

# Exaptation in human evolution: how to test adaptive vs exaptive evolutionary hypotheses

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**Summary** - Palaeontologists, Stephen J. Gould and Elisabeth Vrba, introduced the term “exaptation” with the aim of improving and enlarging the scientific language available to researchers studying the evolution of any useful character, instead of calling it an “adaptation” by default, coming up with what Gould named an “extended taxonomy of fitness”. With the extension to functional co-optations from non-adaptive structures (“spandrels”), the notion of exaptation expanded and revised the neo-Darwinian concept of “pre-adaptation” (which was misleading, for Gould and Vrba, suggesting foreordination). Exaptation is neither a “saltationist” nor an “anti-Darwinian” concept and, since 1982, has been adopted by many researchers in evolutionary and molecular biology, and particularly in human evolution. Exaptation has also been contested. Objections include the “non-operationality objection”. We analyze the possible operationalization of this concept in two recent studies, and identify six directions of empirical research, which are necessary to test “adaptive vs. exaptive” evolutionary hypotheses. We then comment on a comprehensive survey of literature (available online), and on the basis of this we make a quantitative and qualitative evaluation of the adoption of the term among scientists who study human evolution. We discuss the epistemic conditions that may have influenced the adoption and appropriate use of exaptation, and comment on the benefits of an “extended taxonomy of fitness” in present and future studies concerning human evolution.

**Keywords** - Exaptation, Pre-adaptation, Spandrels, Adaptationism, Extended taxonomy of fitness, Operationality.

*“To paraphrase Mr. Huxley in a famous context, I am prepared to go to the stake for exaptation; for this new term stands in important contrast with adaptation, defining a distinction at the heart of evolutionary theory, and also plugging an embarrassing hole in our previous lexicon for basic processes in the history of life”*  
(S.J. Gould, “The Structure of Evolutionary Theory”, 2002, p. 1234)

## A pluralistic taxonomy of fitness

“Ad-aptation” is a pre-evolutionary term that survived the Darwinian revolution, being reconsidered as the feature of a trait which is useful for the individual involved in the struggle for

existence, and at the same time as the process of differential survival of members of a biological population. Like any concept which defines both the process and the product of the process, adaptation is an ambiguous term. In fact, we could define the mechanism of natural selection completely without using the term “adaptation”. Moreover, “adaptation” is seldom quantified, even today, and the degree of “fitness” is a more satisfying concept in evolutionary biology.

Darwin was aware of the teleological remains of the prefix ad- joined with “aptus”, meaning at that time “useful for”, and today “contributing to the fitness of the bearer”. In fact, mixing together the need to search for the remote causes of the evolution of a trait and the teleological fancy of “ad-adaptation”, any evolutionist runs the risk

of reconstructing natural processes as “just-so-stories”: eyes evolved “for” sight, legs “for” walking, and so on. Furthermore, as in George St. Mivart’s objection to natural selection, the idea of a progressive adaptation seems to produce a contradiction between the gradualist assumption about the functioning of natural selection, as a slow and continuous generation-by-generation process, and the assumption of the functionality of any trait that is positively selected. If the wing evolved gradually, with every stage being functional, what was the early phase of a wing for? Is it possible to fly with a small part of a wing? And what about the beginning of a mimicry?

The anti-evolutionary objection of the alleged impossibility to use natural selection to explain the incipient stages of any complex and useful structure composed by an organization of different parts was effectively tackled by Charles Darwin in the sixth chapter of the sixth edition of *The Origin of Species* (1872), where he advanced two different explanatory hypotheses: firstly, a gradual implementation of the structure through natural selection, with a corresponding gradual improvement of the same function; secondly, the evolution of the trait in a frame of primary selective pressures followed by a “functional cooptation” in a new ecological situation where the same structure, or a slightly modified structure, acquires a new function, which is independent from the previous one and unexpected (like a potential “effect” already held in its form). In order to make the second mechanism possible, Darwin supposed that the relationships between forms and functions are not strictly one-to-one, but potentially redundant and flexible (with cooperation of parts, specializations, cooptations).

So we can have classical evolution due to the gradual agency of natural selection maximizing the same function, but also the re-use and recycling of structures already available and previously evolved for other reasons:

*“The illustration of the swim bladder in fishes ... shows us clearly the highly important fact that an organ originally constructed for one purpose, namely, flotation, may be converted into one for*

*a widely different purpose, namely, respiration. The swim bladder has, also, been worked in as an accessory to the auditory organs of certain fishes. All physiologists admit that the swim bladder is homologous, or “ideally similar” in position and structure with the lungs of the higher vertebrate animals: hence there is no reason to doubt that the swim bladder has actually been converted into lungs, or an organ used exclusively for respiration” (p. 148)*

In the final observations of the second edition of *The various contrivances by which orchids are fertilized by insects* (1877) Darwin seems tempted to transform the tinkering of natural selection with forms and structures in a general principle of the theory of evolution (as proposed, moreover, by German marine biologist and founder of the Naples Zoological Station, Anton Dohrn, in his correspondence with Darwin):

*“The regular course of events seems to be that a part which originally served for one purpose, becomes adapted by slow changes for widely different purposes. ... Although an organ may not have been originally formed for some special purpose, if it now serves for this end, we are justified in saying that it is specially adapted for it. On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for its present purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms” (pp. 283-284).*

“Almost every part of each living being served for diverse purposes” is an impressive general statement about nature. Nevertheless, the role of “contrivances” (in other words, the role of trade-offs between structural internal constraints, given by the history of the body plan, and selective functions) has been widely underestimated

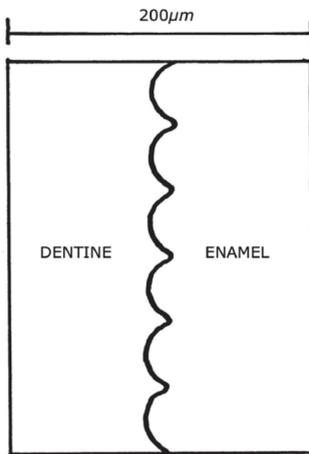
during the process of unification of Mendelism and the Darwinian theory of evolution by means of population genetics. Only the first Darwinian meaning of an improvement by natural selection of one same function ascribed to a structure has been stressed, and functional adaptation has always been a core concept in the study of human evolution, as well as in evolutionary biology in general. In the works of some contemporary authors, this perspective has been stressed even to the point of conceiving natural selection as an anthropomorphic “engineering force”, optimizing the organisms and their behaviours part by part. The use of an “adaptationist” language and the universal equation between current utility of a trait and its historical origin were strongly criticized around 30 years ago (Gould & Lewontin, 1979), as they would prevent evolutionary biologists from being aware of mechanisms that *differ* from direct functional adaptation by optimization and yet *contribute* in shaping living forms.

Palaeontologists Stephen J. Gould and Elisabeth S. Vrba (1982) went further and proposed the neologism “ex-aptation” (that is, “aptus” from a pre-existing, evolved structure or form) to address two mechanisms: 1) *functional shift* (‘type 1’ exaptation in our terminology) in a Darwinian sense, i.e. the re-use by natural selection of a structure with previously different purposes; 2) *functional cooptation from non-adaptation* (‘type 2’ exaptation in our terminology, or “spandrel”), i.e. an evolutionary mechanism which, while leading to useful structures (always “aptations”, after all), is not completely described as a process of standard functional adaptation because the beginning of the emergence of a trait could be non adaptive (like a side effect, a developmental constraint, a structural effect, or a random insertion). ‘Type 2’ exaptation was only sometimes touched on by Darwin, as in the case of the skull sutures: originating as a developmental constraint and then “re-used” in mammals as an adaptation to delivery. It is important to remind the reader that “non adaptive” is different from “non functional”, because we could argue that in many cases the previous “non aptations” had structural or developmental functions. Vrba

& Gould (1986) considered as further cases of exaptation type 2 all the effects that an adaptation at one level of evolution (genes, organisms, groups, populations, species) produces at another level: what is an adaptation at one level could be an exaptation at another (*cross-level spandrels*).

In other words, function does not always precede form: firstly, in evolution, structures could repeatedly change the primary functions they were initially selected for – the process recognized by Darwin in 1872 and later named “pre-adaptation”, the trait being “pre-adapted” for the current utility (a term refused by Gould and Vrba because of its teleological taste) – or, secondly, they could emerge due to structural and historical causes, or for random insertions (neutral mutations, drifts), being later co-opted for some function in different frames of selective pressures. That is why a current function of a structure cannot be used as a default explanation of the past origin and evolutionary history of that structure. Hence the proposal of an “extended taxonomy of fitness” comprising pluralistically: a) standard adaptation (which is not substituted by other processes); b) exaptation type 1, i.e. functional shift or the former “pre-adaptation”; c) and exaptation type 2, i.e. the engagement by natural selection of non-adaptive traits (for further extensions and specifications see Gould & Vrba, 1982; Vrba & Gould, 1986; Gould, 2002).

In a pluralistic taxonomy the problem is not to choose between alternative explanations considered as mutually exclusive in a general sense. Rather, the challenge is that of evaluating case by case the better explanation (adaptive or “exaptive” in type 1 or 2), further calculating the relative frequency in nature of one process or another. The experimental frequency of exaptations (often still called “pre-adaptations” in literature) is today widely recognized (Arnold, 1994), also in University textbooks (Ridley, 2004), mainly in fields such as evolutionary developmental biology, the evolution of cognitive faculties and, since François Jacob’s “Evolution and Tinkering” (1977, where “the final example of tinkering” was “the human brain”), in evolutionary molecular



**Fig. 1 - The scalloped appearance of the dentino-enamel junction (DEJ). Drawn following Shimizu & Macho (2007), Fig. 2.**

biology. Here we consider the welcoming of an “extended taxonomy of fitness” in the study of human evolution.

Some authors (like Dennett, 1995) have criticized the concept strongly because they supposed it implied a suspension of natural selection: on the contrary, as is clear from its history and its precise meaning, exaptation is not incompatible with natural selection, but with an oversimplified representation of it. Other authors (like Pinker, 1994) thought that exaptation does not represent an alternative mechanism, but can always be traced back to classical neo-Darwinian adaptations. However, as we have seen, this is true only for exaptation type 1, not for exaptation type 2 and cross-level spandrels.

A more substantial objection to exaptation is that it is not operationally distinguishable from adaptation: we could call this *the non-operationality objection*. To help cast light on the non-operationality objection, we begin by analyzing the use of exaptation as a working concept in biology: in the next two sections, we briefly review two exemplar studies published in 2007 in *Journal of Human Evolution* which touch on exaptation. The section that follows is dedicated to a commentary of these two research studies regarding the operational

specificity of exaptation. Then we refer to a wide survey (available online) of the use of exaptation in literature since 1982, touching different fields of research in human evolution (morphology and physiology, language, genetics, behaviour etc.). In the final discussion, we draw some conclusions about the epistemic conditions which possibly influence the applicability and operability of exaptation in different research contexts.

### **First case study: the scalloped dentino-enamel junction**

Daisuke Shimizu and Gabriele A. Macho studied the contact surface, inside teeth, between two very different materials: «the hard, brittle enamel and the much softer dentine» (Shimizu & Macho, 2007). This dentino-enamel junction (DEJ) has a “scalloped” appearance in primates (Fig. 1). Recent biomechanical studies seemed to indicate a possible function for this micromorphological structure, i.e. preventing delamination which can occur during mastication. Through 2D and 3D models, Shimizu and Macho tested the mechanical benefits of scallops, showing that scallops actually:

- reduce and discontinue stress concentration, with a resulting crack-stopping effect on enamel;
- reduce sliding between dentine and enamel, so that they are pushed into each other rather than apart.

Being the functional value of scallops ascertained, it could be easily concluded that scalloped DEJ is a dietary adaptation for high bite force and/or hard food, but Shimizu & Macho are cautious in establishing a *causal relationship* between masticatory loads and DEJ microstructure:

*“inferring functional adaptations in evolutionary biology is complicated. For a feature to constitute an adaptation, it must fulfil a number of criteria” (p. 110).*

One of these criteria, considered and evaluated by the authors in this case, is *the consistency*

between scallop formation and inferred bite force. If scallops were a functional adaptation:

- molars would be expected to have generally more-pronounced scallops than the anterior teeth;
- scallops would be expected to be most marked in species that exert high bite forces.

Though scallops *are* functionally advantageous, the comparative data available, albeit scant, do not support the latter two predictions. In search of «some other explanatory model», Shimizu and Macho advance a developmental hypothesis:

*“scallops are a by-product of biophysical processes during ontogeny, which, owing to their functional advantage, are unlikely to be selected against. Consequently, they may be viewed as an example of exaptation in primate biology” (p. 110).*

In particular, scallops may be viewed as a by-product of epithelial folding during odontogenesis in development, *uncorrelated* with functional demands in adulthood, governed by morphodynamic processes and mechanical forces (Shimizu & Macho specify that these processes «can be described also without knowledge of genetic networks»). Observations concerning thick enamelled species, such as the *pronounced* appearance of scallops in fully formed teeth, can be explained by additional biophysical processes upcoming in later stages of ontogeny (e.g. enamel shrinkage during maturation) *exaggerating* unevenness present at the DEJ during early stages of development. In summary, Shimizu & Macho's hypothesis is a combination of exaptation (a structural by-product is co-opted for an incidental subsequent function) and plasticity (a structural feature is enhanced during an organism's ontogeny).

Also, they recognize that, in the absence of scallops, some *other* structure would be supposed to perform the same function:

*“For hominoids [...] scallops may constitute an advantageous mechanism that guards against delamination of enamel from the dentine core during mastication and without the need*

*for further structural reinforcement [...]. In taxa where scallops are not, or are only poorly, developed, other mechanisms that prevent delamination must be identified” (ibid.)*

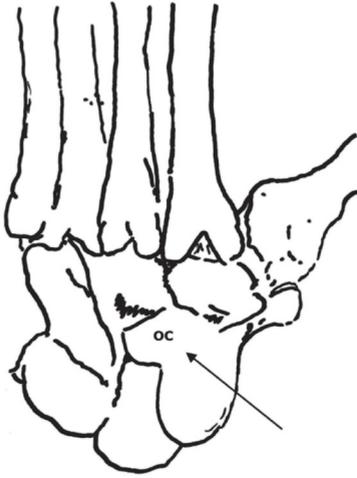
If DEJ were straight, tensile stresses would push the two tissues apart, but in such a case sliding could be prevented through strong structural reinforcements such as von Korff's fibers (see e.g. Bishop et al., 1991). In summary, further studies should be carried out following a pluralistic approach:

*“To ultimately resolve such issues regarding the phylogenetic and functional significance of scallops at the DEJ [...] a large-scale systematic study of scallop morphology and distribution across taxa, sophisticated mechanical testing, and better insights into developmental (i.e., morphomechanic) processes need to be brought together”.*

It must be noted that the question of the origin of scallops (exaptive-adaptive, structural-functional, plastic-genetically determined) is in no way trivial in paleo-anthropology, for scallops, well preserved in fossils, are frequently used to make inferences about phylogeny (species identification and classification, common descent, e.g. Haile-Selassie *et al.*, 2004) and paleo-ecology (scallops as a predictive tool for diet and paleo-environment, e.g. Kay, 1975).

## **Second case study: the scaphoid-centrale fusion**

The fusion of the os centrale to the scaphoid in hominoid carpus (Fig. 2) has been interpreted as a functional adaptation to stress on this joint during quadrupedal locomotion, which is particularly accentuated in knuckle-walking. This functional hypothesis has led to the suggestion that the fusion is evidence for a knuckle-walking common ancestor of the hominine clade (Fig. 3). In modern humans (who are fully bipedal, not-knuckle-walking), the presence of this trait may be either a phylogenetic vestige or an exaptation to a novel function: shear stress during



**Fig. 2 - Redrawing of a carpal drawing of *Hylobates leuciscus* dating back to 1865 (according to Kivell & Begun 2007, Fig. 3). The absence of a line between os centrale (oc) and scaphoid (arrow) in the original drawing has been interpreted as evidence of fusion between these two bones.**

power-grip positions. Since, however, «neither the functional nor the phylogenetic significance of scaphoid-centrale fusion is [so] clear», Tracy L. Kivell and David R. Begun reconsidered the whole matter (Kivell & Begun, 2007), questioning the very assumption that the fusion represents a functional adaptation.

All apes share a tendency to fuse their scaphoid and os centrale, but they differ in the frequency and timing (by heterochrony) of this fusion: there can be a range of intraspecific variability involving sexual dimorphism, pathologies and anomalies, and lateral or bilateral fusion. One must also check whether the fusion occurs under genetic control or as a result of loading (i.e. plasticity). In this regard, Kivell and Begun suspected that available literature lacked adequate sampling, and that there were observational biases, and misinterpretation of ambiguous cases. Therefore, before mapping the distribution of the trait in a complete phylogenetic context, they conducted a primary investigation on all involved species.

Absolute age cannot be used to evaluate and compare the SC fusion in different species with

varying developmental patterns, so Kivell and Begun had to find reliable benchmarks in development to establish the moment when the two bones should be clearly identifiable. Employing a system of age categories based on dental eruption they found that:

*“the scaphoid and os centrale can be identified in well-preserved osteological specimens with DP3 as the last erupted tooth” (p. 328).*

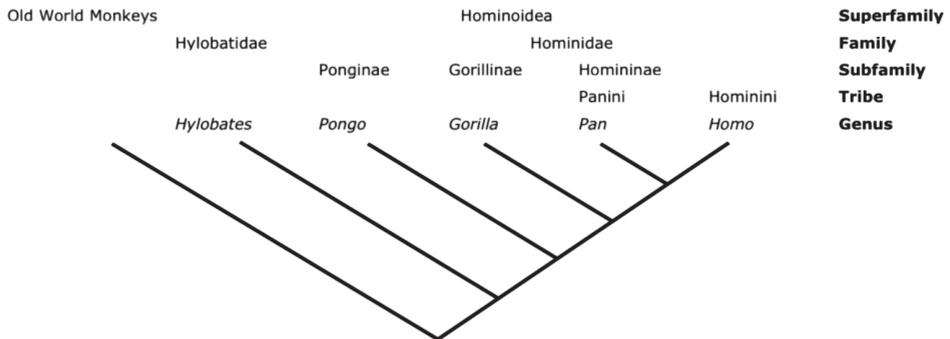
Kivell and Begun’s study indicated that the fusion appears to be primarily under genetic control, because a clear phylogenetic trend can be found among hominoids: in African apes (*Pan*, *Gorilla*) and modern humans fusion occurs in almost all individuals (> 95%) and early in ontogeny, whereas in Asian apes (*Pongo*, *Hylobates*) fusion occurs rarely (circa 7%) and only in adulthood. In non-hominoid primates, a consistent SC fusion – never reported or studied before – has been found in some species of Lemuroidea, but other ontogenetic processes seem to be responsible for it. In fact, it appears to be a convergence with African apes, but no direct correlation with function can be found:

*“Given that most of these [...] taxa are only broadly characterized as vertical clingers and leapers, or include this locomotor behaviour in their positional repertoire, a closer examination of the biomechanics of the postural and locomotor uses of the hands in these taxa is needed to determine the functional implications” (p. 334).*

Neither phylogeny nor size are significantly correlated with the fusion in these Lemuroidea species. In summary, more in-depth analyses of carpal ontogeny, positional behaviour, and functional morphology of these taxa are required.

For Kivell and Begun, «defining a character as “adaptive” is challenging» (p. 336). Function (in this case, that the scaphoid-centrale fusion increases stability during knuckle-walking) has to be demonstrated with several kinds of studies such as:

- *Fossil evidence*: «To convincingly demonstrate that scaphoid-centrale fusion



**Fig. 3 - Up-to-date phylogeny and taxonomy of living higher primates, based on molecular and morphological evidence (drawn after Wood, 2005).**

occurred as an adaptation in African apes, we need fossil evidence that the appearance of this trait (i.e., the most parsimonious hypothesis would suggest this character evolved once in the common ancestor of the hominine clade) coincided with the appearance of knuckle-walking behaviour (associated with corroborative evidence in other parts of the postcranial morphology)» (p. 336). «Fossil evidence for the origins of knuckle-walking coinciding with the appearance of scaphoid-centrale fusion will clarify the adaptive significance of this trait. Evidence for knuckle-walking in a fossil taxon lacking a fused os centrale would weaken or falsify this hypothesis» (p. 338);

- *Biomechanical models and experimental data* on compressive forces, aided by more and more sophisticated computer simulations;
- *The “convergence approach”* analyzing the appearance of that character in unrelated taxa: «A character correlated with the same behaviour in taxa that do not share a recent common ancestor is statistically more likely to be specifically adapted for that behaviour because the effects of phylogeny have been removed» (p. 337).

None of these, however, can conclusively support the functional hypothesis that the SC fusion is an adaptation for stability and compression during knuckle-walking. However, at this point of their research, Kivell and Begun

continue to support this hypothesis, which is the only one currently available:

*“We propose that this is a synapomorphy of the hominine clade functionally associated with digitigrady (knuckle-walking) that is retained in humans as an exaptation for continued stability at the midcarpal and especially lateral carpometacarpal joints” (p. 338).*

The adaptive hypothesis is subject to corroboration through palaeontology as stated before, and more studies are needed to clarify the same trait in Lemuroidea.

### **Exaptation: a working concept in biology**

It may seem odd that even one of the main exaptation enthusiasts in human evolution, Ian Tattersall, seems to expose the argument to the non-operationality objection, dealing with exaptation as a general pattern of evolution in a broad sense and assuming that any evolutionary novelty must be an exaptation:

*“Strange though this might seem, [exaptation] actually reflects a general pattern in evolutionary history. I have already noted that, in evolution, form must precede function and that innovation itself cannot be driven by natural selection.*

*Any novelty has to arise spontaneously as an exaptation, a structure existing independently of any new function for which it might later be co-opted” (Tattersall, 2004, p. 25).*

Ian Tattersall used exaptation as a powerful explanatory hypothesis for a clearly defined subject, though crucial, such as the emergence of symbolic intelligence in *Homo sapiens* during the Palaeolithic Revolution. However, in the citation above he expressed a more radical perspective seeing exaptation (in prevalence type 2) as a general evolutionary pattern. It is noteworthy that Stephen J. Gould himself assumed a similar position at various points in his work. Interestingly, the statement below occurs in the very work where he examined most of the points we make here about the operability of exaptation:

*“I cannot present a ‘review article’ of empirical cases of exaptation, for the defining notion of quirky functional shift might almost be equated with evolutionary change itself, or at least with the broad and venerable subject of, in textbook parlance, ‘the origin of evolutionary novelties” (Gould, 2002, p. 1234).*

But, if exaptation type 2 aspires to the role of general and ubiquitous pattern, replacing adaptation and relegating natural selection as a secondary force of refinement, then a really pluralistic and integrative perspective is avoided, and two possible options remain: either (1) to use the term exaptation in place of adaptation; or (2), more probably and economically, to drop the newest term. However, contrary to this dichotomy, the two studies described above show that at least six directions of research *can* effectively contribute to operationally discern exaptation from adaptation case by case (see also Gould, 2002):

1) *To employ biomechanical studies and models to analyze function:* driven by an adaptationist and selectionist metaphor – according to which adaptation has no need to be tested for – several studies may have too easily attributed functions to structures. The two we described above show that further

observations and tests, aided by new digital techniques for visualization and modelling, are needed to better understand and evaluate the supposed functional value of structures.

- 2) *To test for effective correspondence between structure and function in living and fossil species:* the two studies above are examples of the fact that adaptive hypotheses need to be supported by consistency between the considered structure and function (scallops and high bite force; SC fusion and knuckle-walking). If the distribution of a trait such as the SC fusion is random regarding locomotor behaviour and lifestyle, an adaptive hypothesis is undoubtedly weakened. On the contrary, the “convergence approach” cited by Kivell and Begun can potentially give strong support to an adaptive hypothesis. The amount of intra-specific variation of the structure has to be taken into account and studied. Tighter tests can be done by mapping the occurrence of the structure within the organism (e.g. scallops only in molars).
- 3) *To explore multiple functions of a structure:* functions that are now secondary (and maybe underestimated by researchers) could have been primary in the evolutionary past. As a Darwinian process, exaptation is bound to functional redundancy which allows for gradual shift between functions. For example, Shimizu and Macho state that researchers have considered scallops primarily as a crack-stopping mechanism. Now experimental studies reveal that the latter function has been overestimated: scallops prevent delamination of enamel as their primary function, with crack-stopping as an indirect effect.
- 4) *To explore structural alternatives for the considered function:* e.g. in taxa with poorly developed scallops, or no scallops at all, other structural reinforcement such as Korff’s fibers can prevent teeth enamel delamination. The existence of actual structural alternatives for the same function can weaken the structure-function correspondence necessary for a strictly adaptive hypothesis.

- 5) *To enlarge phylogenetic context and improve knowledge*: an accurate account of the occurrence of the considered trait in a complete phylogenetic tree is the foundation to understand the balance between phylogenetic information (common descent) and functional information (features relative to environment and lifestyle) carried by the trait. Previously unincorporated species (such as Lemuroidea in the SC fusion example) can be added as an external group to the analysis to discern exaptive and adaptive processes. Random distributions could be found, and can be either accepted or used as a basis for further research (as in the case of the SC fusion in Lemuroidea).
- 6) *To improve knowledge concerning ontogenetic and developmental processes underlying the structure*: adaptationist views often rely on the assumption of direct genetic control upon structures. The two studies presented above employ a more integrated view of ontogeny and development. Structures like the SC fusion or a scalloped DEJ can result from usage through the life of organisms, so a study on the timing of the structure (particularly, but not only, the timing before or after birth) can give important clues about the degree of genetic control. Shimizu & Macho's hypotheses concerning «morphodynamic processes and mechanical forces» show that «genetic networks» are only *one* level of factors acting in pre-natal development, which thus requires multiple levels of analysis.

The two studies we considered share a common attitude towards adaptation: if adaptation is *one* of the possible processes leading to a structure in evolution, it cannot be taken for granted and must be demonstrated, and this demonstration is often challenging and demanding. According to an “extended taxonomy of fitness”, a trait contributing to fitness should be named “aptation” in absence of a corroborated theory about the evolutionary mechanism(s) responsible for it (adaptive or exaptive). Also in Giorgio Manzi's reconstruction of human evolution (2007), we see that exaptation is handled as

a general process, but within a pluralistic frame of “interconnected adaptations” and appropriately applied to specific cases, like the evolution of bipedalism or the exaptive effects of developmental mutations in *Homo sapiens*.

We will comment below on the amount of work needed to discern adaptation and exaptation. We note here that such investigations can deepen our knowledge of considered traits and evolutionary processes, avoiding some misinterpretations about phylogeny and functionality in species and organisms.

### A survey of literature

Our survey is fully available online at the URL <http://hdl.handle.net/10281/19392> (complement part I). In the present section, we refer to publications listed therein through bracketed numbers [] followed by the year of publication.

Classic model examples like the Panda's thumb (Gould, 1980) and very recent articles (see cases above) elect *morphological and physiological* aptations as a field for a clear and fruitful employment of the exaptation concept. For many years, however, the use of exaptation in this domain was limited to some publications in cultural anthropology ([57] 1983; [112] 1984; [113], [137] 1986; [141] 1994; [47], [95] 1995) and medicine ([72] 1985; [67] 1997; [19] 2002; [12] 2003; [23], [159] 2004; [160], [20], [158] 2005; [102], [125] 2007; [148], [62] 2009), the latter expressing detailed speculative hypotheses about human morphological and physiological exaptations. There are a few interesting exceptions, which deal with the evolution of physiological traits in humans ([121] 1985; [135] 1996), paleoecology ([65] 1987; [66] 1988), and of morphological traits in our primate relatives ([48] 1986; [142] 1990; [29] 1992; and more recently, [122] 2004; [118] 2009). Despite some exceptions ([143] 1986), paleoanthropologists did not really begin to use the concept in their empirical work until recently ([152] 2002; [10], [58] 2007; see also, of course, [74], [136] 2007, together with the related [110] 2005, and the

anticipatory [117] 1996), with promising results (cf. e.g. [109] 2011).

It is useful to divide the field of *human language* into two non-overlapping sub-areas: (1) studies on language origin and (2) studies on language change.

(1) Since 1990, exaptation has been extensively employed in discussions about the evolutionary origin of language ([111] 1989; [114] 1990; [90] 1991; [105] 1993; [155] 1995; [31] 1999; [27], [75] 2000; [8], [24] 2002; [108], [21] 2007). Our survey shows that contributors in this field, although sharing the concept whereby exaptation has played a role in the origin of language, spent considerable time and energy in trying to make it clear *what* could actually have been exapted in such an evolutionary process (e.g. “cognitive systems”? “calculus categories”? “motor control processes”? “underlying neural organization”? “brain areas”?...). For example, in recent years a remarkable debate started in *Science* ([61] 2002) and has continued in other journals ([115], [45], [69] 2005; [13] 2006), where the focus quickly shifted from exaptation to the general framework concerning the modelling of language. This situation led some authors interested in exaptation and language to point out that the lack of a general theory of language definitely prevents the evaluation of exaptive hypotheses concerning its origin (see [16] 2001; [17] 2002). Meanwhile, a neuro-anatomical approach emerged that began to search for “neural substrates” underlying human language. Born in the 1980s, this research flourished in the late ‘90s ([2] 1997). Even in absence of a complete and shared theory of language, clues coming from analogies and homologies between humans and primates ([38] 1998; [35] 2005; [51] 2006) and functional imaging of neural activity and mirror systems ([9] 2003; [37] 2005; [104], [101] 2007) strengthened the hypothesis that the evolutionary origin of human language happened by cooption for novel functions of pre-existing neural structures and processes (modern human Broca’s area homologous to area F5 in macaques, mirror systems, motor control mechanisms). Our survey shows that a theory of multiple exaptations is

now integrated in the frontier of research into the origin of language ([91] 2006; [64] 2008).

(2) In 1990, the linguist, Roger Lass, introduced an approach in the study of language change which used biological evolution as a model, and considered exaptation as a mechanism with a high relative frequency. He suggested that language contains much “morphological junk” that «as an alternative to being scrapped, gets put to use – albeit a kind of use that has little to do with either efficient communication or the organization of extralinguistic experience» ([83] 1990, p. 814). Lass’s approach was largely welcomed in subsequent years, being applied in the explanation of several peculiar traits of different languages around the world ([70] 1994; [28] 2000; [5], [103] 2002; [41] 2003; [50] 2004). More general works have also been published ([13], [144] 2006). Despite general critiques to the application of evolutionary thinking in linguistics ([34] 2006), exaptation has come to be regarded as a key concept in understanding some important aspects of language change.

*Genetics and molecular biology* appear to be the fields of greatest success of exaptation: a lot of studies have been published showing evidence of functional cooption of genetic sequences and genomic features, and functional shift of (multiple copies of) existing genes (some examples are [22] 1999; [99], [123] 2000; [82] 2002; [124] 2003; [79], [18] 2005; [133] 2004; [52] 2006; [76], [49], [87], [86], [157] 2007; [32] 2008). Moreover, Evo-devo recently showed that evolutionary novelties often consist in differing modulation and genetic regulation of conserved developmental processes ([1] 2007; [30] 2005). Due to their very nature, studies in this field involve humans together with wide taxa such as mammals (e.g. [140] 1999; [4], [88] 2004; [139] 2006; [80], [128] 2007) or vertebrates (e.g. [97] 2005; [11] 2006; [98] 2007). Some papers dealing specifically with human genes, or referring explicitly to human evolution are: [59] 1996; [94], [81] 2001; [134], [78] 2004; [79] 2005; [60] 2006; [116], [132] 2007; [68], [150] 2008.

A complex situation can be found in studies on human behaviour, cognition, culture,

social organization, which we can group here under the general label of *anthropology* (seen as a strongly interdisciplinary field). Early papers used exaptation in studying human behaviours such as tool making, hunting, food cooking and sharing, early weaning, social structure, and the evolutionary origin of culture ([14] 1983; [119], [138] 1989; see also [42] 1994; [120] 1998; [6], [3] 2003; [71] 2005; [85], [43], [156] 2008). Despite this interest, it seems that initially exaptation was poorly known, and some authors tried to introduce the term in debates in order to re-label processes described by others. Meanwhile, exaptation was viewed as a potential source of conceptual change in cognitive sciences as well as in evolutionary theory ([111] 1989; [77] 1999). Various papers have employed exaptation in evolutionary hypotheses about the origin of human cognition ([44] 1993; [84], [149] 1996; [26] 2000; [7] 2007).

In particular, paleoanthropologist, Ian Tattersall (e.g. [145] 2000; [146] 2002; [147] 2004), strongly proposed exaptation as *the* mechanism for the origin of modern human behaviour: current physical abilities of human beings seem to have emerged together with the appearance of anatomically modern humans around 200 000 - 150 000 years ago. However, they remained hidden until some other mechanisms activated them; probably, a cultural stimulus (articulated language) was the main factor that triggered the development of abstractive and symbolic thinking. Therefore, new behavioural and cognitive modes in modern humans would seem to have arisen as exaptations, and this remains one of the most effective and promising explanations for the apparent gap between the evolution of anatomically modern humans and the rapid and global emergence of cognitively modern humans (see also [100] 1989).

The emergence of human behaviours by exaptation compromises strictly gene-based and selectionist explanations of specific behavioural traits in humans. On the one hand, this consequence was actively contrasted by evolutionary psychologists ([25] 1998; [63] 2003; [127] 2008). On the other hand, it induced several

authors to use the concept in making sense of particular, apparently non-adaptive behaviours such as geophagy ([154] 1998), suicide ([129] 2005), or homosexuality ([73] 2000). See also [93] 1996. Exaptation was used in philosophical, psychological and neuro-scientific studies on particular “human universals” such as dreams ([46] 1995), art ([39] 2004), creative thought ([131] 2005), the “rule of thumbs” ([126] 2005). The exaptation concept was also “co-opted” in the context of organizational and societal studies ([92] 2002). Regarding language, a growing emphasis is being put on neuroscience, and in particular on ancestral features like mirror neurons, cortical maps, motor activity co-opted in modern humans ([38] 1998; [21], [36] 2007). Archaeology ([106] 1992; [107], [96] 1998) and technological studies ([33] 2002; [130] 2006; [40] 2007) also became interested in exaptation. To sum up, we find here an early appeal and a gradual acceptance of the concept, which appeared to be a possible explanation in cases where classical selectionist and adaptationist explanations fail.

### Discussion: epistemic conditions influencing the use of exaptation

Our survey demonstrates there is a general acceptance and use of exaptation in all fields of study of human evolution. At the same time, the survey allows us to consider the epistemic conditions which possibly influence its application.

First of all, the strong persistence, in literature, of the term “pre-adaptation” (or “preadaptation”) must be taken into account as a general condition. In a rough count of the occurrences of the two terms in some journals and databases, we found both in varied relative frequencies, with a prevalence of pre-adaptation (exact ratios can be found in the online complement, part II, at <http://boa.unimib.it/handle/10281/19392>). Presently, “pre-adaptation” is preferred by several authors, despite being only partially synonymous to exaptation. As we have seen, Gould & Vrba (1982) proposed exaptation as a *substitution of*

*the term* (because of its misleading finalistic flavour) and an *extension of the concept* of pre-adaptation, including functional cooption of structures which did *not* originate by direct action of natural selection. The choice by some authors and some fields of using “exaptation” instead of “pre-adaptation” can be seen as a welcoming of one or both of these arguments.

Secondly, *the possibility to identify structures* appears to be a *conditio sine qua non* for studies on exaptation to be continued. Based on decoupling between structure and function, these studies are hardly viable in situations where structures and substructures are not clearly distinguishable. As we have seen in our survey, in the study of the evolutionary origin of language, exaptation did have to wait for the appearance of new approaches and (in specific, neuro-scientific) technologies capable of *identifying structures* to be studied – i.e. *what* can possibly have been exapted – in order to fully develop its explaining potential. Differently, exaptation was rapidly spread in evolutionary models of language change (where many recognizable linguistic structures are available) as well as in genetics and molecular biology (where genetic sequences allow a remarkably precise identification). Where conditions do not make it possible to identify structures and substructures (as in non-neuroscientific studies of language or in the last examined field of anthropology), exaptation bears a markedly speculative status, although it still continues the important function of stimulating debate on general evolutionary models, anticipating and directing further research.

Thirdly, tightly bound to the second, is *the possibility of doing research in the multiple directions* we enumerated in the section “Exaptation: a working concept...” above. Again, language origin offers an example. In 2001 and 2002, in evaluating several exaptive hypotheses on the origin of language, the linguist Rudolf P. Botha complained about the impossibility to perform studies about “historical order” (which can be likened to our point 2) and “comparative anatomy” (5) to test exaptive hypotheses (here Botha follows Gould, 1997), whether about language as a

whole or specific components of it, and whether they regard exaptation type I (“preadaptation or functional shift”, Botha, 2002) or type II (“by-product conceptions of language origin”, Botha, 2001). In such a situation, a sufficiently restrictive theory of exaptation is not possible, and exaptive hypotheses cannot be properly tested:

*“...a concise definition of the term “exaptation” or “preadaptation” accompanied by little more than a referential bow in the direction of Charles Darwin, cannot suffice [...] we require a theory of language genesis that assigns a given feature of language the status of “exaptation” in a non-ad hoc and non-arbitrary way [...] a theory of evolution which places general constraints on assigning the status of ‘exaptation’ rather than that of ‘adaptation’ to an arbitrary character or structure” (Botha, 2001, pp. 32-33).*

In absence of such a theory – which is, we can say, operationally specifiable – it is unclear «what kinds of evidence are properly relevant to the appraisal of exaptationist claims». We can observe that, in general, the strength of the non-operationality objection to exaptation appears to be relative to the particular field and moment of study, qualified by the possibility of recognizing structures and performing various kinds of research. In every field of human evolution, such conditions are constantly susceptible to change: even in the study of morphological and physiological features, as we have seen, novel technologies for modelling, visualizing and analyzing features today open new possibilities of research.

Considering examples of morphological and physiological features makes it evident that *the acceptance of an extended taxonomy of fitness seems to be very demanding* for researchers: the possibility of exaptation implies a greater amount of multidirectional work (to identify structures, discuss and evaluate exaptive vs. adaptive hypotheses) than a default acceptance of adaptation. This is even more evident in studies on small and seemingly minor traits such as the dentino-enamel junction or the scaphoid-centrale fusion. We hypothesize that this can influence, and

more specifically delay, the acceptance and use of exaptation together with context-dependent constraints such as the availability of resources and time. From a theoretical point of view, however, these constraints cannot justify the dropping of a concept which can help to clarify important epistemological and methodological issues. The success of broad and demanding studies employing exaptation in extending knowledge about morphological and physiological traits and evolutionary processes is supposed to positively influence the adoption of an extended taxonomy of fitness, at least in the promising field of human morphology and physiology.

In literature, there are particular situations in which *adoption of exaptation seems to be a sort of fall back*, forced by the failure of preferred adaptationist explanations. These cases are frequent, for example, in the multidisciplinary field of anthropology, where conditions second and third (above) are particularly problematic. Our review shows that the situation leads researchers to stress, instead of the exaptation mechanism itself, two aspects related to it: a particular consequence and a correlated theme. It seems that such an emphasis can lead to possible miscomprehension of the concept:

- 1) The stressed *particular consequence* of exaptation is the possibility of accelerated evolutionary change: it appears that the sudden appearance of complex traits such as “human consciousness” cannot be explained by gradual adaptation. In such cases, exaptation seems to be a sort of emergency back door to be used in evolutionary explanations. But it has to be pointed out that the distinctive mark of exaptation is *change of function* (by shift or cooptation), and the latter must be kept distinct from the two other – however correlated – problems which are clearly indicated in an article by Marc Hauser, Noam Chomsky and Tecumseh Fitch (2002, p. 1570):
  - a) *continuity vs. discontinuity*: exaptation of a structure occurring in a taxon does not imply any particular kind or degree of continuity between that taxon and related

taxa (i.e. if we are supporting the exaptation of certain pre-existing structures in the origin of human communication, we are not bound by principle to find a fixed, high continuity or identity between humans and modern primates. Important modification of structures could, in fact, have led to large gaps, so, while exaptation is suitable to explain particular continuities, continuity vs. discontinuity is a completely separate issue, and hypotheses in the two domains cannot be hastily used to support each other);

- b) *graduality vs. saltation*: although exaptation can contribute to explain abrupt evolutionary changes, such as the emergence of “human consciousness” in Tattersall’s hypothesis, the speed of the process is a separate issue, whereas even «a qualitative discontinuity between extant species could have evolved gradually, involving no discontinuities during human evolution». In other words, the possibility of a rapid change is a particular, unnecessary consequence of exaptation. Moreover, historically the term “discontinuity” in evolutionary biology opens the possibility of “saltationist”, anti-Darwinian interpretations which are absolutely unintended and largely unaccepted by the scientific community at present.
  - 2) Often, when exaptation is evoked in explaining rapid change (or, for example, deep continuities between taxa), it happens that its core – functional shift or cooptation – becomes lost in favour of a *correlated theme*: the one about non aptations, constraints and sub-optimality. Exaptation type II implies existence and relevance, in organisms, of: *non-aptations*, i.e. structures with no function, neutral to fitness, which are the raw material to be co-opted for novel functions; *structural constraints*, by which side-effects propagate in the organisms subsequent to every selective pressure, producing by-products and non-aptations. More generally, exaptation (both types) gives an

image of evolution as a suboptimal process, dealing with constrained structures and working like a tinkerer, with limited available material which is ever-changing. For these correlated themes, it is easily understandable for exaptation to draw the attention of researchers who try to make sense of maladaptive, suboptimal, or just bizarre traits. Exaptation has, indeed, much to do with constraints and non-adaptive effects. However, this explanatory route ends up, once again, neglecting the specific core of the concept: functional shift and cooptation (see several articles in our review, e.g. [47]). The meaning of the notion appears to be reduced to “no adaptation” or “oddities”.

In conclusion, since 1982 exaptation has been welcomed and used in research on human evolution. Examples show that it can be a working concept in biology, operationally specifiable and helpful in better understanding human traits and evolutionary processes. A comprehensive literature review reveals various situations: while exaptation has become a key concept in several fields, different epistemic conditions of applicability of the concept can be found. But research in all fields of human evolution appears itself to be in a state of flux, and the correct adoption of the ‘exaptive’ terminology, wherever present, offers an important conceptual and operational clarification. It is thus recommendable to maintain an effort for the diffusion and the correct interpretation of this possible “extended taxonomy of fitness”.

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*[http://boa.unimib.it/bitstream/10281/19392/1/PievaniSerrelliJASS2011online\\_complement.pdf](http://boa.unimib.it/bitstream/10281/19392/1/PievaniSerrelliJASS2011online_complement.pdf). We thank our anonymous referees for their very helpful comments and corrections.*

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