

The Concept of Co-option: Why Evolution Often Looks Miraculous

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Abstract Darwin believed that evolution generally occurred through a series of small, gradual changes. This proposal was counter-intuitive to many people because it seemed likely that “transitional” forms would not survive. Darwin, and later Cuènot, recognized that this problem was easily solved if characters that had evolved for one reason changed their function at a later time with little to no concurrent structural modification, at least initially. In other words, traits that had evolved under one set of conditions were co-opted to serve a different function under a second set of conditions. This meant that organisms carried with them in the structures of their genes, proteins, morphological, physiological, and behavioral characters the potential for rapid evolutionary change, so rapid, indeed, that the process looked miraculous and Lamarckian. In this paper, I discuss some of the paradigm examples of co-option, from genes to behavior.

Keywords Co-option · Preadaptation · Exaptation · Evolution

Darwin believed that evolution generally occurred through a series of small, gradual changes. Oftentimes, though, it appears that evolution has leapt over many of the intermediate forms to arrive rapidly at a later, fully formed stage. These leaps look almost miraculous in retrospect, attributable more to Lamarckian than Darwinian mechanisms (e.g., animals needed jaws, so they grew them). In the following essay, I shall discuss how various researchers have tried to solve the problem of these evolutionary leaps

within a Darwinian framework. This shall involve traveling a long road beginning with Darwin himself and continuing through to the present day. Along the way we will encounter three terms: *preadaptation*, *exaptation*, and *co-option*. No other terminology is needed for the journey.

The History of the Concept in Biology

In chapter VI of *The Origin of Species* (Darwin 1872), Darwin answered objections raised by various authors to his theory of natural selection. One of the major criticisms revolved around the perceived absence of transitional stages (of characters) in either the fossil record or in living species. If natural selection really does operate through a series of small, gradual changes, then the world should be awash in transitional stages. We don't see this in either the fossil record or in the living creatures around us, so where are they?

Darwin formulated numerous answers to this critical question, one of which involved changing the function of an already existing structure. In some cases, this occurred when two organs performed the same function, thus setting the stage for selection to increase the efficiency of one, then modify the second, and now superfluous organ, for a different function. Darwin believed that this type of dynamic was “an extremely important means of transition” (Darwin 1872, p. 175) in evolution. In other cases, an organ that served a major and minor function was modified to serve the latter at the expense of the former. In both of the preceding processes, the starting conditions might be obscured and the “transitional stage” missing. So for example, who other than a good functional morphologist and ichthyologist would think that lungs started their evolutionary journey as a gas bladder, that organ deluxe

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for regulating buoyancy in teleost fishes? Fortunately, we have evidence from basal ray-finned fishes that the gas bladder originally served both functions and has since been modified along two different trajectories. In teleost fishes, gills have assumed all the burden of respiration, while the gas bladder has been sealed off from the gut and now functions in buoyancy. In the lobe-finned fishes, on the other hand, gills eventually disappeared as the gas bladder became increasingly modified to serve as a lung. If the basal ray-finned fishes had gone extinct without leaving a trace of their existence, it would have been difficult to reconstruct this pathway.

Finally, Darwin discussed traits that served no apparent function because they arose as the byproduct of evolutionary processes other than Natural Selection (e.g., the “complex laws of growth”; the “mysterious laws of the correlation of parts”). He believed that such traits were an important part of organismal evolution because they might eventually acquire a function that was necessary for survival in a new environment; “But structures thus indirectly gained, although at first of no advantage to a species, may subsequently have been taken advantage of by its modified descendants, under new conditions of life and newly acquired habits.” (Darwin 1872, p. 186).

In all of the preceding examples, important evolutionary change had been accomplished without creating structures *de novo*. The French biologist Lucien Cuènot (Cuènot 1911; Cuènot 1925) championed the term “preadaptation” for these phenomena. Initially, he believed that preadaptations were traits of little or no importance at their point of origin that played a critical role down the evolutionary road by allowing organisms to invade “des places vides” [unoccupied niches] (Cuènot 1911, p. 417). Unfortunately, his mechanism for how such a shift in functionality could occur was a somewhat confusing amalgam of Darwinian and Lamarckian themes:

“... one could say ... that the need and the organ create function; in the individual functioning changes the organ most efficiently through the effect of usage, and finally selection intervenes to eliminate descendants that cannot handle the new conditions” (Cuènot 1911, p. 417)

This confusion over mechanism clouded his central message: that traits arising under one condition could allow the transition to a new environment/way of life without the need to evolve new structures.

Cuènot spent many years arguing for the importance of preadaptation, building the database of examples much like Darwin sought evidence for selection. During that quest, he expanded the definition of preadaptation to include the co-option of useful traits to serve a new function. So, like Darwin, he considered the gas bladder

to be a preadaptation for the development of lungs and, carrying the argument further, that the gas bladder was a critical preadaptation for the tetrapods’ (animals with four limbs) subsequent invasion of the land. Cuènot was a member of the first generation of geneticists, inspired by Gregor Mendel, attempting to delineate how the units of heredity worked. Many of these early researchers focused on the seemingly random process of mutation, arguing that adaptation was an incidental or accidental byproduct (e.g., mutationist theory of de Vries). From the preadaptation perspective, this created a paradox: if the production of preadaptations was a random process, why, as many good naturalists can attest, did adaptation appear to be so nonrandom, so organized with respect to the environment? Cuènot (Cuènot 1911, 1941, 1951) grappled with the paradox, but never managed to answer it to his, or others’, satisfaction. This paradox eventually led to a split between evolutionary biologists, with the population geneticists on one side and the naturalists, paleontologists, and systematists on the other.

It is thus not surprising that the founders of the New Synthesis were divided over the issue of preadaptation. Dobzhansky (1955) dismissed it, writing “‘preadaptation’ is a meaningless notion if it is made different from ‘adaptation’.” (p. 370). This dismissal missed the point raised by Cuènot that preadaptations might, after their function had been changed (co-opted), appear to be adaptations to the current environment, when in fact they were not; their origin and *raison d’être* predated the current role they fortuitously found themselves playing. Goldschmidt (1940) supported the mutationist theory, reducing preadaptations to random micromutations, arguing that only organisms with “chance hereditary mutant combinations for life under changed conditions” (p. 102) could survive in a fluctuating environment. He echoed Cuènot’s proposal that preadapted individuals might enter an empty niche and there survive and propagate, eventually producing new species. Simpson (1944, 1949; see also Mayr 1963) elaborated on this latter theme, hypothesizing that organisms carried within them a storehouse filled with deleterious and neutral mutations accumulated over time (we might call this historical baggage today), any one or combination of which, under changing conditions, might allow them to move from one adaptive zone (for example living in the water) to another (living on land). Once in the new zone, the population would rapidly undergo an adaptive radiation, filling the zone with new species. So, Simpson believed that the preadapted trait is not adaptive with respect to the environment in which it originated, but that it eventually becomes adaptive in the new zone. In 1944, he concluded that such traits were “of tremendous importance, because they afford an explanation of quick, radical shifts in adaptive types.” (Simpson 1944, p. 80).

Nine years later, Simpson (1953) felt compelled to write that biologists were using the term preadaptation in nine different ways, eight of which assumed the process was adaptive at all stages, and one of which supposed the non-adaptive to adaptive transition. As is so often the case with human beings, for our minds seemed geared to create dichotomies, Simpson's categories were foreshadowed by Darwin's and Cuènot's initial recognition that preadaptations originated in two different ways: (1) a neutral or deleterious trait acquiring an adaptive function in a new environment and (2) a useful (adaptive) trait changing function. The confusion then, surrounds the origin of the trait, was it initially adaptive or not? This confusion aside, the outcome of a preadaptive trait was always the same, evolutionary change happened rapidly because the material for change already existed, for whatever reason, in the organism. Overall then, there was general agreement about the importance of preadaptation, coupled with dissention about which one of two possible pathways was *the* most important to the production of a preadapted trait in the first place.

Mechanism aside, there is a glaring problem with the word "preadaptation" itself. It is teleological; that is, it implies there is a direction or purpose to evolution (to make the trait adaptive), when in fact it is impossible to predict with any degree of accuracy the future of a biological character based on its current state. Evolution does not solve future problems. It is a process of the here and now that has ramifications for the future that we can recognize only in hindsight. In 1982, Gould and Vrba eliminated the specter of teleological terminology by replacing "preadaptation" with the concept of "exaptation". So, for example, consider (again) the gas bladder, which arose long ago in the ancestor of the bony fishes (lobe-finned fishes + ray-finned fishes). At this point in time, it was connected via a duct to the alimentary canal, and from there to the mouth, and is thought to have functioned in both respiration and buoyancy control. Once the bladder was sealed off from the gut (by loss of the duct), it was co-opted several times within the ray-finned fishes to serve an additional, new function: sound production. Specialized sonic muscles beat the gas bladder like a drum in the appropriately named drums and croakers, catfishes, squirrelfishes, and toadfishes. It is at this point in time, when the plesiomorphic¹ (ancestral) character has been co-opted to serve a different function,

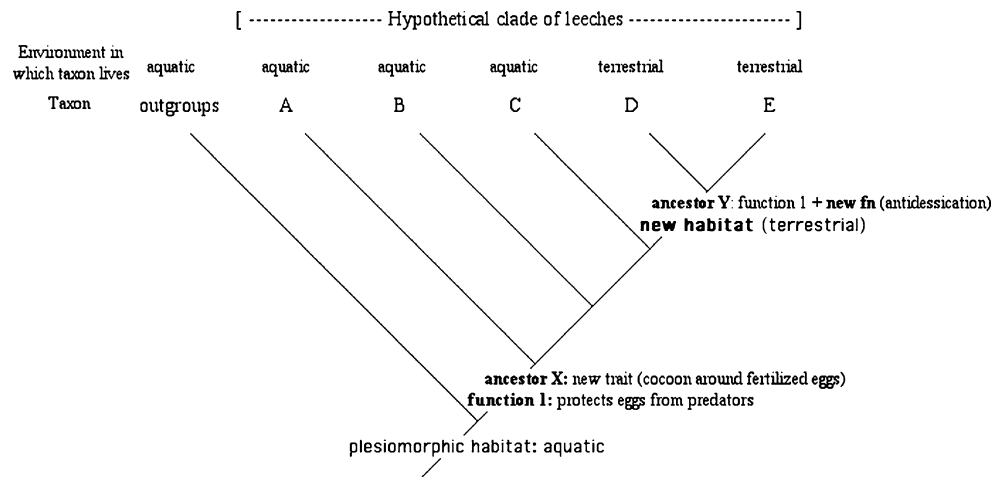
that we call the swim bladder an exaptation for sound production. Gould and Vrba recognized that the dispute about whether the exapted trait was adaptive, neutral or maladaptive at its point of origin was a red herring, albeit an interesting one, and focused instead upon the part of preadaptation with which all previous authors agreed: an exaptation is *a character* that retains its plesiomorphic (ancestral) form *while taking on a new function* (see also Baum and Larson 1991; Arnold 1995; Armbruster 1997). The *process* by which the trait switches function is called co-option² (Gould and Vrba used the more correct form "co-optation", but that has never caught on), a general term encompassing all possible processes. Co-option is critical to Darwinism because, without it, it is often impossible to explain dramatic movements into new environments or the sudden appearance of "new" traits without unintentionally invoking a Lamarckian mechanism. (e.g., fish needed to get from pond to pond to avoid being dried out, *so* they developed limbs, as opposed to fish that *already had limbs* were more successful at getting from pond to pond to avoid being dried out).

The hypothesis that a particular trait has been co-opted is strongly supported by the type of macroevolutionary pattern shown in Fig. 1. In this example, all females from a hypothetical group of leeches produce a thick, proteinaceous cocoon to cover their eggs (the cocoon is the plesiomorphic [ancestral] trait for the group, passed from ancestor "X" to all of its descendants). Let's say researchers have determined that the plesiomorphic function of the cocoon in ancestor X is to deter egg predation. At some point in time, ancestor "Y" colonized land where the cocoon still served its plesiomorphic function (anti-egg predation). One of the problems with living on land is that water is constantly moving out of the organism via evaporation into the surrounding air; organisms tend to dry out, and will die without a constant supply of water to replace that lost by evaporation, and/or ways to store water and decrease its rate of loss to the environment. A thick coating around an egg containing a developing embryo is one way to decrease the rate of water loss. So, the proteinaceous coating may have evolved initially as an anti-predator structure, but now in the new environment, it takes on the additional role of protecting the eggs from desiccation *without any changes to the cocoon itself*. And, as Cuènot proposed, it was the existence of the cocoon that permitted the transition from one environment to another (although this need not happen with every co-opted trait).

¹ Plesiomorphic is a term from phylogenetic systematics that refers to the ancestral state of a character for a given group of organisms. So, for example, if you say that having a special type of enamel called ganoine in the scales is plesiomorphic for ray-finned fishes, what you are saying is that "ganoine in the scales" originated in the ancestor of the ray-finned fish. For a discussion of the terms used in phylogenetic reconstructions of evolutionary pathways and relationships, see Brooks and McLennan 2002; Gregory 2008.

² Co-option entered the English language in 1651 when the Latin word *cooptare* (to choose as a member of one's tribe) was modified to *co-opt* (to select someone for a group or a club by a vote of the members). Somewhere around 1953, *co-opt* assumed a new meaning, to appropriate, take over, assimilate (Online Etymology Dictionary, <http://www.etymonline.com>).

Fig. 1 The evolution of the proteinaceous cocoon in a hypothetical group of leeches. The cocoon originated in ancestor X, where it protected the eggs from predators. The new function (anti-desiccation) in ancestor Y represents the co-option of the plesiomorphic trait, which allowed the leeches to successfully move from an aquatic to a terrestrial environment



The leech example highlights a critical aspect of co-option: it is most robustly studied within a phylogenetic framework because it is inherently historical. We are talking about a two-step process, (1) the origin of a trait followed by (2) a shift in its function at a later point in time. If we had eliminated history from our explanation, we would have concluded that the cocoon was an adaptation for living on land—this implies that the cocoon originated when leeches moved out of the water onto land. At that point, we would then have to invoke random mutations that somehow produced the first cocoon, just in the nick of time for the leeches and their attempted terrestrial colonization. But phylogeny demonstrates that the cocoon existed long before the leeches changed environments, so it wasn't necessary to sit and wait for that one lucky random mutation. In modern parlance then, the cocoon is *not* an adaptation for living on land; it is an adaptation for deterring egg predators and an exaptation for living on land.

The last 15 years of the 20th century has seen the rise of a new star called “evo-devo”; that is, the study of developmental process based on the structure, pattern, and timing of genetic activity with an evolutionary framework. One of the major breakthroughs of this approach has been the discovery that many genes and developmental processes

are remarkably conservative across often vast phylogenetic distances (Plachetzki and Oakley 2007). From this discovery came the (re) recognition that co-option (sometimes called “recruitment”) at the level of genes and proteins has played an important role in the production of evolutionary innovations (for an excellent review of genetic co-option, see (True and Carroll 2002)). There are four types of functional changes at this level depending upon whether co-option is occurring to one gene or a copy of a duplicated gene, and whether the co-opted gene changes function completely or retains its plesiomorphic (ancestral) role as well (Table 1). Overall, the four categories depicted in Table 1 differ primarily in the fate of the plesiomorphic function, which ranges from total loss (category A), through retention (categories B and C) to retention plus some redundancy (category D). This refined examination of co-option builds on Darwin’s insights that one organ may have two functions (category B, Table 1), one organ may undergo a complete change in function (category A, Table 1), and two organs with the same function can be selected to travel different functional pathways (Category C, Table 1).

Although the categories are straightforward, delineating the mechanisms underlying them is more complicated when

Table 1 Fates of co-opted genes under four different evolutionary scenarios

	One gene	Gene duplication (2 copies)
Plesiomorphic function lost	A Direct co-option with a complete functional shift: gene has derived function	C Co-option of a duplicated element, complete functional shift in one of the copies: one copy shows only the derived function, the other retains the plesiomorphic function
Plesiomorphic function retained	B Direct co-option with retention of plesiomorphic function: gene shows both plesiomorphic and derived functions	D Co-option of a duplicated element with retention of plesiomorphic function: one copy shows both plesiomorphic + derived functions, the other retains the plesiomorphic function

discussing the co-option of genes. Research of this type follows a general pathway: (1) sequence a gene, cluster of genes, or, in extreme cases, an entire genome, for as many species as possible; (2) map those data onto a phylogenetic tree for the test species; (3) identify the origin of gene duplication, if any, on the tree; (4) identify the functions of those genes before and after duplication; (5) pinpoint the origin of functional shifts on the phylogeny; (6) search for mechanisms underlying that shift. It is this latter step that is so technologically difficult at the moment, often requiring months or even years of painstaking research to identify one causal factor. The upshot of all this difficulty is that we may be able to identify and answer the “why” of evolution for many genetic co-option events, but we have only an incomplete picture of “how”—for the moment. This is not a permanent gap in our explanatory framework. It is a gap that gets ever smaller and eventually vanishes as our technological prowess advances, increasing the range of problems that become available to the illumination of scientific enquiry.

And Now, For Some Examples

Molecules

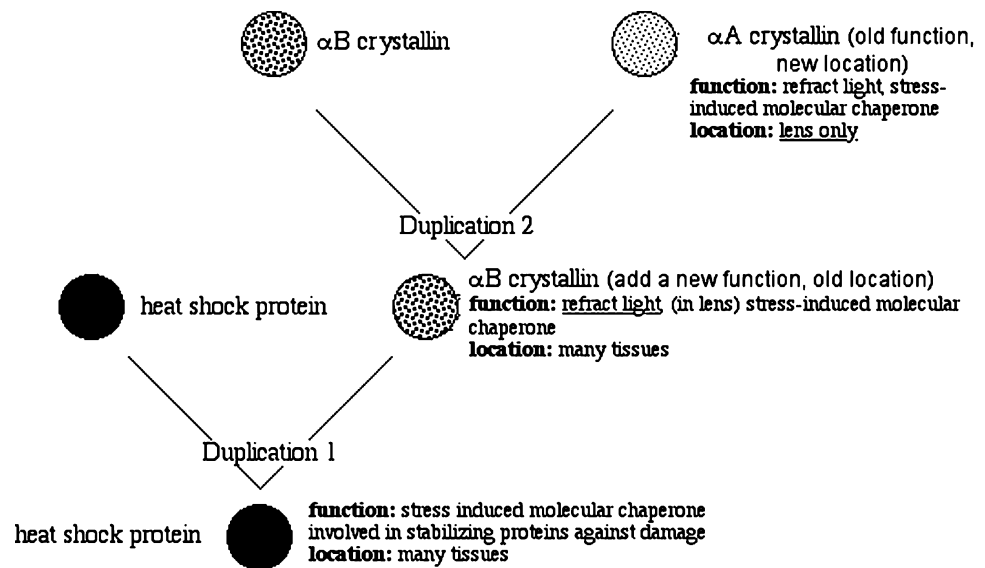
Crystallins are soluble proteins found in the lens of all vertebrates examined to date and some invertebrates (the following summary is taken from (True and Carroll 2002) and references therein). These proteins refract light passing through the lens to form a focused image on the retina. They possess an additional characteristic, the ability to remain stable at very high concentrations for long periods of time, which is critical to functioning in the eye because proteins in that part of the body cannot be repaired or replaced. This is ultimately a story of gene duplication, changes in function and changes in the area in which particular genes are expressed. Molecular analysis indicates that α crystallins are homologous with heat shock proteins, which are involved in stabilizing other proteins under stressful conditions, preventing their degradation. From a protein’s perspective, what more stressful place could there be in the body than the eye, the organ that receives light (photons), which can cause substantial oxidative damage to unprotected proteins (reviewed in (Graw 1997))? Phylogenetic and functional analyses indicated that α crystallins originated following two duplication events (Fig. 2). In the first event one of the copies of a heat shock protein (copy 1) retained its plesiomorphic function (protection against damage) and plesiomorphic location (throughout the body), while the other (copy 2) added a change in function (focusing light) to the old function of protection from degradation in the plesiomorphic location. The second

duplication event involved copy 2; as before, one copy retained the (new) plesiomorphic function³ (focusing light, protection against damage) and the plesiomorphic location (many tissues), while the other copy retained the plesiomorphic function coupled with a change in location (restricted to the lens). This example highlights one of the four categories in Table 1 (the first duplication falls into category D). More importantly, it emphasizes that genetic co-option may involve more than just a change in function; it may also reflect a change in where the gene acts (whole body versus lens only).

Our second example involves a charismatic family of fishes comprising sea horses and pipefish (Syngnathidae). These fish have a very unusual breeding system. Females deposit their eggs on a specialized area along the male’s ventral surface (the *brood pouch*), which he then fertilizes and carries until the babies hatch. In some species, the interaction between developing embryos and dad goes further than just protection from potential predators; the epithelial lining of the brood pouch becomes highly vascularized around individual eggs, which allows nutrients and gases to flow from the blood stream of the father to the embryos (Harlin-Cognato et al. 2006 and references therein). In other words, the male becomes pregnant. During pregnancy, a protein called “patristacin” is produced in the brood pouch of pipefish in the genus *Syngnathus* (Harlin-Cognato et al. 2006). Interestingly, this protein is also active in the liver and/or kidney of many teleost fishes, including pipefishes. This observation implies that patristacin may have initially evolved in conjunction with the liver/kidney then added a new tissue (the brood pouch) to its repertoire with very little change to its original structure (demonstrated by molecular analysis) and function. The *outcome* of that function, however, has shifted from cleansing the body (liver/kidney) to male pregnancy, two

³ When we use the term plesiomorphic we are referring to a very particular point in evolution—the origin of the trait. Traits, however, often continue to change (evolve) past their point of origin and each change becomes the ancestral state for the group it defines. In other words, evolution produces layers upon layers of plesiomorphies. For example, the character “jaws” originated in the ancestor of a large group of animals called the Gnathostomata (which means “jaw mouth” and includes everything from sharks to us) so we would say that jaws are plesiomorphic for the Gnathostomata. Now, jaws have been modified numerous times within that large group. For example, “upper jaw fused to the skull” originated in the ancestor of a small gnathostomatan group called the Holocephali (which means “entire or whole head” and includes the chimeras/rat fish, relatives of sharks and rays), so this new jaw state becomes the new plesiomorphic (ancestral) condition for the group that possesses it, the Holocephali. Evolution is an ongoing process, so the designation of a trait as plesiomorphic is relative; it depends upon which group you are examining. Overall, we would call “jaws” plesiomorphic for the Gnathostomata and sympleiomorphic (this basically means many ancestors removed, like great, great grandmother) for the Holocephali. “Upper jaw fused to skull” is the ancestral (plesiomorphic) state for all species in the Holocephali.

Fig. 2 The evolution of lens specific proteins. The evolutionary pathway involves an initial gene duplication and subsequent co-option of heat shock proteins, followed by another gene duplication of the co-opted gene coupled with a derived change in place of gene expression



very different things. At the moment the precise function of pristinacin has not been determined, nor has the extent of its distribution within the Sygnathidae, so the story is far from complete. Still, this preliminary study does demonstrate that novel structures (in this case the brood pouch) might arise, in part, because some of the genetic underpinnings existed before the origin of the structure itself. In this case, instead of having to produce completely new genetic material in conjunction with the appearance of the novel structure, an old gene was co-opted when a mutation occurred that turned the gene on in a novel location (tissue).

Both of the preceding examples present the *patterns* of molecular co-option. These patterns reflect a complex interaction between the retention of plesiomorphic (ancestral) forms of, combined with changes in, function (what a gene does), time (when a gene is activated), and space (where a gene is activated). On their own, these patterns are insufficient to explain the origin of novel structures because co-option simply provides the material for evolutionary change. In order for it to be evolutionarily relevant, that material, be it an old gene with an old function in a different place or an old gene with a new function, will ultimately have to pass through the filter of selection acting on the phenotype. One effect of such selection might be to fine-tune the plesiomorphic genetic structure by selecting for variants of the co-opted gene that are more efficient in the new context. Gould and Vrba (1982) referred to modifications subsequent to co-option of the exapted trait as “secondary adaptations”.

Morphology

When you survey the history of life on this planet, some changes look downright miraculous. For example, how exactly did vertebrates essay the transition from an aquatic to a terrestrial existence? Traditional approaches to answer-

ing this question went something like this: about 400 million years ago in the Devonian, fishlike creatures hauled themselves laboriously out of the water into the slime and mud, presumably forced there as the bodies of water they lived in dried out or perhaps even boldly going where no fish had gone before in search of food. These fish were without functioning lungs and tetrapod limbs, both of which were thought to have evolved as adaptations to terrestrial life. In order for this to happen, there must have been individuals who already had slight modifications that allowed evolution to begin transforming gas bladders into lungs and fins into limbs. But, how could these variants, all of whom would have been only marginally adapted for living on land, survive long enough to undergo the slow gradual changes selection is thought to make? Put this way, it seems extremely unlikely that any vertebrate could have made that transition, yet we have ample evidence that terrestrial vertebrates do, in fact, exist. How can we untangle this Gordian knot?

The answer was, and is still being, pieced together slowly as more and more Devonian fossils are discovered. Extensive analysis of that evidence in a phylogenetic framework produces a much more plausible, if much less heroic-sounding, tale; one in which lungs and limbs originated and were modified gradually as adaptations to living in warm, shallow, aquatic habitats (Clack 2006 and references therein). As mentioned previously, the gas bladder originated in the ancestor of bony fishes. At some point within the early radiation of the tetrapods, the posterior nostrils moved forward and downwards, splitting the premaxilla and maxilla (upper jaw bones), then backwards along the roof of the mouth (the premaxilla and maxilla re-fused), producing an organism with an opening in the top of the mouth which allowed air to flow from the nose into the mouth and from there to the gas bladder (lungs) even when the mouth was closed (Zhu and

Ahlberg 2004). Close your mouth, take a good deep breath of cold air through your nose, feel that coldness at the top of your throat and you are experiencing the effects of these evolutionary changes. This important evolutionary step allowed our ancestors to breathe air with most of their body underwater and just the tip of the nose (nostrils) elevated above the water surface.

Tetrapod limb evolution involves the change of pectoral and pelvic fins into forelimbs and hindlimbs (arms and legs respectively). It began with the origin of the humerus (upper arm bone) in the ancestor of the Sarcopterygii (lobe-finned fishes), and progressed as shown in Fig. 3. The bones of the upper and forearm, wrist, hand, and rudimentary fingers all evolved in a fin-like structure supplemented with thin, bony rods called lepidotrichia that plesiomorphically provided support for the fin. Functional analysis indicates that the newest member of the tetrapod family tree, *Tiktaalik* (Shubin et al. 2006; Daeschler et al. 2006),

could have propped itself up on these arm-fins and used them to move along the bottom and margins of the rivers and streams in which it lived (Shubin et al. 2006). Tetrapods themselves are characterized by the loss of the lepidotrichia, giving the fin its new “limb” look, the appearance of complex, articulated fingers, possibly allowing the animals to maneuver through shallow, vegetation-rich water (Retallack 2004). The hindlimb appears to have originated in a much shorter period of time; all of the elements of a leg are present in the basal tetrapod *Acanthostega*, although those elements were enclosed in a paddle like structure resembling the forefin of some dolphins (Clack 2006). Mechanistically, changes in the timing and expression of *Hox* genes are thought to be involved in the evolution of limbs. For example, a shift in the area of expression for *Hox d13*, from roughly half, to the entire free (distal) end, of the limb is associated with the development of fingers and toes (Shubin et al. 1997).

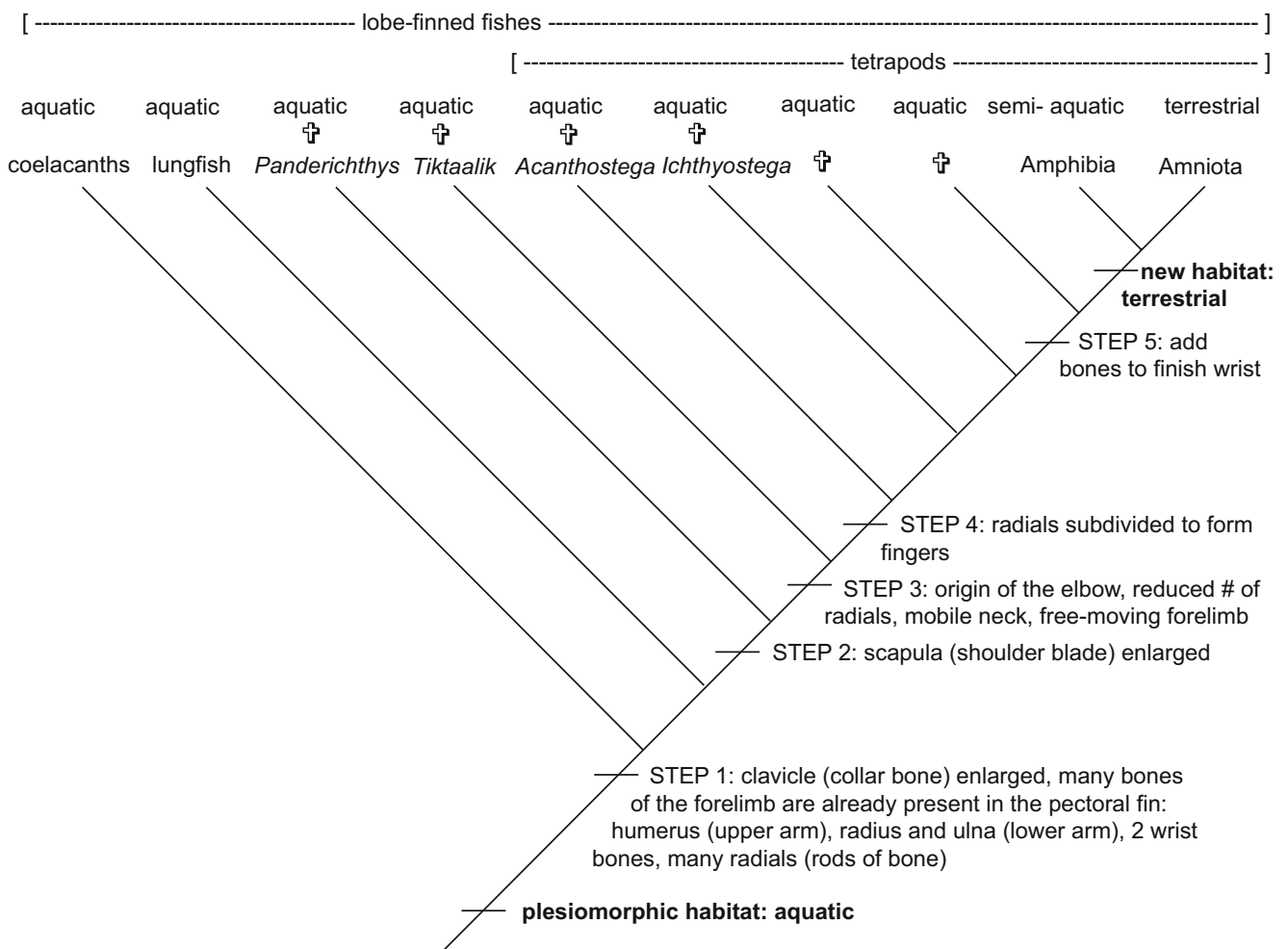


Fig. 3 The evolution of the tetrapod forelimb mapped onto a simplified phylogenetic tree for the lobe-finned fishes (Sarcopterygii). It is important to note that the bones identified on this phylogeny (e.g., the humerus, radius, phalanges) continued to be modified past their

point of origin. The main point, though, remains the same—the tetrapod limb evolved in an aquatic environment and not as an adaptation for living on land. †=extinct species

“Hows” of evolution aside, the important point here is that bones of the tetrapod limbs were laid down, bit by bit, in aquatic animals.

Overall then, did limbs and lungs evolve as an adaptation to living on land, as was once believed? The answer is *No*, these characters existed before vertebrates moved onto land, and may have served a variety of functions, including life as an ambush predator, supporting the body while raising the head up and out of the water to breathe air, and maneuvering through vegetation-rich waters. Was the existence of limbs and lungs in aquatic species a critical prerequisite to the quantum leap from an aquatic to a terrestrial existence? The answer to this question is a resounding *Yes*, without the co-option of these characters vertebrates may never have made that leap: limbs that were once used to maneuver through tangled aquatic habitats, to rest and move along the bottom of shallow estuary, river, and stream margins were co-opted to serve a new function: support and movement on land. This example highlights the subtle but crucial difference between “the environment changed *so* the organism changed,” which is

Lamarckian and the Darwinian formulation “the environment changed and those organisms that *already possessed traits allowing them to survive in the new environment* flourished.” What co-option does not explain, and what may ultimately be the most difficult question to answer, is why some individual tetrapods moved out of the water onto the land in the first place. Co-option cannot answer that question. It can only tell us why those individuals survived when they ventured where no tetrapod had gone before.

Our next example can be titled “things you can do with a bar of cartilage”. The discussion is built around the greatly simplified phylogenetic tree shown in Fig. 4, which you should refer to from time to time to anchor yourself in evolutionary time. Cartilage is a strong yet flexible living tissue made of a collagen, glycoprotein, and water matrix surrounding the cells that produce the matrix (chondrocytes). Your nose and ears are made of cartilage. Now, run your fingers over your upper throat and you are touching your pharynx, one of the most important evolutionary arenas for the deuterostomes (animals that include starfish, sea urchins, lancelets, tunicates, and vertebrates).

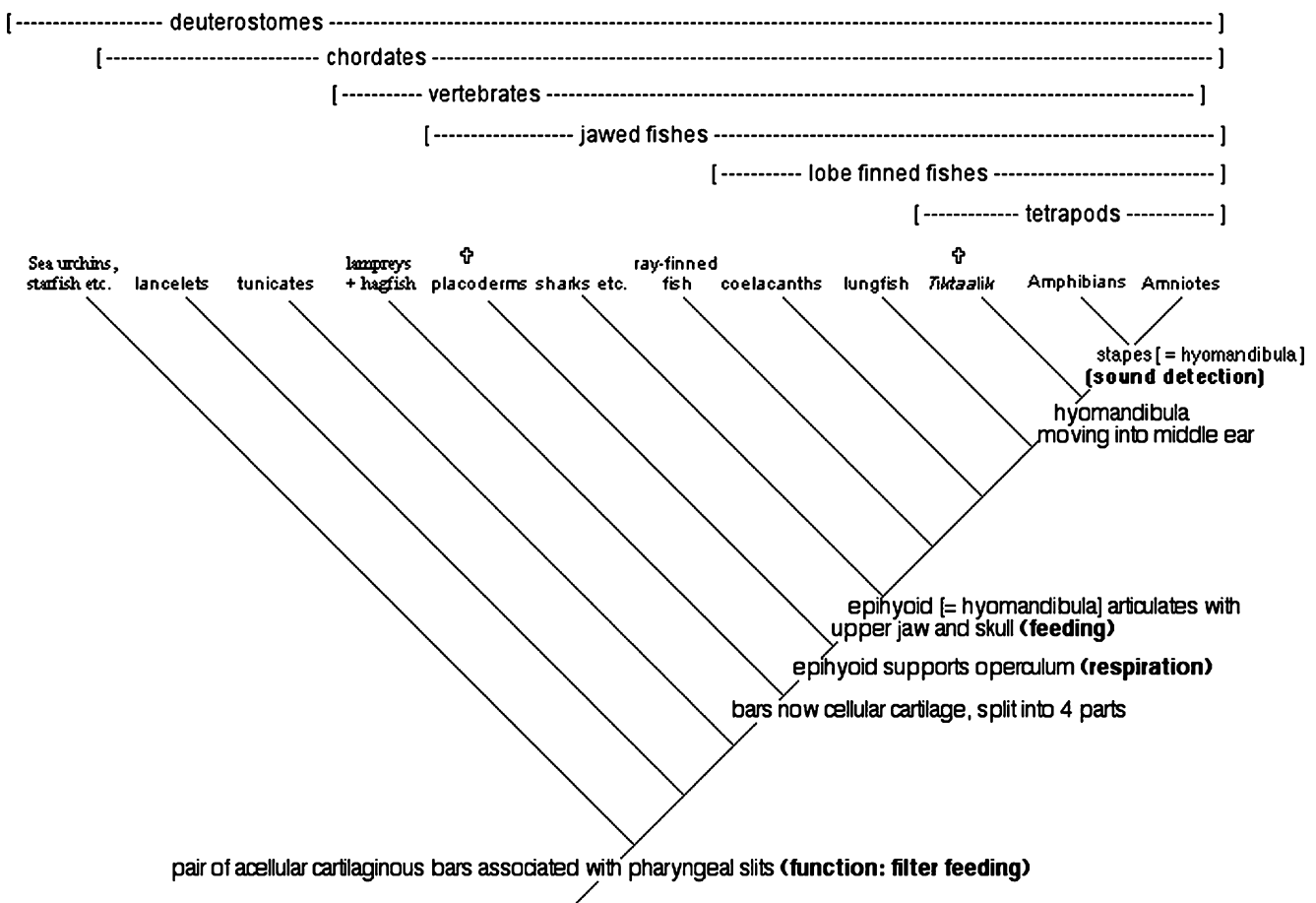


Fig. 4 The evolution of the 2nd pharyngeal slit in the deuterostomes. Both the phylogenetic tree and the evolutionary story have been very simplified, but this does not change the basic observation that a pair of cartilaginous rods that appeared 900 mya in the 2nd pharyngeal slit

were co-opted from their original function in filter feeding to play a role in respiration, predation, and hearing throughout the evolution of the vertebrates. So many different outcomes from one old structure

Nine hundred million years ago, in the ancestor of the deuterostomes (Blair and Hedges 2005), lots of slits appeared in the pharynx (Bourlat et al. 2006), each supported by a pair of acellular cartilaginous bars (Rychel and Swalla 2007). The bars (each pair called an “arch”) supported the slits, helping to hold them open. This was important to early deuterostomes like lancelets and tunicates because they were (and are) filter feeders—they cover the inside of their pharyngeal slits with mucous, which traps tasty food items from the water that is moved in through the animal and out across the slits—so anything that would help hold the slits open would have been selectively advantageous. From these humble beginnings flowed an astonishing number of evolutionary modifications (including jaws but that is another story). Sometime early in the vertebrates, the bars changed from acellular to cellular cartilage (the kind we have in our ears and noses) and each bar was subdivided into four parts, increasing the flexibility of the arch. Here, I will track the fate of the 2nd pharyngeal arch (=hyoid arch); more specifically, one of the four parts of the hyoid arch, the epihyoid. If we leap forward a little in time to the early jawed fishes, we find the epihyoid supporting a structure called the operculum, a cover over the gills that provides protection for the fragile gill filaments from the damaging effects of the external environment. At this point, the function of this part of the original 2nd arch cartilaginous rod has changed from filter feeding to respiration. If we leap forward in time again to Chondrichthyes (cartilaginous fishes—rat fish, sharks, skates, and rays), we find that the epihyoid, now called the hyomandibula, serves as a lever between the upper jaw and the skull. Every time you watch a documentary showing great white sharks tearing chunks off of hapless prey and marvel at the way they seem to push their upper jaws forward, you are seeing the hyomandibula in action as it swings forward around its pivot with the skull to push the upper jaw outwards (Wilga 2002). Interestingly, the hyomandibula has reverted to its original function—feeding—even though the mode, from filter feeding to predation, has changed dramatically.

Now fast-forward yet again to the early tetrapods. The hyomandibula, now a bone built from a cartilaginous template, has been dramatically reduced in size and has moved away from the upper jaw into the middle ear, where it eventually becomes involved in detecting vibrations (sound waves) (Brazeau and Ahlberg 2006). All amphibians, mammals and reptiles have this middle ear bone (now called the stapes) thanks to the modification of the hyomandibula, which itself was a modification of the epihyoid, which itself was one part of the original acellular cartilaginous rod in the two pharyngeal slits that arose in the ancestor of the deuterostomes. No new structures had to appear to support this part of the transition from filter feeding to respiration

to predation to sound detection. All that was required was the co-option, followed by modification, of the basic building blocks that had been laid down 900 mya (for a thought provoking, incredibly readable discussion of the importance of co-option in the evolution of animal bodies, see (Shubin 2008)).

Behavior

Behavior, like morphology, has both structure (what it looks like) and function (what it does). Julian Huxley, a founding father of ethology, had the fundamental insight that behavioral displays often evolve in one context, then change function later in evolution. When the functional change occurs, the trait remains structurally unchanged, but as time passes, certain aspects of the trait may become fine-tuned by selection associated with its new function. The ethologists termed such co-option *ritualization* because in all the examples they uncovered, traits were co-opted to serve a communicative function (Huxley 1966 and references therein). For example, the head-down threat behavior of stickleback fishes is thought to be a ritualized form of digging/biting, something males do when they are tearing apart bits of plants and roots for nest building.

One of the best showcases for the ethologists’ ideas about ritualization was an article published in 1950 by a Dutch ethologist. Daanje (1950) proposed that many of the courtship and agonistic (aggressive/submissive) displays in birds were ritualized forms of locomotory intention movements; in other words, courtship displays were ritualized forms of an individual’s intention to move. So let’s begin with the intention behaviors. Many birds move by hopping, which can be broken into two stages: (1) the bow: bend legs, lower chest, wings slightly expanded, tail pushed upwards, neck drawn into the shoulders and (2) the spring: stretch legs, raise chest, lower wings, tail pushed downwards, neck and head stretched upwards in a straight line. The bow appears in an amplified, frozen form in numerous courtship displays in which the male struts in front of the female, breast lowered, tail upwards and spread, wings expanded (for example, think turkeys and peacocks). The only differences between this display and the “intention to jump” bow are that the legs are (usually) not bent and the wings and tail are maximally expanded. The male house sparrow’s display freezes the action at the point where the male is moving between the bow and the spring: the legs, neck, and body are stretched upwards, but the tail is still held pointing upwards and spread, while the wings are outstretched and slightly downwards. Mallards and other ducks carry ritualization through to include the spring. Their display is a rapid succession of two parts, the male pulls his head towards his shoulders, while elevating and spreading his tail and outstretching his wings (bow), then

he stretches his neck upwards and lowers his tail and wings (spring). Daanje continued on in this documentary vein for 50 pages, so clearly there are many examples of movement behaviors being co-opted to serve a role in courtship displays.

The best-delineated example of behavioral co-option in a phylogenetic context involves changes to the context of a vocalization called the skrraa call in bowerbirds, small passerines related to catbirds, distributed across New Guinea and Australia. Males from 14 of the 19 species build stick structures called “bowers,” which range from a simple avenue between two walls to an elaborate hut with a central pole. They decorate their bowers with a variety of objects, including fruits, berries, flowers, bits of bone, feathers, snail shells, small stones, and even glass fragments. In every species examined to date, a male’s mating success is strongly influenced by the quality of his bower and his vocalizations (Borgia 1985; Borgia and Presgraves 1998). Analysis of the calls from 15 bowerbird species indicated that the skrraa was initially used only in male–male combat then became involved in the male–female courtship dialogue in the ancestor of the *Chlamydera* (spotted bowerbird) group (Fig. 5). That this shift in function does indeed represent co-option is indicated by the fact that calls produced during combat and courtship are similar in terms of structural characteristics; what varies is the context of the call (aggression or sex) and the sex of the receiver (Borgia and Coleman 2000). Interestingly, female spotted bowerbirds prefer males with skrraa calls that

are longer (more similar to the aggressive call (Borgia and Presgraves 1998)). Why would females find a male battle cry, which is after all a signal of intent to attack, so attractive? One possible explanation for this reaction is that more intense courtship reliably signals male vigor so a female can use it to choose a high quality father for her offspring (Borgia 1979; Berglund et al. 1996). If such a dynamic is uncovered for all bowerbirds using the call in both contexts, then we will have evidence for why co-option was successful once it occurred.

Phylogenetic analysis indicates that the aggressive call was intense at the point of co-option (Fig. 5), which begs the question of just how a female “knows” that the male is not going to attack her. Preliminary data indicate that all species with intense calls also have large display areas, implying that co-option occurred under conditions in which the courting pair were far enough apart to provide the female with an escape route if needed. In other words, she doesn’t so much “know” what her mate is going to do, as have a contingency plan in place to counter any aggressive move on his part. This hypothesis is supported by two observations: (1) species in which the display arena has become smaller produce less intense skrraa calls and (2) the species with the most intense courtship displays, the spotted bowerbird, is unique in building an avenue bower with see-through walls that protect the female while she is watching and listening to the courting male (Berglund et al. 1996). Taken together, these data tell us why co-option was permitted in the first place.

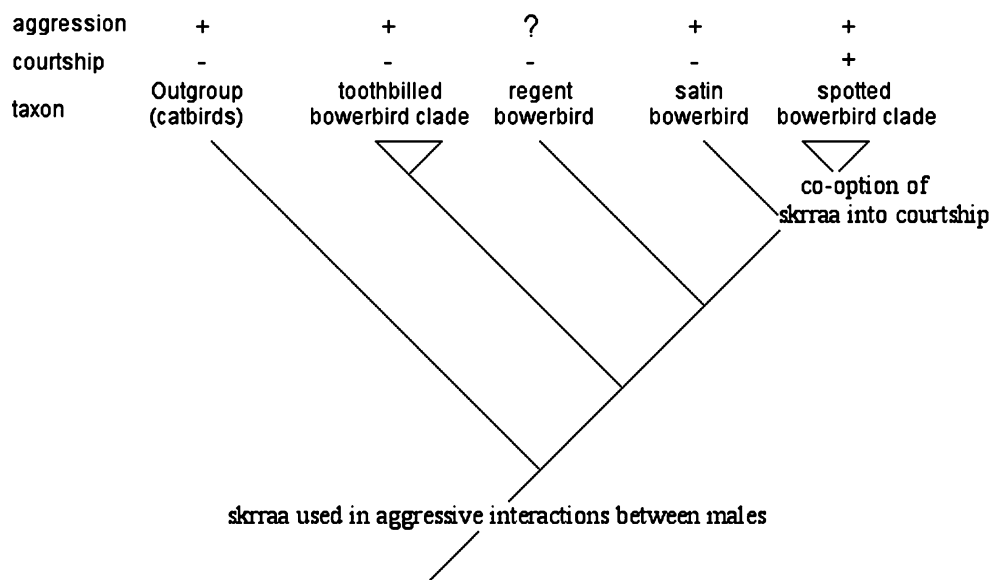


Fig. 5 The evolution of the skrraa call mapped above a simplified phylogenetic tree for the bowerbirds (adapted and modified from Borgia and Coleman 2000). The presence (+) or absence (–) of the skrraa call in aggressive and courtship interactions is mapped above the tree. This example clearly shows when the call was co-opted from

its context in male–male aggression to serve a new function in male–female communication during courtship. *Triangles* at the end of branches indicate a larger, monophyletic group. The spotted group represents five species (in the genus *Chlamydera*), all of whom use the skrraa call in both aggressive and courtships contexts

Conclusion

From time immemorial, humans have noticed that organisms seem to have what they need to survive, that is, they appear to be adapted to their environments. Darwin's proposal that such adaptations emerge through time in slow gradual steps was counter-intuitive to some people because it seemed likely that "transitional" forms would have a hard time of it, being neither "fish nor fowl." Darwin, and later Cuènot, recognized that this problem was easily solved if characters that had evolved for one reason changed their function at a later time without any concurrent structural modifications, at least to begin with. In other words, organisms carried with them in the structures of all their genes, proteins, morphological, physiological, and behavioral characters the potential for rapid evolutionary change; so rapid, indeed, that the process looked miraculous and Lamarckian.

The co-option of traits to serve new functions is not a difficult concept to understand. In fact, we ourselves do it all the time, which is why we speak about "new wine in old bottles" or "rebranding" for the repackaging of ideas, and more recently in keeping with the new management-speak, "repurposing". We are forever finding new functions for old devices, using an old boot as a planter, a fishing rod to fly a kite, a magnifying glass to start a fire, a shell as currency, a berry or a root to dye cloth. The only difference between human and evolutionary co-option is that we purposefully change an object's function, while evolution simply takes advantage of an opportunity with no direction, purpose, or forethought. If an ancestral aquatic tetrapod didn't already possess limbs, it would never have been able to crawl onto the land, and evolution would have followed a different pathway than the one familiar to us today. But those individuals did possess limbs, and there was the land, and here we are, many millions of years later, arguing, discussing, theorizing, and writing about how we got here.

In the Classroom:

One way to get the concept of co-option across to students of any age might be to ask them to go out and search for examples in our own society of:

- (1) object co-option (using a boot as a planter)
- (2) linguistic co-option ("berserk" initially meant "visitor" to the Vikings, but meant something completely different to the "visitees," hence our Anglo-Saxon sense of berserk as "gone wild, out of control, extremely aggressive" etc.; there must be more current examples)
- (3) cultural co-option. So, for example, the website: http://www.avclub.com/content/feature/inventory_13_great_moments_in/2 has 13 examples of how hip-hop has been co-opted by mainstream culture. I don't under-

stand all of the examples (not surprisingly given the generation gap) but my favorite is the co-option of an important hip-hop song, *The Message*, into a cute song to be sung by a baby penguin in the movie *Happy Feet*. In this theme, many of the pivotal songs of the 60s and 70s, including many songs with strong political and social messages, have been co-opted to serve as consumer-soothing, mind-numbing music in grocery stores and malls.

- (4) behavioral co-option in human courtship. For example, providing food gifts for a prospective mate initially was important to her fecundity or was a way for her to judge your success as a hunter. This "provide nuptial gifts" behavior has been co-opted in its most ritualized form on Valentine's Day. "Bring a box of chocolates" now serves to convey a *Homo sapiens*-specific (autapomorphic) message "I love you."

Once the students have the idea of what co-option is, then move into the biological realm. So, for example, (1) feathers initially served a role in insulation in homeothermic organisms and were much later co-opted into flight; (2) limbs/lungs and land (in itself a powerful example of co-option, but also very attractive to teach because it allows you to discuss what the world looked like when all of this limb–lung evolution was happening and to show great diagrams of early fossil tetrapods [*Tiktaalik* is just downright charismatic; you might want to give the students the first chapter in N. Shubin's book to read because he describes how *Tiktaalik* was eventually discovered—showing students how field-based science is actually done]); (3) gliding lizards (a really lovely example because you can get all sorts of great photos from the web: EN Arnold (1995) *Holaspis*, a lizard that glided by accident: mosaics of cooption and adaptation in a tropical forest lacertid (Reptilia: Lacertidae). Bull Nat Hist Mus London 68:155–163); (4) fetal dentition and viviparity in caecilians (another example with a fantastic web page http://www.nhm.ac.uk/about-us/news/2006/apr/news_8032.html showing the traits and behavior. Kupfer et al. (2006) Parental investment by skin feeding in a caecilian amphibian. Nature 440:926–929); (5) the switch from hawkmoth to fly pollination in a group of plants (the story is straightforward [some characteristics of plant morphology that had evolved in conjunction with hawkmoth pollination at night were co-opted to allow the change in pollinators when one species in the group began flowering during the day rather than at night]. This helps demonstrate that co-option is widespread in all living systems, be they plant or animal, and the photographs are beautiful in the paper. Johnson et al. (2002) Specialization for hawkmoth and long-proboscid fly pollination in *Zaluzianskya* section *Nycterinia* (Scrophulariaceae). Bot J Linnean Soc 138: 17–27).

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