Beyond selection

Más allá de la selección

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ABSTRACT

It has been argued that the study of natural selection and quantitative genetics should have a central role in evolutionary thinking and undergraduate teaching in Chile. Extensive operational use of the concept of natural selection may seem consistent with this argument. However, advances of evolutionary knowledge in independent fields such as phylogenetic analysis, developmental evolution, and paleontology cannot be ignored. I argue here that the role of natural selection in contemporary evolutionary biology can be compared to that of Newtonian mechanics in contemporary physics: it can describe a given domain of observations, but it is insufficient to handle the different sources of evolutionary knowledge. Overemphasis on natural selection as the immediate mechanism of evolution may lead to disregard phylogenetic-historical evidence, and to ignore the important evolutionary role of non-adaptive change and epigenetic phenotypic plasticity. Natural selection deals with populations and leads to conceive the environment as a "sieve" of genetic variation, bypassing the role of the environment as a trigger of phenotypic and behavioral diversification. Alternatively, it is possible to conceive how part of the medium participates as an ontogenic niche in the trans-reproductive change or conservation of an ontogenic phenotype. The concept of drift, currently accepted for molecular and developmental change, can be applied to the level of the phenotype as an alternative to the concept of evolution as adaptation by natural selection.

Key words: evolution, history, development, epigenesis, drift.

RESUMEN

Se ha argumentado que el estudio de la selección natural y la genética cuantitativa debiera ocupar un rol central en el pensamiento evolutivo y la enseñanza de pregrado de la evolución en Chile. El extenso uso operacional del concepto de selección puede parecer consistente con este argumento. No obstante, los avances en el conocimiento evolutivo en áreas independientes, como los estudios de análisis filogenéticos, la evolución del desarrollo, y la paleontología, no pueden ser ignorados. Es posible argumentar que el rol de la selección natural en la biología evolutiva puede compararse al de la mecánica newtoniana en la física contemporánea. Puede describir un cierto dominio de observaciones, pero es insuficiente para manejar las diferentes fuentes de conocimiento evolutivo. Un énfasis excesivo en la selección natural como mecanismo inmediato de la evolución puede conducir a desconocer la evidencia filogenético-histórica, y a ignorar el rol evolutivo del cambio no adaptativo y de la

plasticidad fenotípica epigenética. La selección natural trata de poblaciones y conduce a concebir al medio como un "cedazo" de la variación genética, evadiendo el rol del ambiente como un gatillador de diversificación conductual y fenotípica. Alternativamente, es posible concebir cómo parte del medio participa como un nicho ontogénico en la conservación o cambio trans-reproductivo de un fenotipo ontogénico. El concepto de deriva, actualmente aceptado para cambios moleculares y del desarrollo, puede ser aplicado al nivel del fenotipo como una alternativa al concepto de evolución como adaptación por selección natural.

Palabras clave: evolución, historia, desarrollo, epigénesis, deriva.

INTRODUCTION

It is frequently conceived that evolution is a process of adaptive change through natural selection. This can easily lead to consider that evolutionary thinking and undergraduate teaching of evolution should be centered on natural selection. It has been argued that a systematic-taxonomic and historical view of evolution currently prevails in undergraduate courses in Chile, that does not provide a realistic picture of current research on evolution by natural selection and its tools of quantitative genetics (Nespolo 2003). Insufficent teaching of natural selection and quantitative genetics in Chile has been argued to have "devastating consequences for the formation of scientists". The existence in Chile of evolutionary thinking based on structural determinism and autopoiesis rather than natural selection (Maturana & Varela 1973, 1980, 1984, Maturana & Mpodozis 1992, 2000), has further been commented as an outbreak of unscientific and dogmatic thinking (Nespolo 2003). From an alternative point of view, this commentary will discuss the insufficiencies of considering natural selection as a general framework for understanding evolution. I will also argue that in Chile the presence of an approach that is not based on selection is far from being unscientific. Rather, by questioning the concept of evolution as adaptive change, it encourages a discussion that is necessary to grasp the real phenomenological scope of evolution.

CURRENT EVOLUTIONARY RESEARCH:

A CORRECTED PICTURE

Advances in the phylogenetic-historical approach

In order to adequately describe current research in evolutionary biology, it is necessary to understand that the logic of natural selection and quantitative genetics is irrelevant for the treatment of extensive empirical sources of evidence on evolution. The collection of this information can be described as the phylogenetic-historical perspective. The commentary by Nespolo (2003) may provoke the wrong impression that the phylogenetic-historical approach has not undergone significant reinterpretation or expansion of its knowledge. In fact, research and thinking in this independent field has progressed dramatically in recent years, leading to new common methods of research and consensus on several facts. For example, only in the last decade fossil

taxa have been found that are relevant to understand the origin of vertebrates (Shu et al. 1999), birds (Ji et al. 1998, Xu et al. 2003), snakes (Caldwell & Lee 1997), and sirenians (Domning 2001). Only in the 1990's, the number of species of mesozoic birds tripled those discovered in all previous years (Chiappe 1997). Any serious evolutionary study involving the comparison of taxa will require phylogenetic analysis to identify which taxa share a more recent common ancestor. A logic of phylogenetic analysis based on parsimony has been treated mathematically for decades (Hennig 1965) and currently is also aided by molecular evidence, shedding new light on several important evolutionary subjects. For example, new agreements have been arrived according both to morphological and molecular evidence on the affinities of animal phyla (Peterson & Eernisse 2001), and the relationships among the main divisions within amphibians, birds, and mammals (Meyer & Zardoya 2003). Evolutionary biology will always benefit from a historical-systematic perspective, which allows hypotheses on evolutionary mechanisms to be contrasted with available information on how evolution has actually occurred. Examples of historically inspired insight of great importance to the study of evolution are the concepts of phylogenetic constraints, the role of chance and opportunism in events of mass extinction, and the origin of adaptation by exaptation as an alternative to directional selection (Gould & Vrba 1982, Gould 2002). However, all knowledge from the phylogenetic-historic approach is stomped out by the common argument that only the study of natural selection deals with the immediate mechanism of evolution. Evolutionary biologists could therefore ignore the transitions documented by the fossil record, and be generally unaware of the new agreements reached on the phylogenetic relationships among organisms.

In fact, the logic of natural selection and quantitative genetics is insufficient to claim an adequate knowledge of evolution, which must always update the unambiguous information available from the phylogenetic-historical perspective.

For example, it is possible to ask the following question: can population genetics contribute to understand how did the bones articulating the skull and jaw in reptiles end up in the middle ear of mammals? Not much: important evolutionary topics like this must be answered in structural terms. The fossil record shows how previous participation of other bones in a "double" jaw articulation of therapsids (Fig.1) allowed the quadrate and articular bones to change position, while the other bones (dentary and squamosal) were able to keep a functional articulation between the skull and mandible (Caroll 1988, Benton 2002).
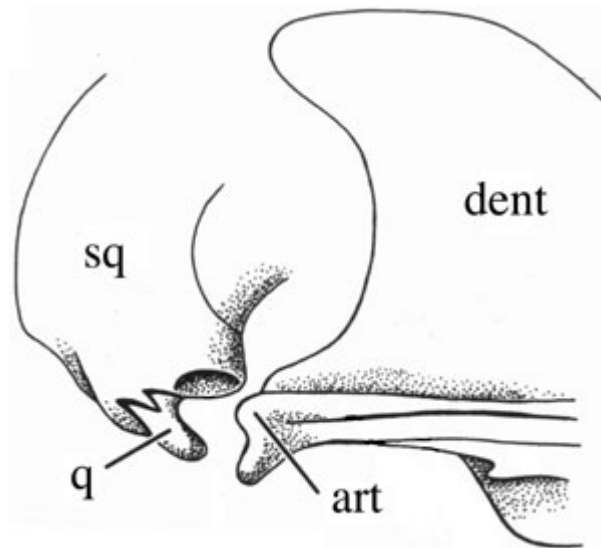
_Fig. 1__:_ The double articulation in the jaw joint of the therapsid cynodont _Probainognathus_, which explains how the articular (art) and quadrate (q) of mammals were able to move into the middle ear, while the dentary (dent) and squamosal (sq) maintained a functional jaw joint. Image taken from Carroll (1988).

La doble articulación en la articulación mandibular del terápsido cynodonto `probainognathus, que explica cómo el articular (art) y el cuadrado (q) de los mamíferos fueron capaces de moverse hacia el oído medio, mientras que el dentario y el escamoso retuvieron una articulación mandibular funcional. Imagen tomada de Carroll (1988).

Evolutionary developmental biology

Natural selection is also clearly insufficient for the study of evolutionary developmental biology (evo-devo), a growing field of research that has delivered remarkable new insight into evolution. The logic of selection can be applied to differential survival within a population, but it is widely acknowledged that selection does not provide a mechanism for the origin of variation. This relates directly to the question on the relationship between development and evolution: how does development "mechanistically" produce and restrict phenotypic variation? (Wagner et al. 2000). Current research within molecular developmental biology has also revealed the actual complexity of the genotype-phenotype relationship (phenogenetics, Weiss 2005), which goes far beyond the concept of quantitative genetics, that small and accumulative effects of several genes determine continuous variation of metric traits. Evolutionary developmental biology has also introduced the comparison among taxa of the embryonic expression patterns of orthologous genes, providing an important new source of evidence for the discussion of homology or convergence of similar traits. For example, several resemblances between protostomes and deuterostomes, previously assumed to be convergences from an adaptationist perspective of evolution, have been found to share a similar molecular-developmental basis. Processes of anterior differentiation, dorsoventral patterning, eye development, peripheral and central nervous system development, cardiac development, gut regionalization, segmentation

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and appendage formation and patterning have all been proposed as conserved developmental mechanisms that were already being utilized in the most recent common ancestor of protostomes and deuterostomes (reviewed by Knoll & Carroll 1999).

Research on developmental evolution is frequently published in several specific journals dedicated to the subject, as well as high-impact developmental, evolutionary, and interdisciplinary journals. According to a review on evolutionary developmental biology, "the evidence for evolution is better than ever. Natural selection in evolution, however, is seen to play less an important role. It is merely a filter for unsuccessful morphologies generated by development. Population genetics is destined to change if it is not to become as irrelevant to evolution as Newtonian mechanics is to contemporary physics" (Gilbert et al. 1996).

NATURAL SELECTION VERSUS NATURAL DRIFT

The evolution of developmental pathways

Although it is possible to state that the evolution of phenotypic traits is caused by the evolutionary modification of their developmental pathways (Hall 1998, Raff 1996), it is important to point out that the evolutionary conservation of a phenotypic trait does not imply the conservation of its developmental pathway. Countless cases of variation in developmental pathways are know (Wagner & Misof 1993), such as variation of the germ layer of origin (endoderm , ectoderm or mesoderm), variation in the early inductive role of tissues, and homeotic transformations (the same structure derived from a different body region). The fact that the developmental pathway of a trait can vary is also evidenced in that genetic and environmental factors can substitute for each other in triggering a certain phenotype, a fact recognized within developmental biology by the use of the terms "phenocopy" and "genocopy". Since in these cases, phenotypes are identical to selection regardless of their genetic or epigenetic triggering, the exchange of genetic or epigenetic triggering of a trait along evolution has been described as an adaptively neutral process of phenogenetic drift (Weiss & Fullerton 2000). Cases where an epigenetically induced phenotype thereafter becomes intrinsically inheritable are discussed under the concepts of genetic assimilation (Waddington 1953, Palmer 2004) and stabilizing selection (Schmalhausen 1949, cited in West-Eberhard 2003). The "Baldwin effect" in turn can describe how traits also may evolve towards increased condition sensitivity, rather than greater genotypic influence (West-Eberhard 2003). Several conceptual and empirical reasons have been exposed to argue that epigenetic plasticity, rather than genetic variation, is frequently involved in the initiation of evolutionary novelty (Newman & Müller 2000, Müller 2003, Palmer 2004), with a role of genes as followers of the phenotype (Maturana & Mpodozis 2000, West-Eberhard 2003).

A renewed concern currently exists among evolutionary biologists over the relevance of epigenetic plasticity in evolution. Unfortunately, epigenetic plasticity is seldom mentioned when natural selection is considered to be the immediate mechanism of evolution. This is because in evolution by natural selection, the effect of the environment is understood to act mainly as a selective agent or "sieve" of genetically determined variation, missing its role as a trigger of phenotypic and behavioral diversification, and starting point of evolutionary changes. Traits without heritability are incorrectly considered to have no evolutionary potential because they do not meet the requisites for evolution "by natural selection" and are frequently considered to be

"noise". Therefore, the actual evolutionary relevance of epigenetic plasticity provides another reason why natural selection should not be ideologically assumed to be the main mechanism of evolution. The theoretical frameworks of genetic assimilation, stabilizing selection, and the "Baldwin effect" have been unable to effectively introduce the evolutionary importance of epigenetic plasticity, and several arguments have been introduced to dismiss them (West-Eberhard 2003). This may be because they are ultimately framed in selective terms, regarding the effects of phenotypic plasticity on fitness and gene frequencies in populations. To study evolution, adequate understanding of the relationship between organism and environment is of evident importance. In fact, full acknowledgement of the developmental and evolutionary importance of epigenetic plasticity is at odds with interpretation of the environment to be ultimately a "sieve" or effector of selection. Although the concept of selection can be used to deal with the relationship to the environment at a population level, it does not deal with the more basic level of the individual. At this level, understanding of the relationship to the environment can be discussed in structural terms. In contrast to conceiving the environment as the effector of selection, focusing on the individual level allows to describe the participation of the environment as an ontogenic niche in the conservation or shifting of an ontogenic phenotype (Maturana & Mpodozis 1992, 2000). The organism is the starting point for the definition of its niche, and the niche itself can be distinguished as part of a greater medium that contains it (Fig 2). The medium, therefore, participates not only as a general container, but it operates fundamentally as the domain of the realization of the ontogenic niche of the living systems that it contains. It provides an independent source of opportunities for the shifting of ontogenic phenotypes, and for the realization of variations in epigenesis along the history of conservation and diversification of lineages (Maturana & Mpodozis 1992, 2000).

The adaptively neutral exchange in the environmental or genetic triggering of the development of a trait described by Weiss & Füllerton (2000) can be described as fitting the proposal that the epigenetic field of possible developmental pathways changes trans-reproductively, even when the ontogenic phenotype-ontogenic niche relationship remains unaltered (Fig 3; Maturana & Mpodozis 1992, 2000). Although the change in the epigenetic field of possible developmental pathways is non-adaptive, note that it defines the possibilities of future shifts in the ontogenic phenotype-ontogenic niche relation. The adaptively neutral exchange between environmental and genetic triggering of the development of traits that are required for survival has the non-trivial consequence of defining which environmental or genetic changes can or cannot occur without losing adaptation.
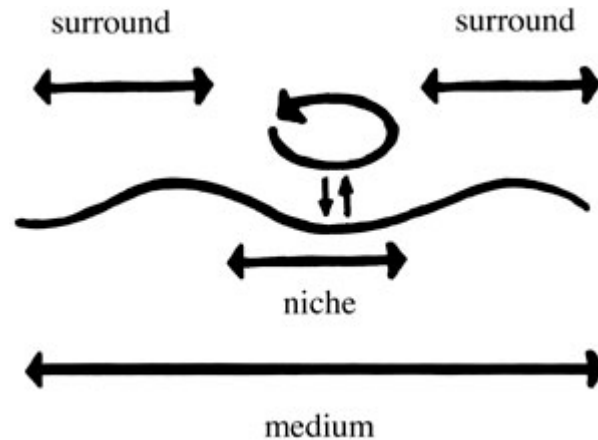
Fig. 2: This figure attempts to evoke the different views that an observer can have of a living system as he or she beholds it and reflects about its existence. As the observer beholds the living system from a distance: (a) the medium appears to him or her as all that he or she may imagine as the great container in which it exists; (b) the niche appears to him or her as that part of the medium with which the living system interacts and which it obscures, so that it can only be shown by the operation of the living system itself: and (c) the ambient or that which surrounds the living system, appears to him or her as that which he or she sees around it but which being part of the medium is not part of its niche. Conceptually, the niche and the ambient together constitute the medium. (figure and legend taken from Maturana & Mpodozis 2000).

Esta figura ilustra las diferentes distinciones que un observador puede realizar respecto del dominio de relaciones de un organismo con su entorno. El medio es distinguido como todo aquello que, a juicio del observador, forma parte del gran continente o ámbito relacional y de interacciones en que el ser vivo existe. El nicho es distinguido como aquella parte del medio con la cual el ser vivo está interactuando, y que por tanto queda oculta al observador, el que puede inducirla solo a partir de las operaciones del propio ser vivo. El ambiente queda distinguido como toda aquella parte del medio que no forma parte del nicho. El nicho y el ambiente juntos constituyen el medio.

Adaptationism: the overestimation of selection

A recent commentary argued that evidence for evolution by natural selection continues to accumulate. To prove this point, 94 recent case studies were listed where estimates of heritability or selection differentials were provided for traits, as well as cases of artificial selection and experimental evolution (Nespolo 2003). However, the basic logic of selection does not require for increasing accumulation of evidence to be accepted, and can be understood through simple qualitative examples, which may or may not belong within the field of biology. A comparison of the role of selection to that of Newtonian mechanics in physics is interesting, since selection can only be used to explain a given domain of observations. The use of "accumulation of replicas" as "accumulation of evidence" ignores the importance of how theories specify the domain of observations they are capable of explaining. Alternatively, an extensive list of case studies of natural selection may be considered to support the frequent occurrence of this evolutionary mechanism in nature. However, most cases listed by Nespolo (2003) do not provide actual evidence of evolution by natural selection. The conceptual framework for evolution by natural selection requires traits to show heritability "and"

to be under selection. Remarkably, only three cases cited in that commentary present estimates of "both" heritability and a directional selection differential for a trait. Moreover, it is well known that the heritability of traits can change depending on environmental conditions (West-Eberhard 2003). Therefore, it is necessary to precise that in such cases heritability was present "under the conditions observed" and that this requisite for evolution by natural selection could disappear under another environmental circumstance. Furthermore, to accept that most evolutionary change occurs by natural selection, this would require a rigorous comparative method to contrast with the frequency of cases in which evolution does not proceed by natural selection (for example, by adaptively neutral drift, or exapted traits that did not originate by selection for current function), specially since Nespolo (2003) admits in the same commentary that non-adaptive processes are commonplace in nature, and that "nothing could be more misleading than to believe in natural selection as the unique cause of evolution". Finally, cases of evolution by artificial selection and experimental evolution certainly do not demonstrate the predominance of natural selection. Evolution by artificial selection is achieved in a homogeneous environment, where environmentally triggered variation is diminished, and genetic differences affecting variation of a trait are made by the researcher to reflect differences in offspring survival. Similar conditions can be rare in nature, especially regarding the directionality of selection as imposed by humans with a well-defined objective. Evolution also requires to be addressed in terms of structural, developmental and phylogenetic constraints, which set limits to the variation available to both artificial and natural selection (Thompson 1917, Whitman 1919, Gould 2002).
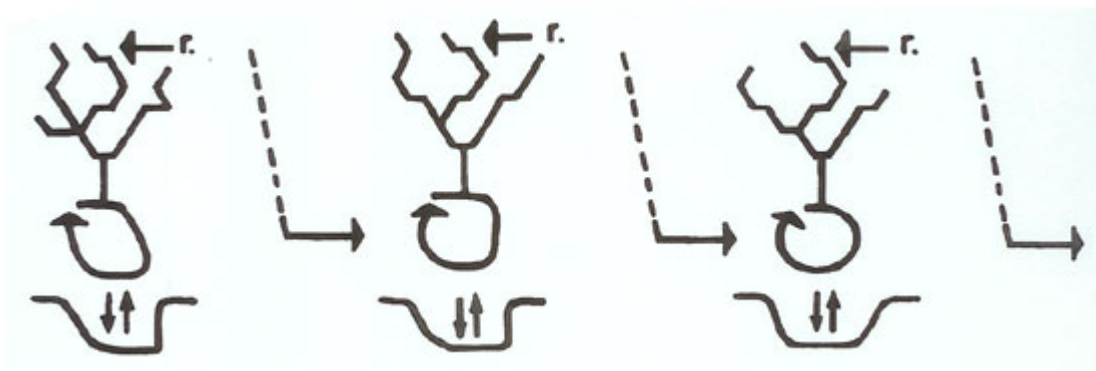

Fig. 3: This figure attempts to illustrate the change or shift of the epigenetic field as well as the change of the genetic constitution that takes place in the course of the generations while the particular ontogenic phenotype/ontogenic niche relation that defines a lineage (and that is epigenetically realized as the arrow and the r indicate), is conserved from generation to generation through systemic reproduction (figure and legend taken from Maturana & Mpodozis 2000).

Esta figura ilustra el corrimiento del campo epigenético, y también de la constitución genética inicial, que ocurren transgeneracionalmente en un linaje, mientras la relación fenotipo ontogénico/nicho ontogénico que define a ese linaje (y que es epigenéticamente realizada, como lo indican la flecha y la r), es conservada generación tras generación a través de la reproducción sistémica.

Natural selection has been argued to have a predictive power that is in contrast with more recent evolutionary frameworks (Nespolo 2003). Evolutionary biology certainly possesses good predictive power that is completely independent of the logic of natural selection. Specially evident examples are the frequent prediction by phylogenetic inference of the discovery of representatives of clades in the appropiate geological time (Norell & Novacek 1992), or the extrapolation of previously described developmental trends such as allometric growth (Gould 1977). The close phylogenetic affinity between *Archaeopteryx* and dinosaurs allowed the prediction that some dinosaurs must have presented feathers (Bakker 1986, Paul 1988) before feathered dromaeosaurid and oviraptorid dinosaurs were actually discovered (Ji et al. 1998, Xu et al. 2001, Xu et al. 2003). In the case of natural selection, despite the mathematical formalization of quantitative genetics, it would certainly be naïve to think this has led to a predictive power comparable to that of Newtonian mechanics. In fact, predictions made in selective frameworks can frequently turn out to be incorrect. Moreover, predictive power achieved within selective frameworks can be argued to always rely heavily on an adequate description and understanding of underlying biological mechanisms and other relevant factors, which in ecology are frequently designated as a whole through a wastepaper-basket use of the term "natural history".

One of the main legacies of Darwinian thinking is the uniformitarian concept that "each slight variation, if useful, is preserved, by … natural selection" (Darwin 1859). It is frequently argued that selection has the power to detect even slight adaptive advantages or disadvantages which become reflected in offspring survival, accumulating slightly beneficial genes and eliminating the slightly negative. However, this way of thinking underestimates the actual relevance of non-adaptive drift and epigenetic plasticity on offspring survival, which can frequently override any small effects of genes (Weiss & Buchanan 2003). The continuous variation of metric traits in quantitative genetics and the assumed accumulation under selection of several genes with small effects is consistent with the Darwinian concept of uniformitarianism. However, one-step genetic or environmental changes can trigger a large spectrum of plasticity, from slight to drastic phenotypic changes, as well as the emergence of traits that are qualitatively different. The limitations of a gradualist, microevolutionary approach as a general framework for evolution have been extensively discussed elsewhere (Gould 2002, West-Eberhard 2003).

Biases of selection: cases from tetrapod limbs

The concept that evolution is a process of adaptation by natural selection has frequently shown inconsistencies with empirical observations of non adaptive evolutionary change, and can be found to mislead from adequate recognition of unambiguous phylogenetic-historic evidence.

One interesting case is provided by the evolution of the development of the bird wing. In the embryos of crocodiles (the closest living relatives of birds), as well as in any pentadactyl amniote, the first digit to initiate cartilage formation is digit 4 (Burke & Feduccia 1997, counting 1-5 from the thumb to the pinky). The fossil record documenting the evolutionary transition from theropod dinosaurs to birds indicates unambiguosly that digits 4 and 5 were lost, retaining digits 1, 2 and 3 in their tridactyl wing (Fig. 4; Padian & Chiappe 1998, Wagner & Gauthier 1999). The development of the wing is unique in that the first digit to initiate cartilage formation is digit 3. It is therefore concluded that the developmental pathway of the forelimb has changed along the theropod-bird transition (Chatterjee 1998), and proposed to be a case of a

homeotic frameshift of digital identity (Wagner & Gauthier 1999). Despite the fact that the evolutionary variation of developmental pathways is well-documented, and that the origin of birds from dinosaurs has been confirmed by several independent sources of evidence (skeletal, tegumental, oological, ethological, and molecular; Padian & Chiappe 1998, Sereno 1999, Prum 2002, 2003, Witmer 2002, Chiappe & Vargas 2003, Zhou 2004, Vargas & Fallon 2005), the assumed predominance of natural selection has allowed for the argument that a change in the embryology of the wing would have no adaptive value, and therefore, that its evolutionary plausibility can be questioned, basically because no reason can be found why this change would be selected for (Feduccia 2002, Galis et al. 2003). Ultimately, it is even argued that birds did not descend from theropod dinosaurs, but rather from ancestors that had lost digits 1 and 5 (Feduccia 2002, 2003).
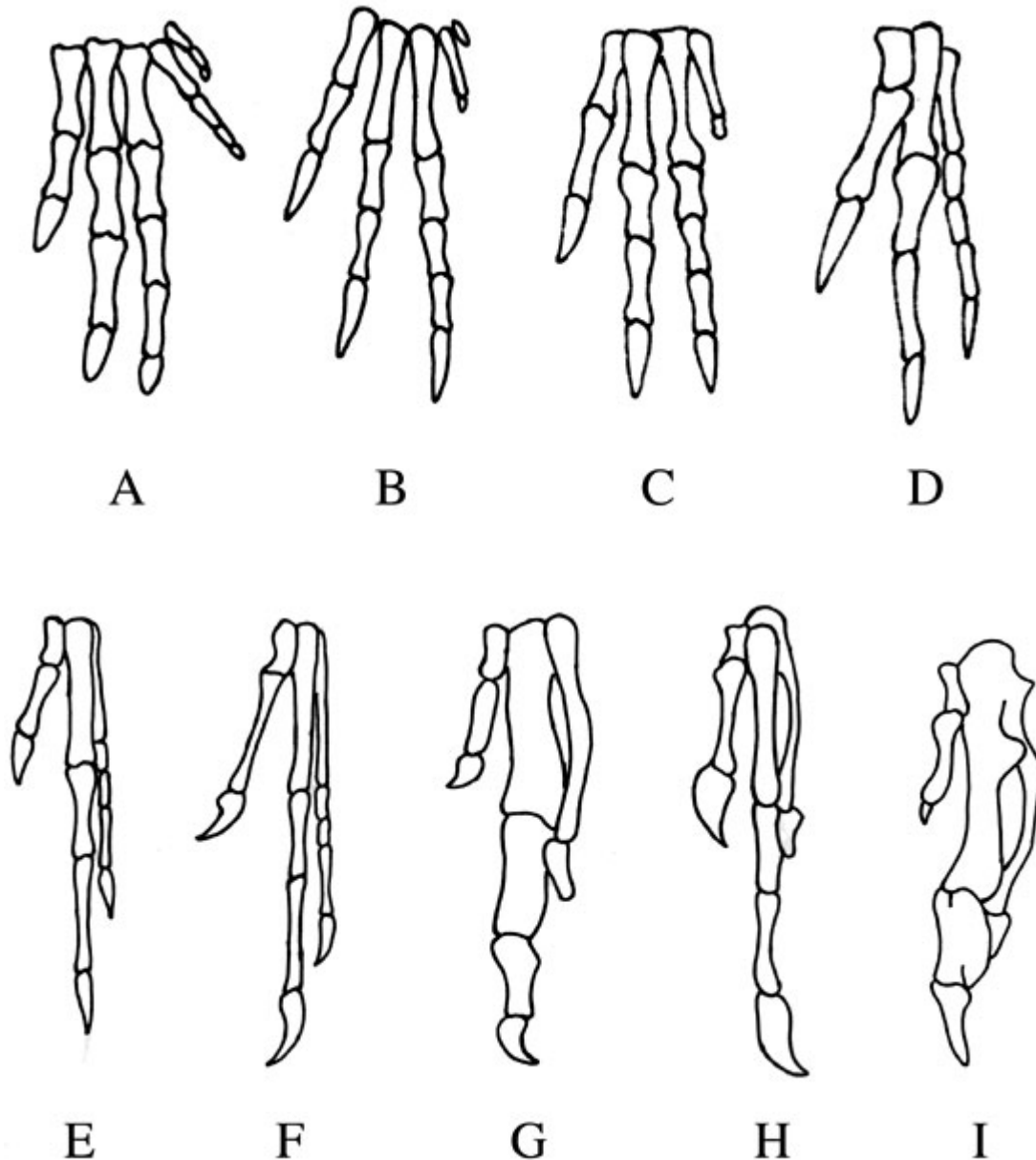
Fig. 4: Phylogenetic-historical evidence unambiguously indicates that birds lost digits 4 and 5, retaining digits 1, 2 and3. Succesive taxa share a more recent common ancestor with modern birds (Neornithes). (A-C) Triassic dinosaurs: (A) the ornithischian *Heterodontosaurus*, (B) the early theropod *Herrerasaurus*, (C) the neotheropod *Coelophysi*s. (D-E) Jurassic theropods: (D) the tetanuran *Allosaurus*, (E) the early maniraptoran *Ornitholestes*. (F-G) Mesosozoic birds: (F) the Jurassic avialae *Archaeopteryx*, (G) the cretaceous enantiornithe *Sinornis.* (H-I) Modern birds: (H) the wing of an *Opisthocomus* (hoatzin) hatchling, (I) the wing of the adult chicken *Gallus*. Modified from Vargas & Fallon (2005).

La evidencia filogenético-histórica indica sin ambigüedades que las aves perdieron los dígitos 4 y 5, reteniendo los dígitos 1, 2 y 3. Los taxa sucesivos comparten un ancestro en común más reciente con las aves actuales (Neornithes). (A-C) Dinosaurios triásicos: (A) ornitisquio *Heterodontosaurus*, (B) terópodo temprano *Herrerasaurus*, (C)

neoterópodo *Coelophysi*s. (D-E) Terópodos jurásicos: (D) tetanuro *Allosaurus*, (E) manirraptor temprano *Ornitholestes*. (F-G) Aves mesosozoicas: (F) Avialae jurásico *Archaeopteryx*, (G) enantiornite *Sinornis.* (H-I) Aves actuales: (H) ala de polluelo de *Opisthocomus*, (I) ala de adulto del pollo *Gallus.* Modificado de Vargas & Fallon (2005).

Adaptationism is evident in this argument against the theropod-bird link. Phylogenetic-historical evidence is discarded before accepting the possibility that even a "rare" event of non-adaptive evolutionary change could have occurred. Further molecular-developmental evidence, however, demonstrates that the development of the wing provides support for the theropod-bird link: the expression pattern of the Hoxd12 and Hoxd13 genes in the chicken wing has been shown to be as expected for a limb with digits 1, 2 and 3, rather than digits 2, 3 and 4 (Pennisi 2005, Vargas & Fallon 2005). In contrast, no expression pattern or molecular marker has been described to support the 2, 3, 4 identification of the wing digits. The best approach is to accept the abundant fossil evidence for the theropod-bird transition, and assume that the wing of birds represents yet another case of adaptively neutral variation in a developmental pathway.

Unfortunately, under an adaptationist point of view, the similarities of theropod dinosaurs and birds can always be interpreted to be convergent solutions to similar adaptive problems. It is considered that phylogenetic analysis based on parsimony cannot deal with "massive convergence" (Feduccia 1999), leading to an ultimately mysterianist attitude towards the subject, which considers (to the outrage of paleontologists) that the origin of birds may be a scientifically unsolvable problem (Feduccia 2002), as in the comment that "the debate over the phylogenetic position of birds seems far from any conclusion (…). Why? Perhaps because where natural selection meets the strict constraints of biomechanics, convergence is inevitable, and separating common inheritance from common function may be near-impossible in a system so highly derived" (Thomas & Garner 1998). Within the subject of bird origins, the concept that natural selection is the main evolutionary mechanism does not pass the test of interdisciplinary integration, failing to agree with what paleontologists consider to be the relevant evidence.

Another case where selective thinking may be misleading regards the evolvability of polydactyly. It is well-known that polydactyly can be observed within intraspecific variation, and that it is inheritable. However, it has been argued that a true case of polydactyly has never occurred at the evolutionary level of interspecific variation (Galis et al. 2001). In some apparent cases, such as the panda's thumb, a sesamoid or pisiform bone is derived into a functional digit-like structure. Given that heritability for polydactly is high within intraspecific variation, and that selection for an extra digit is conceivable, it has been argued that polydactyly may imply some negative side-effect on fitness that constrains its evolutionary occurrence. It has been proposed that selection against polydactyly could be explained because genetic changes required for polydactyly could have pleiotropic effects such as a greater susceptibility to cancer (Galis et al. 2001). This hypothesis therefore provides an adaptive context to understand the apparently non- adaptive constraint on polydactyly. However, the recent discovery of an unambiguously polydactyl aquatic amniote from the Triassic of China (Wu et al. 2003) indicates that the evolutionary occcurence of polydactyly in amniotes is certainly not impossible, a fact that should caution against assuming the generality and pervasiveness of hypothesized adaptive explanations.

The assumption that evolution mostly proceeds by natural selection can lead to "Panglossian" adaptationism and ad-hoc hypotheses of trade-offs as ultimately adaptive explanations for the presence of any apparently non-adaptive or "negative" trait (Gould & Lewontin 1979). Exceptions to hypothesized selective factors can always be explained by previously "unrecognized" advantages or disadvantages which can lead to an ultimately untestable philosophy, where all evolutionary change is allowed or restricted for purely adaptive reasons Although the operational commitment and specialization of some traits is obvious (specially in highly specialized lifestyles), hypotheses of adaptive value of traits can frequently turn out to be insufficiently supported by evidence. Unfortunately, purely hypothetical adaptive considerations are sometimes taken to be more relevant than well-documented phylogenetic-historic facts.

Adaptation and fitness: terms to be revised

Within the study of natural selection, estimates of fitness of individuals cannot rely on the description of traits or mechanisms, but are ultimately judged by offspring survival. This definition of fitness can be controversial, because offspring survival should be considered the result of fitness, rather than its equivalent or cause. As noticed by early opposition to natural selection, the concept of "survival of the fittest" can be argued to be nothing but "survival of the survivors" (Milner 1990). Rather than describe greater offspring survival as a progressive increase in fitness, it can be understood in a more contingential and neutral sense, by full acknowledgement of how non-genetic factors and other circumstances can affect offspring survival. Offspring survival certainly can vary when compared among different individuals. However, differences in offspring survival are not implied to be a direct result of genetic differences among individuals, which can be easily overcome by environmental-circumstantial factors. Unfortunately the concept of fitness as a substitute for offspring survival will continue to mislead towards interpretation of individuals with a greater offspring survival as somehow having a greater "genetic quality" than others. As an alternative, it has been proposed that in a strict sense it is not possible to define adaptation as a variable, such that no individual can be considered intrinsically better adapted than another (Maturana & Mpodozis 2000). Adaptation, considered as the operational congruence and structural coupling of the organism to the environment, is a condition of existence of living systems, and either adaptation is present or the system disintegrates. From this perspective, adaptation does not arise or increase through greater offspring survival, but rather it is a pre-requisite even for reproduction. Evolutionary change does not require for an increase in offspring survival. Conversely, an increase in offspring survival can occur without any evolutionary change. The fact that certain traits cannot change without leading to the disintegration of the organism, does not imply that these traits originated through a competitive process of natural selection for their current function, as exemplified by the occurrence of exaptation (Gould & Vrba 1982).

It is conceivable that a non-adaptive phenotypic trait can become fixed in a population without natural selection, but as a result of a bottleneck or foundation effect. However, even in cases in which differential survival can be found to relate directly to traits of organisms (for example, when only immune individuals survive a disease, or in the classic example of Kettelwell's industrial melanism) , it is legitimate to ask whether this process can only be described as a process of adaptation by natural selection, or if it can in fact be argued to be more contingential and comparable to a bottleneck, specially taking into account that under another circumstance (e.g., another type of sickness), other traits would be selected for. When selection is described to have occurred for a trait, it is possible to consider it as a possible pathway under a specific

circumstance (drift), rather than describing it as a directional, adaptive increase of fitness leading to the final result.

Although it is frequently conceived that evolutionary change is a process of progressive increase in fitness or adaptation through natural selection, it is possible to apply the concept of non-adaptive drift, accepted for the evolution of developmental pathways and evolution at a molecular level (Kimura 1968, Weiss & Fullerton 2000), to the level of the phenotype (Maturana & Varela 1984, Maturana & Mpodozis 1992, 2000, Weiss & Buchanan 2003), conceiving the change and conservation of phenotypes as a neutral process of natural drift (Maturana & Mpodozis 1992, 2000), rather than a process of adaptation through natural selection. Conservation and change of ontogenic (life cycle) phenotypes is established through the trans-reproductive repetition or shifting in the epigenetic pathway that emerges along the organism-environment interaction (Maturana & Mpodozis 1992, 2000). Both genetic and environmental changes in evolution can be described as co-opted to the epigenetic pathway in which adaptation is conserved (Maturana & Mpodozis 1992, 2000).

The epistemological status of natural drift

Epistemologically, the systemic conceptual framework of natural drift (Maturana & Mpodozis 1992, 2000) is not teleological ("finalist"), it does not imply any sort of vitalist or metaphysical reasoning, and does not make any reductionist assumptions. No force is invoked that cannot be observed to operate in the natural world. It is therefore most remarkable that this conceptual framework has been argued to be unscientific and dogmatic, and even framed as holding a potential to fuel creationism (Nespolo 2003). The main argument for this overreaction is that natural drift cannot be falsified. Ironically, it is well-known that the same argument has been used to seriously question the scientific status of natural selection, because no crucial experiment or case can be conceived to prove it wrong (Popper 1976). As discussed by Mayr (1998), when dealing with a general conceptual framework for a complex historical phenomenon such as the evolution of life, an extreme version of falsation is inadequate. Rather, within evolutionary biology, general theories are assessed by contrasting the consistency of their logical predictions with several independent sources of information (see Ahumada et al. 2005). As discussed above, evolutionary biology can have good predictive power, but it cannot be attributed to the sole application of the concept of selection.

Creationists or advocates of "intelligent design" frequently refer to the origin of life as a roadblock to scientific explanation. Natural drift is an explanation of evolution that uses the concept of autopoiesis as a definition of life. The concept of autopoiesis does not recur to any reductionist or vitalist assumptions to explain the origin of life, and as such has received considerable attention in this field (Maturana & Varela 1973, 1980, Bachmann et al. 1992, McMullin 2000, Luisi 2003). Autopoiesis conceives organisms as self-producing units. Reproduction and therefore, evolution, are consequences of autopoiesis (Maturana & Mpodozis 1992, 2000). It is also interesting to point out that, although the metaphysical construct of modern catholic faith currently considers itself compatible with the scientific fact of evolution, it continues to set the limit as to a non-evolutionary origin of a human soul (Vicuña 2004), and further rejects any biological origin of the human mind. Alternatively, all human cognitive experiences can be approached in biological terms of structural determinism (Maturana & Pörksen 2004).

The bold epistemological approach behind natural drift dispels any attempted linking of natural drift to creationism. Similarly, the proposal that natural drift is an actual equivalent to the "daisyworld parable" (a simulation on how a homeostatic, regulative global environment can evolve without natural selection, Watson & Lovelock 1983) is clearly inappropriate. The conceptual framework of natural drift provides a battery of concepts to deal with several important subjects that require attention in evolutionary biology. The only resemblance of natural drift to the "daisyworld parable" is that it does not consider a central role for natural selection.

Creationism is fueled by the mistake of considering "natural selection" and "evolution" to be equivalent, as in the popular misconception of "Darwin's theory of evolution". This leads to confuse the debate on the evolutionary role of selection (which is necessary and appropriate), with the existence of doubt on the phenomenon of evolution in itself. Dobzhansky probably contributed to this confusion with his famous reductionist dictum that "evolution is a change in the genetic composition of populations". The frequent epistemological mistake of reducing a phenomenological domain to another that is assumed to be more fundamental can be recognized and avoided (Lewontin 1974, Maturana & Mpodozis 2000). In fact, a central role for selection and quantitative genetics is not required to acknowledge the phenomenon of evolution in itself. Common ancestry and descent with modification are evident from change and conservation throughout the comparison of the diversity of living and fossil taxa. If this is understood, controversy on the role of selection may cease to be confused with uncertainty on the fact of evolution itself.

CONCLUDING REMARKS

The framework of selection has been applied to several biological levels (genes, cells, organisms, populations, species) and even to non-biological cases (Nespolo 2003). Although this may be considered to reflect the great operational utility of the concept of selection, it has also lead to remarkable controversies: do genes confer fitness to individuals which act mainly as transient vessels, or is the frequency of genes a result of the fitness of individuals? 145 years after publication of "the origin of species", the actual agents of selection are still under discussion, with paradoxical disagreement on the hierarchical priority of selection for one level or another (Gould 2002, Dawkins 1976, West-Eberhard 2003). Even if selection is a highly operational concept, this does not justify conceiving natural selection ideologically as a pre-eminent, fundamental determinant of evolutionary change, that should be central in the study of evolutionary biology (Camus 2000). An ideological approach to selection leads to disregard phylogenetic-historical evidence, dismiss non-adaptive evolutionary change, and underestimate the role of epigenetic phenotypic plasticity. The presence in Chile of alternative conceptual frameworks is in part a response to the insufficiencies of selection for the understanding of evolution (Maturana & Mpodozis 2000).

A historical description of the acceptance of natural selection in the scientific community shows an initial enthusiasm in the late 19th-early 20th century, followed by an important eclipse towards the 1930's when it was almost abandoned. Towards the mid 20th century, the modern synthesis had resurrected Darwinism, and attention focused on the theoretical construct of population genetics, with a dogmatic hardening of the concept of natural selection as the main mechanism of evolutionary change. However, since the 1960´s, research on evolutionary biology has gone far beyond the scope of natural selection and population genetics, with great advances in phylogenetic, historical, molecular, and developmental research. The concepts of

spandrels, exaptation, and non-adaptive change have become well-accepted. Within the actual structure of current evolutionary theory, the study of natural selection and population genetics can be described to coexist with other substantially different branches of evolutionary theory (Gould 2002).

Several researchers have defended that natural selection should have a central role in evolutionary thinking, as it effectively did in the mid 20th century. Some may even consider their own line of evolutionary thinking has "attained maturity" (Nespolo 2003). However, it is evident that a great deal of progress in evolutionary research and thinking is still due, and is not restricted to the study of natural selection. Current evolutionary biology deals with several independent research fields on evolution that are almost absent in Chile, such as paleontology and developmental evolution. We can not expect to develop a truly scholarly vision of evolution if an hegemonic role for selection is defended at undergraduate courses of evolution. Greater interdisciplinary knowledge will be achieved by accepting the growing phenomenological scope of evolutionary biology, and the need for a diversity of theoretical and empirical approaches. New conceptual frameworks are welcome that may help remove the biases facing the recognition of actual evolutionary facts and mechanisms.

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LITERATURE CITED

AHUMADA P, G ASTORGA, K BULL-HEREÑU, C CABRERA, L CAPUTO, C CARMONA, MC CECCHI, N CORTÉS, S CORTEZ, C DORADOR, F FREDES, C GUERRERO-BOSAGNA, P HENNY, C LIBEDINSKY, W MARCELO, N MÁRQUEZ, J MARTÍNEZ, M MEDINA, P OSSA, D PARRA, N POHL, H POTTSTOCK, T OSSANDÓN, P RAZETO, D RUBILAR, C SALAS, F SALINAS, E SEPÚLVEDA, C SOTO, R SUÁREZ, A VARGAS, T VEGA-ZÚNIGA, N VELÁSQUEZ, J VIDAL, C VILLAGRA & CP VILLAVICENCIO (2005) Undergraduate teaching of evolution in Chile: more than natural selection. Revista Chilena de Historia Natural 78: 169-170.

BACHMANN PA, PL LUISI & J LANG (1992) Autocatalytic self-replicating micelles as models for prebiotic structures. Nature 357: 57-59.

BAKKER, RT (1986) The dinosaur heresies. Zebra books, New York, New York, USA. 481 pp.

BENTON MJ (2000) Vertebrate paleontology. Second edition. Blackwell Science, Oxford, United Kingdom. 452 pp.

BURKE AC & A FEDUCCIA (1997) Developmental patterns and the identification of homologies in the avian hand. Science 278: 666-668.

CAMUS PA (2000) Evolution in Chile: natural drift versus natural selection, or the preservation of favoured theories in the struggle for knowledge. Revista Chilena de Historia Natural 73: 215-219.

CALDWELL MW & MSY LEE (1997) A snake with legs from the marine cretaceous of the middle east. Nature 386: 705-709.

CARROL R (1988) Vertebrate paleontology and evolution. W.H. Freeman & Co., New York, New York, USA. 698 pp.

CHATTERJEE S (1998) Counting the fingers of birds and dinosaurs. Science 280: 355.

CHIAPPE LM (1997) Aves. In: Currie P & K Padian (eds) The encyclopedia of dinosaurs: 32-38. Academic Press, New York, New York, USA.

CHIAPPE LM & A VARGAS (2003) Emplumando dinosaurios: la transición evolutiva de terópodos a aves. Hornero 18: 1-11.

DARWIN C (1859) [1977] El origen de las especies por medio de la selección natural. Editorial Edaf, Madrid, España. 533 pp.

DAWKINS R (1976) [1993] El gen egoísta. Salvat Ediciones, Barcelona, España. 407 pp.

DOMNING DP (2001) The earliest known fully quadrupedal sirenian. Nature 413: 625-627. [Medline]

FEDUCCIA A (1999) 1,2,3 = 2,3,4: accomodating the cladogram. Proceedings of the National Academy of Sciences USA 96: 4740-4742.

FEDUCCIA A (2002) Birds are dinosaurs: simple answer to a complex problem. Auk 119: 1187-1201.

FEDUCCIA A (2003) Bird origins: problem solved, but the debate continues. Trends in Ecology and Evolution 18: 9-10.

GALIS F, J VAN ALPHEN & J METZ (2001) Why five fingers? Evolutionary constraints on digit numbers. Trends in Ecology and Evolution 16: 637-646.

GALIS F, M KUNDRÁT & B SINERVO (2003) An old controversy solved: bird embryos have five fingers. Trends in Ecology and Evolution 18: 7-9.

GILBERT SF, JM OPITZ & RA RAFF (1996) Resynthesizing evolutionary and developmental biology. Developmental Biology 173: 357-372. [Medline]

GOULD SJ (1977) Ontogeny and phylogeny. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA. 501 pp.

GOULD SJ (2002) The structure of evolutionary theory. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA. 1,433 pp.

GOULD SJ & RC LEWONTIN (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. Proceedings of the Royal Society of London B 205: 581-598.

GOULD SJ & ES VRBA (1982) Exaptation: a missing term in the science of form. Paleobiology 8: 4-15.

HALL BK (1998) Evolutionary developmental biology. Chapman and Hall, London, United Kingdom. 516 pp.

HENNIG W (1965) Phylogenetic systematics. Annual Review of Entomology 10: 97-116.

JI Q, P CURRIE, MA NORELL & S-A JI (1998) Two feathered dinosaurs from northeastern China. Nature 393: 753-761.

KIMURA M (1968) Evolutionary rate at the molecular level. Nature 217: 624-626. [Medline]

KNOLL AH & SB CARROLL (1999) Early evolution: emerging views from comparative biology and geology. Science 284: 2129-2137. [Medline]

LEWONTIN RC (1974) The genetic basis of evolutionary change. Columbia University Press, New York, New York, USA. 346 pp.

LUISI PL (2003) Autopoiesis: a review and a reappraisal. Naturwissenschaften 90: 49-59. [Medline]

MATURANA H & B PORKSEN (2004) Del ser al hacer. Los orígenes de la biología del conocer. JC Sáez, Santiago, Chile. 239 pp.

MATURANA H & J MPODOZIS (2000) The origin of species by means of natural drift. Revista Chilena de Historia Natural 73: 261-310.

MATURANA H & J MPODOZIS (1992) Origen de las especies por medio de la deriva natural o la diversificaión de los linajes a través de la conservación y cambio de los fenotipos ontogénicos. Museo Nacional de Historia Natural, Publicación Ocasional (Chile) 46: 1-48.

MATURANA H & F VARELA (1973) De máquinas y seres vivos. Editorial Universitaria, Santiago, Chile. 122 pp.

MATURANA H & F VARELA (1980) Autopoiesis and cognition: the realization of the living. D. Reídle Publishing Company, Dordrecht, The Netherlands. 140 pp.

MATURANA H & F VARELA (1984) El árbol del conocimiento. Editorial Universitaria, Santiago, Chile. 172 pp.

MAYR E (1998) Así es la biología. Editorial Debate, Madrid, España. 326 pp.

MCMULLIN B (2000) Remarks on autocatalysis and autopoiesis. Annals of the New York Academy of Science 901:163-74.

MEYER A & R ZARDOYA (2003) Recent advances in the (molecular) phylogeny of vertebrates. Annual Reviews in Ecology and Evolutionary Systematics 34: 311-348.

MILNER R (1990) The encyclopedia of evolution. Facts on File Press, New York, New York, USA. 481 pp.

MÜLLER GB (2003) Embryonic motility: environmental influences and evolutionary innovation. Evolution & Development 5: 56-60.

NESPOLO RF (2003) Evolution by natural selection: more evidence than ever before. Revista Chilena de Historia Natural 76: 699-716.

NEWMAN SA & GB MÜLLER (2000) Epigenetic mechanisms of character origination. Journal of Experimental Zoology B 288: 304-317.

NORELL MA & MJ NOVACEK (1992) The fossil record and evolution. Comparing cladistics and paleontologic evidence for vertebrate history. Science 255: 1690-1693.

PADIAN K & L CHIAPPE (1998) The origin and early evolution of birds. Biological Reviews 73: 1-42.

PALMER AR (2004) Symmetry breaking and the evolution of development. Science 306: 828-833.

PAUL G (1988) Predatory dinosaurs of the world. Simon & Schuster, New York, New York, USA. 464 pp.

PENNISI E (2005) Bird wings really are like dinosaurs' hands. Science 307: 194-195.

PETERSON KJ & DJ EERNISSE (2001) Animal phylogeny and the ancestry of bilaterians: inferences from morphology and 18S r DNA sequences. Evolution & Development 3: 170-205.

POPPER K (1976) El darwinismo como programa metafísico de investigación. Third edition. Tecnos, Madrid, España. 320 pp.

PRUM RO (2002) Why ornithologists should care about the theropod origin of birds. Auk 119: 1-17.

PRUM RO (2003) Are current critiques of the theropod origin of birds science? Rebuttal to Feduccia (2002). Auk 120: 550 -561.

RAFF R (1996) The shape of life. University of Chicago Press, Chicago, Illinois, USA. 520 pp.

SERENO PC (1999) The evolution of dinosaurs. Science 284: 2137-2147.   [Medline]

SHU D-G, H-L LUO, S CONWAY MORRIS, X-L ZHANG, S-X HU, L CHEN, J HAN, M ZHU, Y LI & L-Z CHEN (1999) Lower Cambrian vertebrates from south China. Nature 402: 42-46.

THOMAS ALR & JP GARNER (1998) Are birds dinosaurs? Trends in Ecology and Evolution 13: 129-130.

THOMPSON DAW (1917) [1977] On growth and form (abridged edition). Cambridge University Press, Cambridge, United Kingdom. 346 pp.

VARGAS AO & JF FALLON (2005) Birds have dinosaur wings: the molecular evidence. Journal of Experimental Zoology B 304: 85-89.

VICUÑA R (2004) Alma humana y evolución. Revista de Estudios Médico Humanísticos (Chile) 1: 1.

WADDINGTON CH (1953) Genetic assimilation of an acquired character. Evolution 7: 118-126.

WAGNER GP & BY MISOF (1993) How can a character be developmentally constrained despite variation in developmental pathways? Journal of Evolutionary Biology 6: 449-455.

WAGNER GP & JA GAUTHIER (1999) 1, 2, 3 = 2, 3, 4: a solution to the problem of homology of the digits of the avian hand. Proceedings of the National Academy of Sciences USA 96: 5111-5116.   [Medline]

WAGNER GP, C-H CHIU & M LAUBICHLER (2000) Developmental evolution as a mechanistic science: the inference from developmental mechanisms to evolutionary processes. American Zoologist 40: 819-831.

WATSON AJ & JE LOVELOCK (1983) Biological homeostasis of the global environment: the parable of Daisyworld. Tellus 35B: 284-289.

WEISS KM (2005) The phenogenetic logic of life. Nature Reviews in Genetics 6: 36-46.

WEISS KM & SM FULLERTON (2000) Phenogenetic drift and the evolution of genotype-phenotype relationships. Theoretical Population Biology 57: 187-95.   [Medline]

WEISS KM & AV BUCHANAN (2003) Evolution by phenotype. A biomedical perspective. Perspectives in Biology and Medicine 46: 159-82.   [Medline]

WEST-EBERHARD MJ (2003) Developmental plasticity and evolution. Oxford University Press, New York, New York, USA. 794 pp.

WITMER LM (2002) The debate on avian ancestry: phylogeny, function, and fossils. In: Chiappe LM & LM Witmer (eds) Mesozoic birds: above the heads of dinosaurs: 3-30. University of California Press, Berkeley, California, USA.

WHITMAN CO (1919) Orthogenetic evolution in pigeons. Carnegie Institute of Washington Publications 257.

XU X, Z-H ZHOU & RO PRUM (2001) Branched integumental structures in *Sinornithosaurus* and the origin of feathers. Nature 410: 200-204.   [Medline]

WU XC, Z LI, BC ZHOU & ZM DONG (2003) Palaeontology: a polydactylous amniote from the Triassic period. Nature 426: 516.

XU X, Z ZHOU, X WANG, X KUANG, F ZHANG & YX DU (2003) Four-winged dinosaurs from China. Nature 421: 335-340.   [Medline]

ZHOU Z (2004) The origin and early evolution of birds: discoveries, disputes, and perspectives from fossil evidence. Naturwissenschaften 91: 455-471.   [Medline]