Limits in the evolution of biological form: a theoretical morphologic perspective

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Limits in the evolution of biological form can be empirically demonstrated by using theoretical morphospace analyses, and actual analytic examples are given for univalved ammonoid shell form, bivalved brachiopod shell form and helical bryozoan colony form. Limits in the evolution of form in these animal groups can be shown to be due to functional and developmental constraints on possible evolutionary trajectories in morphospace. Future evolution-limit research is needed to analyse the possible existence of temporal constraint in the evolution of biological form on Earth, and in the search for the possible existence of functional alien life forms on Titan and Triton that are developmentally impossible for Earth life.

1. Limits in evolution: analytic examples

Actual analytic examples of limits in the evolution of biological form in theoretical morphospaces are given in figures 1–3, summarized in table 1, and are discussed in this section of the paper. Theoretical morphospaces are ‘n-dimensional geometric hyperspaces produced by systematically varying the parameter values of a geometric model of form’ [2] and are particularly useful in the analysis of limits in evolution in that they contain computer simulations of both existent and non-existent biological form and hence contain the limit boundary between those two regions of the morphospace (for an overview of the technique of theoretical morphospace analysis, see [1,2]).

In figure 1 is given a two-dimensional plane within a four-dimensional theoretical morphospace of computer-simulated planispiral univalved shell forms created by Raup [3] for the analysis of evolution in ancient nektonic cephalopods. The two dimensions of the space are $W$, the whorl expansion rate of the shell, and $D$, the distance from the coiling axis to the aperture of the shell (for a detailed discussion of the morphospace, see [1]). This morphospace was used by Raup [3] in the analysis of 405 species of ammonoids (Mollusca: Cephalopoda: Ammonoidea), and by Saunders et al. [4] in the analysis of an additional 597 species. Their combined analyses revealed that those shell geometries contained within the polygon boundaries illustrated in the lower left corner of figure 1 exist in actual ammonoids—all other simulated shell forms are geometrically possible but are non-existent in these ancient nektonic cephalopods.

Why did the ammonoids evolve some geometrically possible shell forms but not others? The polygonal boundary line shown in figure 1 maps a hydrodynamic limit to the evolution of shell forms by the nektonic cephalopods within the theoretical morphospace (table 1). Chamberlain [5] measured drag coefficients in flume experiments with model shell forms that have been used to calculate a swimming-efficiency coefficient (SEC) for all of the shell geometries shown in figure 1. All shell forms evolved by the ammonoids have a minimum limit of $SEC = 40$; all shell geometries outside of the polygon in figure 1 have SEC values less than this limit (for example, the non-existent ammonoid shell form shown at the coordinates $W = 3.5, D = 0.5$ has $SEC = 8$).

Not surprisingly, this same hydrodynamic limit holds for shell forms of the other major clade of nektonic cephalopods, the nautiloids (Mollusca: Cephalopoda: Nautiloidea). For example, the convolute shells of the living Nautilus...
have $W = 3.4$ and $D = 0.04$ [3] and are very similar in appearance to the shell form shown at coordinates $W = 3.5$, $D = 0.1$ within the polygon boundaries in figure 1.

A second example of limits in evolution is given in figure 2, which illustrates a plane within a seven-dimensional theoretical morphospace of planispiral bivalved shell forms created for the analysis of evolution in brachiopods [1]. The two dimensions of the space are logarithms of the whorl expansion rate, log $W$, for the dorsal and ventral valves of the brachiopod shell. This morphospace has been used in the analysis of 324 species of biconvex brachiopods (Brachiopoda: Rhynchonelliformes: Rhynchonellata) and has revealed that those shell forms contained within the polygon boundaries illustrated in the centre of figure 2 exist in biconvex brachiopods. As with the ammonoid shell forms, simulated shell forms outside of the polygon are geometrically possible but are non-existent in biconvex brachiopods.

Why do the biconvex brachiopods evolve some geometrically possible shell forms but not others? The polygonal boundary line shown in figure 2 actually maps two separate limits to the evolution of shell forms by biconvex brachiopods within the theoretical morphospace (table 1). The first is an internal volume limit: biconvex brachiopods use a tentacular pumping and feeding organ, the lophophore, to partition the interior of their shells into inhalent and exhalent filtration chambers for the purpose of filter-feeding seawater. The lophophore is coiled in a variety of three-dimensional geometries in living and fossil biconvex brachiopods, and all lophophore coil geometries require sufficient internal shell volume, $V$, to be contained within the external surface area, $SA$, of the shell—a proportion that is measured by a volume-to-surface-area ratio, $V/SA$ [1]. All shell forms evolved by the biconvex brachiopods have a minimum limit of $V/SA = 7$; shell form geometries with $V/SA$ ratios below this limit are non-existent in biconvex brachiopods (for example, the non-existent biconvex brachiopod shell form shown at coordinates dorsal log $W = 13$, ventral log $W = 13$ has $V/SA = 5.5$).

Table 1. Limits in the evolution of cephalopods, brachiopods and bryozoans.

<table>
<thead>
<tr>
<th>Category</th>
<th>Limit Description</th>
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<tbody>
<tr>
<td>Swimming cephalopod shell forms</td>
<td>Hydrodynamic limit: minimum SEC $= 40$ for functional shell forms</td>
</tr>
<tr>
<td>Biconvex brachiopod shell forms</td>
<td>Internal volume limit: minimum volume-to-surface-area ratio $= 7$ for functional shell forms</td>
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<td></td>
<td>Whorl overlap limit: minimum dorsal log $W = 3$, ventral log $W = 2$, for functional shell forms</td>
</tr>
<tr>
<td>Helical bryozoan colony forms</td>
<td>Filtration efficiency limit: minimum colony SAI $= 0.5$ and BDI $= 25$ for functional colony forms</td>
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<tr>
<td></td>
<td>Hydraulic resistance limit: maximum colony SAI $= 7$ and BDI $= 60$ for functional colony forms</td>
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</tbody>
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Figure 1. A theoretical morphospace of computer-simulated ammonoid shell form, where the forms shown within the limits of the polygon boundary in the lower left corner of the figure actually exist in ammonoid cephalopods. Adapted from McGhee [1].

Figure 2. A theoretical morphospace of computer-simulated brachiopod shell form, where the forms shown within the limits of the polygon boundary in the centre of the figure actually exist in biconvex brachiopods. Adapted from McGhee [1].

Figure 3. A theoretical morphospace of computer-simulated helical bryozoan colony form, where the forms shown within the limits of the polygon boundary in the centre of the figure actually exist in helical bryozoans. Adapted from McGhee [1].
Unlike univalved ammonoid shell forms (figure 1), the shell of a brachiopod consists of two separate univalves articulated together (figure 2). This bivalved shell geometry brings us to the second limit in brachiopod evolution: whorl overlap must be absent in both valves of the shell in order for them to be articulated together. Whorl overlap in a univalve occurs whenever $W \times D \leq 1$ (for example, examine the ammonoid shell at coordinates $W = 1.5$, $D = 0.3$ in figure 1 in which the whorls of the shell overlap as $W \times D = 0.45$). It is advantageous for the brachiopod to have low values of $W$ in both valves of the shell as this produces a shell geometry with high values of $V/SA$, yet the brachiopod is limited to values of $W < 1/D$ in its valves because of whorl overlap. For example, the shell at coordinates dorsal log $W = 3$, ventral log $W = 2$ in figure 2 has $V/SA = 11$, and this $V/SA$ value is the maximum possible in the morphospace as all shells with lesser values of $W$ have whorl overlap (as illustrated by the rows of whorl-overlapped unarticulated valves in figure 2, and the two computer simulations in the lower left corner of the morphospace which illustrate impossible geometries in which the whorls of each valve of the shell interpenetrate one another, with the shell material of each valve occupying the same space at the same time in the posterior part of the shell). As biconvex brachiopods typically have dorsal valves with $D = 0.01$ and ventral valves with $D = 0.1$, they are limited to a minimum dorsal log $W = 3$, ventral log $W = 2$ for functional shell forms (figure 2 and table 1).

One last analytic example of limits in evolution is given in figure 3, which illustrates computer simulations in two dimensions of a three-dimensional theoretical morphospace of helical bryozoan colony forms created for the analysis of their evolution by McKinney & Raup [6] and Raup et al. [7]. The two dimensions of the space are ELEV, the rate of climb of the central helix of the colony, and BWANG, the angle between the helix axis and the filtration-sheet whorls of the colony. Helical colony forms have been convergently evolved by several clades of bryozoans, as seen in species of the genera *Archimedes* (Bryozoa: Stenolaemata: Fenestellidae), *Crisalidomenea* (Bryozoa: Stenolaema: Cyclostomata: Crisidae), *Bugula* (Bryozoa: Gymnolaemata: Cheilostomata: Bugulidae) and *Retiflustra* (Bryozoa: Gymnolaemata: Cheilostomata: Flustoidae: Flustriidae). The analysis of 207 colonies of 26 species of these convergent bryozoan colonies [8–10] has revealed that those colonies contained within the polygon boundaries illustrated in the centre of figure 3 exist in helical bryozoans even though, as for the ammonoids and brachiopods, computer simulations reveal that other colony geometries are possible but have never been evolved by the bryozoans.

Why have the bryozoans convergently evolved some geometrically possible helical colony forms but not others? Unlike ammonoid and brachiopod individually shelled animals, the helical bryozoans are colonies of thousands of tiny individual zooids arranged along the branches in the filtration-sheet whorls of the colony. Like the brachiopods, the bryozoans are also lophophorate filter feeders but now, instead of the geometric arrangement of one lophophore within one brachiodp shell form, the geometric arrangement of thousands of tiny lophophores determines the form of the helical colony. Two aspects of the geometric arrangement of the zooids within the colony are measured by a colony surface area index (SAI) and a branch density index (BDI), and analyses have revealed that helical bryozoan colonies maintain minimum limits of SAI = 0.5 and BDI = 25, and maximum limits of SAI = 7 and BDI = 60 [8–10].

The minimum limits of SAI = 0.5 and BDI = 25 appear to be filtration efficiency limits (table 1) in that colonies with colony surface areas and branch densities less than those limits simply do not catch or intercept enough food across their filtration sheets to support the metabolic needs of the colony (i.e. too much water escapes unfiltered through the colony). The maximum limits of SAI = 7 and BDI = 60 appear to be hydraulic resistance limits (table 1) in that colonies with colony surface areas and branch densities higher than those limits impede the flow of water through the colony [11] and dead zones of stagnant water develop within the colony centre (see discussion in [1]). For example, the non-existent colony geometry at coordinates ELEV = 0.50, BWANG = 90 in figure 3 has SAI < 0.5 and, at the other extreme, the non-existent colony geometry at coordinates ELEV = 0.20, BWANG = 10 has SAI = 15.

2. Limits in evolution: theoretical possibilities

The observed empirical limits in the evolution of actual animals illustrated in figures 1–3 are abstracted to theoretical limits in a theoretical morphospace in figure 4. Two types of limit in the evolution of biological form are graphically portrayed within the morphospace of hypothetical forms: limits due to functional constraint (the boundaries of the solid-line rectangle) and limits due to developmental constraints (the boundaries of the dotted-line rectangle). Empirical examples of actual functional constraint limits are illustrated in figures 1–3; these are the hydrodynamic, internal volume, filtration efficiency and hydraulic resistance limits (table 1) discussed in the previous section of the text. Biological forms shown within the limit boundaries shown in figures 1–3 are functional for the animals analysed, forms outside the limit boundaries are not.

An empirical example of an actual developmental constraint limit is seen in the brachiopod whorl overlap limit (figure 2 and table 1). The region of morphospace outside the whorl overlap limit does not contain non-functional forms; rather, this region contains *geometrically impossible*
forms. That is, it is impossible for a brachiopod to develop these forms at all—the question as to whether they are functional or non-functional is moot.

The mapping of the functional and developmental limit boundaries in figure 4 allows us to discern a Venn diagram of four distinct sets of theoretical forms within the morphospace [12]:

1. Form set \( \{f:0\} \): these are the forms, \( f, 0 \), that are non-functional and cannot be developed by life on Earth.
2. Form set \( \{f:1\} \): these are the forms, \( f, 1 \), that are both functional and that can be developed by life on Earth (the shaded region in figure 4).
3. Form set \( \{f:2\} \): these are the forms, \( f, 2 \), that can be developed but that are non-functional and thus lethal for life on Earth.
4. Form set \( \{f:3\} \): these are the forms, \( f, 3 \), that are functional but that cannot be developed by life on Earth.

Empirical examples of members of the form set \( \{f:1\} \) can be seen in all those forms located within the functional-limit polygon boundaries illustrated in figures 1–3, and examples of members of form set \( \{f:2\} \) can be seen in those simulated forms located outside of the functional-limit polygon boundaries. The morphospace region located outside the whorl overlap developmental limit in figure 2 illustrates an empirical example of the morphospace coordinates for members of the form set \( \{f:0\} \). What is not illustrated in figures 1–3 are hypothetical members of theoretical form set \( \{f:3\} \): forms that are functional but that nevertheless cannot be developed by life on Earth. Does such a set of forms actually exist? This is a question that will be considered in the next section of the paper.

A second question recently has been raised by Powell & Mariscal [13], who have argued for the subdivision of form set \( \{f:1\} \) to recognize a new subset of forms:

1. Form subset \( \{f:4\} \): these are the forms, \( f, 4 \), that are functional, developmentally possible, and that actually have been evolved by life on Earth.

The boundaries of the new subset of forms \( \{f:4\} \) within the theoretical morphospace is illustrated by Powell & Mariscal [13] in figure 5. Note that they have drawn these boundaries such that the morphospace region occupied by the members of this form subset is quite small. Powell & Mariscal [13] argued that Gould’s [14] ‘radical contingency thesis’ predicts ‘smaller boundaries around the space of forms that are functional, developmentally possible, and actual’. Gould [14] argued that all evolutionary trends are chains of historically contingent events, and since the actual functional biological forms that have been discovered by evolution are a function of past contingent events there could exist numerous other functional forms that have not yet been discovered purely as a function of history. This concept is older than Gould’s [14] contingency thesis and has been variously called a ‘historical constraint’ or ‘temporal constraint’ in the past (for an extensive discussion of constraint concepts from a theoretical morphologic perspective, see [11]). The most striking feature of Raup’s [15] classic theoretical morphospace study of computer-simulated mollusc shell form was that the overwhelming majority of the morphospace was empty—that there exist numerous geometrically possible shell forms that no mollusc has ever evolved. From the point of view of

natural selection theory, an obvious causal explanation for empty morphospace would be that the forms present in the empty region of morphospace are non-functional; that is, they belong to form set \( \{f:2\} \) (figure 4). However, an alternative point of view could just as easily maintain that such hypothetical non-existent morphologies might function perfectly well in nature but that the process of evolution simply has not produced them yet.

The creation of Powell & Mariscal’s [13] new theoretical subset \( \{f:4\} \) thus requires the existence of an additional new theoretical subset of \( \{f:1\} \)—there should exist members of the functional and developmentally possible form set \( \{f:1\} \) that are not members of the subset of actual forms \( \{f:4\} \). These hypothetical forms belong to the following subset:

2. Form subset \( \{f:5\} \): these are the forms, \( f, 5 \), that are functional and developmentally possible but that nonetheless have not yet been evolved by life on Earth. This subset is here formally defined as \( \{f:5\} = \{f:1\} \setminus \{f:4\} = \{ f | f \in f:1, f \notin f:4 \} \).

The question is now not a question of whether Powell and Mariscal’s subset \( \{f:4\} \) of actual functional forms exists—it does, as can be seen in figures 1–3 for ammonoids, brachiopods and helical bryozoans—but rather whether subset \( \{f:5\} \) exists. If subset \( \{f:5\} \) does not exist, then neither does subset \( \{f:4\} \); that is, if set \( \{f:5\} = \emptyset \) then \( \{f:4\} = \{f:1\} \).

To rephrase the question: are there functional and developmentally possible forms that have not yet been evolved by Earth life? That is, does \( \{f:4\} \) exist as a separate possible form subset? Or does \( \{f:4\} = \{f:1\} \); that is, have all functional and developmentally possible forms for Earth life in fact been discovered by Earth life?

3. Questions for future research

An obvious question for future research concerns the existence or non-existence of form subset \( \{f:5\} \). Is temporal constraint real—can we prove that perfectly functional, developmentally possible biological forms exist that nevertheless have not yet been evolved by life on Earth? In order to answer that question, we must be able to create these non-existent forms and to analyse their functionality, and
the analytic techniques of theoretical morphology allow the researcher to do exactly that [2].

Consider the case of the nektotic cephalopods in figure 1: no active swimming cephalopods exist in the morphospace beyond the minimum limit of SEC = 40. However, the region of morphospace beyond the SEC = 40 limit is not entirely empty of shelled cephalopods—this region was partially occupied early in the evolutionary history of the cephalopods but loosely coiled shell forms were rapidly, and convergently in multiple lineages, abandoned in favour of coiled forms with better streamlining and swimming efficiency [16–20]. Curiously, however, loosely coiled forms were also convergently re-evolved by cephalopods in the Mesozoic; for example, the Cretaceous ammonoid _Cricoceras_ and the Ordovician nautiloid _Aphetoceras_ had shells very similar to the shell form seen at the morphospace coordinates _W_ = 2.5, _D_ = 0.5; shells in which the whorls do not touch. Even more extreme, the Jurassic ammonoid _Spiroceras_ and the Devonian nautiloid _Goldringia_ had shells very similar to that at coordinates _W_ = 4.5, _D_ = 0.7, an odd geometry known as gyroconic in nautiloids.

How could this be, as all of these shell forms have SEC < 40? The answer is that these ammonoids and nautiloids did not swim—they were either planktonic, passively floating up in the water column, or demersal, forms living on the sea bottom [20–22]. Thus, the region of the morphospace with non-functional forms, set { _f_2 }, for the nektonic shell forms were functional forms, set { _f_1 }, for the non-nektonic shell forms. How much of this region of morphospace was occupied by non-nektonic cephalopods? How much of this region of morphospace was occupied by non-nektonic cephalopods?—it is entirely possible that some of the shell forms in the morphospace beyond the SEC = 40 limit boundary illustrated in figure 1 were possible functional shell forms for non-nektonic cephalopods that nevertheless were not evolved by any of the non-nektonic cephalopods. We will not know until someone accepts the challenge to conduct theoretical morphospace analyses of the nektonic shell forms—in elegant computer simulations and morphospaces for these forms have been created [23–25] and simply await data analyses [26].

Consider next the case of the filter-feeding biconvex brachiopods in figure 2: no biconvex brachiopods exist in the morphospace beyond the minimum limit V/SA = 7, and there are good functional reasons why no brachiopods with complex three-dimensionally coiled lophophores exist in this region of the space. However, there existed other brachiopods—the non-biconvex brachiopods (Brachiopoda: Rhynchocheliformes: Strophomenata)—that did occupy some of this region of the theoretical morphospace. Some of the extremely compressed, flattish shell forms of the strophomenides in particular had V/SA ratios as low as 0.5, approaching the absolute limit of V/SA = 0 in which the two valves of the shell fit perfectly together and there is no internal volume space at all between them. These ancient brachiopods developed shell forms with minimum internal volumes to maximum shell surface areas, shell forms with the exact opposite geometry to those found in the biconvex brachiopods.

How could this be? Our best explanation is that the extinct non-biconvex brachiopods used a radically different feeding system from that of the living biconvex ones, a feeding system in which the entire mantle-tissue surface of the interior of the shell was ciliated and gathered food in addition to that gathered by a small, weak lophophore with a simple two-dimensional geometry [27,28]. How many of the shell forms present in the morphospace region beyond the V/SA = 7 limit in figure 2 were evolved by the strophomenate brachiopods is currently not known but we do know that the region of space that contains non-functional forms, set { _f_2 }, for the biconvex rhynchocheliform brachiopods contained functional forms, set { _f_1 }, for the extinct strophomenate brachiopods. At this point, a new morphospace containing non-biconvex concavo-convex and convexi-concave shell forms, in addition to the biconvex spectrum of form shown in figure 2, has been created and the analysis of strophomenate shell form is currently in progress.

Last, in the case of the filter-feeding helical bryozoans, there are no known bryozoan colonies that exist in the empty region of morphospace beyond the limits shown in figure 3. This region of space appears to contain only non-functional forms for bryozoans—but are these forms functional for some other evolutionary clade of organisms with a different mode of feeding? Bryozoan-like fenestrated colony forms have been convergently evolved by both the cnidarians (e.g. the red octocoral _Dictyocanis_), but the only helical colony forms known to me are the flexible skeletons of a few corals, such as the whip black coral _Cirrhipathes_ [29]. These sessile predators have non-erect colony forms that stretch horizontally in water currents, and possess a geometry unlike any of those shown in figure 3 for the bryozoans.

A second question for future research concerns the existence or non-existence of form set { _f_3 }. This question is of major importance to the study of convergent evolution as these hypothetical forms imply that there exists somewhere in the universe an alien set of functional biological forms that cannot be developed by Earth life, and thus these alien life forms would not be convergent on any of the forms of life seen on Earth. Within our own Solar System (since, at present, we can only dream of spacecraft that could take us to other star systems) only the far-distant large planet-like Titan, a moon of Saturn, and Triton, a moon of Neptune, offer physical conditions and chemistries radically different from those found on Earth. It has already been hypothesized [30–32] that Titan might contain life forms that could metabolize acetylene (C₂H₂), using atmospheric hydrogen (H₂) to produce methane (CH₄), analogous to Earth life that metabolizes glucose (C₆H₁₂O₆) with atmospheric oxygen (O₂) to produce carbon dioxide (CO₂).

If life forms exist on Titan, they would belong to form set { _f_3 }, and I predict they would look nothing like life on Earth. The challenge will be to design and send more spacecraft to both Titan and Triton to search for life forms on their surfaces with robot rovers.

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References


