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## Theoretical morphology of tetrapod skull networks

*Morphologie théorique de réseaux crâniens de tétrapodes*

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## ABSTRACT

Network models of the tetrapod skull in which nodes represent bones and links represent sutures have recently offered new insights into the structural constraints underlying the evolutionary reduction of bone number in the tetrapod skull, known as Williston's Law. Here, we have built null network model-derived generative morphospaces of the tetrapod skull using random, preferential attachment, and geometric proximity growth rules. Our results indicate that geometric proximity is the best null model to explain the disparity of skull structures under two structural constraints: bilateral symmetry and presence of unpaired bones. The analysis of the temporal occupation of this morphospace, concomitant with Williston's Law, indicates that the tetrapod skull has followed an evolutionary path toward more constrained morphological organizations.

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## R É S U M É

Les modèles de réseaux crâniens dans lesquels les nœuds représentent les os et les liaisons les sutures ont récemment permis d'apporter un nouveau regard sur les contraintes structurales qui sous-tendent la réduction évolutive du nombre d'os du crâne des tétrapodes, connue sous le nom de loi de Williston. Ici ont été construits des espaces morphologiques génératifs de crânes de tétrapodes, dérivés d'un modèle de réseau nul utilisant des lois de croissance à liaison préférentielle et proximité géométrique aléatoires. Nos résultats indiquent que la proximité géométrique est le meilleur modèle nul qui permette d'expliquer la disparité des structures crâniennes sous une double contrainte: symétrie bilatérale et présence d'os non appariés. L'analyse de l'occupation temporelle de cet espace morphologique qu'explique la loi de Williston indique que le crâne de tétrapode a suivi un itinéraire évolutif vers des organisations morphologiques davantage contraintes.

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## 1. Introduction

The evolution of the tetrapod skull has been extensively studied in comparative morphology. In the early 20th century, a pivotal analysis of changes in the number

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and complexity of skull bones in the evolution of Permian reptiles formed the basis for what is now known as the Williston's Law: an evolutionary trend in tetrapods toward reduction in the number of skull bones (Esteve-Altava et al., 2013a; Gregory, 1935; Sidor, 2001; Williston, 1914). Three complementary causal factors have been proposed to explain the reduction in the number of bones and sutures during tetrapod skull evolution (Sidor, 2001): (1) natural selection favoring more rigid, boxy skulls that improved functional and biomechanical integration in terrestrial vertebrates; (2) developmental and statistical constraints favoring the loss of bones rather than their new formation; and (3) unlikelihood of new bone formation by either genetic or epigenetic mechanisms (see also Rasskin-Gutman and Esteve-Altava, 2008 and references therein, for a review of external and internal processes related to evolutionary trends). Although reversions of Williston's Law are theoretically possible, for example, due to pedomorphosis in the patterns of cranial suture closure, this mechanism has not been reported at a broad scale as a sustained evolutionary process (but see Koyabu et al., 2011; Wilson and Sánchez-Villagra, 2009, for insights on heterochronic shifts in ossification and fusion sequences in mammals).

Recent studies on the evolution of the skull have focused on the analysis of morphological integration and modularity in different groups, such as: hominids (Bastir, 2008; Mitteroecker and Bookstein, 2009; Mitteroecker et al., 2012), mammals (Goswami, 2007; Goswami et al., 2009; Porto et al., 2009), and birds (Bhullar et al., 2012; Klingenberg and Marugán-Lobón, 2013; Marugán-Lobón and Buscalioni, 2009). In addition, the importance of cranial anatomy at all levels of organization has prompted the comparative and evolutionary analysis of gene regulatory networks (Chase et al., 2002; Haberland et al., 2009) and developmental origin of skull embryonic cells (Couly et al., 1993; Santagati and Rijli, 2003), as well as biomechanics and functional morphology (Moazen et al., 2009; Rafferty et al., 2003). These studies show that although the organization of the skull is modular at the genetic, developmental, functional, and morphological level, it still retains a tight integration of parts. As a consequence, the bony elements of the skull, which derive from multiple developmental and evolutionary origins, carry many coordinated functions (e.g., protection and hosting of sensory organs and the brain, feeding, or breathing). To which extent this multi-functional, highly integrated, and modular anatomical structure has occupied the morphospace of all possible tetrapod forms is missing in this picture. Here, we will try to answer this question duly by exploring theoretical morphospaces using network theory; with these tools we can simulate millions of networks that represent possible skulls at a broad macroevolutionary scale, using different null models of growth.

In previous works we have shown that the structure of the tetrapod skull can be efficiently analyzed using network theory (Esteve-Altava et al., 2011, 2013a, 2013b, 2013c; Rasskin-Gutman, 2003). The skull is represented as a network of bones and suture connections; this network has several mathematical properties that can be compared across taxa and during geological time. In particular, we

demonstrated that Williston's Law is a trend of reduction in the number of bones that involves an increase in net structural complexity due to the random loss of poorly connected bones and the selective fusion of the most connected ones (Esteve-Altava et al., 2013a, 2013b). Here, we extend the network analysis of the tetrapod skull by merging network theory with theoretical morphology, using null network models in order to explore systematically the space of possible connections.

## 2. Theoretical morphology and networks

Theoretical morphology appeared in the 1960s beginning with the seminal work of David Raup on the accretionary growth of coiling shells (Raup, 1961, 1962, 1966, 1967, 1968). This methodological approach is based on the construction of a space of possible forms by using a set of generative rules that are formal abstractions of growth patterns (for recent extensive reviews of theoretical morphology and examples of morphospaces, see Dera et al., 2008; McGhee, 1998, 2007). An empirical morphospace including both extinct and extant forms is subsequently superimposed onto the theoretical morphospace; as a result of this mapping, real forms can be analyzed against a background of possible and impossible forms, obtaining a more general picture of how real forms are distributed in nature (Fig. 1).

The dimensions of a morphospace are timeless; this makes theoretical morphology suitable to frame evolutionary patterns of morphological change (McGhee, 1998). A theoretical morphospace describes (or puts into relation) organismal forms with one basic assumption: the morphospace is not occupied uniformly (Rasskin-Gutman and De Renzi, 2009). If the models to generate these forms are carefully chosen, distances among forms and trajectories of occupation within the theoretical morphospace will inform us about underlying causes in development and evolution (Mitteroecker and Huttegger, 2009). In theoretical morphology, the distinction between possible and impossible forms depends on which generative rule is chosen to build the theoretical morphospace. Given a set of parameters, there always will be forms that are impossible either because the generative rule cannot make them or because the combination of those parameters is meaningless. For example, if we consider, by definition, that skull networks cannot be disconnected, then any combination of parameters for each null model that would grow disconnected networks has to be treated as impossible. Also note that we do not impose functional constraints on the exploration of the skull network morphospace, this means that what is biologically possible is a subset of the formally possible, which might be further constrained by functional requirements. Moreover, the set of rules based on morphogenetic processes converts a generative morphospace in a hypothesis of developmental constraint (Rasskin-Gutman, 2003; Rasskin-Gutman and Izpisua-Belmonte, 2004). Indeed, this is how we should look at the null models presented here.

The articulation of skull bones was first analyzed in a theoretical morphology framework in Rasskin-Gutman (2003). There, only 2D bone connectivity networks were

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