (*n* = 28), *Chlamys behringiana* (Middendorff, 1849) (*n* = 20), and *Ch. islandica* (Müller, 1776) (*n* = 8). *Pseudamussium septemradiatus* Müller 1776 (*n* = 30), *Argopecten irradians* (Lamarck, 1819) (*n* = 27), and *Ar. purpuratus* (Lamarck, 1819) (*n* = 23) represented the free-living taxa. For each species, at least eight individuals were included for a total of 206 specimens (see Supplementary material: Appendix C).

We used three-dimensional, landmark-based geometric morphometric methods to quantify shell shape (Bookstein 1991; Rohlf & Marcus 1993; Adams, Rohlf & Slice, 2004;

Zelditch *et al.* 2004). As opposed to linear morphometric methods (e.g. Gould, 1971), this method quantifies shape from coordinates of homologous anatomical structures (landmarks), which include points along curves and surfaces (semilandmarks: Gunz, Mitteroecker & Bookstein, 2005; Mitteroecker & Gunz, 2009) and provides a more complete description of shape. To quantify shell shape, we used 512 three-dimensional landmarks and semilandmarks to ensure that textural information of the shell surface was adequately assessed. Using a NextEngine 3D surface scanner, we obtained high-resolution scans of the left valves of each individual. Each scan was then digitized for the locations of five homologous landmarks, which represented the following anatomical locations: 1, ventroposterior auricle; 2, dorsoposterior auricle; 3, umbo; 4, dorsoanterior auricle; 5, ventroanterior auricle (illustrated by Serb *et al.*, 2011). Eleven semilandmarks were digitized along the ventral edge of the valve and 496 semilandmarks were digitized for the shell surface (for detailed procedures see Gunz *et al.*, 2005; Serb *et al.*, 2011).

We aligned all the digitized specimens using generalized Procrustes superimposition (Rohlf & Slice, 1990). This procedure allows semilandmarks to slide along their tangent directions (Gunz *et al.*, 2005) to minimize Procrustes distance between specimens (one direction for edge semilandmarks and two directions for surface semilandmarks). A set of Procrustes shape coordinates was obtained from the aligned specimens and was used as shape variables in statistical analyses (Bookstein *et al.*, 1999; Mitteroecker *et al.*, 2004; Mitteroecker & Bookstein, 2008). We used the ‘geomorph’ package and routines written by Adams & Otárola-Castillo (2012) for R 2.15.3 (R Development Core Team, 2009) in digitizing the specimens and for morphometric analyses.

To test the hypothesis that species are different in shell shape, we used a nonparametric MANOVA, because the number of variables (1,536) exceeded the number of specimens (206). The Euclidean (Procrustes) distances among individuals were calculated and used to estimate distance variations between species and compared to distance variations within species. Statistical significance was determined using 10,000 permutations (Anderson, 2001). We then performed pairwise comparisons between species to determine whether those species that have the same life habits could be differentiated based on shell shape. For each pair of species, we calculated the difference in average shell shape as the Euclidean distance between species means. We then tested whether pairs of species were more different than expected from chance using permutation, where individuals were randomly assigned to species groups, new means were calculated, and the Euclidean distances between them were estimated (Adams & Collyer, 2007, 2009; Adams, West & Collyer, 2007; Collyer & Adams, 2007). Holm's sequential Bonferroni correction was used to reduce Type I error rate (Rice, 1989). To visualize patterns of variation within and among species, we performed a principal components analysis (PCA). All statistical analyses were performed in R 2.15.3 (R Development Core Team, 2009).

Results

Molecular analyses

The reconstructed phylogeny from the BI analysis is comparable with the phylogeny of Alejandrino *et al.* (2011). Figure 3 highlights the clade of interest and the full phylogeny is provided in Supplementary material (Appendix D). Expanding the number and geographic samples of gliding species recovers two separate monophyletic clades: one clade contains only *A. pleuronectes* (PP = 100) and the second clade includes '*A.*' *balloti* and '*A.*' *japonicum* (PP = 100;

Fig. 3). The latter clade we describe as a new genus, *Ylistrum,* and hereafter refer to *Ylistrum balloti* n. comb. and *Y. japonicum* n. comb. (see Systematic description, below). Constraining *Amusium* and *Ylistrum* to a single clade resulted in a lower likelihood score (constrained: lnL = -46583.94613; unconstrained: lnL = -46450.39651; equally weighted branch lengths), and this topology was significantly less likely given the data ($P = 0.019$) under the Shimodaira-Hasegawa test.

The pairwise comparisons of the 16S rRNA sequences show greater similarity within a single clade than between the two clades (Table 1). Using the conservative p-distance calculation, the percent of nucleotide sequence similarity between *Amusium* and *Ylistrum* ranges from 73.1% to 87.6%. Nucleotide sequence similarity within the *Ylistrum* clade ranges from 90.6% to 99.6%, and from 79.2% to 98.7% among *A. pleuronectes* specimens (Table 1).

Statistical evaluation of shell ribbing variation

For the left valve, the mean number of ribs for *A. pleuronectes* was 23 (range 19–27), while *Y. balloti* and *Y. japonicum* averaged 35 (range 30–45) and 38 (range 35–41) ribs, respectively (Supplementary material: Appendix B). The mean number of ribs for the right valve of *A. pleuronectes* was 23 (range 20–30 ribs), while *Y. balloti* and *Y. japonicum* averaged 44 (range 36–50) and 46 (range 39–51) ribs, respectively (Fig. 4; Supplementary material: Appendix E). In addition to these 93 morphological specimens examined, we found one specimen of *A. pleuronectes* (USNM 1236642: Ban Phe, Rayong Province, Thailand) with an inordinately high number of ribs on the left valve (left = 34; right = 24; Supplementary material: Appendix F). This individual was one of 10 specimens collected from the same location at the same time. While tissues were not available for this individual, DNA sequences from two syntopic specimens phylogenetically place these animals within *A. pleuronectes* (Fig. 3) and 16S rRNA sequence similarity is within the range of clade members (79.2%) (Table 1). Thus, we suspect the inordinately high number of ribs not to indicate another taxonomic unit, but is likely the result of a growth abnormality as the extra ribs were incomplete, not reaching the valve margins (Supplementary material: Appendix F). This specimen was excluded from further analyses. Aside from this one specimen, the range values for internal ribbing patterns of both left and right valves are comparable with other estimates (e.g. Habe, 1964; Raines & Poppe, 2006). Internal ribbing counts for the left valves were statistically different for all pairwise comparisons of species: *A. pleuronectes* vs *Y. japonicum* ($P < 0.0001$), *Y. balloti* vs *A. pleuronectes* ($P < 0.0001$), and *Y. balloti* vs *Y. japonicum* ($P < 0.0001$; Table 2). Internal ribbing counts for the right valves did not statistically differ between *Y. balloti* and *Y. japonicum* ($P = 0.09$; Table 2), but were statistically dissimilar for *A. pleuronectes* and *Y. japonicum* ($P < 0.0001$) and *Y. balloti* and *A. pleuronectes* ($P < 0.0001$). The presence of paired ribs on both left and right valves occurs in all three species and is therefore not a good character in differentiating between the two genera (Supplementary material: Appendix B).

Next, we determined whether the size of the animal might influence the observed differences in ribbing counts. To this end, we quantified and compared internal rib number between smaller and larger specimens *Y. balloti,* and found no statistical difference in the number of ribs for either left ($P = 0.465$) or right ($P = 0.312$) valves. These data suggest that rib number is unlikely to change during ontogeny. We assume that the observed pattern will be consistent in *A. pleuronectes* and *Y. japonicum,* but sufficient samples were unavailable for direct testing. Therefore, rib number should be a reliable character in distinguishing between the two genera even when comparing individuals of different sizes (Fig. 4).

Geometric morphometrics

When we analyzed shell shapes, we found significant variation among species relative to within species (np-MANOVA, $F = 67.63$, $P < 0.0001$, $R^2 = 0.733$). This indicates that at least one species is different in shell shape from another species. In assessing the pairwise shape differences between species using Euclidean distances, we found that the gliding species are significantly different from all byssal attaching and all free-living species ($P \leq 0.0009$; Table 3). Conversely, none of the gliding species differed significantly in shell shape from one another (*A. pleuronectes* versus *Y. japonicum*: $P = 0.0604$; *Y. balloti* versus *A. pleuronectes*: $P = 0.1399$; *Y. balloti* versus *Y. japonicum*: $P = 0.5121$). When we visualized the shell shape variation using PCA, the first three principal components described 80% of the total variation, indicating that the gliding species occupy a separate area of morphospace from the byssally attaching and free-living species (Fig. 5).

Systematic Descriptions

Family Pectinidae Rafinesque, 1815

Tribe Pectinini

Subfamily Pectininae

Amusium Röding, 1798

Amusium Röding, 1798: 165.

Pleuronectia—Swainson, 1840: 388.

Amussium—Agassiz, 1846: 19 (error for *Amusium* Röding, 1798)

Amussium—Herrmannsen, 1846: 47 (unjustified emendation for *Amusium* Röding, 1798)

Type species

Ostrea pleuronectes Linnaeus, 1758.

Description

Size moderate; valves thin, slightly convex, gaping along margins below auricles; small byssal notch; circular shell shape; exterior surface of valves smooth; left valve variable in colour; right valve white; left and right valves bearing an average of 23 internal ribs radiating to margin.

Amusium pleuronectes (Linnaeus, 1758)

(Fig. 1A–C)

Ostrea pleuronectes Linnaeus, 1758: 696, no. 159. Dijkstra, 1999: 399, figs 1C–F (lectotype).

Amusium rumphii Chemnitz, 1784: 284, pl. 61, fig. 595 (invalid publication, ICZN art. 11c).

Amusium magneticum Röding, 1798: 165.

Pleuronectia laevigata Swainson, 1840: 388.

Pecten (*Amussium*) *milne edwardsi* de Gregorio, 1884. de Gregorio, 1898: 6, pl. 1, figs 1, 6.

Amusium pleuronectes australiae Habe, 1964: 2, pl. 1, figs 1, 2.

Amusium pleuronectes nanshaensis Wang & Chen, 1991: 152, 160, fig. 3.

Types

Lectotype (LSL no. 159), paralectotype (MSNP) (Dijkstra, 1999); locality "Habitat in Indiis" (Linnaeus, 1758: 696) [= Indonesia, det. Dijkstra, 1999].

Material examined

USNM 1236646-1236648 (Philippines); USNM 1236643-1236645 (Northern Territory and Queensland, Australia); USNM 1236642 (Thailand); NMNH 254931 (Malaysia). (Supplementary material: Appendices B and C).

Description

Size moderate, maximum height 80–100 mm. Shell disc-shaped, thin, rounded, smooth externally. Valves very slightly convex, compressed near umbo, gaping at anterior and posterior sides; suborbicular to orbicular, umbonal angle *c*. 120°. Auricles small, equal in size, coloration matching valve colour. Left valve variable in colour, from cream to pinkish brown, with variable bluish purple radial lines and intermittent pale dots near umbo; right valve slightly smaller than left, white (Fig. 1A–C). Internal ribbing on both valves; left valve with 19–27 ribs; right valve with 20–30 ribs.

Distribution

Tropical and subtropical Indo-Pacific Ocean.

Remarks

Based on our data, *Amusium s. l.*, which has previously included three species and several subspecies, is herein redefined to include only its type species, *A. pleuronectes* (*Amusium sensu stricto*). A thorough revision of *Amusium* is necessary to investigate the validity of other potential species or subspecies. Here, we aim only to distinguish *Amusium s. s.* from the new genus, *Ylistrum*.

Ylistrum **Mynhardt & Alejandrino, new genus**

Type species

Pecten balloti Bernardi, 1861.

Etymology

Ylistrum comes from the Greek verb γλιστρώ (ylistro), to glide, describing the gliding life habit of this genus. We use the neuter latinized form as the generic name.

Material Examined

MNHN 21185 (New Caledonia); USNM 1236641 (Queensland, Australia); WAM 33076-33088 (Western Australia, Australia); USNM 23947, USNM 229068-229070, USNM 304217, USNM 343967, USNM 753705, USNM 763645, USNM 8181253, USNM 1236649, DMNH 13078, DMNH 20698, DMNH 42249, DMNH 111140, DMNH 155970 (Japan); USNM 333959, DMNH 155970 (China) (Supplementary material: Appendices B and C).

Description

Size large, maximum height up to 120 mm; shell shape disc-like, thin, externally smooth, suborbicular to orbicular, umbonal angle *c*. 120°; valves very slightly convex, compressed near umbo, gaping at anterior and posterior sides; auricles small, equal in size: left valve variable in color from light to dark red-brown, occasionally with irregular light or dark speckling, radial lines present or absent; right valve slightly smaller than left, white, sometimes with brown or yellow ventral margins (Fig. 1D–L); internal ribbing on both valves; left valve with 30-41 ribs, right valve with 36–51 ribs.

Distribution

Subtropical and temperate Indo-Pacific Ocean.

Ylistrum balloti (Bernardi, 1861) new combination

(Fig. 1C, D, G, H, K, L)

Pecten balloti Bernardi, 1861: 46-48, pl. 1, fig. 1.

Amusium balloti—Iredale 1939: 369–370. Dijkstra, 1988: 3–4.

Amusium japonicum balloti—Habe, 1964: 4–5, pl. 1, fig. 5, pl. 2, fig. 6.

Types

3 syntypes MNHN 21185; lectotype here designated height 86 mm x length 85 mm; 2 paralectotypes 98 mm x 98 mm and 93 mm x 93 mm; type locality New Caledonia.

Material examined

Thirty-seven specimens from ten localities (eight in western Australia, one in eastern Australia, one in New Caledonia) (Supplementary material: Appendices B and C).

Description

Size moderate, up to a maximum of 110 mm in height. Shell disc-shaped, thin, rounded, smooth externally. Valves very slightly convex, compressed near umbo, gaping at anterior and posterior sides; suborbicular to orbicular, umbonal angle *c*. 120°. Auricles small, equal in size. Exterior colour of left valve reddish, covered with a concentric pattern from the umbo to ventral margin of many thin brown lines and violet-brown spots, light brown or pale reddish stripes transverse valve height; auricles often similar in colour to base colour of left valve (Fig. 1G); exterior of right valve white or pale brown, with concentric, irregularly sized violet-brown spots; valve interior white, becoming a pink, brown, or yellow tint along the margins of one or both valves; interior ribbing on both valves, 30-38 on left valve, 36-49 on right valve.

Distribution

New Caledonia; western, northern and eastern Australia.

Ylistrum japonicum **(Gmelin, 1791), new combination**

(Fig. 1B, F, J)

Ostrea japonica Gmelin, 1791: 3317.

Amusium japonicum—Röding, 1798: 165.

Amusium japonicum f. taiwanense Dijkstra, 1988: 4 (invalid infrasubspecific name).

Amusium japonicum taiwanicum Habe, 1992: A12 (new name for *Amusium japonicum formosum* Habe, 1964).

Types

Not traced.

Material examined

Twenty specimens from 18 localities (Supplementary material: Appendices B and C).

Description

Size large, up to maximum 110 mm in height. Shell disc-shaped, thin, rounded, smooth externally. Valves very slightly convex, compressed near umbo, gaping at anterior and posterior sides; suborbicular to orbicular, umbonal angle *c*. 120°. Auricles small, equal in size. Exterior colour of left valve dark red to reddish-brown or light brown, with light brown concentric lines radiating from umbo to ventral edge; auricles darker in colour than base of left valve; exterior right valve white. Interior of both valves white, left valve sometimes with brownish margin, interior right valve almost always with yellow margin (Fig. 1F); interior radial ribbing on both valves, 35–41 on left valve, 39–51 on right valve; paired ribs sometimes present on either valve.

Distribution

Northwest Pacific Ocean (Hong Kong, China; Taiwan; Japan).

Remarks

Valve colour and the pattern of concentric lines and spots differ between the two *Ylistrum* species. In *Y. japonicum*, auricles generally are darker than the base colour of the left valve and only *Y. balloti* has spots in a concentric pattern on both left and right valves. Internal rib count could not be used to differentiate between the two *Ylistrum* species as counts had completely overlapping ranges. Their geographical distributions are not known to overlap. Additional molecular sampling will be needed to address the validity of species within *Ylistrum*.

Comparison of genera

Ylistrum can be separated from *Amusium* based on several morphological features, including size, number of ribs and coloration (Table 4). *Ylistrum* species are typically larger, reaching 120 mm in height as compared to 100 mm in *Amusium*; however, number of ribs and coloration are better characteristics to separate the two genera as they do not appear to be age dependent.

Ribbing data have been used previously to define the three different *Amusium s. l.* species (Fig. 4; Bernardi, 1861; Habe, 1964; Dijkstra, 1988), but their reliability has not been rigorously tested. Our statistical analysis suggests that internal ribbing is a reliable character in distinguishing between the two genera. *Ylistrum* has a significantly greater number of internal ribs on both valves (Table 1; Supplementary material: Appendix B), with 30–45 and 36–51 ribs on left and right valves, respectively. On average, the number of ribs in *Ylistrum* differs between left and right valves, the right valve always having a greater number of ribs than the left. In contrast, *Amusium* bears between 19–27 internal ribs on the left valve and 20–30 ribs on the right and, on a single individual, the number of ribs tends to be similar between valves.

Coloration of the left valve is variable in both genera, but general patterns can be observed. *Ylistrum* typically has a reddish hue and lacks conspicuous radial lines on the exterior left valve (Fig. 1D, G, J), while *Amusium* appears cream, pinkish or light brown and bears obvious radial lines that are bluish or purple (Fig. 1A). It is important to note that colour may be variable when examining specimens from different localities, in which case ribbing may be more reliable in separating the two genera (Fig. 1B, C cf. E, F, H, I, K, L).

Discussion

We conducted a multigene phylogenetic analysis of *Amusium s. l.* based on representative sampling across its distributional range and showed that this group was not monophyletic. The resulting topology confirms two well supported and well separated clades of *Amusium s. l.* (Fig. 3), with greater genetic variation between clades than within a single clade for the 16S rRNA marker (Table 1). Furthermore, members of these molecularly-defined clades can be reliably distinguished from one another by the number of internal ribs on the left and right valves (Table 2; Fig. 4). We demonstrate that a combination of molecular and morphological characters effectively differentiates two morphologically convergent scallop lineages, *Amusium* and *Ylistrum*. Therefore, to communicate better this hitherto hidden biological diversity, we describe a new genus, *Ylistrum*, which includes *Y. balloti* and *Y. japonicum.* As a result, *Amusium* is now monotypic and includes only the type species, *A. pleuronectes*.

While our data support the recognition of a new genus of gliding scallop, these data are insufficient to address the taxonomic status of species within *Ylistrum*. This was due, in part, to the scarcity of molecular-grade specimens of *Y. japonicum.* Thus, while our molecular dataset aided in the recognition of a new genus, it did not allow us to test formally the monophyly of *Y. balloti* and *Y. japonicum*. In our morphological dataset, with larger sample size of *Y. balloti* and *Y. japonicum*, we found that the internal rib count could not be used to differentiate between the two species as counts had completely overlapping ranges. Thus, future studies with larger molecular sampling will be necessary to address taxonomy of *Ylistrum* species.

The fact that *Ylistrum* and *Amusium* have been previously classified in a single genus is not surprising as the shells are qualitatively similar. Even with the application of quantitative methods, like the geometric morphometrics approach used here, there are no significant differences in shell shape among the three gliding species (Table 3), as they occupy the same area of morphospace (Fig. 5). Accordingly, the morphologically conserved shell shape of *Ylistrum* and *Amusium* supports the hypothesis that two different lineages of scallops have converged on a remarkably similar shell shape in response to an ecological niche or the biomechanical constraints associated with gliding (Serb *et al.*, 2011).

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Table 4.1 **-** Pairwise genetic distances of 16S rRNA between specimens of *Amusium pleuronectes*, *Ylistrum balloti* and *Y. japonicum*. Asterisks (*) indicate the *Ylistrum* specimens. Values below the diagonal indicate percent sequence similarity; pairwise comparisons above the diagonal are presented as a heat map, with dark shades representing higher similarities between sequences. Abbreviations match specimen labels in Fig. 3 and specimens listed in Appendix A.

	SL76 WA*	SL78 WA*	SL03 QL*	SL04 QL*	SL02 QL*	SL01 JP**	SL05 QL*	GB01 NC*	SL01 QL*	SL0 2PH	SL0 7PH	SL0 3PH	SL0 1PH	SL0 1AU	SL0 2AU	GB0 1AU	GB0 2AU	GB0 3AU	GB1 0CN	GB1 9TH	GB1 7TH	GB1 8TH	GB1 5TH	SL0 3TH	SL0 1TH
SL76 WA*																									
SL78 WA*	99.6																								
SL03 QL*	98.8	98.6																							
SL04 QL*	99.0	98.8	99.6																						
SL02 QL*	99.0	98.8	99.4	99.6																					
SL01 JP**	98.1	97.9	98.3	98.6	98.6																				
SL05 QL*	95.1	94.9	95.8	96.0	95.8	94.7																			
GB01 NC*	93.6	93.4	94.3	94.3	94.0	93.0	90.6																		
SL01 QL*	96.8	96.6	97.9	97.7	97.5	96.4	94.2	94.2																	
SL02 PH	87.3	87.6	87.3	87.1	87.1	86.9	83.5	84.7	85.6																
SL07 PH	87.3	87.6	87.3	87.1	87.1	86.9	83.5	84.7	85.6	98.7															
SL03 PH	87.1	87.3	87.1	86.9	86.9	86.7	83.3	84.4	85.4	98.5	98.5														
SL01 PH	85.9	86.1	85.9	85.7	85.7	85.5	83.0	83.2	84.3	97.3	97.3	97.0													
SL01 AU	86.9	87.1	87.3	87.1	87.1	86.9	83.5	84.9	85.6	97.0	97.0	97.0	95.5												
SL02 AU	86.9	87.1	87.3	87.1	87.1	86.9	83.5	84.9	85.6	97.0	97.0	97.0	95.5	98.7											
GB01 AU	85.0	85.2	85.2	85.2	85.2	85.0	81.6	84.9	84.3	93.2	93.2	93.2	91.7	94.7	94.7										
GB02 AU	84.4	84.7	84.7	84.7	84.7	84.4	81.0	85.3	84.8	92.6	92.6	92.6	91.1	94.1	94.1	94.1									
GB03 AU	84.7	84.9	84.4	84.4	84.4	84.2	80.8	85.1	84.6	94.1	94.1	93.9	92.7	92.6	92.6	92.6	93.0								
GB10 CN	74.5	74.7	74.2	74.2	74.2	74.0	74.2	74.2	74.3	83.3	83.3	83.0	82.9	81.8	81.8	81.8	81.8	83.3							
GB19 TH	74.5	74.7	74.2	74.2	74.2	74.0	74.2	74.2	74.3	83.3	83.3	83.0	82.9	81.8	81.8	81.8	81.8	83.3	83.3						
GB17 TH	73.9	74.1	73.7	73.7	73.7	73.4	73.7	73.7	73.7	82.7	82.7	82.5	82.3	81.2	81.2	81.2	81.2	82.7	82.7	82.7					
GB18 TH	74.2	74.5	74.0	74.0	74.0	73.8	74.0	74.0	74.1	83.0	83.0	82.8	82.7	81.5	81.5	81.5	81.5	83.0	83.0	83.0	82.5				
GB15 TH	74.7	74.9	74.5	74.5	74.5	74.2	74.5	74.5	74.5	82.0	82.0	81.8	81.7	81.3	81.3	81.3	81.3	82.0	82.0	82.0	81.4	81.8			
SL03 TH	76.0	76.2	76.0	75.8	75.8	75.5	75.8	73.1	74.5	86.5	86.5	86.3	86.2	84.8	84.8	81.0	80.4	81.9	81.2	81.2	80.6	81.0	79.9		
SL01 TH	76.8	77.0	76.6	76.6	76.6	76.4	76.6	76.7	76.9	85.0	85.0	84.8	84.7	84.0	84.0	83.8	83.9	84.9	80.3	80.3	80.8	80.1	79.5	79.2	

Table 4.2 - Results of t-test comparing pairwise ribbing counts between *Amusium pleuronectes* (*n* = 42), *Ylistrum balloti* (*n* = 40) and *Y. japonicum* (*n* = 11). Pairwise comparisons (*P*-values) in bold font indicate significant values ($P < 0.05$).

Right valve →	*A. pleuronectes*	*Y. balloti*	*Y. japonicum*
Left valve ↓			
A. pleuronectes		**$P = 1.71e^{-43}$**	**$P = 2.25e^{-11}$**
Y. balloti	**$P = 1.29e^{-31}$**		$P = 0.09$
Y. japonicum	**$P = 1.04e^{-13}$**	**$P = 3.31e^{-04}$**	

Table 4.3 - Statistical assessment of pairwise differences in shell shape between pectinid species. Values above the diagonal are probabilities (based on 10,000 random permutations). Values below the diagonal are Euclidean distances treated as the amount of shape difference between species (values significant at $P < 0.05$ after Holm's sequential Bonferroni correction shown in **bold**).

	Y. balloti	*Ch. behringiana*	*Ar. irradians*	*Ch. islandica*	*Y. japonicum*	*A. pleuronectes*	*Ar. purpuratus*	*Ca. sentis*	*P. septemradiatus*
Y. balloti		0.0001	0.0001	0.0001	0.5121	0.1399	0.0001	0.0001	0.0001
Ch. behringiana	**0.072305**		0.0001	0.1082	0.0001	0.0001	0.0001	0.0288	0.0086
Ar. irradians	**0.104875**	**0.052485**		0.0225	0.0001	0.0001	0.0004	0.0001	0.0001
Ch. islandica	**0.096015**	0.033922	0.043696		0.0001	0.0001	0.0151	0.0182	0.0037
Y. japonicum	0.013613	**0.073921**	**0.107465**	**0.096582**		0.0604	0.0001	0.0001	0.0002
A. pleuronectes	0.022318	**0.064888**	**0.094707**	**0.086418**	0.029704		0.0001	0.0001	0.0009
Ar. purpuratus	**0.128142**	**0.068142**	**0.046631**	0.04656	**0.128818**	**0.12048**		0.0001	0.0001
Ca. sentis	**0.076855**	0.030167	**0.063131**	0.044754	**0.079007**	**0.066436**	**0.081421**		0.0017
P. septemradiatus	**0.052522**	0.034879	**0.063996**	**0.053072**	**0.055138**	**0.042716**	**0.087636**	**0.038237**	

Table 4.4 - Distinguishing features used to separate *Amusium* from *Ylistrum*.

	Amusium	*Ylistrum*
Maximum height	100 mm	120 mm
Number of internal ribs (left)	19-27	30-45
Number of internal ribs (right)	20-30	36-51
Coloration of left valve	Cream, pinkish, light brown	Reddish
Radial lines on left valve exterior	Bluish-purple	Absent
Marginal coloration	Absent	Present

Figure 4.1 - External shell morphology and internal shell ribbing. **A–C.** *Amusium pleuronectes* 80.56 mm shell height, Ban Phe, Rayong Province, Thailand. **D–F.** *Ylistrum japonicum*, 92.71 mm shell height, Oyano Island, Kumamoto, Japan. **G–I.** *Y. balloti*, 86.00 mm shell height, Nuu Island, New Caledonia. **J–L.** *Y. balloti*, 47.15 mm shell height, Rottnest Island, Western Australia, Australia. **A**, **D**, **G**, **J.** Outer views of left valves. **B**, **E**, **H**, **K**. Inside views of left valves. **C**, **F**, **I**, **L.** Inside views of right valves.

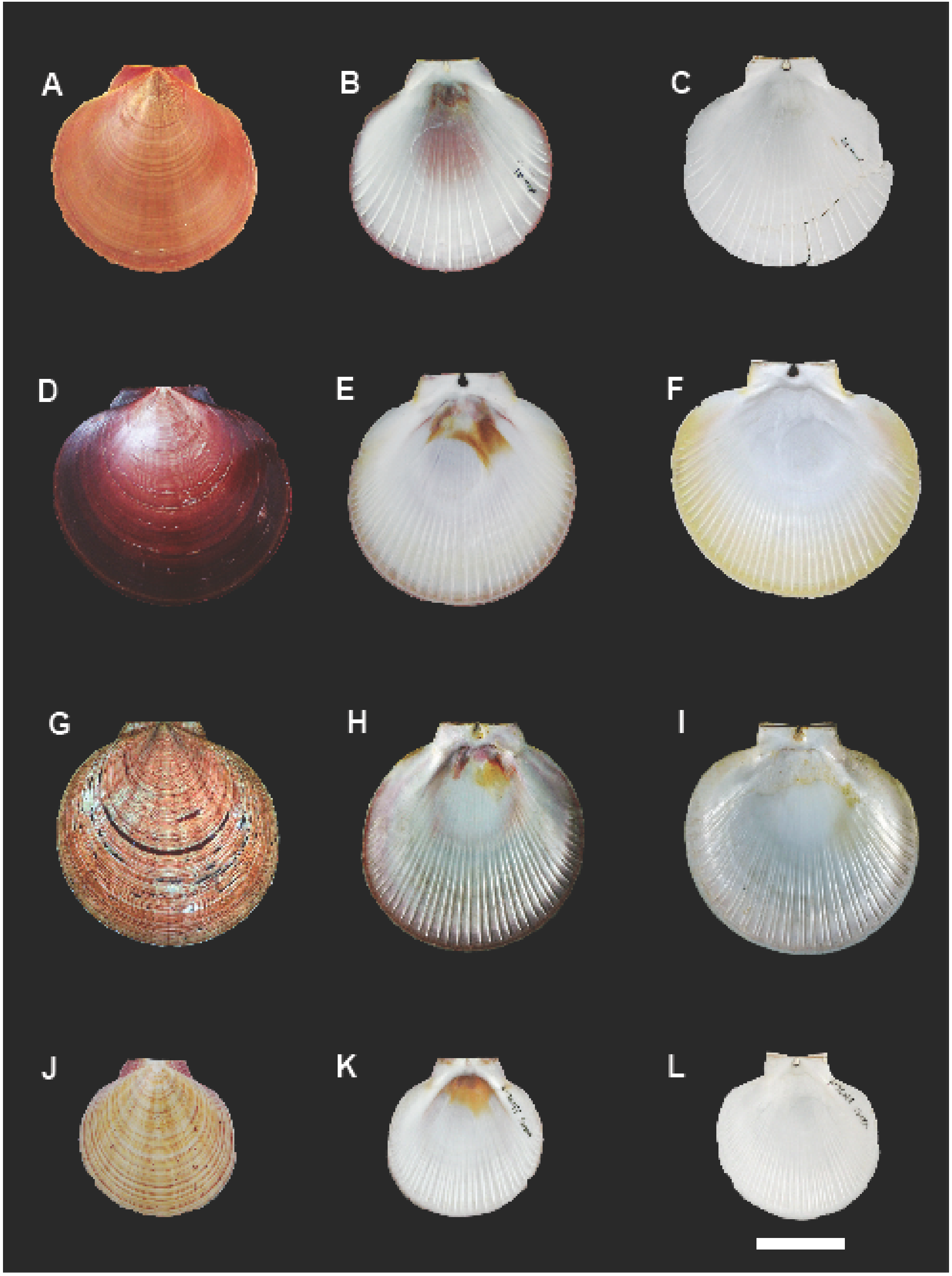


Figure 4.2 - Localities of molecular samples examined for *Amusium pleuronectes*, *Ylistrum balloti* and *Y. japonicum*.

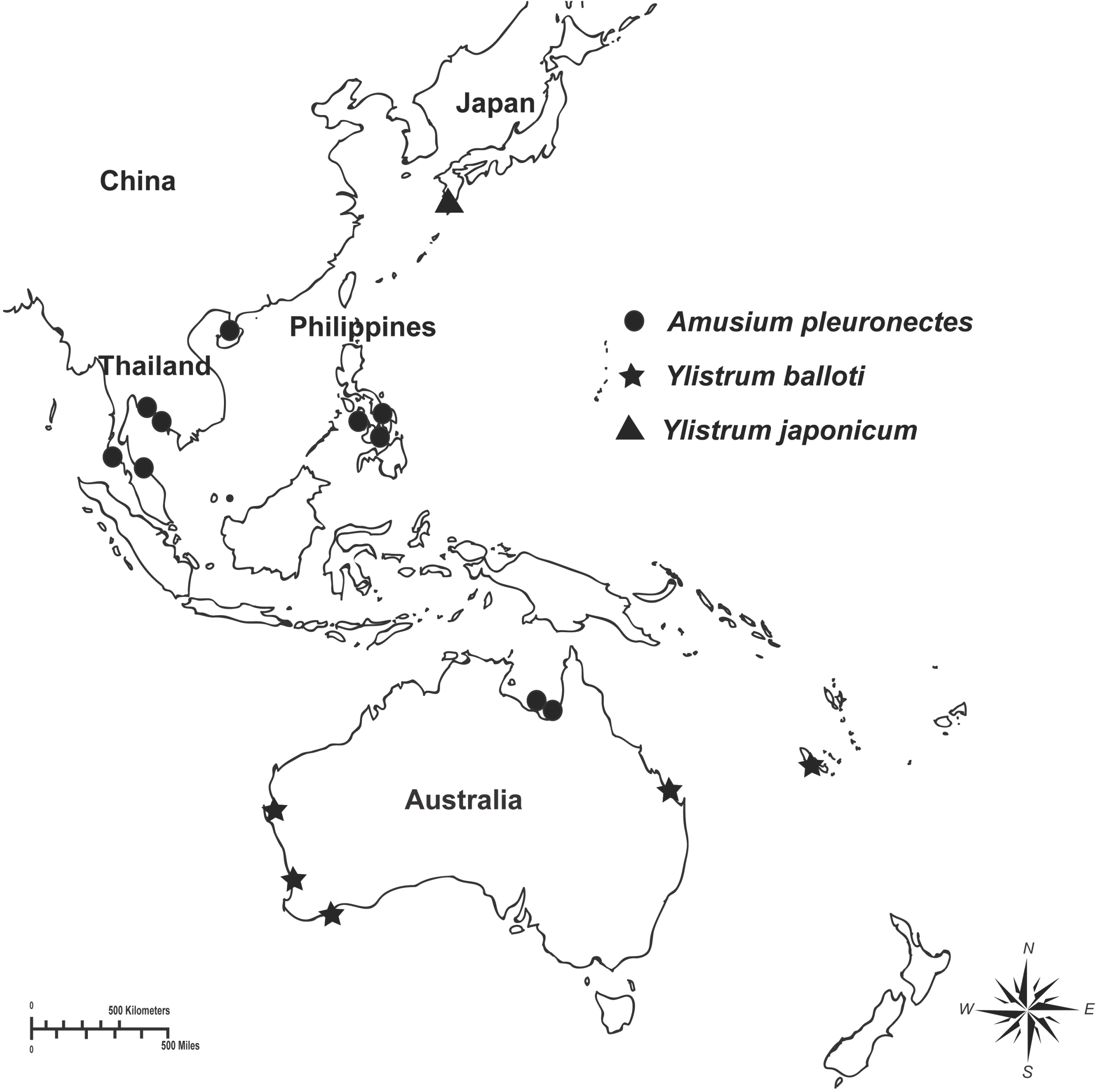


Figure 4.3 - Phylogenetic relationships of Pectinidae inferred by Bayesian inference (BI) of histone H3, 28S rRNA, 12S rRNA and 16S rRNA gene regions. Only the clade that contains gliding lineages is shown. The complete BI phylogeny is shown in Supplementary material: Appendix D. Branches with less than 50% support (posterior probabilities) were collapsed. Generic assignments are based on our revised classification. Labels for *Amusium* and *Ylistrum* specimens are as follows: source (SL, Serb Lab; GB, Genbank), unique numerical identifier, and country (AU, Australia; CN, China; JP, Japan; NC, New Caledonia; PH, Philippines; QL, Queensland, Australia; TH, Thailand; WA, Western Australia, Australia) (see Fig. 2 for map of locations).

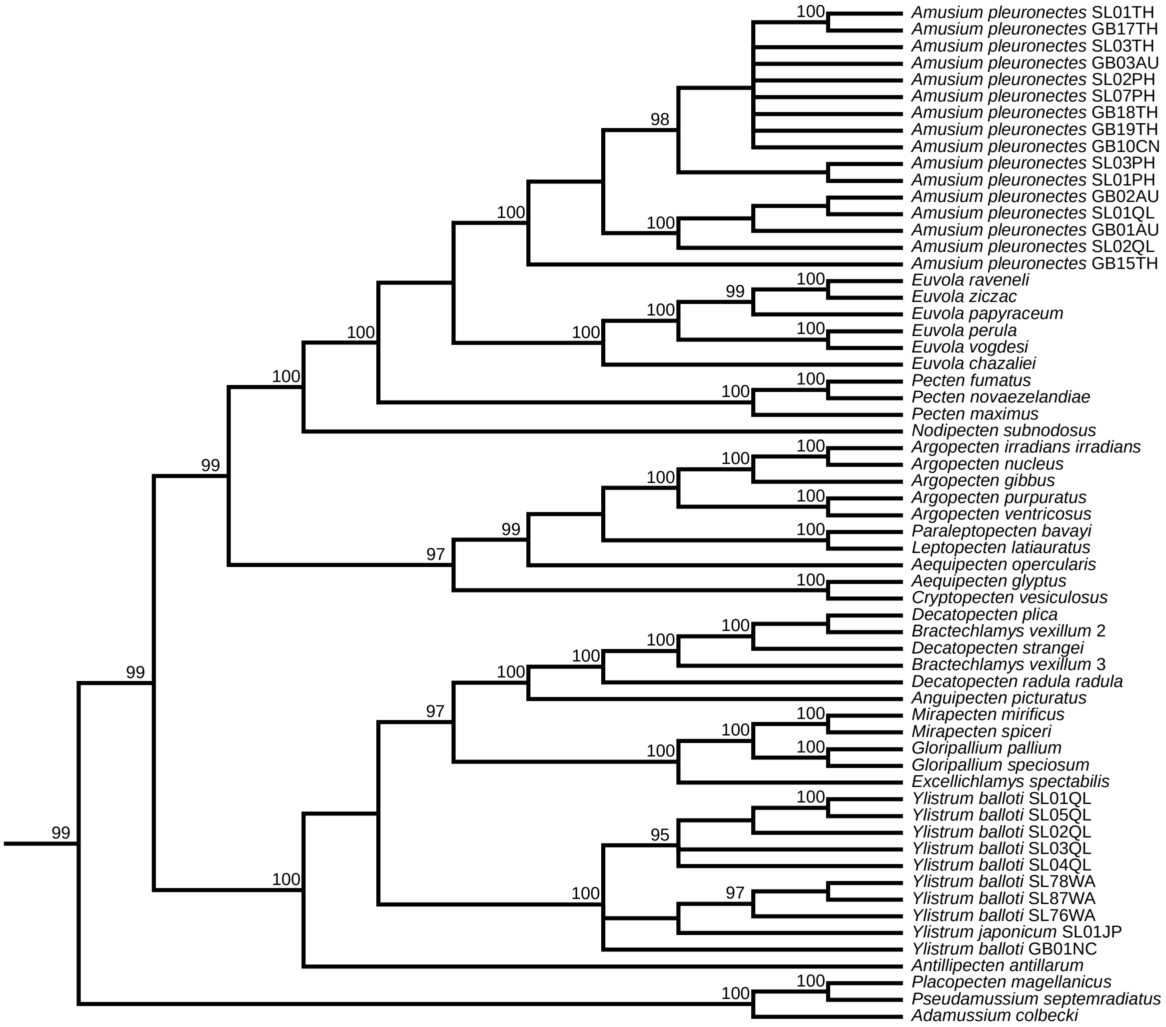


Figure 4.4 - Histograms illustrating the distribution of internal ribbing counts for left (**A**) and right valves (**B**) of specimens of *Amusium pleuronectes*, *Ylistrum balloti* and *Y. japonicum* (see Supplementary material: Appendix B for rib counts of specimens).

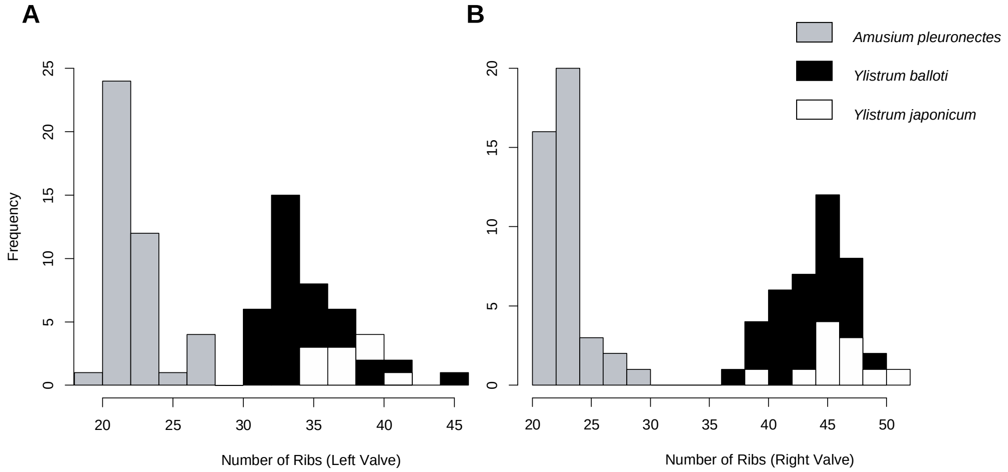
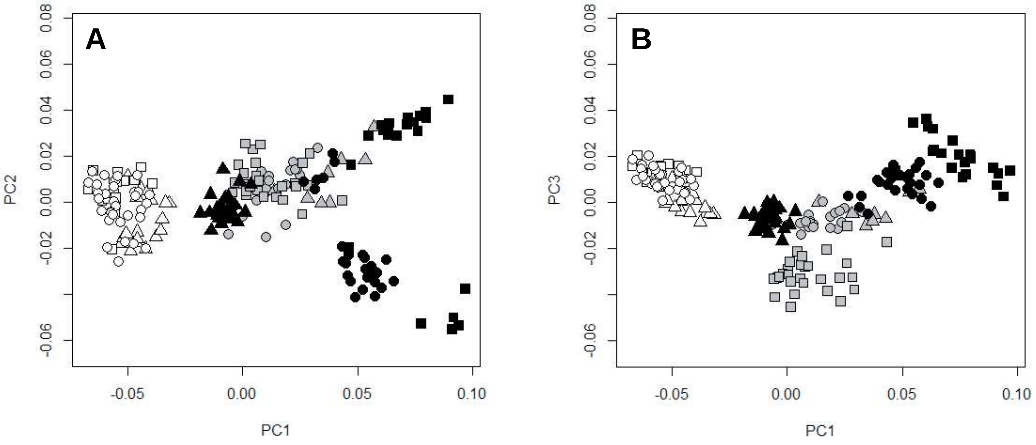


Figure 4.5 - Principal component plots of shell shape variation for the nine species used in this study. The first three principal components (PC) of shell shape variation are 62%, 11% and 8%, respectively. **A.** PC1and PC2 axes. **B.** PC1 and PC3 axes. Symbols for species: white squares, *Ylistrum japonicum*; white circles, *Y. balloti*; white triangles, *Amusium pleuronectes*; black triangles, *Pseudamussium septemradiatus*; grey circles, *Chlamys behringiana*; grey triangles, *Ch. islandica*; grey squares, *Caribachlamys sentis*; black circles, *Argopecten irradians*; black squares, *Ar. purpuratus*.



Supplementary Material 4.1 - List of specimens examined for the molecular phylogeny. Museums are represented by the following abbreviations: FLMNH = Florida Museum of Natural History, Gainesville, Florida, United States; WAM = Western Australian Museum, Perth, Australia.

Species	**Specimen Identification**	**Collection Number**	**Locality**	**12S rRNA**	**16S rRNA**	**Histone 3**	**28S rRNA**
A. pleuronectes	GB01AU	--------	Gulf of Carpentaria, Australia	JF339085.1	JF339128.1	--------	--------
A. pleuronectes	GB02AU	--------	Gulf of Carpentaria, Australia	JF339070.1	JF339129.1	--------	--------
A. pleuronectes	GB03AU	--------	Gulf of Carpentaria, Australia	JF339087.1	JF339130.1	--------	--------
A. pleuronectes	GB10CN	--------	Lingao, Hainan, China	--------	GU119962	--------	--------
A. pleuronectes	GB15TH	--------	Andaman Sea, Krabi Province, Thailand	--------	DQ640835	--------	--------
A. pleuronectes	GB17TH	--------	Gulf of Thailand, Trat Province, Thailand	--------	DQ873917	--------	--------
A. pleuronectes	GB18TH	--------	Gulf of Thailand, Naratiwas Province, Thailand	--------	DQ873918	--------	--------
A. pleuronectes	GB19TH	--------	Gulf of Thailand, Naratiwas Province, Thailand	--------	DQ873919	--------	--------
A. pleuronectes	SL01QL	QLD1	West Karumba, Queensland, Australia	HM630500	HM630501	HM630502	HM630503
A. pleuronectes	SL01PH	CPG1	Guus Island, Pres. Carlos P. Garcia, Bohol, Philippines	***KC879117***	***KC879118***	***KC879120***	***KC879119***

Species	**Specimen Identification**	**Collection Number**	**Locality**	**12S rRNA**	**16S rRNA**	**Histone 3**	**28S rRNA**
A. pleuronectes	SL01TH	1	Gulf of Thailand, Rayong Province, Thailand	EU379415	EU379469	EU379523	HM630508
A. pleuronectes	SL02QL	QLD2	West Karumba, Queensland, Australia	HM630496	HM630497	HM630498	HM630499
A. pleuronectes	SL02PH	CPG2	Guus Island, Pres. Carlos P. Garcia, Bohol, Philippines	***KC879121***	***KC879122***	***KC879124***	***KC879123***
A. pleuronectes	SL03PH	CBY3	Calbayog, Samar, Philippines	***KC879113***	***KC879114***	***KC879116***	***KC879115***
A. pleuronectes	SL03TH	3	Gulf of Thailand, Rayong Province, Thailand	HM630504	HM630505	HM630506	HM630507
A. pleuronectes	SL07PH	RXS7	Manila Market, Roxas City, Philippines	***KC879125***	***KC879126***	***KC879128***	***KC879127***
D. radula	280376	UF280376	Sulawesi Island, Indonesia	***KC879129***	HM630492	HM630493	HM630494
Y. balloti	GB01NC	--------	New Caledonia	JF339055.1	JF339127.1	--------	--------
Y. balloti	SL01QL	1	Bundaberg, Queensland, Australia	HM540088	HM540089	HM540090	HM540091
Y. balloti	SL02QL	2	Bundaberg, Queensland, Australia	EU379379	EU379433	EU379488	HM540092
Y. balloti	SL03QL	3	Bundaberg, Queensland, Australia	EU379380	EU379434	EU379489	HM540093
Y. balloti	SL04QL	4	Bundaberg, Queensland, Australia	HM540094	HM540095	HM540096	HM540097

Species	**Specimen Identification**	**Collection Number**	**Locality**	**12S rRNA**	**16S rRNA**	**Histone 3**	**28S rRNA**
Y. balloti	SL05QL	5	Bundaberg, Queensland, Australia	HM540098	HM540099	HM540100	HM540101
Y. balloti	SL76WA	WAM 33076_1	Rottnest Island, Western Australia, Australia	***KC879130***	***KC879131***	***KC879132***	--------
Y. balloti	SL78WA	WAM 33078_1	South Denham Sound, Shark Bay, Western Australia, Australia	***KC879133***	***KC879134***	***KC879135***	--------
Y. balloti	SL87WA	WAM 33087_1	Point Ann, Western Australia, Australia	***KC879136***	--------	***KC879138***	***KC879137***
Y. japonicum	SL01JP	1	Oyano Island, Kumamoto, Japan	HM622706	HM622707	HM622708	HM622709

Supplementary Material 4.2 - List of specimens examined and counts for ribbing data. DMNH = Delaware Museum of Natural History, Wilmington, Delaware, United States; MNHN = Muséum National d'Histoire Naturelle, Paris, France; WAM = Western Australian Museum, Perth, Australia.

Specimen number	**Species**	**Location**	**# Ribs (L)**	**Paired (L)**	**# Ribs (Rt)**	**Paired (Rt)**	**Life stage**
WAM 33076.2	*Y. balloti*	Rottnest Island, Western Australia, Australia	34	Yes	41	Yes	Juvenile
WAM 33076.3	*Y. balloti*	Rottnest Island, Western Australia, Australia	38	Yes	45	Yes	Juvenile
WAM 33076.4	*Y. balloti*	Rottnest Island, Western Australia, Australia	34	Yes	44	Yes	Juvenile
WAM 33077.1	*Y. balloti*	Rottnest Island, Western Australia, Australia	35	Yes	42	Yes	Juvenile
WAM 33077.2	*Y. balloti*	Rottnest Island, Western Australia, Australia	36	Yes	43	Yes	Juvenile
WAM 33077.4	*Y. balloti*	Rottnest Island, Western Australia, Australia	35	Yes	44	Yes	Juvenile
WAM 33078.2	*Y. balloti*	South Denham Sound, Shark Bay, Western Australia, Australia	30	Yes	44	Yes	Juvenile
WAM 33078.3	*Y. balloti*	South Denham Sound, Shark Bay, Western Australia, Australia	33	No	49	No	Adult
WAM 33078.4	*Y. balloti*	South Denham Sound, Shark Bay, Western Australia, Australia	34	Yes	42	Yes	Juvenile
WAM 33079.2	*Y. balloti*	South Denham Sound, Shark Bay, Western Australia, Australia	35	No	45	No	Juvenile
WAM 33079.3	*Y. balloti*	South Denham Sound, Shark Bay, Western Australia, Australia	34	Yes	46	Yes	Juvenile
WAM 33079.4	*Y. balloti*	South Denham Sound, Shark Bay, Western Australia, Australia	33	Yes	41	Yes	Juvenile
WAM 33080.3	*Y. balloti*	South Denham Sound, Shark Bay, Western Australia, Australia	37	Yes	46	Yes	Juvenile
WAM 33080.4	*Y. balloti*	South Denham Sound, Shark Bay, Western Australia, Australia	34	No	46	No	Juvenile
WAM 33081.2	*Y. balloti*	North West Peron, Shark Bay, Australia	37	No	45	Yes	Adult
WAM 33081.3	*Y. balloti*	North West Peron, Shark Bay, Australia	34	Yes	43	Yes	Juvenile
WAM 33082.2	*Y. balloti*	North West Peron, Shark Bay, Australia	35	Yes	48	Yes	Adult
WAM 33082.3	*Y. balloti*	North West Peron, Shark Bay, Australia	33	Yes	44	Yes	Juvenile
WAM 33082.4	*Y. balloti*	North West Peron, Shark Bay, Australia	32	Yes	46	Yes	Juvenile
WAM 33083.3	*Y. balloti*	Houtman Abrolhos Islands, Australia	34	Yes	41	Yes	Juvenile
WAM 33083.4	*Y. balloti*	Houtman Abrolhos Islands, Australia	32	Yes	39	Yes	Juvenile
WAM 33084.2	*Y. balloti*	Doubtful Islands, Albany, Western Australia, Australia	32	No	42	No	Adult
WAM 33084.3	*Y. balloti*	Doubtful Islands, Albany, Western Australia, Australia	33	No	39	No	Adult
WAM 33084.4	*Y. balloti*	Doubtful Islands, Albany, Western Australia, Australia	35	Yes	48	Yes	Adult
WAM 33085.2	*Y. balloti*	Quoin Head, Fitzgerald River National Park, Western Australia, Australia	32	Yes	39	No	Adult
WAM 33085.3	*Y. balloti*	Quoin Head, Fitzgerald River National Park, Western Australia, Australia	32	Yes	36	Yes	Adult
WAM 33085.4	*Y. balloti*	Quoin Head, Fitzgerald River National Park, Western Australia, Australia	34	No	45	No	Adult

Specimen number	Species	Location	# Ribs (L)	Paired (L)	# Ribs (Rt)	Paired (Rt)	Life stage
WAM 33086	*Y. balloti*	Hassell Beach, Bald Island, Western Australia, Australia	33	No	48	No	Adult
WAM 33087.2	*Y. balloti*	Point Ann, Western Australia, Australia	33	No	40	No	Adult
WAM 33087.3	*Y. balloti*	Point Ann, Western Australia, Australia	34	Yes	43	Yes	Adult
WAM 33088.2	*Y. balloti*	Point Ann, Western Australia, Australia	36	Yes	48	Yes	Adult
WAM 33088.3	*Y. balloti*	Point Ann, Western Australia, Australia	35	Yes	48	Yes	Adult
1	*Y. balloti*	Bundaberg, Queensland, Australia	38	Yes	48	Yes	Adult
2	*Y. balloti*	Bundaberg, Queensland, Australia	37	No	48	No	Juvenile
3	*Y. balloti*	Bundaberg, Queensland, Australia	37	No	46	No	Juvenile
4	*Y. balloti*	Bundaberg, Queensland, Australia	40	No	46	Yes	Juvenile
5	*Y. balloti*	Bundaberg, Queensland, Australia	45	Yes	50	Yes	Juvenile
MNHN21185	*Y. balloti*	New Caledonia	42	Yes	48	Yes	Adult
MNHN21185	*Y. balloti*	New Caledonia	41	Yes	46	Yes	Adult
MNHN21185	*Y. balloti*	New Caledonia	39	No	45	No	Adult
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	23	No	24	No	Juvenile
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	21	No	22	Yes	Juvenile
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	23	Yes	23	Yes	Juvenile
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	27	Yes	25	Yes	Juvenile
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	24	Yes	24	Yes	Juvenile
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	27	Yes	27	Yes	Juvenile
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	22	No	21	Yes	Juvenile
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	22	No	24	Yes	Juvenile
	A. pleuronectes	Ban Phe, Rayong Province, Thailand	25	Yes	25	Yes	Juvenile
QLD1	*A. pleuronectes*	West Karumba, Queensland, Australia	23	No	22	Yes	Juvenile
QLD2	*A. pleuronectes*	West Karumba, Queensland, Australia	22	No	22	Yes	Juvenile
	A. pleuronectes	West Karumba, Queensland, Australia	23	No	22	Yes	Juvenile
	A. pleuronectes	West Karumba, Queensland, Australia	22	No	24	Yes	Juvenile
	A. pleuronectes	West Karumba, Queensland, Australia	22	No	24	Yes	Juvenile
	A. pleuronectes	West Karumba, Queensland, Australia	22	No	25	Yes	Juvenile
	A. pleuronectes	Mornington Island, Queensland, Australia	23	No	24	Yes	Juvenile
	A. pleuronectes	Mornington Island, Queensland, Australia	22	No	24	Yes	Juvenile
	A. pleuronectes	Mornington Island, Queensland, Australia	22	No	24	Yes	Juvenile

Specimen number	Species	Location	# Ribs (L)	Paired (L)	# Ribs (Rt)	Paired (Rt)	Life stage
	A. pleuronectes	Mornington Island, Queensland, Australia	23	No	24	Yes	Juvenile
	A. pleuronectes	Mornington Island, Queensland, Australia	21	Yes	23	Yes	Juvenile
	A. pleuronectes	Mornington Island, Queensland, Australia	24	No	24	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	23	No	23	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	21	No	22	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	23	No	23	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	22	Yes	Adult
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	23	No	22	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	22	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	23	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	23	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	21	Yes	20	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	19	No	20	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	23	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	23	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	21	No	22	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	23	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	22	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	21	No	22	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	No	22	Yes	Juvenile
	A. pleuronectes	Groote Eylandt, Northern Territory, Australia	22	Yes	23	Yes	Juvenile
CPG	*A. pleuronectes*	Guus Island, Pres. Carlos P. Garcia, Bohol, Philippines	27	No	22	Yes	Juvenile
RXS	*A. pleuronectes*	Roxas City, Capiz, Philippines	24	No	28	Yes	Adult
CBY	*A. pleuronectes*	Calbayog City, Samar, Philippines	27	No	30	Yes	Juvenile
DMNH013078	*Y. j. japonicum*	Japan	38	No	51	Yes	n/a
DMNH013078	*Y. j. japonicum*	Japan	36	No	50	Yes	n/a
DMNH013078	*Y. j. taiwanense*	Japan	35	Yes	39	Yes	n/a
DMNH013078	*Y. j. taiwanense*	Japan	40	Yes	45	Yes	n/a
DMNH020698	*Y. j. japonicum*	Kiushiu, Awa, Kagoshima, Japan	38	No	48	Yes	n/a
DMNH042249	*Y. j. japonicum*	West Kyushu Island, Japan	41	Yes	47	Yes	n/a

Specimen number	Species	Location	# Ribs (L)	Paired (L)	# Ribs (Rt)	Paired (Rt)	Life stage
DMNH111140	*Y. j. japonicum*	Kyushu, Japan	39	Yes	46	Yes	n/a
DMNH111140	*Y. j. japonicum*	Kyushu, Japan	39	Yes	47	Yes	n/a
DMNH155970	*Y. j. japonicum*	Bay of Tosa, Japan	36	No	45	No	n/a
DMNH229009	*Y. j. taiwanense*	Aberdeen Bay, Hong Kong, China	40	Yes	45	Yes	n/a
	Y. j. japonicum	Oyano Island, Kumamoto, Japan	37	No	43	No	Juvenile

Supplementary Material 4.3 - List of specimens examined in the geometric morphometric analysis. Museums are represented by the following abbreviations: DMNH = Delaware Museum of Natural History, Wilmington, Delaware, United States; LACM = Natural History Museum of Los Angeles County, Los Angeles, California, United States; FLMNH = Florida Museum of Natural History, Gainesville, Florida, United States; USNM = National Museum of Natural History, Washington D.C., United States; WAM = Western Australian Museum, Perth, Australia; YPM = Yale Peabody Museum of Natural History, New Haven, Connecticut, United States.

Species	**Specimen identification**	**Collection number**	**Locality**
Y. balloti	ball01L	WAM 33084.3	Doubtful Islands, Albany, Western Australia, Australia
Y. balloti	ball02L	WAM 33085.3	Quoin Head, Fitzgerald River National Park, Western Australia, Australia
Y. balloti	ball03L	WAM 33084.2	Doubtful Islands, Albany, Western Australia, Australia
Y. balloti	ball04L	WAM 33087.2	Point Ann, Western Australia, Australia
Y. balloti	ball05L	WAM 33088.2	Point Ann, Western Australia, Australia
Y. balloti	ball06L	WAM 33087.3	Point Ann, Western Australia, Australia
Y. balloti	ball07L	WAM 33086	Hassell Beach, Bald Island, Western Australia, Australia
Y. balloti	ball08L	WAM 33085.4	Quoin Head, Fitzgerald River National Park, Western Australia, Australia
Y. balloti	ball09L	WAM 33084.4	Doubtful Islands, Albany, Western Australia, Australia
Y. balloti	ball10L	WAM 33088.3	Point Ann, Western Australia, Australia
Y. balloti	ball11L	WAM 33085.2	Quoin Head, Fitzgerald River National Park, Western Australia, Australia
Y. balloti	ball12L	WAM 33081.2	North West Peron, Shark Bay, Australia
Y. balloti	ball13L	WAM	North West Peron, Shark Bay, Australia

Species	Specimen identification	Collection number	Locality
		33081.3	
Y. balloti	ball14L	WAM 33078.3	South Denham Sound, Shark Bay, Western Australia, Australia
Y. balloti	ball15L	WAM 33082.2	North West Peron, Shark Bay, Australia
Y. balloti	ball16L	WAM 33078.4	South Denham Sound, Shark Bay, Western Australia, Australia
Y. balloti	ball17L	WAM 33082.4	North West Peron, Shark Bay, Australia
Y. balloti	ball18L	WAM 33082.3	North West Peron, Shark Bay, Australia
Y. balloti	ball19L	WAM 33080.4	South Denham Sound, Shark Bay, Western Australia, Australia
Y. balloti	ball20L	WAM 33079.3	South Denham Sound, Shark Bay, Western Australia, Australia
Y. balloti	ball21L	WAM 33077.2	Rottnest Island, Western Australia, Australia
Y. balloti	ball22L	WAM 33077.1	Rottnest Island, Western Australia, Australia
Y. balloti	ball23L	WAM 33076.3	Rottnest Island, Western Australia, Australia
Y. balloti	ball24L	WAM 33080.3	South Denham Sound, Shark Bay, Western Australia, Australia
Y. balloti	ball25L	WAM 33079.2	South Denham Sound, Shark Bay, Western Australia, Australia
Y. balloti	ball26L	WAM 33076.2	Rottnest Island, Western Australia, Australia
Y. balloti	ball27L	WAM 33078.2	South Denham Sound, Shark Bay, Western Australia, Australia
Y. balloti	ball28L	WAM	Rottnest Island, Western Australia, Australia

Species	Specimen identification	Collection number	Locality
		33077.4	
Y. balloti	ball29L	WAM 33076.4	Rottnest Island, Western Australia, Australia
Y. balloti	ball30L	WAM 33079.4	South Denham Sound, Shark Bay, Western Australia, Australia
Y. balloti	ball31L	WAM 33083.3	Houtman Abrolhos Islands, Australia
Y. balloti	ball32L	WAM 33083.4	Houtman Abrolhos Islands, Australia
Ch. behringiana	behr01	1	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr02	2	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr03	3	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr04	4	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr05	5	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr06	6	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr07	7	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr08	8	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr09	9	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr10	10	Monti Bay, Yakutat, Alaska, United States
Ch.	behr11	11	Monti Bay, Yakutat, Alaska, United States

Species	Specimen identification	Collection number	Locality
behringiana			
Ch. behringiana	behr12	12	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr13	13	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr14	14	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr15	15	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr16	16	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr17	17	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr18	18	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr19	19	Monti Bay, Yakutat, Alaska, United States
Ch. behringiana	behr20	20	Monti Bay, Yakutat, Alaska, United States
Ar. irradians	irra01	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra02	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra03	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra04	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra05	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra06	DMNH	Wellfleet Harbor, Massachusetts, United States

Species	Specimen identification	Collection number	Locality
		40205	
Ar. irradians	irra07	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra08	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra09	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra10	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra11	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra12	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra13	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra14	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra15	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra16	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra17	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra18	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra19	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra20	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra21	DMNH	Wellfleet Harbor, Massachusetts, United States

Species	Specimen identification	Collection number	Locality
		40205	
Ar. irradians	irra22	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra23	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra24	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra25	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra26	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ar. irradians	irra27	DMNH 40205	Wellfleet Harbor, Massachusetts, United States
Ch. islandica	isla01	YPM 7448	Newfoundland
Ch. islandica	isla02	LACM 167522	Iceland
Ch. islandica	isla03	LACM 167521	Newfoundland
Ch. islandica	isla04	LACM 167522	Iceland
Ch. islandica	isla05	LACM 177789	Newfoundland
Ch. islandica	isla06	LACM 118060	Massachusettes
Ch. islandica	isla07	LACM 177790	Iceland
Ch. islandica	isla08	LACM 177788	Iceland
Y. japonicum	japo17	USNM818253	Honshu Island, Japan

Species	Specimen identification	Collection number	Locality
Y. japonicum	japo18	USNM753705	Kyushu Island, Japan
Y. japonicum	japo19	USNM753705	Kyushu Island, Japan
Y. japonicum	japo20	USNM763645	Honshu Island, Japan
Y. japonicum	japo21	USNM763645	Honshu Island, Japan
Y. japonicum	japo22	USNM229069	Kyushu Island, Japan
Y. japonicum	japo23	USNM229069	Kyushu Island, Japan
Y. japonicum	japo24	USNM229069	Kyushu Island, Japan
Y. japonicum	japo25	USNM229069	Kyushu Island, Japan
Y. japonicum	japo26	USNM229069	Kyushu Island, Japan
Y. japonicum	japo27	USNM229068	Kyushu Island, Japan
Y. japonicum	japo28	USNM229068	Kyushu Island, Japan
Y. japonicum	japo29	USNM333959	Fuzhou, China
Y. japonicum	japo30	USNM229070	Honshu Island, Japan
Y. japonicum	japo31	USNM343967	Kyushu Island, Japan
Y. japonicum	japo32	USNM343967	Kyushu Island, Japan

Species	**Specimen identification**	**Collection number**	**Locality**
Y. japonicum	japo33	USNM304217	Honshu Island, Japan
Y. japonicum	japo34	USNM304217	Honshu Island, Japan
Y. japonicum	japo35	USNM023947	Honshu Island, Japan
Y. japonicum	japo36	USNM023947	Honshu Island, Japan
A. pleuronectes	pleu01	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu02	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu03	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu04	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu05	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu06	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu07	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu08	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu09	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu10	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu11	USNM254931	Borneo Island, Malaysia

Species	Specimen identification	Collection number	Locality
A. pleuronectes	pleu12	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu13	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu14	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu15	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu16	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu17	USNM254931	Borneo Island, Malaysia
A. pleuronectes	pleu18	USNM254931	Borneo Island, Malaysia
Ar. purpuratus	purp02	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp03	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp04	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp05	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp06	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp07	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp08	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp10	UF337447	Paracas Bay, Peru

Species	**Specimen identification**	**Collection number**	**Locality**
Ar. purpuratus	purp11	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp12	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp13	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp14	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp15	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp16	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp17	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp18	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp19	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp20	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp21	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp22	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp23	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp24	UF337447	Paracas Bay, Peru
Ar. purpuratus	purp25	UF337447	Paracas Bay, Peru
Ca. sentis	sent01	UF374737	Biscayne Bay, Florida

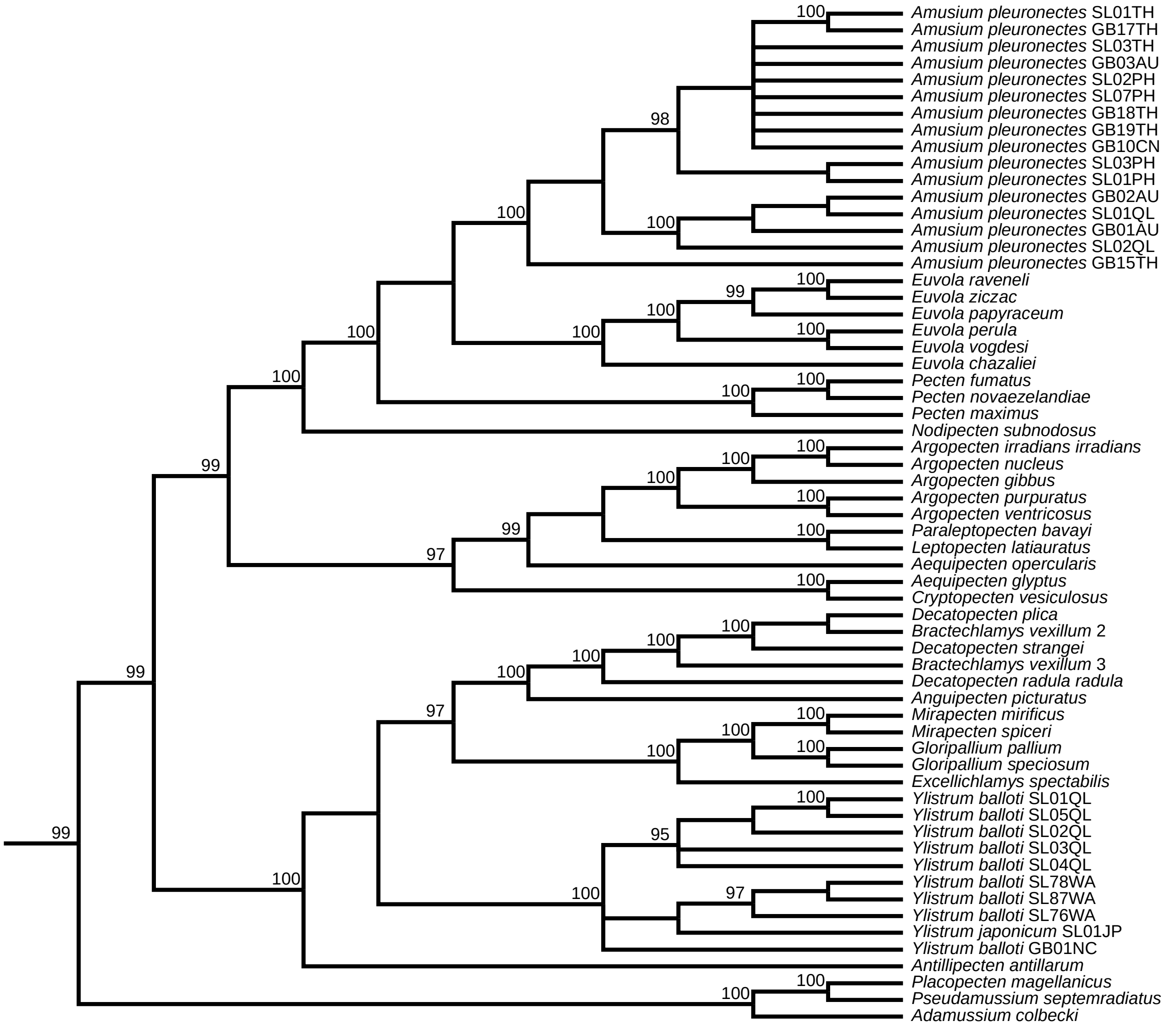
Species	**Specimen identification**	**Collection number**	**Locality**
Ca. sentis	sent02	UF374737	Biscayne Bay, Florida
Ca. sentis	sent03	UF374737	Biscayne Bay, Florida
Ca. sentis	sent04	UF374737	Biscayne Bay, Florida
Ca. sentis	sent05	UF374737	Biscayne Bay, Florida
Ca. sentis	sent06	UF374737	Biscayne Bay, Florida
Ca. sentis	sent07	UF374737	Biscayne Bay, Florida
Ca. sentis	sent08	UF374737	Biscayne Bay, Florida
Ca. sentis	sent09	UF374737	Biscayne Bay, Florida
Ca. sentis	sent10	UF374737	Biscayne Bay, Florida
Ca. sentis	sent11	UF374737	Biscayne Bay, Florida
Ca. sentis	sent12	UF374737	Biscayne Bay, Florida
Ca. sentis	sent13	UF374737	Biscayne Bay, Florida
Ca. sentis	sent14	UF374737	Biscayne Bay, Florida
Ca. sentis	sent15	UF374737	Biscayne Bay, Florida
Ca. sentis	sent16	UF374737	Biscayne Bay, Florida
Ca. sentis	sent17	UF374737	Biscayne Bay, Florida
Ca. sentis	sent18	UF374737	Biscayne Bay, Florida
Ca. sentis	sent19	UF374737	Biscayne Bay, Florida
Ca. sentis	sent20	UF374737	Biscayne Bay, Florida
Ca. sentis	sent21	UF374737	Biscayne Bay, Florida
Ca. sentis	sent22	UF374737	Biscayne Bay, Florida
Ca. sentis	sent23	UF374737	Biscayne Bay, Florida
Ca. sentis	sent24	UF374737	Biscayne Bay, Florida
Ca. sentis	sent25	UF374737	Biscayne Bay, Florida
Ca. sentis	sent26	UF374737	Biscayne Bay, Florida
Ca. sentis	sent27	UF374737	Biscayne Bay, Florida

Species	Specimen identification	Collection number	Locality
Ca. sentis	sent28	UF374737	Biscayne Bay, Florida
P. septemradiatus	sept01	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept02	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept03	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept04	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept05	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept06	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept07	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept08	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept09	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept10	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept11	USNM 62645	Loch Fyne, Scotland

Species	**Specimen identification**	**Collection number**	**Locality**
P. septemradiatus	sept12	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept13	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept14	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept15	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept16	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept17	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept18	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept19	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept20	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept21	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept22	USNM 62645	Loch Fyne, Scotland

Species	**Specimen identification**	**Collection number**	**Locality**
P. septemradiatus	sept23	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept24	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept25	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept26	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept27	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept28	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept29	USNM 62645	Loch Fyne, Scotland
P. septemradiatus	sept30	USNM 62645	Loch Fyne, Scotland

Supplementary Material 4.4 - Molecular phylogeny of the Pectinidae generated by Bayesian inference of a four-gene dataset comprised of Histone H3, 28S rRNA, 12S rRNA, and 16S rRNA DNA sequences. Dashed box highlights the clade that contains gliding lineages (Fig. 3). Posterior probabilities >50 are shown at the nodes. Generic assignments are based on our revised classification. Data source, unique identifier, and country of origin for *Amusium* and *Ylistrum* specimens are as follows: SLC = Serb Lab; GB = Genbank; AU = Australia; CN = China; JP = Japan; NC = New Caledonia; PH = Philippines; QL = Queensland, Australia; TH = Thailand; WA = Western Australia, Australia (see Fig. 2 for map of locations).



Supplementary Material 4.5 - Descriptive statistics of *Amusium pleuronectes*, *Ylistrum balloti*, and *Ylistrum japonicum* shell ribbing for left and right valves.

Species		**Left valve**	**Right valve**
A. pleuronectes (n=42)	Mean	23	23
	Range	19-27	20-30
	St. dev.	1.69	1.87
Y. balloti (n=40)	Mean	35	44
	Range	30-45	36-50
	St. dev.	3.05	3.25
Y. japonicum (n=11)	Mean	38	46
	Range	35-41	39-51
	St. dev.	1.92	3.29

CHAPTER 5. SUMMARY AND CONCLUSIONS

In this dissertation work, I investigated the evolution of life habits and shell shape of scallops. I have found repeated evolutionary patterns of life habits and shell shapes, and I have uncovered hidden taxonomic diversity in a lineage of scallops that was masked by convergent evolution of shell shape. Comparing my work to current classification systems for the Pectinidae (Raines & Poppe 2006, Waller 2006, Dijkstra 2014), it is evident that schemes largely based on morphological data do not take convergence into account. Failing to recognize convergence can lead to a false assumption that species with similar morphologies are closely related (Wiens et al 2003). My dissertation study demonstrates a need to revise current classification systems by incorporating molecular data. Currently, I am expanding the taxonomic and genetic sampling of scallops in an attempt to unify all existing phylogenetic hypotheses for scallops, from species to Superfamily Pectinoidea.

Scallops exhibit a diverse array of life habits, including byssal attaching, nestling, cementing, free-living, recessing, and gliding. However, the evolutionary patterns of these traits are unknown among scallops, which limits our understanding of how such phenotypic diversity evolved. In Chapter 2, I reconstructed the scallop phylogeny to provide the basis for comparative studies carried throughout the dissertation. To do this, I amplified 12S ribosomal RNA, 16S ribosomal RNA, 28S ribosomal RNA, and the histone H3 protein-coding gene to reconstruct the scallop phylogeny employing Maximum Likelihood and Bayesian Inference methods. I then mapped the scallop life habits on the phylogeny and reconstructed the life habits at the nodes to identify the evolutionary trajectory from ancestors to descendants. With the exception of the nestling life habit, which evolved once in scallops, the other life habits arose multiple times, independently through both convergent and parallel patterns. The results of this study provide a foundation to investigate the evolutionary processes that generate biological diversity.

A study by Stanley (1970) indicated that the diversity of bivalve shell shapes could be limited by life habits. If this were accurate, then we would expect shell shapes to follow similar convergent patterns as life habits. In Chapter 3, I quantified shell shapes of scallops to investigate the patterns of shape diversity and evolution within the family. I used a three-dimensional scanner to capture images of the left valves of scallops. Then I digitized the images using fixed landmarks, sliding edge and sliding surface semi-landmarks for shape analyses. I statistically compared the shell shapes based on life habit categories to determine the degree of disparity among and within each life habit. I also used the phylogeny to reconstruct ancestral shell shapes at the node to trace the evolutionary trajectory of shell shape. I found that a reduction in auricles is the best evidence of shell shape convergence between the two groups of gliding scallops with respect to other life habit groups. Remarkably, they diverged with respect to shell surface curvature suggesting two shape optima for the gliding life habit. These results show that some characters of shell shape (reduced auricles) may be important for the gliding life habit while others (degree of shell curvature) are not.

The reconstructed phylogeny from Chapter 2 indicates that the gliding genus *Amusium* is polyphyletic, and the study in chapter 3 shows the shell shapes are convergent. To investigate the taxonomic classification of *Amusium*, I gathered additional data to describe a new genus of scallops, *Ylistrum*, separating the polyphyletic *Amusium* genus. In Chapter 4, I analyzed the 16S rRNA gene sequences of multiple individuals of the three species historically classified in the *Amusium* genus to assess genetic similarity and phylogenetic grouping. I also used landmark-based geometric morphometrics to statistically compare quantitative shell shapes between the three species. Lastly, I tested whether *Ylistrum* could be differentiated from *Amusium* based on the number of internal ribs, which is a trait previously used for classification of *Amusium* species. I found that *Ylistrum* is genetically distinct from *Amusium* according to the 16S rRNA gene. Both genera form separate monophyletic clades that are distantly related to one another. While molecular data suggests separate taxonomic groups, shell shapes indicate similarities, supporting the convergent evolution found in Chapter 3. In contrast, internal ribbing number was found to be a useful trait in determining taxonomic grouping as *Ylistrum* species have a greater number of internal ribs than *Amusium*. Through this study, I have uncovered taxonomic diversity masked by morphological convergence, highlighting the importance of molecular and other phenotypic traits for use in taxonomic classifications.

This study provides some support for the ubiquity of repeated evolution, which is important in understanding common selection pressures in similar environments. However, evolutionary predictability is more elusive as the link between form and function may not be strong, possibly due to genetic or developmental constraints. Lastly, this dissertation work emphasizes the need for all types of data including molecular, morphological, and behavioral data to accurately assess taxonomic classifications of taxa. Although repeated phenotypic traits can provide insight on evolutionary trajectories, they can also hide taxonomic diversity that underestimate biodiversity.

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