

The paradox of gradualism: phyletic evolution in two lineages of lymnocyprid bivalves (Lake Pannon, central Europe)

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Abstract.—Patterns preserved in the fossil record are of the highest importance in addressing questions about long-term evolutionary processes, yet both the description of pattern and its translation into process can be difficult. With respect to gradual phyletic change, we know that randomly generated sequences may exhibit characteristics of a “trend”; apparent patterns, therefore, must be interpreted with caution. Furthermore, even when the claim of a gradual trend can be statistically justified, interpretation of the underlying mechanisms may be challenging. Given that we can observe populations changing rapidly over tens or hundreds of years, it is now more difficult to explain instances of geologically gradual (as opposed to punctuated) change.

Here we describe morphologic change in two bivalve lineages from the late Miocene Lake Pannon. We evaluate change according to the model-based methods of Hunt. Both lineages exhibit size increases and shape changes over an interval of nearly 4 million years. Size and two shape variables in the conjungens lineage are best fit by a model of directional evolution; remaining shape variables mostly conform to unbiased random walks. Body-size evolution in the diprosopum lineage is also significantly directional but all shape variables are best fit by the unbiased random walk model; the small number of sampling intervals available for this lineage ($n = 6$) makes determination of the actual pattern more difficult. Model-fitting results indicate that the parallel trajectories of increasing log shell height over time in the two lineages can be accounted for by an underlying trend shared by both lineages, suggesting that the size increases may be a shared response to the same cause. The pace of phenotypic change, measured as Lynch’s Δ , is slower than the neutral expectation for all size and shape traits.

Our examples illustrate well the paradox of gradualism; the sequences exhibit significant directional morphological evolution, but rates of change as measured over the long-term are apparently too slow for directional selection or even drift to be the cause. Viewing long-term phenotypic evolution in terms of populations tracking peaks on adaptive landscapes is useful in this context. Such a view allows for intervals of directional selection (during times of peak movement—resulting in the overall trends we can detect) interspersed with intervals of stasis (during times of peak stability—resulting in overall changes that appear to proceed more slowly than the neutral expectation). The paradox of gradualism thus reduces to (1) peak movements and their drivers, which are not restricted in rate as are population-genetic drivers, and (2) the maintenance of stasis, on which no consensus exists.

We can identify no environmental parameter in the central European Neogene that exhibits consistent change across the interval of gradual morphologic change. It may be that in Lake Pannon the long-term persistence of generally ameliorating conditions (plentiful resources and habitat space, few predators or competitors) resulted in geologically slow but consistent peak shifts, which in turn facilitated size increase and shape change in these lineages.

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Introduction

Patterns preserved in the fossil record are critical to interpreting evolutionary processes, yet both the description of pattern and its translation into process remain controversial. Eldredge and Gould (1972) stimulated considerable empirical work on the fossil expression of species-level change, but taking these studies at face value is often not advisable

because one’s perception of pattern may be biased in various ways (Eldredge and Gould 1972; Fortey 1985).

With respect to identifying gradual change, it has been demonstrated that randomly generated sequences may exhibit the characteristics of a “trend” (e.g., Raup 1977; Bookstein 1987). For this reason, a number of studies have proposed methods for testing

stratophenetic series against a null model of random change. These methods are generally based on the rates of change between consecutive samples (Lynch 1988, 1990; Gingerich 1993, 2001), the relative magnitude of change (Bookstein 1987, 1988; Roopnarine et al. 1999; Roopnarine 2001; see also Sheets and Mitchell 2001a,b), or the consistency in direction of change (Raup and Crick 1981). In general, if a series has greater rates, magnitude, or consistency of change than expected in a random sequence, directional selection can be invoked. It is important to remember that an inference of randomness implies only that the assemblage of forces acting on the lineage in question was too complex for our methods to untangle, not that there were no deterministic forces at work (see Raup 1977; Roopnarine 2001; Hunt 2006). Unfortunately, these tests are generally prone to Type I errors (rejecting the null hypothesis when it is true [Hannisdal 2006]) and Type II errors ([accepting the null when it is false; Roopnarine et al. 1999; Sheets and Mitchell 2001b; Bell et al. 2006]). Hunt (2006) devised an alternative approach for likelihood-based fitting of three evolutionary modes (directional change, random walks, and stasis). This approach has the advantage of comparing the relative statistical support for different models on equal footing, without giving any one model privileged null status.

Even when the pattern of a gradual trend can be clearly identified, interpretation of the underlying processes is challenging. Given the preponderance of punctuated change in the fossil record, coupled with the fact that we can observe populations changing rapidly on time scales of tens or hundreds of years, it is now much more difficult to explain instances of geologically gradual change. In his final book, S. J. Gould (2002: p. 836) states: "I do not think we have even begun to explore the range of potential explanations for the puzzling phenomenon of anagenetic gradualism. I, at least, find the subject very confusing and challenging." The paradox of geologically gradual change is this: if change is driven by directional selection, it ought to proceed rapidly on geologic time scales. Quantitative models show that change occurring over

million-year time scales requires such miniscule numbers of selective deaths per generation that random factors would certainly swamp out any long-term trend (Lande 1980). Thus, the evolutionary pattern that was once our expectation (and Darwin's) has now become more challenging for evolutionary biologists to explain.

The purpose of this paper is to describe the morphological changes in two lineages of lymnocardiid bivalves from ancient Lake Pannon. Lake Pannon occupied the Pannonian basin in central Europe from 11.6 to 4 Ma. It was a large, long-lived, brackish to nearly freshwater lake that harbored a spectacular evolutionary radiation of bivalves and gastropods (including 900 described species [e.g., Papp et al. 1985; Geary et al. 2000, 2002]). Among the described lineages are many examples of apparently gradual change, punctuated change, and stasis (e.g., Geary 1990, 1992, 1995; Müller and Magyar 1992). As Fortey (1985) maintained, confidence in the reality of the punctuated patterns is reinforced by their co-occurrence with the gradual patterns (and vice versa).

The sequences we describe here have been noted by earlier authors (Lörenthey 1894; Basch 1990; Lennert et al. 1999; Szonoky et al. 1999), but never described in detail or quantified. We selected these particular lineages because they are reasonably well represented in fossil collections and because they appear to change gradually over several million years. Our purpose here is not to provide an assessment of the relative frequencies of different evolutionary modes, but rather to describe the evolutionary patterns present in these two lineages, to evaluate the measured changes according to the methods of Hunt (2006) and Lynch (1990), and to assess the underlying processes in the paleoenvironmental context of the European late Miocene.

Background

Geologic Context.—The Pannonian Basin (Fig. 1) is one of a chain of extensional basins that developed in the Mediterranean zone of convergence between the Eurasian and African plates in the Cenozoic (Horváth et al. 2006). In terms of hydrography and biogeog-

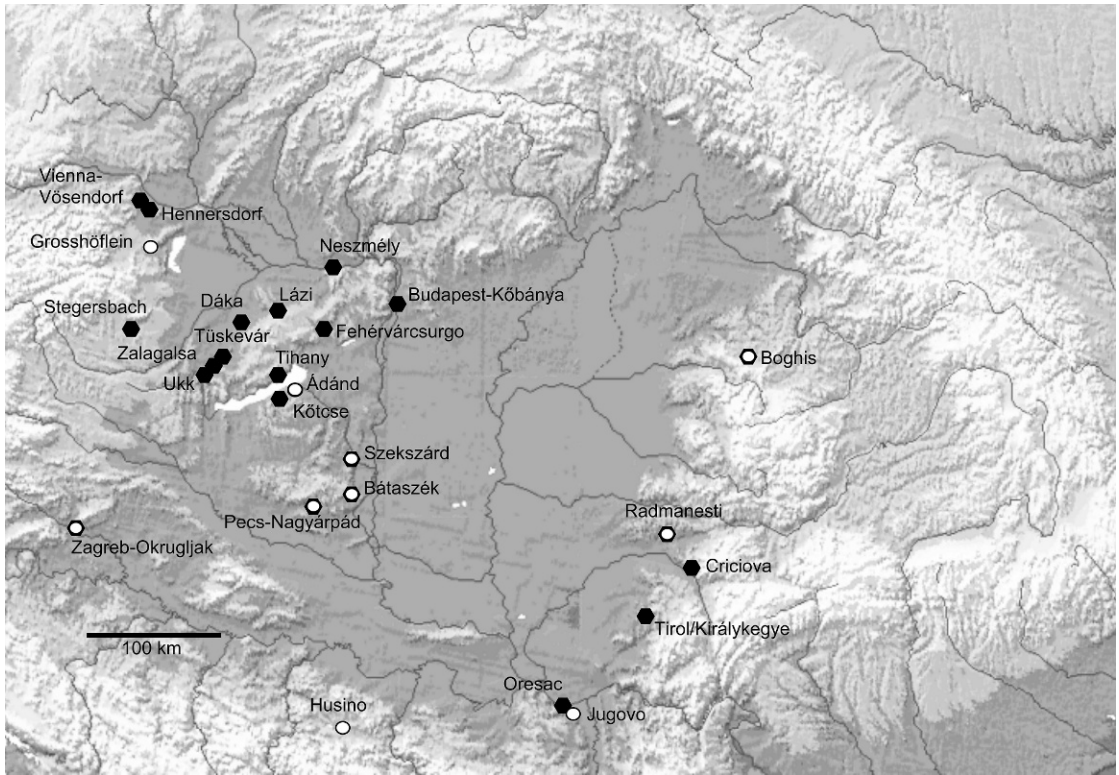


FIGURE 1. Map of the Pannonian Basin with localities noted. Vienna, Budapest, and Zagreb are noted for general reference (alongside collecting localities in their immediate vicinities). Coniungens lineage localities are represented by black hexagons; diprosopum lineage localities are represented by white circles; localities with both lineages present are represented by black hexagons enclosing white circles. Base map after Microsoft Encarta World Atlas.

raphy, the basin was isolated from the Mediterranean Sea for most of the Neogene. Instead it belonged to the Paratethys, an inland water body that connected a series of epicontinental basins from the Alps to the Central Asian Aral Lake. By the beginning of the late Miocene, a combination of tectonic activity and eustatic sea-level fall had effectively isolated the Pannonian Basin fauna from that of other paratethyan basins and from the marine system (Kazmer 1990; Rögl 1998; Magyar et al. 1999a; Harzhauser et al. 2004; Popov et al. 2004, 2006;). Following this isolation, a nearly complete turnover in the faunal assemblages indicates that the environment shifted from marginal marine to lacustrine brackish (Papp et al. 1974, 1985; Nagymarosy and Müller 1988; Müller et al. 1999; Harzhauser and Piller 2007). Brackish conditions prevailed until the Early Pliocene in open lake environments; fresh (or considerably less brackish) water characterized the

deltaic environments that became widespread by the middle of the late Miocene (Geary et al. 1989; Harzhauser et al. 2007). The term Lake Pannon refers to the lake through its entire late Miocene and earliest Pliocene history.

Clastic material in the Pannonian Basin was derived from the uplift of the Alps and Carpathian Mountains (Kovacic and Grizelj 2006; Thamó-Bozsó et al. 2006). Sediment was initially trapped in marginal basins such as the Vienna and Transylvanian Basins; by approximately 9–10 Ma, these marginal basins were filled (Harzhauser et al. 2004; Krézsek and Filipescu 2005) and sedimentation proceeded from the northwest and northeast toward the south (Vakarcs et al. 1994; Magyar et al. 1999a). An interconnected system of deltas formed along the northern shoreline of the lake (Pogacsas et al. 1988; Jiricek 1990; Juhasz 1992; Vakarcs et al. 1994; Magyar et al. 1999a) and completely filled the basin by roughly the middle of the Pliocene.

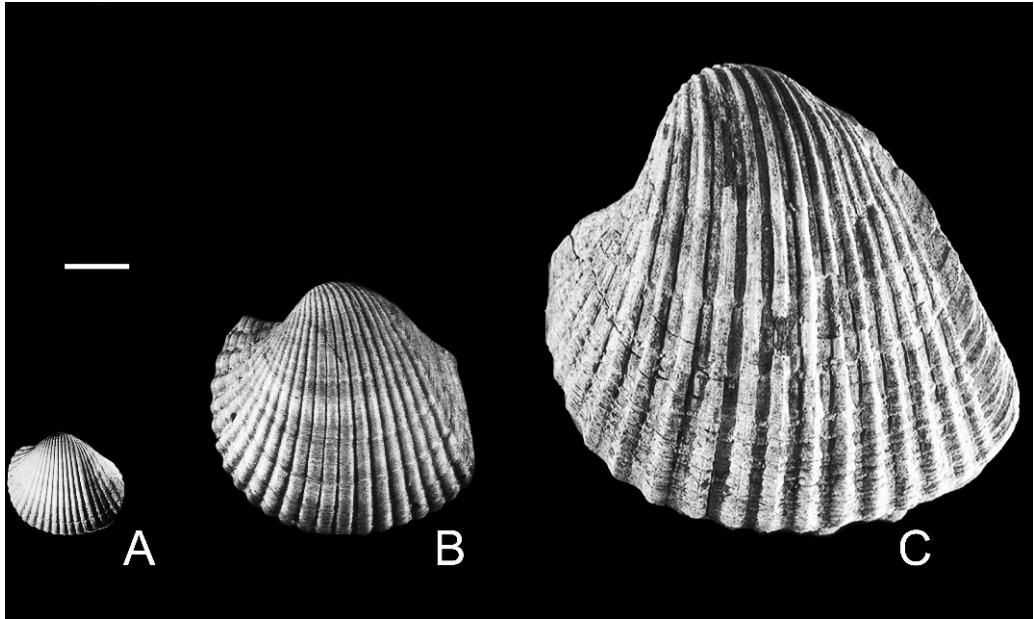


FIGURE 2. Species of the conjungens lineage. A, *Lymnocardium conjungens*. B, *L. penslii*. C, *L. schmidtii*. Scale bar, 1 cm.

Uplift of marginal parts of the basin since the Pliocene resulted in the current exposures (Cloetingh et al. 2002; Horváth et al. 2006; Magyar and Sztanó 2008).

Systematics.—Our specimens belong to six described species from two well-defined phyletic lineages. Both lineages fall within the Lymnocardiini (Schneider and Magyar 1999), but they are not sister groups. Phylogenetic analysis (Schneider and Magyar 1999) indicates that each lineage is a monophyletic unit and stratigraphic evidence (described below) supports their interpretation as anagenetic, species-level lineages.

The conjungens lineage (Fig. 2) includes (from oldest to youngest) *L. conjungens* (Hornes), *L. penslii* (Fuchs), and *L. schmidtii* (Hornes). These species are characterized by two anterior lateral teeth in the right valve, ribs that are triangular in cross-section and separated by intercostal spaces, and a posterior gape. Schneider and Magyar's (1999) cladistic analysis included 47 taxa (species of Lymnocardiinae plus outgroups; 29 characters, 155 character states). *Lymnocardium conjungens* and *L. penslii* are sister species in this analysis; *L. schmidtii* was not included.

What we refer to here as the diprosopum lineage (Fig. 3) includes (from oldest to

youngest) *L. subdiprosopum* (Stevanovic), *L. diprosopum* (Brusina), and *L. arpadense* (Hornes). Basch (1990) assigned *L. diprosopum* and *L. arpadense* to the subgenus *Podravini-cardium* (his research did not extend into the older units containing *L. subdiprosopum*). Schneider and Magyar's (1999) analysis unites these three species into a clade, with the stratigraphically younger *L. diprosopum* and *L. arpadense* as sister species. Species in the diprosopum lineage bear robust hinge teeth and many flat, closely spaced ribs. The right valve typically has one anterior lateral tooth, but sometimes the anterior-dorsal margin has a protruding structure like a rudimentary second tooth above the first one. In the cladistic analysis, the three species differ in only three of 29 characters: the development of a moderate lunule in *L. arpadense*, the loss of the posterior gape after *L. subdiprosopum*, and shell shape (discussed below).

Paleoecology.—Species of the endemic genus *Lymnocardium* occupied littoral and sublittoral habitats in Lake Pannon; they did not live in the deepest parts of the lake. Members of the conjungens lineage are generally known from littoral deposits and from storm beds that were redeposited in sublittoral environments. Individuals are most often found in fine to

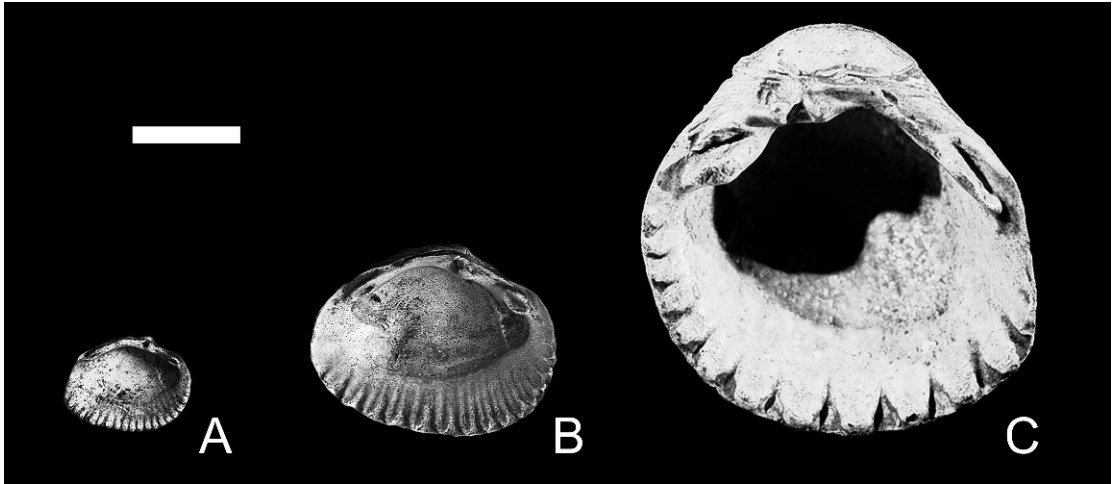


FIGURE 3. Species of the diprosopum lineage. A, *Lymnocardium subdiprosopum*. B, *L. diprosopum*. C, *L. arpadense*. Scale bar, 1 cm.

coarse-grained sands or even gravel. The accompanying fauna usually includes a wide variety of grazing gastropods, particularly *Melanopsis*, which indicates a water depth of several meters (<10–15 m). Younger members of this lineage may appear in deeper, sublittoral settings as well. *Lymnocardium schmidti* from Báticaszék, for instance, is found in silty claymarl, which also harbors specialized deep-water pulmonate snails and lacks *Melanopsis* or other shallow-water taxa (Lennert et al. 1999). (These sublittoral specimens differ from “normal” *L. schmidti* in having sharper ribs.) The water depth in such sublittoral environments is estimated to have been a few tens of meters.

In contrast, members of the diprosopum lineage invariably come from coarse-grained littoral or storm deposits (e.g., Báticaszék [Lennert et al. 1999]). Reworking by waves has eroded many of the shells.

Although a number of important outcrops no longer exist and detailed information on the sedimentologic context of their fossils is not available, the outcrop at Báticaszék (from the relatively young *dainellii* zone) exhibits an interesting distinction between the conjungens and diprosopum lineages. Members of the conjungens lineage are found in the sublittoral silts, whereas members of the diprosopum lineage occur only in the intercalated storm beds. Thus, although both

lineages are predominantly littoral, in the Báticaszék outcrop the difference between their habitats is clearly reflected in their patterns of occurrence.

Materials and Methods

Specimens.—We used 403 specimens from 25 localities, representing six countries in the Pannonian Basin (Fig. 1 and Appendix). The specimens came from our own personal collections and from the following museums or individuals: Magyar Állami Földtani Intézet (MÁFI), Magyar Természettudományi Múzeum (TTM), Eötvös Loránd Tudományegyetem Őslénytani Tanszék (ELTE), Szegedi Tudományegyetem Földtani és Őslénytani Tanszék (SZTE), Hrvatski Prirodoslovni Muzej (HPM), Prirodnjacki Muzej Beograd (PMB), Naturhistorisches Museum Wien (NHMW), Institut Royal des Sciences Naturelles de Belgique (IRSNB), and Josef Paul Lueger (JPL).

Specimens from a given locality typically come from a single, relatively small outcrop and thus belong to a single biozone. For purposes of this study, we combined localities belonging to each biozone.

Biostratigraphy.—The regional biostratigraphy for Lake Pannon deposits (Fig. 4) is based mainly on endemic molluscs, ostracodes, and dinoflagellates (Papp et al. 1985; Stevanovic et al. 1990; Magyar et al. 1999b). Correlation of

Age (Ma)	Stage	Polarity	Chron	Mammal zone	Biozones of Lake Pannon deposits			
					microplankton	molluscs		
						profunda	sublittoral	littoral
6	Messinian	[Black bar]	C3r	MN13	Galeacysta etrusca	"Dreissenomya" digitifera	Congeria rhomboidea	Prosodacnomya vutskitsi
			C3An					Prosodacnomya dainellii
7	Messinian	[Black bar]	C3Ar	MN12	Galeacysta etrusca	"Dreissenomya" digitifera	Congeria rhomboidea	Prosodacnomya carbonifera
			C3B					
8	Tortonian	[Black bar]	C4n	MN11	Spiniferites validus	"Dreissenomya" digitifera	Congeria praerhomboida	"Lymnocardium" decorum
			C4r					
9	Tortonian	[Black bar]	C4An	MN10	Spiniferites paradoxus	"Dreissenomya" digitifera	Congeria praerhomboida	"Lymnocardium" ponticum
			C4Ar					
10	Tortonian	[Black bar]	C5n	MN9	Spiniferites paradoxus	Congeria banatica	Congeria czjzeki	Lymnocardium soproniense
11	Tortonian	[Black bar]	C5r	MN7-8	Pontadinium pecsvaradensis	Congeria banatica	Congeria czjzeki	Lymnocardium schedellianum
					Spiniferites bentorii oblongus			Congeria hoernesii
								Congeria ornithopsis
								"Lymnocardium" praeponicum
								Mecsekia ultima

FIGURE 4. Biostratigraphic zonation scheme for Lake Pannon (updated from Magyar et al. 1999b; polarity timescale after Lourens et al. 2004; correlation of European mammal zones follows Agustí et al. 2001).

Pannonian Basin sediments with the global stratigraphic system is made possible through mammal, radiometric, and magnetostratigraphic data (Elston et al. 1994; Rögl and Daxner-Höck 1996; Magyar et al. 1999b, 2007).

Because the lineages of focus here are found predominantly in littoral deposits, we use the littoral mollusk biozones (see Fig. 4). Our material requires and allows some modifications in the zonation for the purpose of this study. Samples from the conjungens zone can be divided into two groups, an older and a younger one, based on the accompanying mollusk species and stratigraphic considerations (Magyar et al. 2000). The same applies to the two samples from the vutskitsi zone; we suggest that the Pecs-Nagyárpád (Árpád) material is younger than the Szekszard material, judging from the strong similarity of the previous to terminal Miocene faunas in Slavonia (Szonyky et al. 1999). Thus, samples of the conjungens lineage can be sorted to eight stratigraphic levels, whereas those of the diprosopum lineage to six (the oldest representatives of this lineage are known from the younger part of the conjungens zone only, and the ponticum zone failed to yield fossils of this lineage).

Morphometrics.—We used traditional morphometrics and eigenshape analysis to quantify variation and change. Traditional morphometric characters were measured from images of the shell interiors so that features of the dentition as well as overall shape could be captured. Measured lengths and angles, as well as the ratios calculated from them, are shown in Figure 5 and described in its caption.

For eigenshape analysis, we used traces of the shell outline (taken from the same images). Images of right valves were flipped horizontally before tracing in order to correspond to images of left valves.

Morphometric characters and traces for eigenshape analysis were captured using NIH Image. The series of x-y coordinates representing the shell outlines were entered into QuicKurve.004 (Walker 1998) to reduce the number of points to 50. We used Standard Eigenshape (MacLeod 1999; http://www.morpho-tools.net/standard_es.html) for eigenshape analysis.

In total, we measured 232 individuals from the conjungens lineage and 171 individuals from the diprosopum lineage. Many of the characters that exhibit phyletic change in

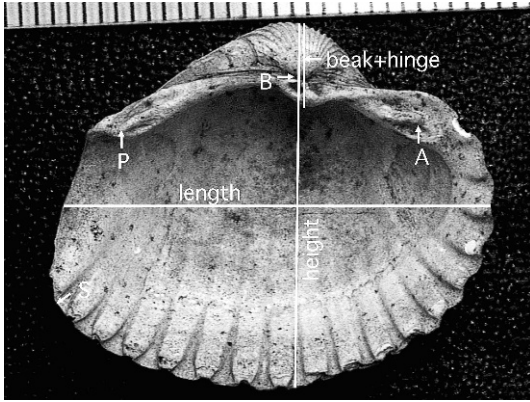


FIGURE 5. Morphometric measurements. Shell height was measured perpendicular to length, with height passing through the beak, and length terminating at the anteriormost margin of the shell. The points S (dorsal-most sulcus on the posterior margin), P (posterior cardinal tooth), A (anterior cardinal tooth), and B (beak) were used to define the angles ABP, APS, PAS, ABS, and BPS. "Anterior length" was defined as the portion of shell length anterior to the line along which height was measured. "Beak + hinge" was measured along the height from the dorsalmost point of the shell to the lowest edge of the hinge. "Hinge height" was measured from the line segment BP (and perpendicular to it) to the edge of the hinge furthest from this line. From these measurements, the following ratios were derived: Length/Height, AnteriorLength/Length, "RelativeBeak-Height" = beak + hinge/Height, "HingeCurve" = hinge height/length of BP.

these lineages also exhibit ontogenetic change. Because the primary focus of this paper is change over time, we used "adults only" in the analyses presented here. We defined adults as all those individuals whose shell height was 70% or more of the maximum for that biozone. Defined in this way, we had 122 individuals from the conjungens lineage and 106 individuals from the diprosopum lineage. The description and analysis of ontogenetic change in these lineages will be the focus of a separate paper.

Statistical Analysis of Evolutionary Sequences.—Using the likelihood-based methods of Hunt (2006), we fit the evolutionary trajectory of each measured trait to models corresponding to the three standard modes of evolution: directional change, unbiased random walk, and stasis. The unbiased random walk model occurs in discrete time increments; for each of these an evolutionary transition (= "step") is drawn at random from a distribution with a mean (μ_{step}) of zero and a variance of σ_{step}^2 . Because the

mean step is zero, unbiased random walks are inherently nondirectional, although portions of such sequences may visually appear trended. Directional evolution was modeled as a generalization of the unbiased random walk that allows the mean step to be different from zero. (This model was called a general random walk by Hunt [2006].) Traits tend to increase over time when μ_{step} is positive, and decrease when μ_{step} is negative; when μ_{step} is exactly zero this model reduces to its special case, the unbiased random walk. Finally, following Sheets and Mitchell (2001b), we modeled stasis as uncorrelated Gaussian fluctuations around a static mean. Further details on these models, their parameterization, and their statistical properties can be found elsewhere (Hunt 2006, 2008a). This trichotomy of evolutionary modes is now standard (Raup and Crick 1981; Bookstein 1987; Gingerich 1993; Roopnarine 2001; Hunt 2006), but it does differ somewhat from the original formulation of Eldredge and Gould (1972), who did not recognize random walks as a distinct mode, and whose notion of stasis was broader, encompassing all cases for which lineages show little net change over time.

The three models considered here differ in their complexity; stasis and directional evolution have two parameters each, whereas an unbiased random walk has only a single parameter. Because more complex models generally have a log-likelihood advantage, we use the Akaike Information Criterion (AIC) as a measure of model support that balances goodness-of-fit and model complexity. This metric is computed as $-2\ln(L) + 2K$, where $\ln(L)$ is the log-likelihood and K is the number of free parameters in the model (Akaike 1974). We used the bias-corrected version of this metric, AIC_C , which is more appropriate when sample sizes are modest, as in the present analyses (Hunt 2006). The relative support for different models is conveniently summarized by converting AIC_C scores into Akaike weights. These weights sum to one across all candidate models, and are convenient measures of the relative evidential support each model receives (Anderson et al. 2000).

Because body-size trends were similar in the conjungens and diprosopum lineages (see

below), we performed additional analyses to test if they shared the same underlying evolutionary dynamics. We compared four models that differed as to whether evolutionary dynamics were (1) shared or separate across the two lineages, and (2) directional or random walks. Note that shared dynamics models do not correlate specific evolutionary changes, but rather assume that body size in these two lineages is evolving according to the same underlying rules (Hunt 2006).

To better understand the microevolutionary processes involved in shaping the evolution of these measured traits, we used the rate metric proposed by Lynch (1990) to compare the pace of evolutionary divergences with the expectation of neutral genetic drift. This metric, called Δ , can be computed from the maximum-likelihood estimate for the step variance of the unbiased random walk model: $\Delta = \sigma_{step}^2 / (2V_P)$. The numerator is the maximum-likelihood estimate of the step variance from the unbiased random walk model (Hunt 2006). In the denominator, V_P is the population phenotypic variance, estimated as the average sample variance pooled across all samples. Under genetic drift, Δ is governed by the rate of neutral mutational input and is expected to range between 5×10^{-5} and 5×10^{-3} (Lynch 1990). This range of Δ is based on per-generation mutational input, and time must therefore be measured in generations. We estimate that generation time for these lineages was approximately one to two years (e.g., Tyler-Walters 2007), and use the higher of these two figures in the calculations (results are unchanged if single-year generations are assumed instead). Calculated values of Δ that lie below or above the neutral range imply the action of natural selection. Low values suggest an evolutionary history with substantial intervals of stabilizing selection; values exceeding the neutral range likely result from diversifying selection. The formula given for Δ differs from the ANOVA-based calculations presented by Lynch (1990). This equation is equivalent, and follows from the finding that populations at mutation-drift equilibrium evolve as a random walk with a step variance equal to twice the phenotypic

variance introduced by mutation each generation (Lynch and Hill 1986).

The above methods treat sample ages as if they were known without error, but ages are approximations based on assigning strata to regional biozones, which are in turn correlated to global chronology. There are uncertainties in both steps of age determination, but it is difficult to constrain the exact nature of this uncertainty so that it may be incorporated formally into the statistical analysis (as in Hannisdal 2007). Instead, we explored with simple simulations the consequences of age-model error for our conclusions. We focused on the amount of elapsed time between adjacent samples because this is the relevant quantity in the likelihood calculations (Hunt 2006). These durations range from 0.2 to 1.9 Myr in the two analyzed lineages. For each time-series of trait values, we simulated 1000 new sequences with the same means, variances, and samples sizes, but with some error added to the elapsed times between adjacent samples. Errors were drawn from a uniform distribution that bracketed an observed duration by 50% of its value on either side. For example, the simulated values for an observed duration of 0.4 Myr were drawn uniformly between 0.2 and 0.6 Myr. This 50% value was chosen to be conservative as it implies a rather high degree of chronostratigraphic error.

Each analyzed sample does not necessarily represent a single time slice, but more typically represents a time-averaged aggregation across a biozone. It has been suggested that this aggregation has the potential to bias results in favor of directional evolution even when evolution is not truly directional (B. Hannisdal personal communication 2009). This might occur if time-averaging smoothes some of the true variability of evolutionary changes, and thus allows more of the evolutionary change to be ascribed to directionality. We explored this suggestion with simulations, using the observed sample sizes, ages, phenotypic variance, and evolutionary divergences of the trait eigenshape 2 in the conjungens lineage (this trait was chosen because it shows the strongest evidence for directionality, see below). We did find that,

for sequences with highly aggregated samples (i.e., each sample was drawn from populations spanning an entire biozone), there was an average increase in support for directional change over the unbiased random walk, relative to the situation in which each biozone was represented by a single population. However, the effect was not large: the mean difference in Akaike weight averaged 0.05. Moreover, the samples in both lineages under study were not so highly aggregated as this simulation implied, generally including individuals from only a few different sampling localities (conjugens median = 2, range from one to seven sites; diprosopum median = 1.5, range from one to three sites) and most localities include fossils from a single horizon only. When these modest levels of aggregation are incorporated into the simulations, model supports from the aggregated sequences do not differ from sequences that are simply subsampled without time-averaging (see also Hunt 2008a for model-selection performance under a variety of simulated conditions).

Results

General Morphospace Occupation in the Conjugens Lineage.—In the eigenshape analysis for the conjugens lineage, the first eigenshape describes the overall roundness or angularity of the shell outline and explains 71% of the overall variance. Specimens with low values for eigenshape 1 are generally smooth, rounded, and symmetrical in outline; specimens with high values are angular and asymmetrical, characteristically with a more elevated beak, a sharper posterior margin, and an elevated anterior corner to the hinge margin. Eigenshape 1 does not correlate strongly with any particular morphometric variable, but exhibits moderate correlations with ABP (0.40; the angle from the anterior tooth to the beak to the posterior tooth) and RelativeBeakHeight (0.54; the proportion of shell height represented by the beak and hinge).

Eigenshape 2 explains 10% of the overall variance and also describes overall shell shape. Specimens with low values for eigenshape 2 are boxy (length roughly equal to

height) with an elevated beak; specimens with high values for eigenshape 2 are more elongate and are relatively flat across the beak. Eigenshape 2 correlates strongly with Length/Height (0.71), RelativeBeakHeight (0.83), and HingeCurve (-0.60 ; the curvature of the posterior part of the hinge). Additional eigenshapes explain very small percentages of the overall variation, generally do not exhibit consistent change over time or among localities, and are difficult to characterize in terms of shell features.

The relative distinctiveness and position of conjugens lineage samples is shown in Figure 6, which plots a morphospace of shell height and eigenshape 2. The separation of samples from different biozones is readily apparent, as is the overall association between shape and size in this lineage.

Morphological Change through Time in the Conjugens Lineage.—Several characters exhibit apparently gradual change over the nearly 4-million-year interval examined. Foremost among these is shell size (Fig. 7A). Shell height exhibits a maximum of 17 mm in the oldest samples (conjugens zone), and increases to 73 mm in the dainellii zone. Although specimens in the upper zones are relatively few, the very robust samples sizes in the lower zones ensure that shell size early on was indeed considerably smaller than it was higher in the section. Thus, we see a greater than fourfold increase in shell size in the conjugens lineage.

Shell shape also changes dramatically in the conjugens lineage over time, and is well captured by several variables (Figs. 7B–D, 8). The second eigenshape and the second principal component exhibit the most consistent change over time (Fig. 7B,D). The principal components analysis of nine shape characters from the conjugens lineage generated four factors, which explain, respectively, 35%, 24%, 19%, and 12% of the original variance. Size measurements were left out of the analysis so that shape could be studied more directly. The principal components are defined by the following variables (variables that dominate PC loadings are indicated in parentheses, along with the sign of the relationship): PC1 (BPS[+], APS[+], PAS[–]); PC2 (Length/Height[–],

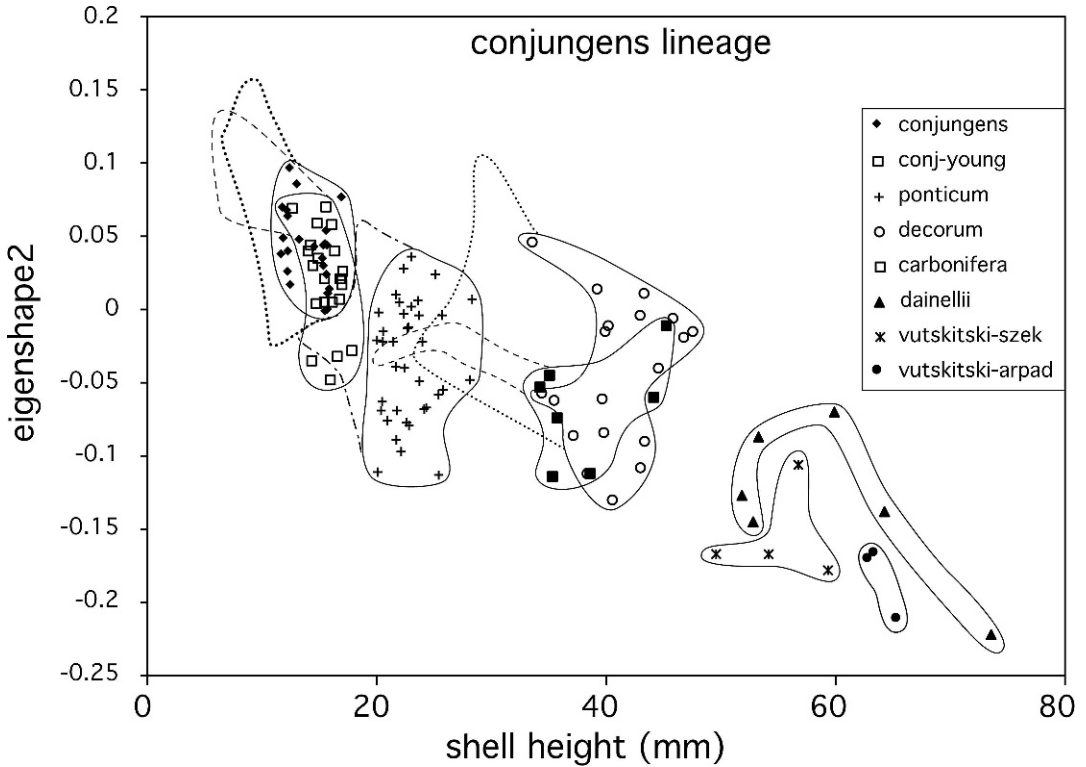


FIGURE 6. A representation of morphospace for the conjungens lineage. "Adult" shells (defined as all those individuals within a biozone whose size is at least 70% of the maximum for that zone) are plotted as individual symbols. Solid lines have been drawn around the adult specimens from each biozone. Dotted or dashed lines extending from each cloud encircle the morphospace occupied by juveniles from that biozone (those individuals that were excluded by the 70% cutoff). Samples from the conjungens zone are the oldest; those from the vutskitski zone are the youngest (see Fig. 4).

RelativeBeakHeight[+], HingeCurve[+]); PC3 (ABP[+], ABS[+]); PC4 (AnteriorLength/Length[+], hingeCurve[-]). Other multivariate variables exhibit weak to moderate directional change (PC4, eigenshape 4) or no net change (PC 1 and PC3, eigenshapes 1 and 3). PC1 is plotted here for comparison (Fig. 7C).

The morphometric variables that exhibit consistent and pronounced changes over time include Length/Height (Fig. 8A), RelativeBeakHeight (Fig. 8B), the proportion of the shell length that lies anterior to the beak (AnteriorLength/Length, Fig. 8C), and HingeCurve (Fig. 8D). Over time, shells become more boxy (less elongate), the beak becomes very pronounced and moves anteriorly, and the hinge becomes more curved.

The timing of change in different variables differs somewhat. For instance, Length/Height (Fig. 8A) appears to decrease steadily across the first four biozones and remain

static thereafter. HingeCurve, on the other hand, is static across the first three biozones and then increases steadily after that (Fig. 8D). Thus, although the overall effect appears gradual, the pattern of change differs among characters.

Testing Evolutionary Models in the Conjungens Lineage.—Relative statistical support for the three evolutionary models—directional evolution, random walk, and stasis—is summarized in Table 1. Size (as represented by log shell height) and two composite shape variables (HingeCurve and eigenshape 2) are best fit by the directional evolution model. Of these, the support for directional change is strongest for eigenshape 2; this model garners 90% of the Akaike weight for this sequence. Most other variables, including four measures of shape change that appear to change gradually (Fig. 8), show a mixture of support for both directional and unbiased random

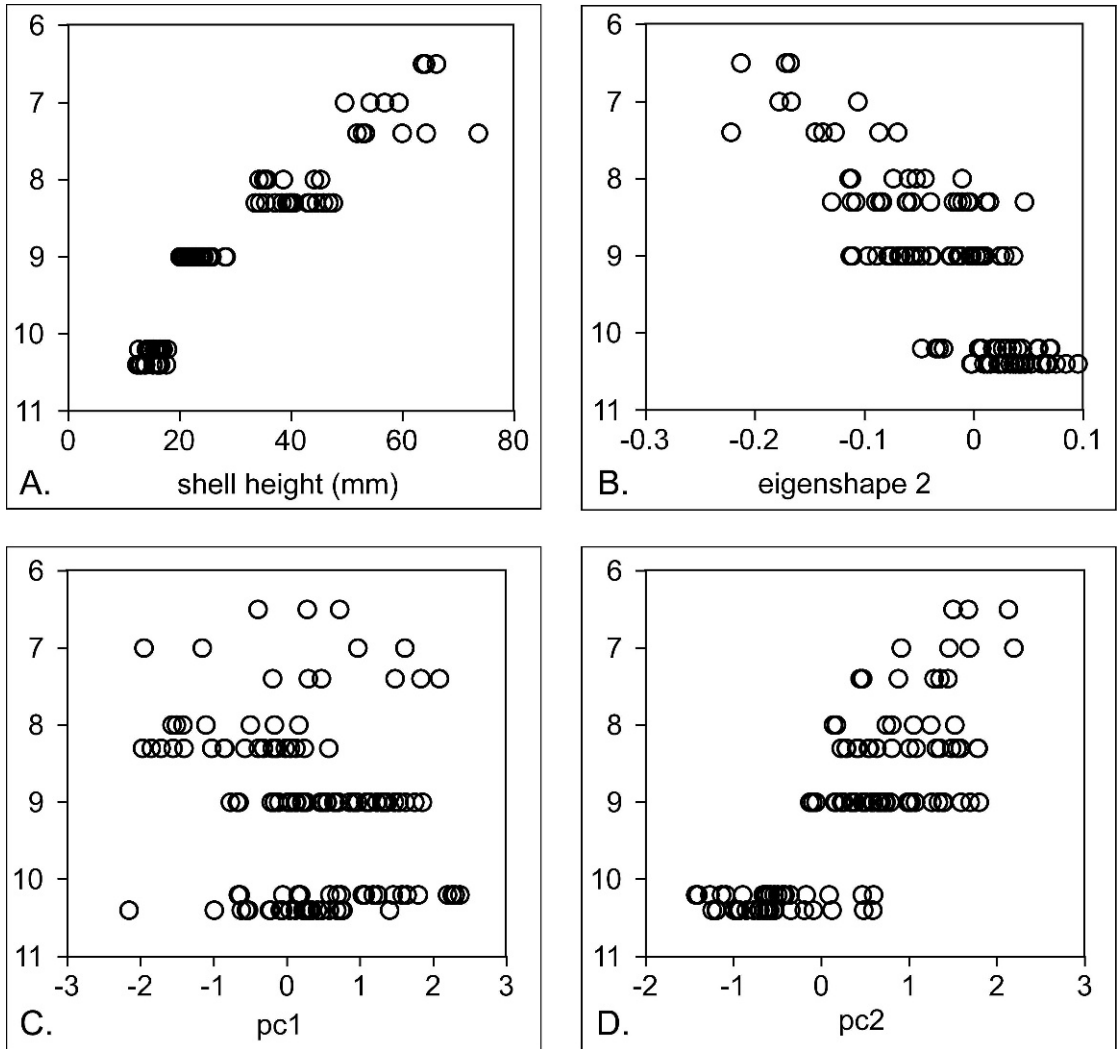


FIGURE 7. Size and multivariate shape change over time in the conjungens lineage. Vertical axis is age estimate in Ma. A, Shell height. B, Eigenshape 2. C, PC1. D, PC2. Log shell height, eigenshape 2, and PC2 are best fit to a model of directional change. PC1 is best fit by the stasis model.

walk models, usually with somewhat greater support for the latter (Table 1). In contrast, there is not much support for stasis; only two traits (PC1 and PC3) have more than marginal support for this model. This minimal support for stasis holds despite the fact that sampling error can exaggerate the support for stasis in evolutionary trajectories (Hannisdal 2006; Hunt 2008a). In general, the model-fitting results are not too sensitive to age-model error (Table 1). The same models garner significant support in the sequences with simulated age-model error as in the original data, although the exact Akaike weights can

shift 0.1 or 0.2 units depending on the details of the sample ages (Table 1). Similarly, model results do not appear sensitive to the value of the size cutoff used to define adults.

Calculation of Lynch's Δ reveals that all measured traits, even those with directional trends, evolve at a pace that is slower than the neutral expectation (Table 1).

General Morphospace Occupation in the Diprosopum Lineage.—A principal components analysis of nine shape characters (ABP, ABS, BPS, APS, PAS, Length/Height, RelativeBeakHeight, AnteriorLength/Length, and Hinge-Curve) from the diprosopum lineage generated

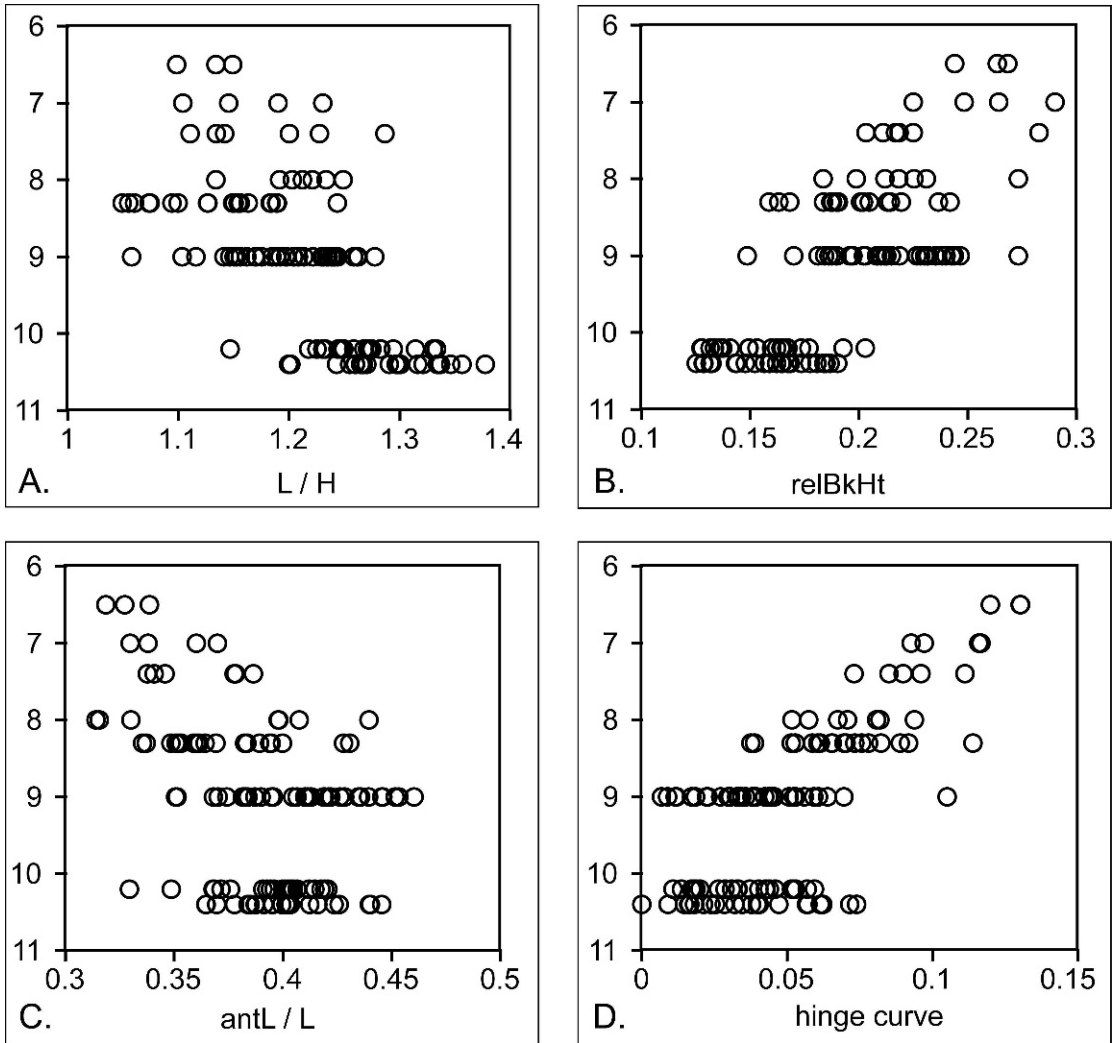


FIGURE 8. Shape character change over time in the conjungens lineage. Vertical axis is age estimate in Ma. A, L/H (ratio of shell length to height). B, Relative beak height. C, antL/L (ratio of anterior length to length). D, Hinge curve (see Fig. 5 caption). Despite the appearance of gradual change, these variables are best fit to the unbiased random walk model.

five factors, the first three of which explain, respectively, 40%, 28%, and 13% of the original variance. The principal components are defined by the following variables: PC1 (L/H[+], ABP[+], ABS[+]); PC2 (BPS+, APS+, PAS-); PC3 (antL/L[+], hingeCurve[-]).

Figure 9 is a representation of morphospace occupation in the diprosopum lineage using the first principal component and shell height (including adults only). As with the conjungens lineage, samples in the diprosopum lineage exhibit good separation in morphospace that is temporally consistent and corresponds to biozone.

Morphological Change through Time in the Diprosopum Lineage.—As in the conjungens lineage, several characters in the diprosopum lineage exhibit apparently gradual change. An increase in shell size is again the most obvious part of the pattern (Fig. 10A). Shell height exhibits a maximum of 12.6 mm in the oldest samples (conjungens zone) and increases to 44.4 mm in the youngest samples, representing a 3.5-fold increase.

In the eigenshape analysis for the diprosopum lineage, the first two axes explain 64.8% and 9.9% of the overall variance, and appear to describe overall shell roundness. Both

TABLE 1. Results of fitting evolutionary models to measured traits in the conjungens lineage. Given are the Akaike weights for each model, with the value for the best-supported model in bold. Directional evolution was modeled according to the general random walk model. Under the Akaike weight for the best-supported model are given the ranges of Akaike weights from the middle 90% of simulations that incorporate age model error (see text). Estimates of Δ are expected to range between 5×10^{-5} and 5×10^{-3} for neutral genetic drift; the rightmost column indicates that the pace of evolutionary changes in all variables is slower than the neutral expectation.

Trait	Akaike weights			Δ	Drift verdict
	Directional evolution	Unbiased random walk	Stasis		
Length/Height	0.201	0.620 (0.52, 0.67)	0.178	1.7×10^{-6}	Too slow
Ln Height	0.684 (0.44, 0.81)	0.315	0.001	1.4×10^{-5}	Too slow
RelativeBeakHeight	0.303	0.689 (0.64, 0.75)	0.007	1.7×10^{-6}	Too slow
HingeCurve	0.544 (0.37, 0.75)	0.455	0.001	1.1×10^{-6}	Too slow
AnteriorLength/Length	0.244	0.670 (0.59, 0.70)	0.086	5.4×10^{-7}	Too slow
Eigenshape 1	0.189	0.714 (0.64, 0.78)	0.097	1.3×10^{-7}	Too slow
Eigenshape 2	0.900 (0.72, 0.97)	0.099	0.000	1.2×10^{-6}	Too slow
Eigenshape3	0.108	0.777 (0.709, 0.808)	0.115	3.1×10^{-7}	Too slow
PC1	0.065	0.527 (0.36, 0.62)	0.408	1.5×10^{-6}	Too slow
PC2	0.397	0.595 (0.43, 0.71)	0.007	1.8×10^{-6}	Too slow
PC3	0.024	0.182	0.794 (0.71, 0.88)	3.5×10^{-6}	Too slow
PC4	0.217	0.716 (0.66, 0.74)	0.067	1.5×10^{-6}	Too slow

correlate strongly with Length/Height (0.89 and -0.82 , respectively) and ABP (0.77 and -0.65 , respectively).

As observed in the conjungens lineage, shells in the diprosopum lineage become more boxy (less elongate) over time (Fig. 3). Accompanying trends in the height and position of the beak observed in the conjungens lineage (RelativeBeakHeight and AnteriorLength/Length) are not observed in the diprosopum lineage. The morphometric variables that exhibit the most consistent and pronounced changes over time in the diprosopum lineage include the first principal component (Fig. 10B), the second eigenshape (Fig. 10C), the angle ABP (anterior cardinal tooth–beak–posterior cardinal tooth; Fig. 10D), and Length/Height (Fig. 10E). RelativeBeakHeight (Fig. 10F) and HingeCurve exhibit weak change over time.

Testing Evolutionary Models in the Diprosopum Lineage.—The statistical support for each of the three candidate modes of evolution in

the diprosopum lineage is presented in Table 2. Body size (log shell height) is best fit by a model of directional evolution, but all other traits are best accounted as unbiased random walks. Even those shape traits that visually appear to trend over time (eigenshape 2, PC1) garner little support for the model of directional evolution. The lack of support for the directional evolution and stasis models is mostly a consequence of the relatively few samples available for this lineage. Our measure of model support (AIC_C) has a parsimony penalty term that is particularly severe when sample size is low, so that the cost incurred going from one to two parameters is much greater when there are five evolutionary transitions (as in the diprosopum lineage) than when there are seven (as in the conjungens lineage). As a result, the unbiased random walk model receives most of the support because it has one parameter fewer than the other two models. Although six samples are sufficient

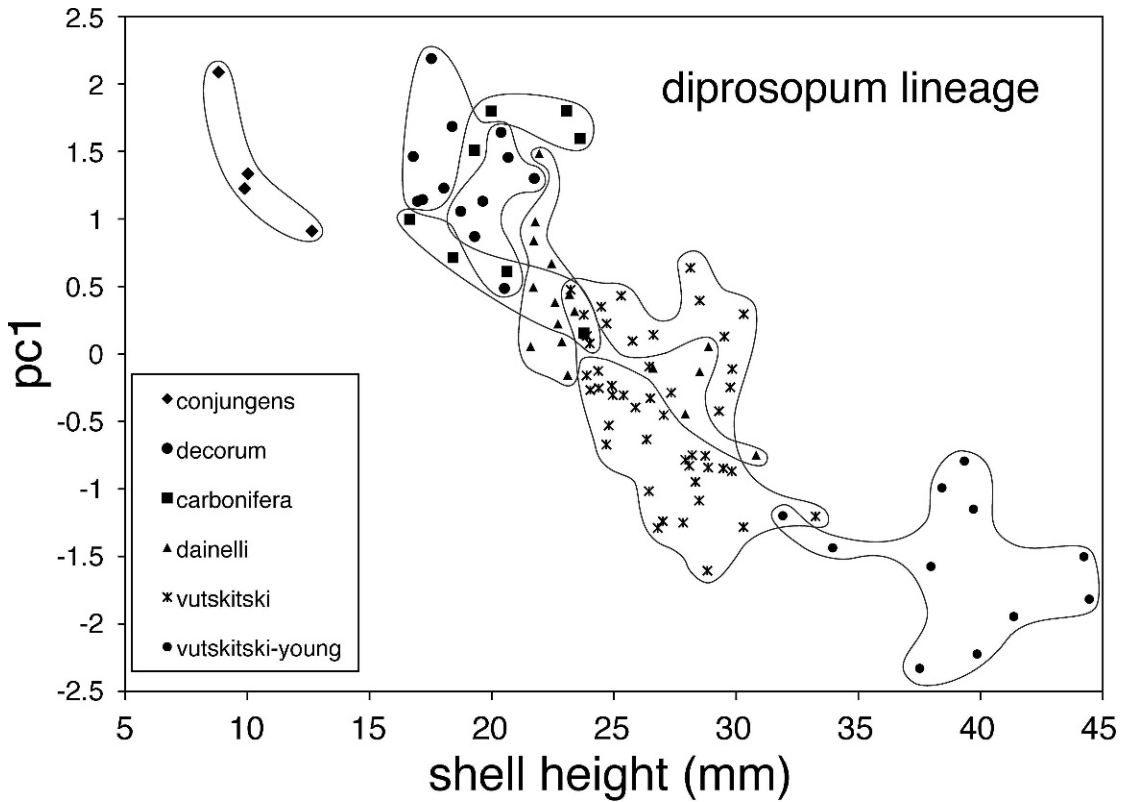


FIGURE 9. A representation of morphospace for the diprosopum lineage. Only “adult” shells are plotted, defined as all those individuals within a biozone whose size is at least 70% of the maximum for that zone. Samples from the conjugens zone are the oldest; those from the vutskitski zone are the youngest (see Fig. 4).

to document that substantial evolutionary divergence has occurred within a lineage, they are not enough to infer with confidence the nature of the underlying evolutionary dynamics. Because relative model fits for this lineage were not very informative, we did not perform simulations to explore age-model error.

As in the conjugens lineage, values of Δ for all measured traits in the diprosopum lineage indicate evolutionary changes slower than the neutral expectation (Table 2).

Body Size Dynamics in Both Lineages.—Parameter estimates for the general random walk model are similar for body size in both lineages; the directionality parameters (μ_{step}), in particular, are nearly identical (conjugens: 0.39 log units per Myr, diprosopum: 0.36 log units per Myr). This similarity in directionality is evident in the nearly parallel trends of body size over this interval (Fig. 11). This impression of similarity is borne out by more formal comparisons of evolutionary models

across the two sequences. Models that imply separate evolutionary dynamics between the lineages do not offer sufficient log-likelihood gains to compensate for their extra parameters, and together account for a negligible portion of the total Akaike weight (models 3 and 4, Table 3). By far the best-supported model indicates that the two lineages show similar, and inherently directional, evolutionary dynamics for body size (model 2, Table 3).

Discussion

Trends in paleontological data have long been a focal point for both investigation and controversy. Here we describe apparent trends in both size and shape in two bivalve lineages, some of which hold up under quantitative scrutiny, some of which do not. As Bell et al. (2006) emphasize, it is often difficult to reject neutral evolution, even when directional selection is the most likely mechanism at work (see also Hunt et al. 2008).

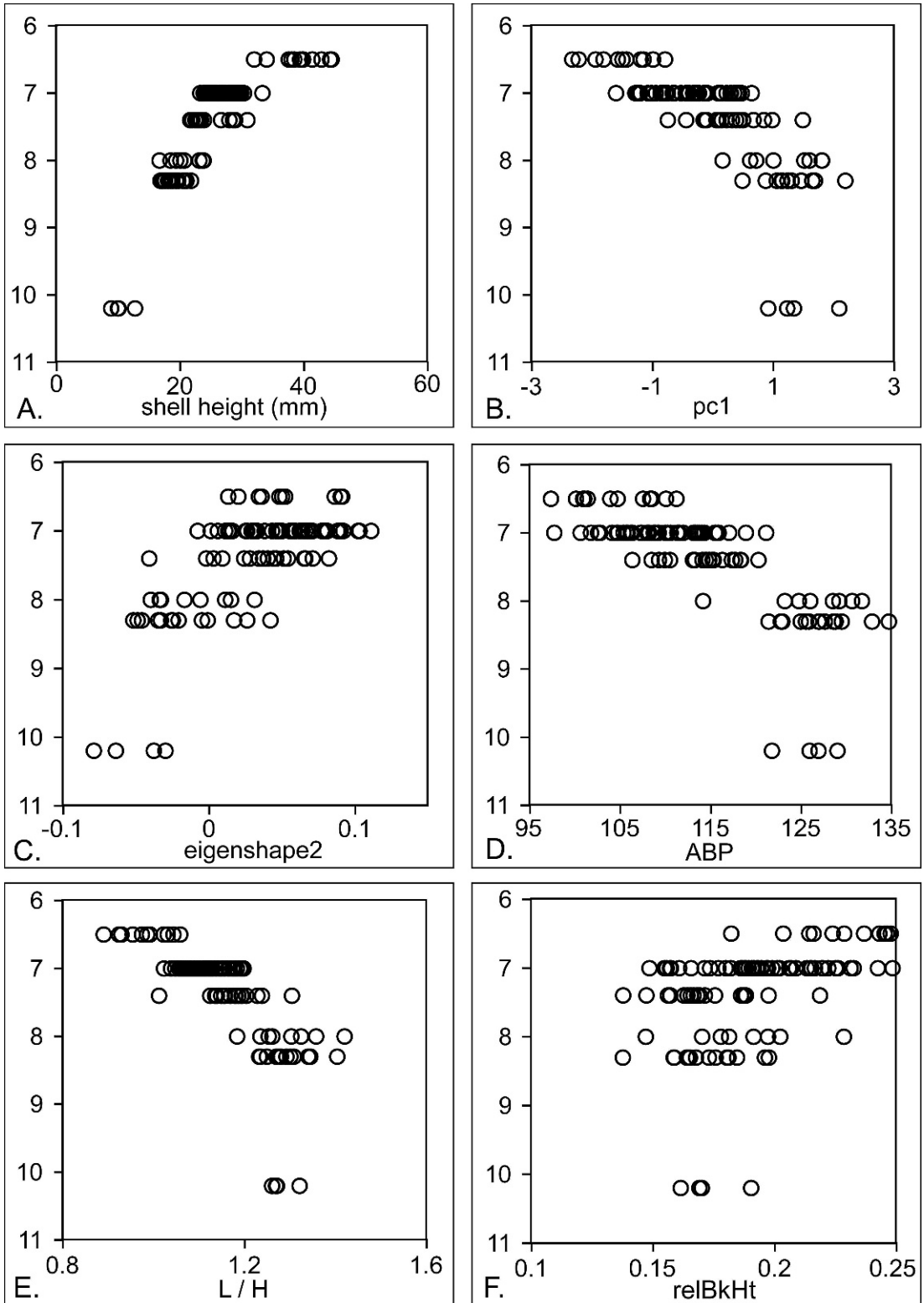


FIGURE 10. Size and shape change over time in the diprosopum lineage. Vertical axis is age estimate in Ma. A, Shell height. B, PC1. C, Eigenshape 2. D, ABP (angle, in degrees, from the anterior cardinal tooth-beak-posterior cardinal tooth). E, L/H (ratio of shell length to shell height). F, Relative Beak Height (portion of the shell height dorsal to and including the hinge). Despite the appearance of gradual change, all traits are best fit to the undirected random walk model.

TABLE 2. Results of fitting evolutionary models to measured traits in the diprosopum lineage. Given are the Akaike weights for each model, with the value for the best-supported model in bold. Directional evolution was modeled according to the general random walk model; conventions as for Table 1. Age model error results not presented because too few samples were available to reliably determine evolutionary mode.

Trait	Akaike weights			Δ	Drift verdict
	Directional evolution	Unbiased random walk	Stasis		
In Height	0.753	0.237	0.010	1.2×10^{-5}	Too slow
Length/Height	0.095	0.896	0.009	5.1×10^{-6}	Too slow
AnteriorLength/ Length	0.039	0.886	0.075	7.6×10^{-9}	Too slow
HingeCurve	0.032	0.884	0.085	2.3×10^{-6}	Too slow
RelativeBeakHeight	0.050	0.889	0.061	1.6×10^{-6}	Too slow
ABP	0.094	0.900	0.006	3.0×10^{-6}	Too slow
ABS	0.092	0.900	0.008	1.6×10^{-6}	Too slow
APS	0.048	0.896	0.056	3.2×10^{-7}	Too slow
BPS	0.029	0.786	0.185	2.7×10^{-7}	Too slow
PAS	0.034	0.879	0.087	1.6×10^{-7}	Too slow
Eigenshape 1	0.048	0.941	0.010	4.1×10^{-6}	Too slow
Eigenshape 2	0.191	0.798	0.010	9.5×10^{-7}	Too slow
Eigenshape 3	0.039	0.785	0.177	1.8×10^{-8}	Too slow
Eigenshape 4	0.035	0.865	0.100	4.6×10^{-6}	Too slow
PC1	0.132	0.861	0.007	3.4×10^{-6}	Too slow
PC2	0.026	0.706	0.268	2.4×10^{-7}	Too slow
PC3	0.034	0.813	0.153	1.4×10^{-6}	Too slow

For some of the cases presented here, the lack of support for the model of directional evolution may be partly related to the nature of the AIC_C , which imposes large penalties for additional parameters at low n . Thus, for short sequences, the log-likelihood advantage of the directional evolution model must be very large to overcome its substantial parsimony penalty relative to the unbiased random walk. Never-

theless, it is also likely that many apparently trended sequences are more plausibly explained by the unbiased random walk because the underlying dynamics are not strongly directional. Sampling additional strata, or improved correlations that would enable finer subdivision of existing stratigraphic zones, would permit more confident determinations of evolutionary dynamics in these lineages.

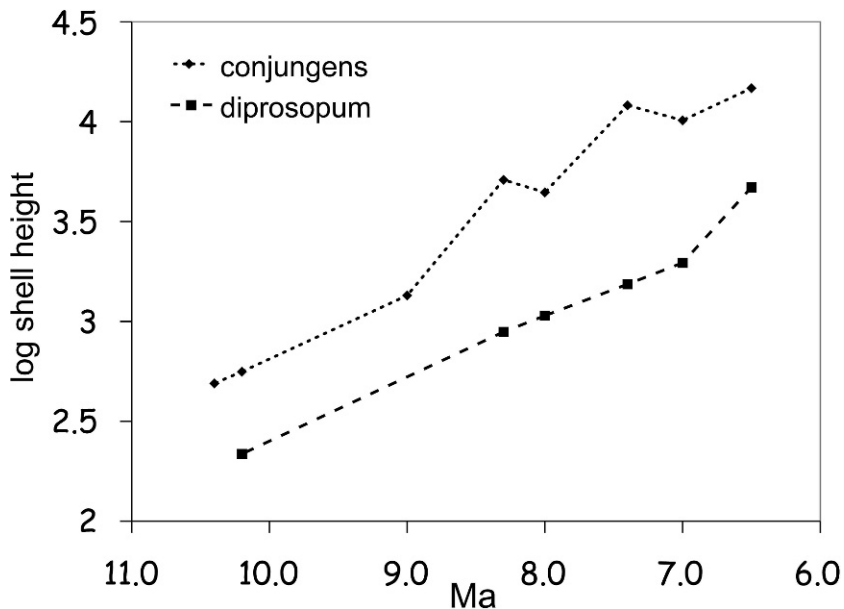


FIGURE 11. Log shell height over time in the two lineages, showing their parallel trajectories.

TABLE 3. Results of fitting evolutionary models to body size evolution in the conjungens and diprosopum lineages. The models differed according to whether evolution dynamics were the same (shared) or different (separate) in the two lineages, and whether evolution was directional (general random walk) or not (unbiased random walk). The Akaike weight for the best-supported model is in bold. K = the number of parameters in the models; $\ln(L)$ is the log-likelihood.

No.	Evolutionary model	K	$\ln(L)$	AIC _C	Akaike weight
1	Dynamics shared & nondirectional	1	-1.08	4.55	0.006
2	Dynamics shared & directional	2	5.45	-5.57	0.957
3	Dynamics separate & nondirectional	2	-1.04	7.40	0.001
4	Dynamics separate & directional	4	6.33	1.06	0.035

Evolution of body size and some shape traits in the conjungens lineage are gradual in the sense of exhibiting significant trends over time. In addition to directionality, the term “gradual” sometimes is taken to imply an evolutionary dynamic that is smoothly continuous, rather than punctuated (e.g., Fortey 1985). Models of punctuated evolution can be evaluated within an AIC-based framework, but they require sequences with more samples than those analyzed here (Hunt 2008b: p. 364). Therefore, although these data indicate substantial and directional evolution in some traits, they are not extensive enough to evaluate claims about the continuity or homogeneity of evolution.

Ecophenotypy is always a concern when dealing with fossil sequences, but we do not believe it contributes in any significant way to the patterns we describe here. This assertion is based principally on the magnitude of the observed morphologic change, which greatly exceeds what is typical for ecophenotypy (e.g., Wilk and Bieler 2009); in units of within-population standard deviations, net size changes are 15 units (conjungens lineage) and 13 units (diprosopum lineage), whereas the largest shape differences are 6 units (eigenshape 2 in the conjungens lineage) and 5 units (PC1 in the diprosopum lineage). Furthermore, these changes are not ephemeral, nor are they correlated with any lithologic, geographic, or paleoecologic variable that might be indicative of facies (see Geary 1992).

The Paradox of Gradualism.—The sequences analyzed here illustrate well the apparent paradox of gradual change. On the one hand, we see strong support for changes in size and shape that are directional. Furthermore, the parallel nature of size change in the two lineages is consistent with a shared response

to a common cause, presumably from a change in their shared environment. Calculation of Lynch’s Δ for these sequences, however, yields rates of evolution too slow for sustained directional selection or even drift to be the cause. Thus, the change would seem to be driven by directional selection, but the required selective advantage is unrealistically small when stretched over millions of years.

This juxtaposition of results also suggests a possible resolution to the paradox, a resolution best envisioned with the aid of the adaptive landscape (Simpson 1944; Arnold et al. 2001). It is clear that traits often have intermediate optima (Travis 1989; Schluter 2000; Kingsolver et al. 2001; Benkman 2003; Brooks et al. 2005; Pfennig et al. 2007), and that populations can climb adaptive peaks quickly, even on ecological time scales (e.g., Reznick et al. 1997; Thompson 1998; Hendry and Kinnison 1999; Huey et al. 2000; Kinnison and Hendry 2001; Thomas et al. 2001; Carroll et al. 2007; Hunt et al. 2008). At geologic time scales, however, the pace of change within lineages is more likely determined by the dynamics of the adaptive peaks themselves, rather than the ability of any population to move across the landscape. Thus, whereas the population-genetic drivers (selection, drift) that control the movement of populations on adaptive peaks are constrained to result in rates of change that fall within certain limits, the ecological or physical drivers of peak movements are under no such constraints. In this view, the abundance of fossil sequences that exhibit stasis and random-walk patterns, and the rarity of long-term directional change (Hunt 2007) largely reflect the temporal dynamics of selective conditions; fossil species seldom show sustained directional change because environmental and biotic

conditions usually do not change gradually in the same direction for millions of years. This claim can be tested by compiling and analyzing modes of change in paleoenvironmental proxies and biotic conditions over time scales similar to the durations of species.

If the pace of change is dictated by the forces that determine peak movements, the phenomenon of geologically gradual change no longer represents a paradox per se, but leads instead to two important questions. First, what factors resulted in the desultory yet ultimately consistent directional peak movements over time? The answers here presumably lie in the realm of paleoenvironment and/or paleoecology, and are discussed below.

Ironically, the second question relates to the maintenance of stasis (the issue Gould and Eldredge always maintained was the most unorthodox component of punctuated equilibrium [e.g., Gould and Eldredge 1986]). If the overall rate of change is viewed as the result of faithful tracking of adaptive peaks, and if populations respond whenever the peak they are on happens to move, what keeps them on the peak for those extremely long intervals in between? The slower-than-drift divergences observed here have been noted in many other paleontological studies (e.g., Cheetham and Jackson 1995; Clegg et al. 2002; Bell et al. 2006; Hunt 2007), and there exists no shortage of views as to the mechanisms responsible, including stabilizing selection (Estes and Arnold 2007), possibly in conjunction with habitat tracking (Eldredge 2003), genetic or other constraints (Eldredge and Gould 1972; Hansen and Houle 2004), and spatially structured populations (Lieberman et al. 1994, 1995; Lieberman and Dudgeon 1996; Eldredge et al. 2005).

Environmental Context.—With respect to possible environmental drivers, temperature and/or salinity should be promising candidates for physical drivers across this time interval; the late Miocene is an interval of global cooling, and younger faunas from Lake Pannon are of a considerably fresher water character than are early faunas. Studies of oxygen isotopes in Lake Pannon shell material over the interval ca. 10–7 Ma reveal decreases in $\delta^{18}\text{O}$ ranging from 0.2 to 4–6‰

(Geary et al. 1989; Mátyás et al. 1996; Harzhauser et al. 2007; Geary unpublished data), which may reflect changes in humidity and the isotopic composition of inflow rather than decreases in salinity or increases in temperature (Mátyás et al. 1996). Thus, even though cooling temperatures would fit with global paleoclimate patterns and with the general association of large body size with cooler temperatures (“Bergmann’s Rule” [for examples and discussion of this phenomenon in ectotherms, see Strauch 1968; Van Voorhies 1996; Partridge and Coyne 1997; Huey et al. 2000; Angilletta et al. 2004]), there is no direct evidence for consistent cooling in Lake Pannon environments from ca. 10–7 Ma (and in fact isotopic data trend in the wrong direction). With respect to salinity, faunal patterns suggest that the overall freshening of lake waters happened in several major steps rather than steadily over this interval.

The overall stratigraphic context for this interval involves an ongoing infilling of the basin, but this basinwide situation is not reflected in a systematic shallowing-upward of our fossil-bearing localities. All of our samples come from comparable paleodepths, irrespective of their stratigraphic position. We observe no systematic facies differences or trends in grain size that might correlate with the morphological patterns described here.

The interval of gradual morphologic change in the conjungens and diprosopum lineages began during a time of relatively high humidity, subsequently crossed a significantly drier interval (including the Vallesian Crisis), and then continued into a succeeding interval of slightly increased moisture (Lueger 1978; Mátyás et al. 1996; Fortelius et al. 2006; Ivanov et al. 2006; Kovac et al. 2006; Nargolwalla et al. 2006; van Dam 2006). Thus, changes in humidity and their attendant influence on food availability seem an unlikely driver for unidirectional peak shifts across this interval.

Another possible selective mechanism for larger size is the introduction of a predator, the best escape from which can be the attainment of a large (unwieldy) body size. Although we cannot rule out this possibility, there is no supporting evidence for intense

predation pressure on the mollusks of Lake Pannon (such as numerous broken, peeled, or repaired shells), nor is there direct evidence of abundant predators (very few fish or crustacean fossils).

In the absence of an obvious environmental driver, we suggest that whatever the surrounding climatic conditions, the local lacustrine environment was generally highly favorable for these bivalves. In bivalves, larger size is generally correlated with greater fecundity (Jablonski 1996). One disadvantage of large size is the attendant delay in reproduction necessary to reach it (although this is not always the case [e.g., Seed and Brown 1977]). In general, selection favoring larger size should result when conditions change so that organisms can grow faster, such as with an increased food supply, or mortality rates decrease (Kozłowski and Teriokhin 1999), as with, for example, decreasing frequencies of physical disturbance or increasing suitable habitat. In other words, the disadvantage of delayed reproduction is more likely to be outweighed by the advantage of greater ultimate fecundity when local conditions are stable and favorable (e.g., Gould 1977). In Lake Pannon, long-term favorability may have slowly shifted adaptive peaks so as to result in the directional patterns we observe.

Hypotheses about the factors contributing to size increase in these lineages can be tested with data on the relative contributions of elevated growth rate and greater longevity to larger size in these and other lineages; such data are available through sclerochronologic analysis (work in progress). In addition, taking a more comprehensive view of both environmental proxies and morphologic patterns in a wider variety of molluscan lineages may help narrow the range of possible contributing factors.

Summary

1. We describe morphologic patterns in two lineages of lymnocardiid bivalves, both of which exhibit size increase and shape change over an interval of nearly 4 million years. The size increases and changes in

many shape variables visually appear gradual over time. When evaluated according to the models of Hunt (2006), size and two shape variables in the conjungens lineage are best fit by a model of directional evolution; most other shape variables in this lineage conform to unbiased random walks. Body size in the diprosopum lineage is significantly directional, but all shape variables are best fit by the unbiased random walk model. The small number of sampling intervals available for this lineage ($n = 6$) makes determination of the actual pattern difficult.

2. When measured as Lynch's Δ , the pace of phenotypic change is slower than the neutral expectation for all size and shape traits in both lineages.
3. Size increases in the two lineages (as measured by log shell height over time) exhibit parallel trajectories, suggesting comparable directionality. We tested this possibility by fitting a set of models to the two sequences. The data strongly support the model in which evolutionary dynamics are shared and directional across the two lineages, suggesting that the size increases may be a shared response to the same cause.
4. These lineages exemplify the paradox of gradualism; they exhibit significant directional morphologic evolution but rates of change as measured over the long term are apparently too slow for directional selection or even drift to be the cause. We propose that the paradox can be resolved by considering that intervals of directional selection occurred during times of peak movement and resulted in the overall trends we detect. These intervals were interspersed with intervals of stasis during times of peak stability, the overall result of which is rates of change that appear slower than the neutral expectation. The movement of adaptive peaks is not restricted in rate (as are population-genetic drivers of change) and may proceed at a geologically gradual pace.
5. We can identify no environmental parameter that exhibits consistent change across the interval of gradual morphologic

change. We speculate that the long-term persistence of generally ameliorating conditions (plentiful resources and habitat space, few predators or competitors) resulted in geologically slow but consistent peak shifts, in turn facilitating size increase and shape change in these lineages.

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Appendix

Age estimation, locality, and sample size for each biozone.

Biozone	Age (Ma)	Locality	<i>n</i> (adults)
Conjungens lineage			
Conjungens (older)	10.4	Vösendorf, Austria	22
		Hennersdorf, Austria	2
Conjungens (younger)	10.2	Stegersbach, Austria	19
		Boghis/Szilagybagos, Romania	3
Ponticum	9.0	Dáka, Hungary	20
		Ukk, Hungary	6
		Fehérvárcsurgo, Hungary	5
		Lázi, Hungary	2
		Zalagalsa, Hungary	2
		Neszmély, Hungary	1
		Tuskevar, Hungary	1
Decorum	8.3	Radmanesti, Romania	13
		Kőbánya, Hungary	4
		Criciova, Romania	1
		Tihany, Hungary	1
Carbonifera	8.0	Oresac, Serbia	6
		Kőtcse, Hungary	1
Dainellii	7.4	Bátaszék, Hungary	3
		Királykegye, Romania	2
		Okrugljak, Croatia	1
Vutskitsi (older)	7.0	Szekszárd, Hungary	4
Vutskitsi (younger)	6.5	Pecs-Nagyárpád, Hungary	3
Diprosopum lineage			
Conjungens	10.2	Grosshöflein, Austria	2
		Boghis/Szilagybagos, Romania	1
		Husino, Bosnia-Herzegovina	1
Decorum	8.3	Radmanesti, Romania	14
Carbonifera	8.0	Ádánd, Hungary	7
		Jugovo, Serbia	1
Dainellii	7.4	Bátaszék, Hungary	16
		Okrugljak, Croatia	2
Vutskitsi (older)	7.0	Szekszárd, Hungary	50
Vutskitsi (younger)	6.5	Pecs-Nagyárpád, Hungary	12