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Many ways of being human, the Stephen J. Gould's legacy to Palaeo-Anthropology (2002-2012)

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Summary - *As an invertebrate palaeontologist and evolutionary theorist, Stephen J. Gould did not publish any direct experimental results in palaeo-anthropology (with the exception of Pilbeam & Gould, 1974), but he did prepare the stage for many debates within the discipline. We argue here that his scientific legacy in the anthropological fields has a clear and coherent conceptual structure. It is based on four main pillars: (1) the famed deconstruction of the "ladder of progress" as an influential metaphor in human evolution; (2) Punctuated Equilibria and their significance in human macro-evolution viewed as a directionless "bushy tree" of species; (3) the trade-offs between functional and structural factors in evolution and the notion of exaptation; (4) delayed growth, or neoteny, as an evidence in human evolution. These keystones should be considered as consequences of the enduring theoretical legacy of the eminent Harvard evolutionist: the proposal of an extended and revised Darwinism, coherently outlined in the last twenty years of his life (1982–2002) and set out in 2002 in his final work,* The Structure of Evolutionary Theory. *It is in the light of his "Darwinian pluralism", able to integrate in a new frame the multiplicity of explanatory patterns emerging from different evolutionary fields, that we understand Stephen J. Gould's legacy in palaeo-anthropology today, both in terms of provocative shocks to comfortable visions of human evolution and, above all, in terms of specific scientific predictions about future research.*

Keywords - *Punctuated Equilibria, Contingency, Exaptation, Neoteny, Darwinian pluralism.*

Stephen J. Gould's legacy has been studied with regard to his political and sociological thought (Prindle, 2009), his style of communication and writing (Selzer, 1993), his famous public controversies and intellectual provocations (Sterelny, 2001), his role as a historian and philosopher of science (Shermer, 2002), his ability to write remarkable works on the history of science based on primary sources (frequently available on the bookshelves of his antiquarian book collection: see Gould, 1987b, 2000). Less attention has been devoted until now, ten years after his death, to his proper scientific and epistemological legacy in many evolutionary fields and not only in his parochial competencies as a palaeontologist. Two remarkable exceptions are: Vrba & Eldredge (2005); Allmon *et al.* (2009). The latter presents a detailed and apparently complete bibliography of Gould's work (814 titles, at pp. 335–379).

The role of Stephen J. Gould's ideas in palaeo-anthropology is an excellent example of indirect theoretical influence between a general scientific "research programme" (Pievani, 2012a) – that is evolutionary thought at large – and one of its strikingly changing sub-fields, the study of human evolution. As an invertebrate palaeontologist (Gould, 1969, 1970b) and evolutionary theorist, Stephen J. Gould (now: SJG) did not publish any direct experimental results in palaeo-anthropology (with the exception of Pilbeam & Gould, 1974), but was able to prepare the stage for many debates within the discipline, frequently concerning some implicit, powerful but misleading concepts applied to human evolution. As for strictly technical contributions in formal paleo-anthropological literature, Shermer quantified 13 publications in the huge amount of SJG's technical papers (479) (Shermer, 2002). In the scheme in the following pages we see the continuous

Scheme - Stephen J. Gould's Chrono-Bibliographical sketch. The complete SJG's bibliography, compiled by Warren D. Allmon and based on the list maintained by SJG's secretary, Agnes Pilot, includes 814 titles, of which 154 peer-reviewed (Allmon* et al*., 2009). It allows to draft a sketch of the main entangled theme s of SJG's work between 1965 (first item recorded) and 2002, in ten phases. We grasp here his continuous interest for human evolution (through the underlined items) until at least 1996.

1 - 1965-1968, ALLOMETRY AND SIZE IN ONTOGENY AND PHYLOGENY: THE SCIENCE OF FORM

(land snails from Bermuda, Bahamas; *Cerion, Gryphaea*)

2 - 1972, ELDREDGE & GOULD – PUNCTUATED EQUILIBRIA, AN ALTERNATIVE TO PHYLETIC GRADUALISM.

(1973-1974: stochastic models of phylogeny, with D.M. Raup, T.J.M. Schopf and D.S. Simberloff; 1974: size and scaling in human evolution, with D. Pilbeam; 1974: evolution of the brain and intelligence, letter to *Science*; 1974: the central role of retardation and neoteny in the evolution of man, Burg Wartenstein Symposium; first essays about human races, IQ and racist arguments; 1975: more papers about allometry, also in primates; 1974-1975: first papers about mass-extinctions; 1976: bushes and ladders in human evolution; 1977: Punctuated Equilibria, the tempo and mode of evolution reconsidered)

3 - 1977 (*ONTOGENY AND PHYLOGENY*) EVOLUTION AND DEVELOPMENT

(1977: papers about progressionism, the problem of perfection, the episodic nature of evolutionary change, the return of hopeful monsters; 1977-1978: attacks against "the selfish gene" and socio-biology; 1978: the panda's thumb; 1979: the importance of heterochrony in evolution)

4 - 1979, GOULD & LEWONTIN – THE SPANDRELS OF SAN MARCO AND THE CRITIQUE OF THE ADAPTATIONIST PROGRAMME

(1979-1980: Piltdown revisited; 1979: a biological homage to Mickey Mouse; 1980: is a new and general theory of evolution emerging?; 1980: the evolutionary biology of constraints; 1980: what is intelligence?)

5 - 1981, *THE MISMEASURE OF MAN* (NEW EDITION IN 1996)

(1981: constraints and oddities in evolution; 1981: palaeontology plus ecology as palaeobiology; 1982: macroevolution)

interest for human evolution in SJG's ten phases of scientific production, at least until 1996.

But what matters is the global theoretical impact of his work (Tattersall, 2013). The indirect contribution was not ephemeral and occasional, or case by case according to his famous series of three hundred essays in *Natural History* magazine (carefully gathered in ten volumes; for an essential compendium, see McGarr & Rose (2006)). It was instead the structural consequence of what seems the most important and enduring theoretical legacy of the eminent Harvard evolutionist: the proposal of an extended and revised Darwinism, coherently outlined in the last twenty years of his life (1982–2002) and depicted in his monumental and impervious work, *The Structure of Evolutionary Theory* (2002a).

Gould as a Darwinian

The discoveries accumulated in the ten years since his death would have thrilled SJG and we can easily imagine how many more essays he

Scheme - continued.

6 - 1982, GOULD & VRBA – EXAPTATION. THE MULTILEVEL THEORY OF EVOLUTION. THEORETICAL TURNING POINT: HE BEGINS THE FOUNDATION OF HIS "DARWINIAN PLURALISM" AS AN EXTENDED AND REVISED THEORY OF EVOLUTION.

(1982: the meaning of Punctuated Equilibria and its role in validating a hierarchical approach to macroevolution; 1982: Darwinism and the expansion of evolutionary theory; 1982: the uses of heresy, about Goldshmidt's hopeful monsters; 1983: the hardening of the Modern Synthesis; 1984: morphological channelling by structural constraints; 1984: human equality as a contingent fact of history; 1984: challenges to neo-Darwinism and their meaning for a revised view of human consciousness, The Tanner Lectures on Human Value, Cambridge University, April 30)

7 - 1986, VRBA & GOULD, CROSS-LEVEL SPANDRELS.

(1986: Punctuated Equilibria at the third stage, with N. Eldredge; 1987: asymmetry of lineages and the direction of evolutionary time, with N.L. Gilinsky and R.Z. German; 1987: Darwinism defined; 1987, book *Time's Arrow, time's cycle*; 1988: against the idea of progress in evolution; 1988: the uses of heterochrony; 1988: a novel notion of Neanderthal)

8 - 1989, *WONDERFUL LIFE* - EVOLUTIONARY CONTINGENCY AND THE SUPREMACY OF VARIATION

(1989: Punctuated Equilibria in fact and theory; 1989: mass extinctions and asteroids; 1991: Exaptation, a crucial tool for an evolutionary psychology; 1991-1993: the Burgess Shale case and debates; 1992: ontogeny and phylogeny, revisited and reunited; 1993: species selection on variability, with E.A. Lloyd; 1993: debates with Daniel C. Dennett; 1994: tempo and mode in the macroevolutionary reconstruction of Darwinism)

9 - 1996, *FULL HOUSE* – EVOLUTION WITHOUT PROGRESSIONISM

(1996: new edition of *The Mismeasure of Man*; after 1996, no more updating about paleo-anthropology; 1996-1997: debate with R. Dawkins about the growth of complexity in evolution; 1997: the exaptive excellence of spandrels as a term and prototype, in *PNAS*; 1997: the pleasures of pluralism in evolution, against the "Darwinian fundamentalism"; 1997: on Punctuated Equilibria, *Science*, with N. Eldredge; 1998-1999: levels of selection and the units of Darwinism; 2001: theory of hierarchical selection)

10 - 2002, *THE STRUCTURE OF EVOLUTIONARY THEORY* - THE EXPANSION OF EVOLUTIONARY THEORY AND DARWINIAN PLURALISM.

would have dedicated to the exuberant tree of human evolution. The chapters of *Wonderful Life* (1989), with its analytical criticisms of the "ladder of progress" in human evolution – our most influential "iconography of hope" – and the history of the fortune of this misleading image within palaeo-anthropology, are by now classic reading in the philosophy of biology, an example of shining scientific prose, even leaving aside the powerful but still controversial reinterpretation of the Burgess Shale (Collins, 2009). The intuitive power of the linear and anagenetic way of seeing hominid evolution is still evident in the popularisation of science (Pievani, 2011b). Thus its deconstruction – as an untestable and culturally embedded idea of general improvement – is still current and welcome, showing that evolution is not necessarily a transition from simple to

complex, from inferior to superior, from "archaic" to "modern". Thanks to SJG, we know that the present is not the key to reconstruct, retrospectively, the past (Gee, 1999). With his highly imaginative writing, SJG tried to separate human evolution from human hopes, from satisfying (but false) tales, canonical legends, and any tendency to hubris. This is clearly the first pillar of his legacy in anthropological science.

The controversies SJG raised about the metaphors applied in human evolution – intended as proofs of preferred human thoughts – were useful mainly within the field, helping to reinforce empirically a theoretical "normalisation" of human evolution through a branching model of diversification of species, typical of the broader phylogenetic tree of primates (Harrison, 2010). The alleged exception of human evolution, with its linear succession of only one species after another at every stage of our natural history (Dobzhansky, 1962; Mayr, 1963), failed under the weight of evidence accumulated since the 1980s (but being incomplete already in 1950s). In this process of experimental updating, SJG helped scientists to understand the role of old and inadequate concepts, thanks to his peculiar archaeology of scientific ideas. He filled up the "theoretical vacuum" in which paleoanthropologists and human anatomists were largely trained after mid XX century (Tattersall, 2013).

He concentrated on the jargon with new attention, distinguishing "evolution" and "progress" (Gould, 1996), trend and finality, and stressing the ambiguous and appealing fashion for using linear terms like "missing link". It is interesting to note that even in this case SJG was in tune with the original Darwinian pluralism, confirming again that the supposed anti-Darwinian meaning of his legacy is completely groundless (Gould, 1995). When the young English naturalist wrote his "Transmutation Notebooks", the very early image of evolution in his mind (drafted in the astonishing page of July 1837, starting with the note "I think") was not just the "tree of life", but an "irregularly branched tree", without any hierarchy of importance between the branches and similar to the anarchy of a coral, with dead branches composing the great part of the structure (Darwin, 1987).

Even the tree of life could reveal a linearity (at least in the growing diversity of species, with more and more complex adaptations) and the young Darwin was sceptical about that linearity, preferring an irregularly branched model with different densities of species in the genera depending on environmental conditions. The controversial "bushy tree" of human evolution proposed by SJG should also be understood in this historical sense of a convergence with the original Darwinian pattern. The "coral of life" that we see in Darwin's early notebooks is astonishingly similar to the current phylogenetic tree of hominin species (Tattersall, 2009a): so, "ever since Darwin" (Gould, 1977a) in human evolution as well.

It is not by chance that Darwin drafted that coral of life before his generalisation of the principle of the slow gradualism of evolution (the only figure in *The Origin of Species*, twenty years later, is a quite different tree of species, with gradual divergence). This is a crucial detail because SJG's point is not the degree of "bushiness" or the number of species. The reasonable objections against any hurried proliferation of newly baptised species (White, 2003; Wood & Harrison, 2011) are not a refutation of his initial proposal, for two reasons. First, even the most vehement "lumpers" have to accept today an irregularly and clearly non minimalist branching tree of human evolution (with at least four genera: *Ardipithecus*, *Australopithecus*, *Paranthropus*, *Homo*), and the debate in palaeo-anthropology is about the degree of methodological parsimony in adding new species or varieties. Second, the point for SJG is not the contingent number of new or unobserved or misinterpreted hominin species, but the theoretical background of the branching model itself (Gould, 1980). His legacy is related to the reasons for the diversity of species in human evolution, according to which the path of human evolution is not a ladder of progress. And here we find the second pillar of SJG's legacy in palaeo-anthropology today: Punctuated Equilibria and their significance in human macro-evolution as a directionless "bushy tree" of species.

Punctuated Equilibria: Tempo and mode of a contingent evolution

Punctuated Equilibria and the extended role of both allopatric speciation and stasis (Eldredge, 1971; Eldredge & Gould, 1972) was a standard case of theoretical challenge in evolutionary thought, with a series of stages: (a) early "revolutionary" phase, against the "influential paradigm" or "conventional prejudice" of phyletic gradualism intended as the core of the application of Modern Synthesis to palaeontology; (b) defensive reactions of the "orthodox" scholars (about the punctuated rate of speciation and the empirical reality of the stasis); (c) extension of the theory (Gould & Eldredge, 1977, 1986, 1993; Eldredge & Gould, 1997); (d) later, more moderate considerations and pondering about the effective theoretical impact of Punctuated Equilibria among the patterns of speciation; (e) in the end, integration in a more pluralistic evolutionary canon and in textbooks (Futuyma, 1998; Stearns & Hoekstra, 2005).

In opposition to some simplistic reconstructions (Orr, 2002), the debate is not concerned with a marginal epiphenomenon surrounding a monolithic paradigm or, on the contrary, a radical crisis of its core. Otherwise, it could mean an extension and revision of its structure, remaining nevertheless compatible with other components and patterns of it (Somit & Peterson, 1992). The result is a structure of the theory of evolution, intended as a research programme (Pievani, 2012a), that is more articulated in a pluralistic frame, more realistic in its assumptions about the currently available evidence, with revision of previous restrictive concepts (regarding the "universality" of some patterns) hardened in the protective belt of the late version of the Modern Synthesis in the 1960s (now: MS) (Gould, 2002a).

According to Ernst Mayr (1963, 1970), the birth of a new species presumes a heterogeneity of populations within the same species: small populations that, separating themselves from their parent species for geographical reasons, diverge morphologically to the point of breaking off the genetic flow from their original populations. Mayr's hypothesis had actually been preceded by the unpublished thoughts of the young Charles Darwin in his "Transmutation Notebooks" (Eldredge, 2005; Pievani, 2009) and by Simpson's "quantic speciation". In any case, Mayr had deemed it to be "internal" and consistent with the Neo-Darwinian paradigm (Mayr, 1991). In 1972, Eldredge and Gould interpreted it as an authentic turning point in evolutionary thought and in the vision of natural history. The onset of a new species does not just derive from a gradual, genetic-type transformation, extended to a whole population and within the same habitat: rather, speciation can be a phenomenon of rapid divergence of a peripheral population, with subsequent changes in geographic distribution, and long periods of stasis.

After decades of debate, the general consensus around the mechanisms of speciation is now that we need to consider a multiplicity of processes and modes of birth of new species (punctuated in some ecological circumstances and gradual in others), a multiplicity of possible rates of speciation (including the palaeontological reality of stasis), and a multiplicity of levels of change (from an ecological and a genealogical point of view). The main methodological stance today is a calculation of the relative experimental frequencies of one pattern (punctuationism and stasis) with respect to another (gradualism and trends) (Pagel *et al.*, 2006), and not a radical alternative between incompatible patterns. We now have a more pluralistic set of explanations, still consistent with an extended and updated Neo-Darwinian core. As Niles Eldredge significantly pointed out, "At heart Steve was a neo-Darwinian always. As am I – and so are we all" (Eldredge, 2013).

SJG, together with Eldredge, is deservingly credited with having broadened the range of evolutionary patterns, illuminating problems that were missing or defined away in the previous setting of evolutionary research: geographic speciation as punctuated innovation; stasis; evolutionary trends. What we see in Punctuated Equilibria is precisely a theoretical balance between points of rupture from past methodological stances within MS population genetics (like phyletic gradualism *sensu* Williams (1966)) and points

of theoretical continuity (for a detailed historical reconstruction of Punctuated Equilibria paper and following debates: Sepkoski, 2012).

The points of rupture are:

- rapid punctuations in the birth of new species are not due to imperfections of the geological record;
- species are natural and real units ("individuals" in SJG) of evolution, not conventional entities;
- speciation is not only extrapolated as anagenesis within populations or as gradual divergence, but is frequently cladogenetic, with high frequency of allopatric processes;
- speciation is connected with major episodic evolutionary changes;
- wide diffusion of apparent stasis in natural histories.

The points of continuity with the MS are:

- the evolutionary mechanisms in action during the speciation are still Darwinian;
- gradual trends are not excluded and they could emerge in groups of related species as a result of sorting among species;
- allopatric processes are not exclusive of but complementary with sympatric or parapatric speciations in other environmental conditions;
- above all, punctuation and stasis stand at the level of the geological scale of species life, so they do not clash with normal mechanisms of change at the level of populations of organisms (Gould, 2002a).

Points of rupture and points of continuity are consistent with each other because of the different scaling of evolutionary causality, a crucial issue for SJG. In this necessary and continuous updating of the MS (without radical "paradigm shifts") and in the consequent theoretical pluralism, we see that the novelty of Punctuated Equilibria was not only related to the rates of speciation (the axis of time in representing evolution), a matter given undue weight in debates, with confusions between Punctuated Equilibria and versions of "saltationism" (Dennett, 1995). The novelty was mainly related to the ecological, bio-geographical and macro-evolutionary conditions surrounding speciation processes (the axis of space in representing evolution: Vrba & Eldredge, 1984; Eldredge, 1989), like climate instability, geophysical disruptions, ecological barriers, fragmentation of habitats, and their consequences (turnover pulses, habitat tracking, mass or regional extinctions, cohabitation of species, and possible hybridisations). Then, not only the "tempo" but also the "mode" of evolution (Eldredge, 2013).

The enduring significance of Punctuated Equilibria is the relative independence and the effectiveness of macro-evolutionary patterns (not always reducible to micro-evolutionary ones), the concept of "species" as a discrete entity, and the primary role of ecological and geographical factors (Eldredge, 1995, 1999). The physical structure and distribution of populations inside any species becomes a crucial variable in order to understand the production of diversity inside the tree of hominins. In SJG, genomes, organisms and groups (even species for some characters like the degree of internal genetic variability) are different, inherently hierarchical levels of evolving "Darwinian units": autonomous, inter-dependent and integrated levels of the organisation of life. In Lloyd & Gould (1993), species selection on "variability" (intended as a good species-level trait associated with genuine species-level fitness) was depicted as a major force of macroevolution.

In the background of these "multilevel theories of evolution" (like that formulated in different ways, without multilevel selection and with an interplay between a genealogical hierarchy and an ecological hierarchy, by Niles Eldredge (2008)), we find precisely the reasons for the diversity of species shown by the irregularly branched tree of human evolution today, reasons first underlined by Niles Eldredge and Ian Tattersall (1982). It was a methodological turning point: after the proposal of Punctuated Equilibria, the long debated and supposed gaps in the fossil record became actual information, in paleo-anthropology as well. So, leaving the controversy about the number of species aside,

we see the typical plurality of patterns outlined in SJG's work:

- repeated episodes of speciation;
- phases of great diversification of species and subsequent extinction, during periods of ecological instability in Africa, like those around two million years ago (a pattern found in hominins and other mammals as well, according to Elisabeth Vrba); this is a macro-evolutionary scheme that corresponds well to the model of "experimentation and decimation" proposed by Gould (1989; 1995);
- species apparently more stable in time and long-lived (like *A. afarensis*, *P. boisei* and *H. erectus*);
- in contrast, "comet-species" in local regions (like apparently *A. bahrelgazali* and *A. garhi*);
- great geographical expansions, with successive allopatric diversification in varieties, sub-species and new species (as apparently in *H. ergaster* for the first "out of Africa" and *H. heidelbergensis* for the second "out of Africa") (Tattersall, 2009a; Manzi, 2011);
- not a cumulative succession of new adaptations coordinated in many species, but episodic innovations in single species, intended as peculiar mosaics of traits (Tattersall, 1999), as in the case of the many different ways of bipedalism in early hominins;
- as an integration to the previous pattern, the cumulative trend of encephalisation in the genus *Homo* may have been produced by "species sorting" processes;
- bursts of ephemeral cultural innovation in small groups of humans due to demographic expansions and contractions in specific regions like South Africa (Jacobs & Roberts, 2009);
- the reconstruction of the phylogenetic tree of populations of *Homo sapiens* on the planet, starting from the speciation which occurred in Africa about 200,000 years ago, and of the somehow corresponding tree of cultural and linguistic diversification, have traced the contours of a similar branching model of recent evolutionary diversifications, with paths of expansion among historical and geographical contingencies (Cavalli Sforza *et al.*, 1994; Cavalli Sforza & Pievani, 2012).

He was really prescient about the discovery of new branches in the human tree and the picture of human evolution today would probably have satisfied SJG's curiosity and expectations. He would comment enthusiastically on the discovery of at least five human forms still living together in the Old World 50,000 years ago (Gibbons, 2010), after three or more great diasporas out of Africa in species of the genus *Homo*. In these patterns we appreciate a real and irreversible scientific (and epistemological) legacy of his work, the second pillar of our reconstruction here: not the use of radical provocative metaphors, like the "jumps" between species or the "bush" of human evolution – afterwards appropriately revised – but the role of macro-evolutionary, biogeographical and ecological factors in human natural history, with *Homo sapiens* as a small, late twig on the enormously arborescent bush of life.

The dependence of our evolution on external (and frequently accidental) circumstances – like the Great Rift Valley formation and the Pleistocene climate oscillations – is also the key to understanding the central concept of contingency in SJG (Gould, 1991, 1993; Pievani, 2011b). It does not mean that human evolution occurred exclusively "by chance", but through an entanglement of functional factors (produced by selective pressures), structural constraints, and historical contingent events: an interplay between random events and regularities (Gould, 2002a). *Homo sapiens*, an improbable and tiny branch at the end of a luxuriant tree of species, is a "glorious accident of history" in SJG for these scientific and epistemological reasons. Like any other species, we are not at the top of a process of perfect optimisation, but we are the offspring of the material and contingent relationships between localised populations and ever-changing environments. The massive contingency of human evolution means that particular events, or apparently meaningless details, were able to shape irreversibly the course of natural history.

Structures and functions in human evolution

Contingency means that evolution has to be interpreted not only as a process in time – with the risky "great narratives" produced in our minds by the teleological preferences (Girotto *et al.*, 2008) – but also as a process occurring in a material space: the ecological and geographical space, which is not "for us" but in which we have to survive. From Darwin to SJG this is the first (external) source of limitation for any adaptive process, which is relative to specific populations subject to local, external and ever-changing circumstances. Thus adaptation, as originally formulated by Darwin, is always a limited and temporary functional result, far from perfection.

Furthermore, adaptation has also in SJG a second (internal) source of limitation – the set of physical, structural and developmental constraints that influence or canalise any functional tuning of adaptive traits (Gould, 1993). It is also for this reason that natural history is so filled with quirkiness, happenstance and unpredictable outcomes. Natural selection does not have indefinite freedom to shape organisms, and the process of adaptation is sub-optimal. The same selective pressure could have a range of adaptive outputs and solutions, according to the different internal constraints of the organisms, and contingent circumstances. Evolution is an irreversible process, with its specific historical patterns. As SJG repeated, history matters (Gould, 1987b) and after Darwin natural history acquires for the first time a scientific status. This idea of a continuous trade-off between functional and structural pressures in evolution (external factors and internal factors in SJG's language) should be considered as the third pillar of SJG's legacy to palaeo-anthropology: his biological formalism and structuralism (Gould, 1983, 1987b). As Niles Eldredge recently stressed, "Steve, at heart, was first and always a morphologist and developmentalist" (Eldredge, 2013).

In a foundational essay of 1982, SJG and Yale palaeontologist Elisabeth S. Vrba circumscribed the whole set of potentially useful characteristics as "aptations", identifying the subsets of characteristics shaped for a specific reason that then become, by different circumstances, available to selection for another function (Gould & Vrba, 1982). Therefore, the hypothesis is that we should not consider all cases where there is a real change in function, with structure remaining the same or just slightly modified, to be "ad-aptation". Rather we should speak of "ex-aptation" in all those cases where there is co-optation for new functions of structures employed in the past for other functions (exaptation type 1, functional cooptations, at different levels, from molecular to morphological ones). In a more radical sense of the term, exaptation also includes the cases where the initial traits had no function at all, being just neutral insertions or structural constraints (exaptation type 2, cooptation by non-aptations, or "spandrels"). In exaptation type 1 a functional pressure is always ongoing, in exaptation type 2 we have at least one stage of the process without natural selection in action (Pievani, 2003). Exaptation could also be a trait originating at one level of evolution for adaptive reasons (genomes, organisms, groups, species), then having side-effects at other levels (cross-level spandrels) (Vrba & Gould, 1986), like in case of exaptations conferring emergent fitness at higher levels (Gould & Lloyd, 1999).

In other words, an organ's current usefulness and its historical origin should be seen as separate in some cases. An early adaptation could have later unexpected side-effects in different circumstances and selective pressures. Natural history in SJG, like in François Jacob at the molecular level (1978), seems an opportunistic and flexible "tinkering", always reorganising the available material. Morphology does not necessarily represent a functional optimisation of the organic structure in relation to its environment. As clearly shown by early hominin adaptive strategies, and by their singular mosaics of innovations species by species, evolution is an exploration of different contingent possibilities and not the fine-tuning of the same functional mainstream.

SJG (with Richard Lewontin) outlined an extended taxonomy of evolutionary phenomena, remarkable in human evolution as well, in

which the general class of emerging evolutionary innovations (aptations) includes purely casual innovations (i.e. through genetic drifts, another process depending on the physical structure of populations inside the species), correlations by exaptation, and standard Darwinian adaptations. Thus evolutionary pluralism does not lead to the negation of adaptation as an evolutionary reality, rather it redefines the concept of adaptation as it must consider that organisms and environmental niches are co-evolutionary subjects bearing internal historical constraints and channels of growth.

In the history of the idea of "functional cooptation" in Darwin (in the sixth edition of *The Origin of Species* (1872) as an answer to the objection of the "incipient stages of complex structures"), then "pre-adaptation" in Ernst Mayr and the MS, then in the more radical sense of "exaptation" (Gould & Vrba, 1982; Vrba & Gould, 1986) and "spandrels" by structural non-aptations (Gould & Lewontin, 1979), we see the same equilibrium between elements of theoretical continuity and elements of rupture. It is clear in the current literature that we do not need a conflation between standard adaptations and exaptations, but an "extended taxonomy of fitness" (Gould, 2002a) made basically by three typologies of processes: (1) classical Darwinian adaptations by natural selection; (2) functional shifts, by natural selection, from a previous function to a secondary one; (3) spandrels and other side effects with no adaptive reasons in their beginning, possibly co-opted by natural selection in new external conditions (Pievani, 2003).

Also in this case we have points of rupture with the MS in its "adaptationist" version. The current usefulness does not always correspond to the historical origin and points of continuity with the Neo-Darwinian core of evolutionary thought: natural selection remains pervasive, but frequently finding contingent trade-offs with the internal constraints of organisms. The result is far from the classical lyrical descriptions of perfect organic design and harmonious adaptations. Thirty years later, exaptation is a term widely used in different evolutionary fields ranging from paleontology to molecular biology. According to Jürgen Brosius - with SJG author of a paper about the processes of functional cooptation of neutral elements in the genome (Brosius & Gould, 1992) - even if much of the neutral nomenclature was not accepted by the scientific community (being too complex), however the concept of exaptation at the genomic level clearly has conquered the field of molecular biology and especially molecular evolution.

The role of exaptation also in human evolution cannot be underestimated today and is gaining growing empirical confirmation (Manzi, 2006, 2007), with all the caveats necessary in terms of application of the concept and empirical verification of the exaptive models (Pievani, 2011a; Pievani & Serrelli, 2011). According to Tattersall, it is impossible to understand the evolution of our first innovation, the architectural re-organisation of bipedalism, without a consideration of its immediate adaptations (in Eastern and Southern African habitats becoming gradually drier and with greater open spaces) and its exaptive side-effects in hominin societies and behaviours (1999). SJG was one of the most convicted theorists of bipedal locomotion as the first and major innovation at the base of our divergent tree, with different early solutions in archaic hominins and a large temporal gap with the growth of the brain in the genus *Homo*, at least three million years later.

Another proliferating source of exaptations is precisely the growing and plastic brain in genus *Homo*, with its direct selective pressures and then a range of amazing re-utilisations for functions completely disjointed from the original ones. It seems also highly promising the application of the concept of exaptation in order to fill up the apparent gap between the anatomical speciation of *Homo sapiens* and the belated emergence of cognitively modern behaviors: after a first phase of "exaptive equipment", an ecological and social trigger in Africa could have pushed forward both a rapid cultural innovation and a final wave of populations of *Homo sapiens* out of Africa (Tattersall, 2009b; Pievani, 2012b).

So, according to Tattersall, we have to recognize that exaptation is now a crucial pattern in the history of innovation in the human clade

(Tattersall, 2012). The notion of exaptation, capturing the connection between morphological potential and the production of functional innovations through a kind of opportunistic "tinkering", introduces into the "nature of history" an important principle of redundancy as the "foundation of creativity" (Gould, 1980). For SJG evolution is a process that abounds in redundancies and imperfections, and adaptation could be a collateral effect rather than a direct optimisation. Biology is a field of potentialities, and not determinations. Functional flexibility seems directly proportional to the capacity of organisms to react by natural selection to changes in their environmental rules. Complex organisms exist thanks to imperfections, to multiplicity of use and redundancy. In this frame SJG inscribed the contingent success of *Homo sapiens*, a highly exaptive species, at the end of our irregularly branched tree.

With the notion of exaptation, SJG powerfully challenged also the adaptationism and the atomistic separation of adaptive traits (or "modules") that dominated early sociobiology and then evolutionary psychology (Gould, 1978, 1987a). His warning of the dangers of the adaptationist and not falsifiable "just so stories" in evolutionary reconstructions of human behaviours and psychological faculties were based on the idea that the present (*Homo sapiens* as it is now, as a biological and cultural species) is not the right key to understand the past, because these narratives tend to use the past as a progressive justification of this present intended as the only possible one (Buller, 2005).

Even as scientists, we are dazzled too much by the apparently good functional designs in nature and behaviours. The role of ever-changing environments (and not mythical and unrealistic "ancestral adaptive environments"), the historical and geographical contingencies, niche constructions, exaptations and spandrels could become antidotes and theoretical tools for a new generation of evolutionary psychologists. Considering the recent developments of literature in evolutionary psychology, and leaving aside the initial heated debates, we see that the provocative role of SJG has been effective in this field as well.

The child is man's real father

Ex-aptation is coined from Latin "aptus" (useful, suitable) and "ex" (starting from) a previous form or structure. It means that natural selection acts in a context of historical and structural constraints, finding trade-offs with previously settled forms, that show their power specifically in developmental constraints. We should recall that the favourite hypothesis supported by SJG about the emergence of the genus *Homo*, and the causes of its uniquely derived anatomy, was that a speciation from one of the branches of Australopithecines took place by a process of modification of the mechanisms of development. Specifically, a preservation of youthful characteristics which was not strictly speaking adaptive, called "neoteny" or juvenilisation, had many exaptive side-effects, including the allometric growth of the brain (Gould, 1974, 1977b, 1980).

The child is man's real father, he wrote in 1977 (Gould, 1977a). He thought that the delayed growth was crucial in human evolution, re-animating the studies of heterochrony in paleo-anthropology. According to Ian Tattersall (2013), the "size and scaling" paper published in *Science* by David Pilbeam and SJG in 1974 was very influential in the field, highlighting the role of ontogeny and neoteny in human evolution (Pilbeam & Gould, 1974). A selective trade-off between the costs of a more fragile offspring and the advantages of a prolonged period of imitative and social nurture separated our evolutionary path through paedomorphism, with *Homo sapiens* as a later expression of this trend (Gould, 1977b). Because of this developmental retardation, the following anatomical and neural reorganization, and the broadening of the space for individual experiences, *Homo sapiens* becomes for SJG a pool of new evolutionary possibilities.

This hypothesis is receiving corroboration (Manzi, 2007) and testifies the topicality of SJG's approach to human evolution. The African speciation of *Homo sapiens* is probably related to a genetic re-organisation including a slower development and a longer period of parental dependence, during which the experimentation of

behaviours not strictly associated with survival and new ways of cultural transmission could have been favoured. According to recent research (under debate) based on dental evidence and skull development (Smith *et al.*, 2010), the ontogenetic neotenic trend reaches its maximum in *Homo sapiens*, and in our closest cousin, *Homo neanderthalensis*. Some physical anthropologists (Falk, 2009) think that neoteny, and the prolonged vocal contact between mothers and offspring in bipedal primates, could also be related to the evolution of articulated language.

More generally, this is another example of extension of the evolutionary research programme. A small mutation in developmental timing triggers a range of exaptive effects, including the successful behavioral flexibility of *Homo sapiens*, highlighting the importance of "size and scaling in human evolution" (Pilbeam & Gould, 1974). Furthermore, in the frame of a renewed MS, the evidence of a huge amount of variations and sequences inside the genome with no adaptive or selective origin is accepted with the cost of a robust quantitative and mathematical integration in the models. As in the case of punctuationism, we need a calculation case by case of the relative frequencies of selective patterns and drift patterns when we look inside the structure of the genome. SJG was able to underline the most fruitful fields of research that threatened the inclusive capacity of the MS, showing that they were touching supporting ribs of the theoretical architecture of the MS and in some cases adding entire new domains of experimental evidence that claimed for a powerful theoretical updating.

The discovery of families of genes and hierarchies of genes, with a hitherto underestimated complexity of genetic regulation, changes the very idea of the genome, the machinery of mutations and phenotypic effects, the definition of the concept of "gene". The "raw material" of any evolutionary process is no longer so "raw", as SJG anticipated. Evo-Devo, prefigured by SJG already in 1977 in his prescient book *Ontogeny and Phylogeny*, suggests a crucial role for the constraints to variation, for the internal developmental constraints, for systems innovations, functional cooptations, and changes with a modular logic (Gould, 1977b; Carroll, 2005; Minelli & Fusco, 2008). Following SJG's interest in the history of biological structuralism (already in: Gould, 1966, 1970a, 1972), 1977 is a very early date for understanding that a huge amount of evolutionary changes could be related to mutations in ontogenetic development (particularly in the case of heterochrony), long before the successes of molecular developmental genetics. The field of epigenetics has now enlarged the range of the sources of variation and inheritance. Phenotypic and developmental plasticity modifies the relationships between genomes, phenotypes and ecological niches (West-Eberhard, 2003). And again, the "niche construction" hypothesis (Odling-Smee *et al.*, 2003) is a new way to see the active role of organisms in evolution and the reciprocal modifications of organisms and niches.

The neotenic hypothesis for the evolution of the genus *Homo*, and particularly for *Homo sapiens* – mixing genomic reorganisation, developmental constraints, Evo-Devo, adaptations and exaptations – is a result of this pluralistic way of seeing evolutionary explanations. It should be considered as the fourth pillar of SJG's legacy to palaeo-anthropology: the attempt to understand human uniqueness in terms of "evolvability", the very possibility of future evolution. For each of these lines of research we need more data and a careful consideration of the real theoretical impact. Anyway, the capacity for painless assimilation of scientific novelties by the MS seems to be progressively declining. The problem is no longer one of partial "incompleteness", but the adequacy of the whole conceptual structure of the theory (Gould, 2002a). SJG was thinking that we need not a completely new theory but a new kind of Neo-Darwinism, revised and extended. Palaeoanthropology has been an excellent candidate to test the experimental fruitfulness of this approach.

An iconoclastic but strictly scientific legacy

SJG suffered a well-known negative side-effect of popularity, clearly described by Michael

Shermer: "one's celebrity with the general public was thought to be inversely proportional to the quantity and quality of real science being done" (Shermer, 2002, p. 36). For our approach about SJG and palaeo-anthropology, it is useful to separate the past contents of public debates – too radical because of SJG's polemic attitude itself – and the specific, scientific and experimental, legacy of his ideas, as in the case of the application of Evo-Devo to *Homo sapiens* and the neotenic hypothesis. Observers were enamoured with the polemic side of SJG's work, because of his tendency to radicalise and extend his ideas beyond their logical and empirical limits (Allmon, 2009), as in the case of the connection between Punctuated Equilibria and his Marxist education (Gould & Eldredge, 1977). Punctuated Equilibria for SJG became much more than a theory of allopatric speciation and stasis: rather it was a general theory of change across varied domains (the "punctuational paradigm" in Gould (2002a)). However, if our focus of attention is concentrated on the famous "heterodox fights" in which SJG hyperbolically engaged in public controversies – especially in the provocative papers of the early 1980s about mass-extinctions, hopeful monsters and the elusive concept of "species selection" – we lose the general novelty and influence of his approach, which was primarily scientific and epistemological. SJG left a coherent intellectual framework, that we need to understand before criticising it. It was his "view of life", his idea of the nature of history.

For example, his incendiary battle against any biological and genetic foundation of the concept of "human race" (Gould, 1981) – another case of a good challenge subsequently confirmed by overwhelming data – was full of scorching criticisms against the politically conservative prejudices of many scientists. SJG never concealed his partisanship and preference, stressing the role of sociological factors in any scientific enterprise. He frequently struggled against three epistemological "myths": (1) the scientist without cultural and social biases; (2) the scientist as a diligent inductivist hero, a collector of neutral facts without preconceptions; (3) the linear or "Whig" historiography of science (Gould, 1981, 1987b). Science is a human, fallible activity, full of glories and mistakes.

Fossils do not speak by themselves, empirical data are impregnated by theories and background knowledge. Ironically, according to his critics (Lewis *et al.*, 2011), some aprioristic cultural beliefs could have biased his own severe analysis (1981) of Samuel G. Morton's unconscious manipulations of the anthropometric measurements and ranking of skulls belonging to different "races" (in *Crania Americana*, 1839). Any scientist is unconscious victim of his preconceptions (polygenism in Morton's case), including the egalitarian and liberal SJG. But he always added that "vigilance and scrutiny" were the only palliations, and he reached his conclusions with integrity and conviction. Then, as Tattersall pointed out, "in a paradoxical way Steve had proved his own point" (Tattersall, 2013). What matters here is the great picture: he faced strong cultural biases (i.e. about the human intelligence as a unitary and inheritable object), and undoubtedly his combat against any use of genetic reductionism to support racism and discrimination was on the right side of the controversy. Other scientists feel the need to pursue his battle, being aware that the concept of human race (and "racial" drugs) is still misused in medicine literature (Barbujani & Colonna, 2010).

Furthermore, despite his tireless stressing on cultural biases, he was not a sociological relativist, and never abandoned his scientific rationalism and even objectivist realism: "I remain an old-fashioned, unreconstructed scientific realist" (Gould, 2002a, p. 969; see also Gould 1987a). So, even if Morton was one of his political straw men, it must be recalled that his crusade in *The Mismeasure of Man* (1981) was against the more general scientific attitude of measuring what is not measurable, attaching "universal essences" to human disparities, a crusade still being fought today. Furthermore, his battle against the biological identity of human races was based not only on his political ideas but mainly on his strong assent to the "out of Africa" hypothesis: so to a unique, recent speciation of *Homo sapiens* with

subsequent wide mobility and cultural diversifications. He fairly understood that this model was incompatible with the natural creation of subvarieties and racial genetic barriers.

The strong genetic equality of every human being, with slight differences mainly at the level of individuals and not races, was a scientific argument, according to the first evidence suggested by Richard Lewontin (Gould, 1985). But SJG added something more, showing the different epistemologies behind the two competing hypotheses; a progressive idea of linear evolution by global cumulative stages in the old "multiregional" hypothesis, and a pluralistic pattern of speciations, diversifications and cohabitations, in the "out of Africa" hypothesis (Gould, 1989). His campaign against human races was thus right in the end, and he was right because of the most important reasons.

Saying "he was right", we would like to stress that SJG, apart from his political engagement, made precise scientific predictions – risky predictions because of their possible refutation – that we can test now, ten years later: the bushy tree of hominin evolution; bipedalism as earliest trigger; neoteny; ecological contingencies; and so on. But polemical attitudes attract excessive reactions. Nothing in exaptation and historical contingency leads to the conclusion that *Homo sapiens* is an evolutionary "discontinuity" or that SJG supposed non-naturalistic ways of explanation, as asserted by Daniel Dennett in his harsh and unfair criticism (1995). SJG's appeal to evolutionary humility was exactly the contrary – a naturalistic way of seeing *Homo sapiens* as a part of a contingent process and not its culmination. He reinforced the idea that in the process of "becoming human" we cannot find any special mechanism: the human tree is just like that of other mammals.

What SJG did is an application of his Darwinian pluralism to human evolution, and the evidence of the last ten years seems to confirm the concrete complexity of the process he depicted. Conversely, the ultra-Darwinian and strictly functionalist approaches to human evolution appear more and more speculative with respect to the facts discovered in the natural histories of the numerous human species. These histories are far from a battle of selfish genes or the result of a universal pan-selectionist logic. The non-reductionist attitude of SJG was not ontological, nothing like a rejection of naturalism and Darwinism, but methodological: a proposal of explanatory pluralism for scientists dealing with the rhythms, the levels and the mechanisms of evolution. In a word, with "history".

In SJG, nature is never the repository of moral norms or the inspiration for ethical arguments (Gould, 1981, 1991), and cultural evolution has radically different patterns from biological evolution. This is not because the human species is something completely separated by nature (Gould, 1983), an ontological leap, but because the human species is a contingent innovation in natural history, a unique result of natural processes, able to contradict their logic through its intelligence and cultural evolution, as we have already read in the final lines of Darwin's *The Descent of Man* (1871). The epistemological guideline for SJG was the battle against any form of anthropocentrism (cosmological, evolutionary, ethical, environmentalist) and mythological progress (Gould, 1993), not questioning the completely natural condition of our species. In that sense he was a follower of the standard naturalistic view, enriched by a pluralistic methodology in the evaluation of the different levels of analysis of human behaviour. Darwin's revolution must be completed, he wrote (1995), even if he probably underestimated (with his wishful thinking about the "non overlapping magisteria": Gould, 1998, 1999) the clash between the radical idea of evolutionary contingency and the religious zeal for a teleological path in natural history (De Caro & Pievani, 2010).

We appreciate here a final cultural legacy, not yet as cultivated as it deserves, of SJG the "humanistic naturalist" (Gould, 1998) interested in the deep similarities between natural and human sciences (and arts) as a global process of human inquiry and fullness of life (Gould, 2003). His coherent and analytical criticism of any form of teleological and progressive

"evolutionism" could be a way to reconstruct in the future the broken bridge between cultural anthropology and evolutionary studies. If this enduring misunderstanding between two traditions of research is really due to the misleading ideas of "progress" roughly applied in anthropology by evolutionists in the past – with potential discriminatory effects and reductionist justifications of essential diversities within the human species - thanks to SJG we have the opportunity to restore the relationships on the base of an epistemological "evolution of evolutionary thought". After SJG we do not have the "evolutionism" of decades ago, so cultural anthropology could now show that the misunderstanding was due to the old progressive background of "evolutionism", and not to an enduring and implicit prejudice against naturalism itself. Also in this case SJG's work is a provocative and open challenge.

Science is culture, in its general sense, and SJG was not only a scientist but an opinion maker and a popular writer, stretching the bounds of scientific literature in his own way (Allmon, in Allmon *et al.*, 2009). For that reason he was subjected to a great deal of unfair and personal criticisms, sometimes provoked by his iconoclastic attitude as well (Sterelny, 2001). Nevertheless, his idea that any over-specialism could become sterile without scientific creativity, and his tireless emphasis on the communication of science as a professional obligation (Gould, 2000, 2002b), made a great contribution to seeing evolutionary thought as a part of the public scientific culture. In so doing, facilitating the communication between disciplines and exploiting the history of ideas, he also helped to understand evolution as a set of integrated areas of research, in which palaeo-anthropology would not be a marginal branch of the marginal branch of palaeontology (redeemed by Punctuated Equilibria), but a rapidly growing field of evidence at the centre of the contemporary evolutionary research programme.

Whether right or wrong in his specific proposals, SJG stimulated research and revisions like no other (Lewontin, 2008). The four pillars described here are not atomised ideas, but a conceptual structure, a scientific oeuvre with a fundamental logic and interconnectedness across academic boundaries. They represent a proposal for the renovation of palaeo-anthropology based on SJG's peculiar way of being a "Darwinian pluralist".

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