

The Geometry of Evolution Adaptive Landscapes and Theoretical Morphospaces

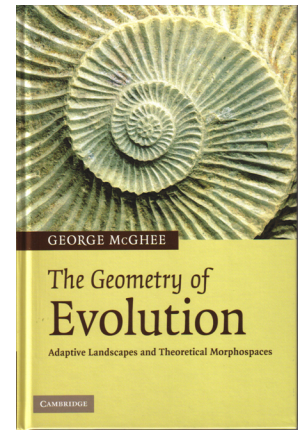
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By George McGhee
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This slim book aims at demonstrating that the concept of S. Wright's adaptive landscape can be presented in terms of the evolutionary model referred to by the author as "theoretical morphospaces," namely the geometrical representation of biological form, known or unknown. Much of the material presented is not new, a fair proportion of it being derived from results of S. Wright, D. Raup, D.W. Thompson, and others, dating back to 1915. The general principles of what is covered in an essential part of the book can, however, be found in the excellent text *Principles of Paleontology* by D.M. Raup and S.M. Stanley (1971) and it is therefore curious that this book is not referred to. Several interesting models are discussed in the later chapters, drawn from aspects of the work of the author and his associates. It is clear from the beginning that the presentation is weighted in favour of certain theories and in a manner that I cannot but find borders on the uncritical at times. In the following I confine myself to topics that I believe could have been treated better, or crucial research that has unfortunately not been considered despite its importance.

There is no doubt that Wright's fitness landscape is a useful theoretical concept. A large part of the text is devoted to presenting some of the details of the concept and examples discussed which the author believes provide unequivocal support for its validity. Brief mention is made of R.A. Fisher (cast in the role of detractor), the renowned

mathematician and geneticist, but that is all. One learns little more than that Fisher seems to have gone wrong. (NB the landscape with a single adaptive peak that figures in the adaptivity chapters, is more correctly rendered as a "Fujiisan" landscape; "Fujiyama" is an inappropriate "gaijin" reading of the Japanese (Kanji) characters for the volcano.) It is worth noting that the British geneticist John Maynard Smith (*Evolutionary Genetics*, 1989) pointed out that the shifting balance theory of Wright has frequently been misunderstood with respect to the importance of peak-shifts. The geneticist J. Crow (*Basic Concepts in Population, Quantitative and Evolutionary Genetics*, 1986), commenting on the shifting-balance theory, argued that it requires a special population structure that in his experience is seldom to be expected in nature. He stressed that Fisher's "alternative model" requires an adaptive surface more akin to waves and troughs reflecting environmental changes, rather than a static landscape. Crow's view is that both protagonists may turn out to be correct, like the blind Indian sages and the elephant. Fisher's process is theoretically responsible for minor changes to



improve fitness, whereas occasional new novel types involve a random element and occur by a Wrightian process; however, more than half a century after Wright's theory was put forward, the issue is according to Crow, still unresolved. This aspect of the Fisher-Wright disagreement could have been elucidated by reference to Crow's work. In this connexion, McGhee's book would have profited from a more unbiased approach to the subject matter. Why not include an account of the manifestation of dwarfing in mammals of Mediterranean islands, such as the pygmy elephants and hipopotami of Cyprus, which would seem to be a good example of one of Wright's models? (Most recently, the "hobbits" of Flores are being viewed by one research group in the light of island speciation and dwarfing.)

In 1940 Gayle Scott promoted the idea that ammonite shell shapes were possibly indicative of particular marine environments in the Texan region, ranging from abyssal to strandline. This fanciful idea was taken up by some palaeontologists, but soon withered away due to a lack of convincing observations. This notwithstanding, Scott's construction shows up occasionally in general textbooks in palaeontology. The elements of Scott's idea appear in the present volume as an example of modelling iterative evolution in lateral shell-shape. I am at a loss to understand from whence the factual basis for the modelling derives and what the two categories of shell-form are supposed to be telling us. It is quite possible that such situations could arise, but not as an interchangeable process and not as a one-and-only solution. One factor that incites caution concerns what the model requires to be regarded as "significant" sea-level differences. Here we touch on a common malaise that bedevils so many palaeoecological reconstructions, namely the ignorance of what takes place in the real world. In order to construct a useful model of transgressional histories it is necessary to understand what the components of sea-level shifts can be. It is well known that the classical region for studying the effects of sea-level changes is the Cretaceous-Paleogene of the Sahara. It was for the epicontinental sea of the Saharan Cenomanian that the Austrian Eduard Suess more than 100 years ago recognized the role of tectono-eustasy. Raymond Furon, the doyen of African geology, was to take the geological and palaeoecological aspects further in the thirties and forties.

Tectono-eustatically powered shifts in sea-level are due to the factors of seafloor spreading and ridge-growth/subsidence. Tectono-eustatic

changes of sea-level can seldom do more than change the water-level much more than 100-200 metres, usually less, and over a long interval of time. Nils-Axel Mörner, in a celebrated paper in the *Journal of Geology* from 1976, identified not only the transgressional mechanics of Suessian eustasy, but reviewed its role in relation to glacial eustasy, coastal basin tectonics and gravitationally controlled changes of sealevel (geoidal eustasy) of local significance. The model of iterative evolution for ammonite shells suggested by McGhee, whereby the same morphologies are repeated by "daughter species" in a stereotyped mode controlled uniquely by the depth of the sea, suffers from a lack of reality. It requires that the oceanic stock remains as a reservoir at "depth", available for producing "high sea-level" complementary morphologies, and with, one assumes, intact DNA-profiles. However, oceanic conditions are not static, even for short periods of time, and certainly not over the millions of years the "yo-yo model" (this is my term) would require. The evidence available for the "high sea-level" periods in the history of the Saharan inundations of the Albian to Maastrichtian fail to convey any impression of differentiation in shell morphology of the type envisaged by the "yo-yo model", as I have observed during many years of fieldwork in West and North Africa. Moreover, the consensus of opinion arrived at by several workers is that the epicontinental inundations can hardly have exceeded a few hundred metres at most (in a mondial perspective). Moreover, the tectono-eustatic phases in the Sahara, other than imperfectly, cannot be related to what went on at different times in the several coastal basins of Africa (and South America). Here, local tectonics decide where land and sea are located - but this does not encompass sea-level other than marginally, as has been eloquently documented by Richard V. Dingle, one of the few expert palaeontologists who is equally at home in the intricacies of basin tectonics.

With respect to the molecular biological aspect, that is the fixed status, tacitly assumed for the ammonite DNA-profiles it is worth considering the case of the "living fossil" *Lingula anatina*, which in the Northern Pacific Ocean deviates from the condition of panmixia, there being notable differences in sequences of a *cox1* region of mitochondrial DNA and an intron region of the nuclear EF-1a gene over relatively short geographical distances (K. Endo, T. Ozawa and S. Kojima 2001, *Marine Biology* 139). The shell morphology of the lingulas does not differ, yet the molecular biological

properties of some populations are such as to justify making a case for species status for them.

Another problem besetting the “yo-yo model” concerns the unavoidable effects of oceanic currents. The puzzling identical patchy distribution patterns of the weakly mobile living nautilus and coelacanths are now seen by specialists as being the result of dispersal by intermittently active deep-sea currents. Enforced migration of living organisms by oceanic currents may therefore be exemplified by reference to the role of deep-sea currents in relocating the coelacanth *Latimeria* to the Celebes (Sulawesi) in Indonesia together with *Nautilus pompilius*. These are not strong swimmers and cannot successfully hold their own against intermittently active powerful submarine currents (television programme aired in 2004 in the Discovery Science Channel by Professor Hans W. Fricke, [Max Planck Institute, Frankfurt/Main]).

J. Gerritsen in 1984 applied a type of energy bookkeeping model to mobile marine organisms in terms of specific power resulting from feeding, less power spent foraging, less standard metabolism. Application of the model to shelled cephalopods suggests that they were not functionally capable of maintaining cruising predation, owing largely to energy costs, apart from the case of small oxynotes under special circumstances. Many forms would have been able to manage ambush-predation (as indeed is typical of the octopus) and many more, a scavenging mode of feeding, or browsing (Reyment 1988. A foraging model for shelled cephalopods. In: J. Wiedmann and J. Kullmann (eds.), *Cephalopods – Present and Past*, p.687-703). Gerritsen’s model applied to cephalopods imposes a definite constraint to palaeontological reconstructions based on suppositional lifestyle modelling. It goes without saying that the ornamental status of the ammonite animal would have been the most important ingredient in determining its motility. Hence, a factor that must be of importance concerns the part played by shell-ornament and polymorphism in ammonites. One possible interpretation is that predators of some sort could be a triggering cause. A classical example of such morphological variability is that of contiguous polymorphism in barnacles. The controlling ecological factor determines indirectly the geographical distribution of the ornamental morphs in that the predator is bound to some particular environment, usually related to depth and/or wave-action. In this example, the relationship between the carnivorous gastropod *Acanthina angelica* and the acorn barnacle *Chthamalus anisopoma* is marked by intense

predation which results in the virtual (local) extinction of the normal morph in the shore-zone in which the gastropod operates. The alternative morph is hood-shaped and is difficult for the predator to attack. Outside the zone occupied by the gastropod only the normal morph develops because of its greater fitness. Even if we could apply this kind of polymorphism, namely patch-bound monomorphism, to the ammonite-coiling-depth problem, it would be no easy task to defend a static evolutionary situation (over millions and millions of years), not least in the absence of information on what has caused intrapopulational ornamental variability in a great number of ammonite species.

The application of the Reverend Henry Nottidge Moseley’s mathematically derived results (1834) for the significance of the logarithmic spiral for studying growth in ammonite shells leads to a consideration of David Raup’s pictures of outlines of ammonite shells obtained by varying the input parameters. McGhee’s enthusiasm tends to get out of hand as for example when he anoints Raup as the “founder of theoretical morphology”. The originator of the concept *Morphologie* is usually attributed to J.W. von Goethe. In von Goethe’s mind the field was very broad and one that he let expand the more he surveyed the subject. Application to Botany took place in the hands of Auguste St. Hilaire (*Morphologie Végétale*). The zoological counterpart was produced by Ernst Haeckel in 1866 (*Generelle Morphologie der Organismen*). In 1887 Wiley started publishing their *Journal of Morphology*, which is still being produced and which has always contained a fair proportion of experimental and theoretical work, including mathematical analyses of growth in molluscs—for example S. and M. Löwtrup (2005, vol. 197): *The morphogenesis of molluscan shells: a mathematical account using biological parameters*.

Raup’s contribution is concerned with producing an array of shell shapes in lateral aspect using what is essentially a computer friendly simplification of Moseley’s solution. It has proven very useful for many practically oriented studies, not only with respect to ammonites but also other molluscan shells. Useful as David Raup’s work is, one can go further. D.W. Thompson produced a text on *Growth and Form* in 1915, formally issued in 1917. Thompson put forward many important theories and ideas in his book. One of these was a transformation procedure whereby one shape was transformed into another by a geometrical mapping (the method of cartesian coordinates). In essence, the idea is to be found, well illustrated, in the geometrical hand-

books of the Hungaro-German artist Albrecht Dürer (1471-1528), namely *Vier Bücher von menschlichen Proportionen*. This graphical device is appealing to the eye and moreover can be exploited in some evolutionary studies. Thompson, who was acquainted with Dürer's work, did not go beyond a simple freehand procedure and never tried to consider the mathematics of this operation in any of the later editions of his book. Thompson's graphical procedure suffers from the disadvantage attendant upon its inability to yield quantitative information and J. Huxley in 1932 noted that the figures were not produced by computation. Huxley's *Problems of Relative Growth* (1932) is one of the great classics of evolutionary geometry, not least because of the introduction of the concept of allometry. That it is not mentioned in McGhee's survey is astonishing. For years, there does not seem to have been a mathematical solution for producing the Thompsonian transformation. That is until Fred L. Bookstein turned his attention to the problem and came up with an elegant solution that has turned out to be of supreme importance in the study of shape relationships in organisms. It later transpired that the same general theory had been published about the same time by the English mathematician D.G. Kendall, in a fundamental paper on the geometry of Shape Manifolds. Bookstein's work was couched in biological terms, whereas Kendall's was given a more general framework, largely divorced from biological constraints, and intensely mathematical. Bookstein began by studying affine transformations. This was later expanded to encompass non-affine transformations. From this beginning in the mid-1980s what has become to be known as *Geometric Mor-*

phometrics has burgeoned into a science of its own. Coverage of the field in relatively accessible terms can be found in the textbook by I.L. Dryden and K.V. Mardia, *Statistical Shape Analysis* (1998). Bookstein's monographic analysis *Morphometric Tools for Landmark Data: Geometry and Biology* (1991) would seem to warrant more than a passing reference, granted that it must be regarded as one of the most important biometrical texts to have appeared over the last 100 years. Not only has Bookstein put Thompsonian transformations on a firm basis, but gone much further and opened the portals to an amazingly rich field of research in geometrical aspects of evolution in a wider field than was ever suspected in the days of Thompson and Huxley. An account of some of the results of Bookstein and his many associates would have made the Thompson section alive and relevant instead of redundant (see also SUNY Stony Brook Morphometrics site: life.biosunysb.edu/morph/). There is a vast literature on various topics in Geometric Morphometrics and many generally oriented books dealing with practical biological aspects.

Notwithstanding that the development of models in theoretical biology is an indispensable activity, it is essential that the step be made from conjecture to fact and that relevant research be considered and not arbitrarily excluded for reasons unexplained. Verification of the parts played by oceanological and palaeogeographical factors, should be at the base of models such as the iterative evolution sketch for the lateral aspect of ammonite shells. Finally, would not a better title for the book have been *Aspects of the Geometry of Evolution?*