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Morphological convergence of shell shape in distantly related scallop species (Mollusca: Pectinidae)

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Morphological convergence is a central concept in evolutionary biology, but convergent patterns remain understudied in nonvertebrate organisms. Some scallop species exhibit long-distance swimming, a behaviour whose biomechanical requirements probably generate similar selective regimes. We tested the hypothesis that shell shape similarity in long-distance swimming species is a result of convergent evolution. Using landmark-based geometric morphometrics, we quantified shell shape in seven species representing major behavioural habits. All species displayed distinct shell shapes, with the exception of the two long-distance swimmers, whose shells were indistinguishable. These species also displayed reduced morphological variance relative to other taxa. Finally, a phylogenetic simulation revealed that these species were more similar in their shell shape than was expected under Brownian motion, the model of character evolution that best described changes in shell shape. Together, these findings reveal that convergent evolution of shell shape occurs in scallops, and suggest that selection for shell shape and behaviour may be important in the diversification of the group.

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ADDITIONAL KEYWORDS: adaptation – convergent evolution – geometric morphometrics – mollusc.

One of the most compelling patterns observed in evolutionary biology is that of morphological and behavioural convergence amongst species inhabiting similar environments at different geographical locations. Evolutionary convergence frequently occurs when environmental factors exert strong selection pressures on the taxa in those environments, generating similar phenotypic responses amongst them (Losos, 1992; Losos *et al*., 1998; Rüber, Verheyen & Meyer, 1999; Rüber & Adams, 2001; Melville, Harmon & Losos, 2006; Stayton, 2006). Convergence can also occur from functional or biomechanical requirements, when species exploit a common trophic niche and respond evolutionarily to those selective constraints (Herrel *et al*., 2008; Vincent *et al*., 2009). Patterns of convergent evolution provide strong evidence of a link between the selective forces shaping trait evolution and the evolutionary responses to those forces. As a consequence, convergent evolution has long been treated as evidence of adaptation (e.g. Pagel, 1994; Schluter, 2000; Blackledge & Gillespie, 2004; Harmon *et al*., 2005), and the instances of convergent evolution seen in nature demonstrate that in at least some circumstances, common selective pressures can generate repeated and predictable evolutionary responses (Losos *et al*., 1998).

A conspicuous feature in bivalve evolution is the broad diversity of behaviour and shell shape exhibited throughout the group (Kauffman, 1969; Stanley, 1970, 1975, 1988; Seed, 1980; Savazzi, 1982). Bivalves are found in a wide range of freshwater and marine habitats and often display particular behaviours associated with their ecological niche (Stanley, 1970,

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1972). Species from phylogenetically disparate families frequently occupy common environments and display behavioural habits that are alike (e.g. Stanley, 1970: fig. 6). These similar phenotypes demonstrate that distinct behaviours have evolved multiple times in bivalves, suggesting the possibility of adaptive evolution (Stanley, 1970, 1975). In addition, species occupying similar niches sometimes exhibit similarity in particular morphological elements of their shells (e.g. Trueman, Brand & Davis, 1966; Stanley, 1981; Watters, 1994; Checa & Jimènez-Jimènez, 2003), indicating that shell shape may be convergent as well (Kauffman, 1969; Stanley, 1970). However, these anatomical observations are largely qualitative and descriptive; a quantitative test of the hypothesis of morphological convergence has not been performed.

Bivalved scallops of the family Pectinidae Rafinesque, 1815 are a good system to examine convergent evolution, as several species exhibit long-distance swimming via jet propulsion (Gould, 1971; Morton, 1980; Joll, 1989; Ansell, Cattaneo-Vietti & Chiantore, 1998). Although all nonpermanently attached scallop species have the ability to swim for short distances (< 1 m) to escape predators or seek more favourable surroundings, few species can swim greater than 5 m in a single swimming effort (Brand, 2006). Long-distance swimming (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 (Morton, 1980; Joll, 1989; Ansell, Cattaneo-Vietti & Chiantore, 1998). This swimming phase also contains a glide component, where the animal is propelled forward while the valves are held closed (Manuel & Dadswell, 1993; Chang, Davison & Demont, 1996; Ansell *et al*., 1998). Neither a level swimming phase nor a glide component is present in short distance swimming (Marsh, Olson & Guzik, 1992; Ansell *et al*., 1998; Donovan *et al*., 2002), making this a unique behaviour in scallops. Interestingly, long-distance swimming has evolved multiple times in the Pectinidae (Puslednik & Serb, 2008 and below). In addition, long-distance swimming scallops possess shells that are qualitatively similar in overall shape (Stanley, 1970; Hayami, 1991; Millward & Whyte, 1992), suggesting the possibility of repeated coevolution between this unique behaviour and the morphological attributes that may contribute to it. This observation further suggests that long-distance swimmers have evolved a single anatomical solution to a common ecological problem.

One effective way to test convergent evolution and morphological constraint is to quantitatively examine morphological variation in multivariate morphospace (e.g. Stayton, 2006; Revell *et al*., 2007). In instances where there is a tight correlation between shell shape and functional performance, the morphology of that organism is predicted to be under strong selection, resulting in a narrow area of morphospace being occupied by that behavioural group. Alternative morphologies exhibited by members of that behavioural group that fall outside of the optimal region will have lower performance as compared to individuals exhibiting more ‘typical’ morphology. Based on such functional considerations, we can predict that phylogenetically distant species with similar performance or functional needs will converge on the same region of morphospace (Vincent *et al*., 2009). For scallops, if effective long-distance swimming requires a specific shell shape, we predict that species exhibiting this behaviour will be morphologically constrained because of the functional demands of this behaviour. In this study, we use three-dimensional (3D) landmark-based geometric morphometric methods to quantify shell shape for the first time, and to compare patterns of variation in shell shape within and amongst taxa. We examined shells of seven species of scallops representing a wide shape range to address the following hypotheses:

1. If long-distance swimmers are convergent in shell shape, we predict that they will occupy the same area in morphospace.
2. When phylogeny is taken into consideration, we predict that long-distance swimmers will be more similar in shell shape to each other than they are to species not displaying this behaviour, such as epifaunal free-living and byssal attaching species.
3. We predict that morphological disparity (multivariate variation) in long-distance swimmers will be less than the disparity observed in species not exhibiting this behaviour.

We examined these hypotheses by first identifying multiple origins for the long-distance swimming behaviour through the estimation of ancestral states on a molecular phylogeny. We then evaluated shell shape morphology for selected taxa that display a range of behavioural habits, and assessed patterns of shell shape within and amongst species. Finally, we determined whether long-distance swimmers exhibited patterns consistent with the hypothesis of morphological convergence, and evaluated this hypothesis using both nonphylogenetic and phylogenetically informed approaches.

MATERIAL AND METHODS

Ancestral state reconstruction

To determine phylogenetic relationships amongst scallop species, we added two new species [*Carib-*

achlamys sentis (Reeve, 1853) and *Chlamys behringiana* (Middendorff, 1849)] to a published multigene data set from Puslednik & Serb (2008) for a total of 42 scallop and nine outgroup species. The dataset of one nuclear (Histone H3) gene and two mitochondrial (12S and 16S rRNAs) genes was analysed using Bayesian inference (BI) in MRBAYES v.3.1.2 (Huelsenbeck & Ronquist, 2001). Bayesian parameters, gene partitions, a list of taxa examined, and GenBank accession numbers are provided in Puslednik & Serb (2008). Gene sequences for *Ca. sentis* and *Ch. behringiana* are available in GenBank (*Ca. sentis*: GU953232–GU953234; *Ch. behringiana*: FJ263632, FJ263661, FJ263641).

We used the BI topology for ancestral state reconstruction. Behavioural habits of extant species were determined from the literature and were organized into five behavioural habit classes. Brief definitions of behavioural habits are described in Table 1. A character matrix was constructed using standard categorical data (0, unknown behaviour; 1, cementing; 2, byssal attaching; 3, free-living; 4, recessing; 5, long-distance swimming). We then estimated ancestral states on the Bayesian topology using likelihood methods in MESQUITE 2.6 (Maddison & Maddison, 2009), which generate ancestral conditions that maximize the probability that the observed states would evolve under a stochastic model of evolution (Schluter *et al*., 1997; Pagel, 1999). The one parameter Markov k-state (Mk1) model was applied in the likelihood analysis and assumes a single rate for all character state transitions (Lewis, 2001). Likelihood-ratio tests at respective nodes tested alternative states. Differences in log-likelihoods larger than 2.0 rejected the higher negative log-likelihood value, whereas values smaller than 2.0 provided ambiguous character-state reconstruction.

MORPHOMETRIC ANALYSIS

Of the taxa included in the phylogenetic analysis, we selected seven species that are represented in museum collections as lots that include at least 20 individuals per location for a total of 178 individuals examined (see Appendix). These species exemplify the major behavioural habits exhibited by scallops, including long-distance swimming (Table 1). Although long-distance swimming occurs in seven pectinid species, the majority (four) of these species were believed to belong to a single genus, *Amusium* Röding, 1798 (Hertlein, 1969). A recent phylogenetic analysis using molecular data by Puslednik & Serb (2008) determined that *Amusium* is not a monophyletic group but forms two distantly related clades, suggesting that long-distance swimming has evolved at least twice in the family. We sampled species from each of these two clades, represented by *Amusium pleuronectes* (Linnaeus, 1758) ($N = 18$) and '*Amusium*' *balloti* (Bernardi, 1861) ($N = 32$). Long distance swimming has been characterized in these two species by Joll (1989) and Morton (1980), respectively. Thus, our sample contained two distantly related species found in different clades that exhibited long-distance swimming. The five remaining species represent two other behavioural groups and an intermediate behaviour. *Caribachlamys sentis* ($N = 28$) and *Chlamys behringiana* ($N = 20$) are two byssal-attaching species (Valh & Clausen, 1980; Waller, 1993). Two closely related, free-living epifaunal species, *Argopecten irradians* (Dall, 1898) ($N = 27$) and *Argopecten purpuratus*

Table 1. Descriptions of predominant behavioural habits used in ancestral state reconstruction

Behavioural habit*	Description	Species in morphometric comparison
Cement	Permanently attaches to hard or heavy substratum by right valve (Waller, 1996)	
Byssal attaching	Temporarily attaches to a substratum by byssus threads; can release and reorientate (Brand, 2006)	*Chlamys behringiana* (Valh & Clausen, 1980); *Caribachlamys sentis* (Waller, 1993)
Recess	Excavates cavity in soft sediment; full/partial concealment (Sakurai & Seto, 2000; Brand, 2006)	
Free-living	Rests above soft sediment or hard substratum (Stanley, 1970)	*Argopecten irradians*; *Argopecten purpuratus* (Clark, 1965)
Long-distance swimming	Able to swim >5 m/effort; includes a level swimming phase with a glide component (Chang *et al*., 1996; Brand, 2006)	*Amusium pleuronectes* (Morton, 1980); '*Amusium*' *balloti* (Joll, 1989)

*Behaviours ordered from least to most mobile/active.
Species included in the morphometric analyses are placed in behavioural classes.

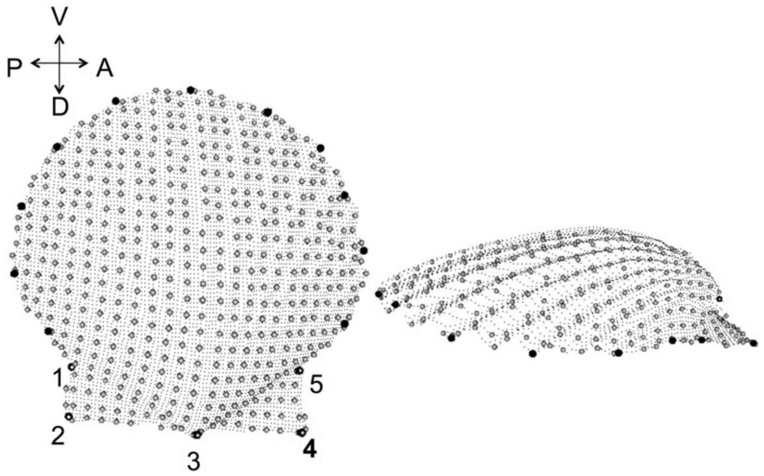

Figure 1. Three-dimensional surface scan of the left valve of a representative scallop, with the positions of 506 landmarks and semilandmarks indicated. Fixed landmarks are shown as numbered, open circles (Landmark 1: ventroposterior auricle, 2: dorsoposterior auricle, 3: umbo, 4: dorsoanterior auricle, 5: ventroanterior auricle), semilandmarks along the ventral edge of the valve are shown as closed circles, and surface semilandmarks on the scallop valve are shown as grey circles. Dorso-ventral and antero-posterior axes are provided.

(Lamarck, 1819) ($N = 23$) were also sampled (Clark, 1965; Marsh *et al*., 1992). Finally, we included a species (*Pseudamussium septemradiatus*, $N = 30$) that can be classified as 'intermediate' in its behaviour. *Pseudamussium septemradiatus* (Müller, 1776) is found on soft mud substrate and is more active than species occurring on hard substrates (i.e. byssal attachers or free-living) (Allen, 1953). Allen (1953) suggested that intermittent swimming prevents *P. septemradiatus* from sinking in the soft mud. However, there are no detailed reports describing specific components of the swimming behaviour and it is unknown if the swimming phase of *P. septemradiatus* has a glide component.

We used landmark-based geometric morphometric methods to quantify overall shell shape (Bookstein, 1991; Rohlf & Marcus, 1993; Adams, Rohlf & Slice, 2004; Zelditch *et al*., 2004). These methods quantify the shape of anatomical objects from the coordinates of homologous locations, after the effects of nonshape variation are mathematically held constant. An important advantage of this approach is that shape information from homologous anatomical structures (landmarks), as well as points along curves and points on anatomical surfaces can be included in the same analysis (points on curves and surfaces are termed semilandmarks: see Gunz, Mitteroecker & Bookstein, 2005; Mitteroecker & Gunz, 2009). Together, these provide a more complete description of shape, and thus a more rigorous quantitative comparison of the external anatomy of organisms. In this study, we used 506 three-dimensional landmarks and semilandmarks to quantify shell shape and shell surface texture. We chose to use a large number of landmarks to ensure that the textural information of the shell surface was well quantified by our procedure. First, we obtained high-resolution surface scans of the left valve of each individual using a NextEngine 3D surface scanner. We then digitized the locations of five homologous landmarks on each scan, which represented the following anatomical locations: (Landmark 1: ventroposterior auricle, 2: dorsoposterior auricle, 3: umbo, 4: dorsoanterior auricle, 5: ventroanterior auricle). Next we digitized 11 semilandmarks along the ventral edge of the valve. Finally, we quantified the general shell surface by digitizing 490 semilandmarks on the surface of each scan, following the procedure outlined in Gunz *et al*. (2005). To accomplish this we produced a mesh of 490 relatively evenly spaced surface semilandmarks on a single specimen and treated this as a template. We then used the thin-plate spline to warp the template to a second specimen, using the fixed and edge landmarks as points of correspondence between the template and the specimen. The points on the scan nearest to the 490 points on the template were then taken as the surface semilandmarks for that specimen. This was then repeated on all specimens to obtain surface semilandmarks for each (Fig. 1). We utilized this procedure to capture the general shape of the shell surface because the number of ridges per shell was not consistent amongst species or amongst specimens within a species, and as such, strict homology of these ridges could not be determined.

Once all specimens were digitized, we aligned them using a generalized Procrustes superimposition (Rohlf

& Slice, 1990). During this procedure, semilandmarks were permitted to slide along their tangent directions (Gunz *et al.*, 2005) so as to minimize Procrustes distance between specimens: one direction for semilandmarks on edges, two directions for semilandmarks on surfaces (sliding based upon minimizing bending energy yielded equivalent results). From the aligned specimens, a set of Procrustes shape coordinates were obtained, and used as shape variables in subsequent statistical analyses (e.g. Bookstein *et al.*, 1999; Mitteroecker *et al.*, 2004; Mitteroecker & Bookstein, 2008). We performed all digitizing and morphometric analyses in R 2.91 (R Development Core Team, 2009) using routines written by the authors (D. C. A. and E. O. C.).

To test the hypothesis that species differed in overall shell shape, we used nonparametric MANOVA (NP-MANOVA). NP-MANOVA was used because the number of variables (1518) greatly exceeded the number of specimens. With this approach, the Euclidean (Procrustes) distances amongst individuals in morphospace were calculated, and from these distances variation between groups was calculated and compared to variation within groups. Statistical significance was determined using 10 000 permutations (for details see Anderson, 2001). Next, to determine whether species belonging to the same behavioural groups could be distinguished on the basis of shell sculpture, we performed pairwise comparisons between species. For each pair of species we calculated the difference in average shell shape as the Euclidean distance between species means. We then evaluated 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 (for similar procedures see: Adams & Collyer, 2007, 2009; Adams, West & Collyer, 2007; Collyer & Adams, 2007). We also performed a principal components analysis (PCA) to visualize patterns of variation within and amongst species. Representative surface scans from each species were used to facilitate biological interpretation of these findings.

As shared evolutionary history can affect morphological similarity amongst species (Felsenstein, 1985) we also performed a phylogenetically informed analysis to evaluate whether the long-distance swimmers were more similar to one another in shell shape than was expected under various models of character evolution. To accomplish this, we compared the fit of shell shape to the phylogeny using a Brownian motion model and an Ornstein–Uhlenbeck (OU) model. As the OU model did not provide a significantly better fit (results not shown), we used a Brownian motion model of evolution for all subsequent analyses. We then assessed shell shape similarity with phylogenetic simulation (Garland *et al.*, 1993), as the number of shape variables greatly exceeded the number of species. To do this, we first calculated the observed shape differences amongst species as the Euclidean distances amongst species means in the morphological data space. We then calculated the test statistic ($T_{\mathrm{obs}} = D_{LD\text{-}Swim} - \bar{D}_{Swim\text{-}NonSwim}$), which quantified the degree of morphological similarity between the two long-distance swimmers ($D_{LD\text{-}Swim}$) relative to the mean morphological similarity of long-distance swimmers to the remaining species ($\bar{D}_{Swim-NonSwim}$). We then simulated shell shape along the phylogeny using a Brownian motion model of evolution, and recalculated T. The proportion of simulated T-values (of 9999) greater than the observed was used as a test of significance (see Garland *et al.*, 1993). Finally, to test the hypothesis that morphological variation was smaller in species exhibiting long-distance swimming, we calculated the morphological disparity for each species (*sensu* Foote, 1993) from the Euclidean distances amongst individuals (see Anderson, 2001). The pairwise differences amongst species' disparities were then determined, and statistically evaluated using a permutation procedure (the permutation procedure held morphological differences amongst species constant: see Hollander *et al.*, 2006b; also Adams & Collyer, 2009). Our biological hypothesis predicted that long-distance swimmers would exhibit less morphological disparity; therefore, we used a one-tailed testing procedure, where the difference in morphological disparity was examined, rather than the absolute value of the pairwise differences (see Hollander *et al.*, 2006b). We used sequential Bonferroni adjustment in our probability assessments of each pairwise comparison (Rice, 1989). All statistical analyses were performed in R 2.91 (R Development Core Team, 2009).

RESULTS

ANCESTRAL STATE RECONSTRUCTION

Phylogenetic relationships amongst the 42 species were strongly supported by Bayesian analyses (Fig. 2) and are similar to those in Puslednik & Serb (2008). All nodes had posterior probabilities greater than 85% except for three nodes in a large clade of byssal attachers, which did not affect ancestral state estimations. Ancestral state reconstruction for behavioural classes identified two unambiguous origins of long-distance swimming in the Pectinidae: the first is a clade that includes *Am. pleuronectes* and the second is the '*Am.*' *balloti* lineage (Fig. 2). The reconstructed ancestral state for the node leading up to *Am. pleuronectes* was recessing, whereas the ancestral behavioural state for the lineage including '*Am.*' *balloti* was

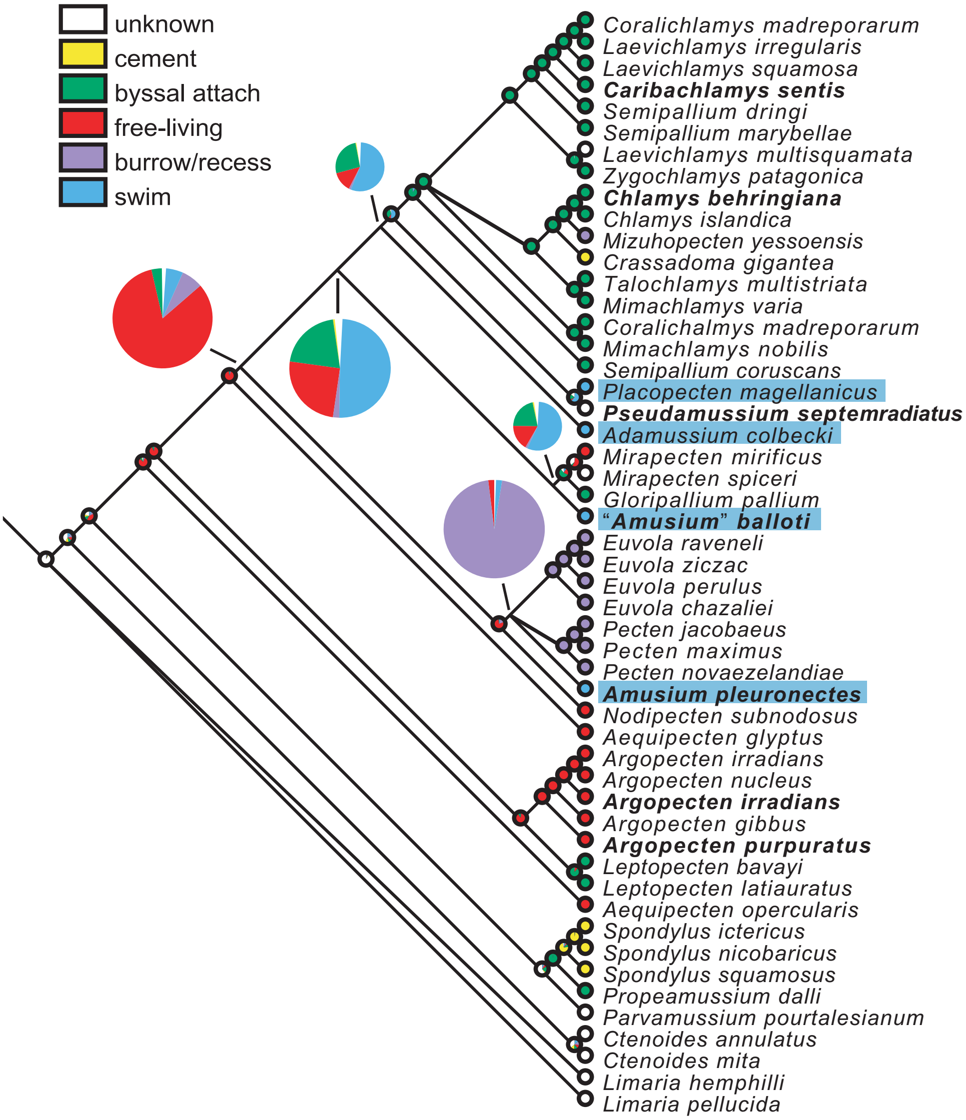

Figure 2. Maximum likelihood estimation of ancestral behaviours using a symmetrical likelihood model (Mk1) on an independently derived multigene Bayesian majority-rule consensus tree. Pie diagrams show character states and their proportion at each node. Taxa highlighted in blue represent long-distance swimming species; taxa in bold represent the seven species examined in our quantitative morphometric analyses of shell shape.

free-living. These data support a convergent pattern of behavioural evolution under a phylogenetically based definition (Revell *et al.*, 2007).

MORPHOMETRIC ANALYSES

Using NP-MANOVA, we found significant variation amongst species relative to within species ($F = 69.12$, $P < 0.0001$, $R^2 = 0.708$), indicating that at least one species differed from the others in shell shape. Pairwise comparisons confirmed these findings, indicating that nearly every species differed significantly from every other species (Table 2). As such, species from distinct behavioural groups, as well as species from the same behavioural group were significantly different in shell shape. The single exception to this pattern was found between the long-distance swimming species (*Am. pleuronectes* and '*Am.*' *balloti*), which were not significantly different in shell shape. When examined from a phylogenetic perspective, we found that the long-distance swimmers were significantly more similar to one another than expected under a Brownian motion model of evolution ($T_{\text{obs}} = 0.0573$; $P_{\text{rand}} = 0.0309$). Thus, shared evolutionary history was not sufficient to explain their degree of phenotypic similarity.

Table 2. Statistical assessment of pairwise differences in shell shape between species

	Amusium pleuronectes	*'Amusium' balloti*	*Argopecten irradians*	*Argopecten purpuratus*	*Chlamys behringiana*	*Caribachlamys sentis*	*Pseudamussium septemradiatus*
Amusium pleuronectes	0	0.0683 NS	0.0001	0.0001	0.0001	0.0001	0.0001
'Amusium' balloti	0.025271	0	0.0001	0.0001	0.0001	0.0001	0.0001
Argopecten irradians	**0.101694**	**0.097673**	0	0.0001	0.0001	0.0001	0.0001
Argopecten purpuratus	**0.126472**	**0.120306**	**0.040458**	0	0.0001	0.0001	0.0001
Chlamys behringiana	**0.071253**	**0.065465**	**0.066356**	**0.092344**	0	0.0006	0.0011
Caribachlamys sentis	**0.073565**	**0.067704**	**0.058188**	**0.078985**	**0.044976**	0	0.0041
Pseudamussium septemradiatus	**0.0546**	**0.047089**	**0.060339**	**0.082532**	**0.043114**	**0.034331**	0

Euclidean distance is treated as the amount of shape difference between species, and is found below the diagonal; probabilities (based on 10 000 random permutations) are found above the diagonal (NS, not significant).
Significant values are in bold.

When morphological disparity was examined, we found that the long-distance swimming species (*Am. pleuronectes* and *'Am.' balloti*) exhibited considerably less within-species morphological variation as compared to the remaining species (Table 3). Further, statistical comparisons of disparity revealed that in all cases, these differences were statistically significant (Table 3). These analyses revealed that the degree of morphological variation in the two long-distance swimming species was significantly less than what was observed in the species from other behavioural groups. Amongst the remaining five species, *P. septemradiatus* had the smallest within-species disparity (Table 3).

Visualizing shell shape variation using principal component analysis reflected the statistical findings above. The first principal component axis (PC1) described 57% of the total variation, and described a pattern of nearly continual variation from free-living species to byssal attaching species to long-distance swimmers (Fig. 3). The shell shape of *P. septemradiatus* occupies the morphospace between byssal attaching and long-distance swimming species (Fig. 3). The behavioural groups could be distinguished on the basis of shell shape along PC1; however, there was also significant separation between species within behavioural groups when viewed along both PC1 and PC2. In particular, both free-living species formed distinct clouds in morphospace, as did both byssal attaching species (Fig. 3). Importantly, the one notable exception to this pattern was the long-distance swimmers *Am. pleuronectes* and *'Am.' balloti*, which overlapped considerably in morphospace (Fig. 3). This finding was consistent with the statistical analyses described above (Table 3). In addition to the separation between species, differences in disparity were also evident amongst species. In particular, both *Am. pleuronectes* and *'Am.' balloti* displayed considerably less variability as compared to the remaining species.

Morphologically, the continuum of shell shape variation represented an anatomical gradient from smooth-shelled species to species exhibiting distinct ribs/ ridges on their shells. This pattern is evident when comparing 3D surface scans of representative individuals along PC1 (Fig. 3). In addition to alteration in shell sculpturing, there was a clear change in auricle size, shape, and symmetry. Smooth-shelled species exhibited a relative reduction in auricle size as compared to other behavioural groups and these auricles were relatively more symmetric and created a flared edge to the hinge line. On the other extreme of shell shape, byssal-attaching species exhibited a relative elongation of their anterior auricle, resulting in a straight, asymmetric hinge along the antero-posterior axis. Interestingly, these anatomical

Table 3. Within-species morphological disparity

	Disparity (D)	D_{pleuro}-D_{Other}	P_{rand}	D_{balloti}-D_{Other}	P_{rand}
Amusium pleuronectes	3.7006×10^{-4}				
'Amusium' balloti	4.7786×10^{-4}				
Argopecten irradians	9.6605×10^{-4}	**–0.000596**	**0.0041**	**–0.000488**	**0.0095**
Argopecten purpuratus	2.1983×10^{-3}	**–0.0018282**	**0.0001**	**–0.00172**	**0.0001**
Chlamys behringiana	9.6971×10^{-4}	**–0.0005996**	**0.0083**	**–0.000492**	**0.0156**
Caribachlamys sentis	1.0412×10^{-3}	**–0.0006711**	**0.0011**	**–0.000563**	**0.0027**
Pseudamussium septemradiatus	7.9178×10^{-4}	**–0.0004217**	**0.0271**	**–0.000314**	**0.0483**

Differences in disparity measures between *Am. pleuronectes* and *'Am.' balloti* versus all non-long-distance swimmers are displayed, along with their probabilities (based on a permutation procedure using 9999 iterations: see Material and methods).
Significant values based on sequential Bonferroni adjustment are shown in bold.

changes correspond closely to functional differences of the shell. Mechanistically, the longer anterior auricle adds support to the byssal attachment site and prevents overturning of the animal (Stanley, 1970) (Fig. 3A). When compared to byssal attaching (*Ch. behringiana*, *Ca. sentis*) or free-living species (*Ar. irradians*, *Ar. purpuratus*), the long-distance swimming species (*Am. pleuronectes*, *'Am.' balloti*) exhibit a unique shape with larger umbonal angles, which increases the shell area perpendicular to the direction of movement (i.e. 'aspect ratio'). This circular shape of the shell disk results in an increased lift/drag ratio when compared to byssally attached forms (Stanley, 1970; Gould, 1971).

DISCUSSION

Morphological convergence is an important phenomenon in evolutionary biology as it provides both multiple independent tests of the phenotypic response to a particular selective regime, and a way to study adaptation at the macroevolutionary scale (Larson & Losos, 1996). The rampant morphological convergence in shell form amongst bivalves illustrates the structure–function relationship as a response to similar selective forces. These selective forces acting on shells may include a range of environmental factors and functional/biomechanical requirements. For the swimming species of the Pectinidae, similarity in shell shape appears to be dictated by locomotive ability; i.e. locomotor performance. Under this scenario, shells of swimming species should converge on the most effective morphology for movement regardless of species relatedness. In this paper, we first demonstrated that long-distance swimming evolved at least two times within the Pectinidae using an independent molecular phylogenetic analysis. Using ancestral state reconstruction, we confirmed that the two swimming lineages evolved from ancestors exhibiting different behavioural habits. We then examined the shells of seven scallop species representing a range of behavioural habits. We found that the shells of two unrelated, long-distance swimming species converged on a specific morphology and occupied a narrow region in morphospace. For these two long-distance swimming species, there is clear morphological convergence. In addition, these swimming species displayed a significantly reduced degree of morphological disparity as compared to species from other behavioural groups. Finally, shared evolutionary history was not sufficient to explain the similarity in shell shape between long-distance swimmers. Thus, the patterns revealed in this study, distinctness of morphological type and a reduction of morphological variation, correspond closely to what is expected for a trait under strong selection and functional constraints.

The shell shape variation that we observed amongst species in this study also generated a particular pattern in morphospace; where long-distance swimming species were found at one extreme of morphospace, more sedentary species at the other extreme, and intermediate swimming species were between the two. Thus, our analyses identified a morphological gradient that corresponded closely to the known gradient in the behavioural habits of these species. These findings suggest the hypothesis that the observed differences in shell shape may have resulted from divergent selection, generated by biomechanical factors required for swimming in some species and physical factors required for protection against predators in other species. If this hypothesis is correct, there exists a functional trade-off in shell shape, such that having a smooth, streamlined surface and reduced weight may benefit swimming performance, but at the expense of protecting the animal within the shell, and vice versa. Indeed, such divergent evolution in shell shape has previously been

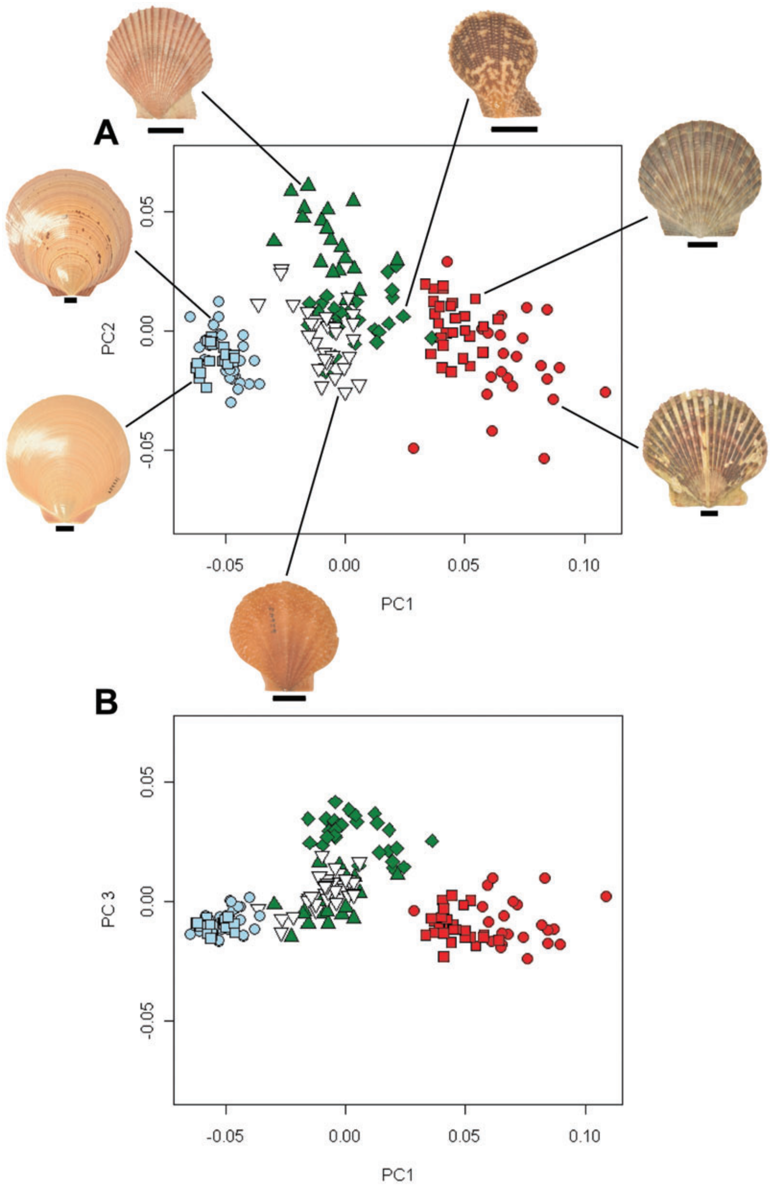

Figure 3. Principal component plot of shell shape variation for specimens used in this study. The first three principal component (PC) axes explain 75.8% of the total variation in shell shape (PC1 = 57.3%; PC2 = 11.6%; PC3 = 6.9%). (A) Shape variation along PC1 and PC2 with photographs of representative individuals for each species. Scale bars = 1 cm. (B) Shape variation along PC1 and PC3. Species are designated as: *Amusium pleuronectes* (blue squares), *'Amusium' balloti* (blue circles), *Argopecten irradians* (red squares), *Argopecten purpuratus* (red circles), *Chlamys behringiana* (green triangles), *Caribachlamys sentis* (green diamonds), *Pseudamussium septemradiatus* (white inverted triangles).

identified in other species. For example, the gastropod *Littorina saxatilis* (Olivi, 1792) displays a smaller, thin-shelled ecotype in habitats where biomechanical constraints owing to wave action represent a major selective pressure, and displays a larger, thicker shelled ecotype in alternative habitats where defence against predation is critical for survival (see Reid, 1996; Johannesson, 2003; Hollander, Adams & Johannesson, 2006a; Hollander *et al.*, 2006b). Analogous patterns in other species have also been identified (e.g. Appleton & Palmer, 1988; Trussell, 1996; DeWitt, Robinson & Wilson, 2000). Our study represents one of the first putative instances of such a pattern in adult bivalves, suggesting the possibility that functional trade-offs and selective divergence may be important for the evolutionary diversification of this group (see also Freeman & Byers, 2006). It should be noted however that we examined only seven of the roughly 250 recognized scallop species (Brand, 2006; Dijkstra, 2009). Although our data support morphological convergence between two swimming species from the *Amusium* and '*Amusium*' clades, we predict that other long-distance swimming species may also be convergent. This prediction should be formally examined. Future experimental and comparative studies are therefore required to determine whether or not this pattern is general to the entire family.

Interestingly, we found that the species intermediate in its swimming ability (*P. septemradiatus*) was also intermediate in its shell morphology. Specifically, *P. septemradiatus* lies between the long-distance swimmers and the more sedentary species in morphospace, indicating an intermediate morphology between byssal attachers and long-distance swimmers. In addition, *P. septemradiatus* exhibited reduced variation in shell shape, although its disparity was not as low as was seen in *Am. pleuronectes* and '*Am.*' *balloti*. This finding suggests the hypothesis that intermittent swimming behaviour in *P. septemradiatus* has exerted some degree of selection on shell shape, although perhaps not to the same degree as in *Am. pleuronectes* and '*Am.*' *balloti*. In terms of shell shape, *P. septemradiatus* displays distinct rounded ribbing along its shell, but these ribs are fewer in number (four to ten) than in the more sedentary species (e.g. *Ar. irradians*, 14–24; *Ca. sentis*, up to 50). Thus, *P. septemradiatus* is relatively smoother than the sedentary species, but more rugose than the two long-distance swimmers. This morphology suggests that intermittent swimming may be adequately accomplished via a morphology that is neither 'swimmer-like' nor 'sedentary-like.' If this hypothesis is correct, we predict that other intermittent swimmers, such as *Swiftopecten swiftii* (Bernardi, 1858) and *Delectopecten* Stewart, 1930, will display a similar morphology to *P. septemradiatus*, and will overlap with it in morphospace.

In this study, we identified strong morphological and behavioural similarity in shell shape between two distantly related species experiencing similar functional demands. A phylogenetic analysis of behaviour revealed that long-distance swimming evolved multiple times, revealing that this behaviour evolved as a result of convergent evolution. Combining these findings we hypothesized that two unrelated species exhibiting long-distance swimming were morphologically similar as a result of functional convergence. Although this morphological hypothesis derives logically from the available evidence, it should be noted that other historical processes have not been fully considered. Indeed, morphological similarities amongst extant taxa can evolve from a number of causal processes, including evolutionary convergence and evolutionary parallelism (*sensu* Revell *et al*., 2007). Distinguishing between these alternative explanations requires examining the trajectories of morphological evolution obtained from a phylogenetic framework (Revell *et al*., 2007). Thus, although it is likely that the similarity in shell shape between two long-distance swimmers is the result of evolutionary convergence, a more comprehensive comparative analysis with complete taxon sampling, combined with a robust and comprehensive phylogeny for Pectinidae, is required to fully distinguish this hypothesis from the alternative of evolutionary parallelism.

Finally, we note that most studies of morphological convergence and adaptation have focused on vertebrates, where examples are found in all major lineages (e.g. fish: Fryer & Iles, 1972; Rüber & Adams, 2001; amphibians: Wiens, Chippindale & Hillis, 2003; reptiles: Stayton, 2006; Revell *et al*., 2007; birds: Van Tuinen *et al*., 2001; Grant *et al*., 2004; mammals: Kelt *et al*., 1996). Although convergent evolution in vertebrates is well documented, we know far less about such patterns in other animal groups. Part of the reason for the paucity of nonvertebrate examples may simply reflect the fact that fewer invertebrate species are used as models to study adaptation. Indeed, if the patterns seen in vertebrates are representative, they suggest that convergent evolution should be far more prevalent across the animal kingdom than is currently known, as vertebrates comprise only about 5 per cent of all animal diversity. Thus, we recommend that future work on convergent evolution focus more heavily on nonvertebrate taxa, to determine whether similar patterns and processes are observed. In particular, we feel that the Mollusca represent an attractive system for studying patterns of morphological evolution and adaptation. Mollusca is the second largest animal phylum, including about 93 000 named living species, with an estimated 200 000 living species and 70 000 additional fossil taxa (Brusca *et al*., 2003; Ponder & Lindberg, 2008). Although a number of studies have examined patterns of phenotypic change, particularly in gastropod shell shape as an evolutionary trade-off or response to predation pressures (e.g. Vermeij, 1982; Hollander *et al*., 2006b; Edgell & Rochette, 2008; Lakowitz, Bronmark & Nystrom, 2008) or as a physiological response to extreme ambient temperatures (e.g. Phifer-Rixey *et al*., 2008; Harley *et al*., 2009), this phylum generally remains under-utilized as an evolutionary model for such questions. Within the Mollusca, bivalves exhibit a wide range of morphological variation, which is closely linked to their life history and ecology. Furthermore, in some lineages, shell shape appears to be more a consequence of biomechanical requirements rather than a response to predation (but see Freeman & Byers, 2006). Our study has demonstrated the first instance of morphological convergence in bivalves as a result of biomechanical selective pressures, and suggests the possibility that this pattern may be more widespread. Thus, like vertebrates, bivalves provide the opportunity to examine the evolutionary responses to disparate selection pressures (predation and biomechanical requirements) to understand how these pressures have shaped the evolution of diversity.

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APPENDIX

Specimens examined to quantify shell shape. For each, the left valves of individuals from both in-house collections as well as collections of the Delaware Museum of Natural History (DMNH), Florida Museum of Natural History (FLMNH), Smithsonian Institution (USNM), and Western Australian Museum (WAMS) were examined. Taxa studied include:

Amusium pleuronectes ($N = 18$). Borneo Is., Malaysia. 7 January 1908. USNM 254931. (pleuronectes-1, pleuronectes-2, pleuronectes-3, pleuronectes-4, pleuronectes-5, pleuronectes-6, pleuronectes-7, pleuronectes-8, pleuronectes-9, pleuronectes-10, pleuronectes-11, pleuronectes-12, pleuronectes-13, pleuronectes-14, pleuronectes-15, pleuronectes-16, pleuronectes-17, pleuronectes-18).

'Amusium' balloti ($N = 32$). Shark Bay, Australia. 15 January 2007. (WAMS 33084.3 = balloti1, WAMS 33085.3 = balloti2, WAMS 33084.2 = balloti3, WAMS 33087.2 = balloti4, WAMS 33088.2 = balloti5, WAMS 33087.3 = balloti6, Bald Isl #3 = balloti7, WAMS 33085.4 = balloti8, WAMS 33084.4 = balloti9, WAMS 33088.3 = balloti10, WAMS 33085.2 = balloti11, WAMS 33081.2 = balloti12, WAMS 33081.3 = balloti13, WAMS 33078.3 = balloti14, WAMS 33082.2 = balloti15, WAMS 33078.4 = balloti16, WAMS 33082.4 = balloti17, WAMS 33082.3 = balloti18, WAMS 33080.4 = balloti19, WAMS 33079.3 = balloti20, WAMS 33077.2 = balloti21, WAMS 33077.1 = balloti22, WAMS 33076.3 = balloti23, WAMS 33080.3 = balloti24, WAMS 33079.2 = balloti25,

WAMS 33076.2 = balloti26, WAMS 33078.2 = balloti27, WAMS 33077.4 = balloti28, WAMS 33076.4 = balloti29, WAMS 33079.4 = balloti30, WAMS 33083.3 = balloti31, WAMS 33083.4 = balloti32).

Argopecten irradians (*N* = 27). Wellfleet Harbor, MA. 1970. DMNH 40205. (irradians-ls1, irradians-ls2, irradians-ls3, irradians-ls4, irradians-ls5, irradians-ls6, irradians-ls7, irradians-ls8, irradians-ls9, irradians-ls10, irradians-ls11, irradians-ls12, irradians-ls13, irradians-ls14, irradians-ls15, irradians-ls16, irradians-ls17, irradians-ls18, irradians-ls19, irradians-ls20, irradians-ls21, irradians-ls22, irradians-ls23, irradians-ls24, irradians-ls25, irradians-ls26, irradians-ls27).

Argopecten purpuratus (*N* = 23). Paracas Bay, Peru. FLMNH 337447. (purpuratus2, purpuratus3, purpuratus4, purpuratus5, purpuratus6, purpuratus7, purpuratus8, purpuratus10, purpuratus11, purpuratus12, purpuratus13, purpuratus14, purpuratus15, purpuratus16, purpuratus17, purpuratus18, purpuratus19, purpuratus20, purpuratus21, purpuratus22, purpuratus23, purpuratus24, purpuratus25).

Chlamys behringiana (*N* = 20). Yakutata, AK. 2007. (behringiana1, behringiana2, behringiana3, behringiana4, behringiana5, behringiana6, behringiana7, behringiana8, behringiana9, behringiana10, behringiana11, behringiana12, behringiana13, behringiana14, behringiana15, behringiana16, behringiana17, behringiana18, behringiana19, behringiana20).

Caribachlamys sentis (*N* = 28). Biscayne Bay, FL. FLMNH 374737. (sentis-1, sentis-2, sentis-3, sentis-4, sentis-5, sentis-6, sentis-7, sentis-8, sentis-9, sentis-10, sentis-11, sentis-12, sentis-13, sentis-14, sentis-15, sentis-16, sentis-17, sentis-18, sentis-19, sentis-20, sentis-21, sentis-22, sentis-23, sentis-24, sentis-25, sentis-26, sentis-27, sentis-28).

Pseudamussium septemradiatus (*N* = 30). Loch Fyne, Scotland. 1846. USNM 62645. (septem-1, septem-2, septem-3, septem-4, septem-5, septem-6, septem-7, septem-8, septem-9, septem-10, septem-11, septem-12, septem-13, septem-14, septem-15, septem-16, septem-17, septem-18, septem-19, septem-20, septem-21, septem-22, septem-23, septem-24, septem-25, septem-26, septem-27, septem-28, septem-29, septem-30).