Evolutionary Studies

Jaume Bertranpetit
Juli Peretó *Editors*

Illuminating Human Evolution: 150 Years after Darwin

Springer

Evolutionary Studies

Series Editor

Naruya Saitou, National Institute of Genetics, Mishima, Japan

Everything is history, starting from the Big Bang or the origin of the universe to the present time. This historical nature of the universe is clear if we look at evolution of organisms. Evolution is one of most basic features of life which appeared on Earth more than 3.7 billion years ago. Considering the importance of evolution in biology, we are inaugurating this series. Any aspect of evolutionary studies on any kind of organism is a potential target of the series. Life started at the molecular level, thus molecular evolution is one important area in the series, but non-molecular studies are also within its scope, especially those studies on evolution of multicellular organisms. Evolutionary phenomena covered by the series include the origin of life, fossils in general, Earth–life interaction, evolution of prokaryotes and eukaryotes, viral and protist evolution, the emergence of multicellular organisms, phenotypic and genomic diversity of certain organism groups, and more. Theoretical studies on evolution are also covered within the spectrum of this new series.

Jaume Bertranpetit • Juli Peretó
Editors

Illuminating Human Evolution: 150 Years after Darwin

Springer

Editors
Jaume Bertranpetit
MELIS-Universitat Pompeu Fabra
IBE, Institut de Biologia Evolutiva
(UPF-CSIC)
Barcelona, Spain

Juli Peretó
Institut de Biologia Integrativa de Sistemes
I2SysBio
Universitat de València-CSIC
Paterna, Spain

ISSN 2509-484X ISSN 2509-4858 (electronic)
Evolutionary Studies
ISBN 978-981-19-3245-8 ISBN 978-981-19-3246-5 (eBook)
https://doi.org/10.1007/978-981-19-3246-5

The translation was done with the help of artificial intelligence (machine translation by the service DeepL.com). A subsequent human revision was done primarily in terms of content.
Translation from the Spanish language edition: “Iluminando la evolución humana: Ciento cincuenta años después de Darwin” by Jaume Bertranpetit and Juli Peretó, © Unitat de Cultura Científica i de la Innovació de la Universitat de València 2021. Published by Publicacions de la Universitat de València. All Rights Reserved.
© The Editor(s) (if applicable) and The Author(s), under exclusive license to Springer Nature Singapore Pte Ltd. 2022
This work is subject to copyright. All rights are solely and exclusively licensed by the Publisher, whether the whole or part of the material is concerned, specifically the rights of reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Singapore Pte Ltd.
The registered company address is: 152 Beach Road, #21-01/04 Gateway East, Singapore 189721, Singapore

Preface

The book you have in your hands comes from a very simple purpose: to pay tribute to Charles Darwin on the 150th anniversary of the publication of the book *The descent of man, and selection in relation to sex,* first published in 1871. For that we began with a local project: the publication of a monography in the series of the Catalan Society of Biology (SCB), ascribed to the Institute of Catalan Studies (IEC) and having the headquarters in Barcelona. Even if exceeding the standard length of the monographies, it was published as Volume 71 of the *Treballs de la Societat Catalana de Biologia*, in our language, Catalan, at the end of 2021.

For that we had a double purpose: the study of the social context of Darwin and his time and the state of the art of the studies on human evolution and sexual selection, considering all aspects that Darwin examined and those that emerged later and now are important disciplines in our understanding of our own evolution.

We could have done a stricter follow-up of Darwin's work, following in parallel chapters the state of the present knowledge, but we decided to do otherwise to introduce more easily those views that he did not consider, like art or genetics. Thus, the general structure is not the same, even if all Darwin's views are discussed in the different chapters of this book.

The set of authors are different from the predominant Anglo-Saxon monographies and edited books. In this case all are internationally recognized researchers but not mainly based in the USA. Thus, many authors are working in different places in Spain, with strong representation of Barcelona and Valencia. This is an added value to have a view from the "periphery" of first-class science.

At the same time, we offered the University Press of the University of Valencia (*Publicacions de la Universitat de València* [*PUV*]) the possibility of publishing it in Spanish. They enthusiastically did a fantastic job publishing it in a book format that has been widely appreciated.

A short time later, Professor Naruya Saitou, recognizing the wide interest of the book, suggested us to offer its publication in English to Springer translated from the Spanish texts kindly provided by PUV. In a strict and smooth process, Springer offered us the publication in English in its series of Evolutionary Studies. We are very grateful for the acceptance of the proposal and the professionality of the editorial team.

Darwin was a genius and paved exquisitely the path of evolutionary anthropology. Let's hope this book is a worthy heir of his wealth.

Barcelona, Spain	Jaume Bertranpetit
Valencia, Spain	Juli Peretó

Contents

Chapter 1
Light Would Be Thrown: Human Evolution 150 Years After Darwin

Juli Peretó and Jaume Bertranpetit

Abstract In 1871 Charles Darwin published *The descent of man, and selection in relation to sex*, his first major contribution to the natural explanation of the origin of mankind, a subject deliberately omitted from his better known work *The origin of species*. Convinced that the time was ripe to address this thorny issue in public, Darwin produces a book that is, in form and substance, profoundly Victorian. It reflects his prejudices of class, gender and (imperial) nation, while at the same time laying the foundations for our contemporary view of human evolution without any supernatural intervention. This commemorative collection offers us a broad and diverse overview of current knowledge about the origins of humanity.

Keywords Victorian era · Sexual selection · Human races · Scientific image · Human phylogeny

On February 24, 1871, the first edition of *The descent of man, and selection in relation to sex* (*Descent*, from now on) went on sale and, before the end of the year, counting reprints, 8000 copies were in circulation. It was Charles Darwin's first book to make a financial profit, even though he was already an established and popular author (Fig. 1.1). Despite the unfavourable reports about the opportunity to publish the text, the sense of his publisher John Murray was not wrong: a strictly natural explanation of the origin of humans could attract the attention not only of specialists but also of the general public. In the same year of publication, translations appeared in Dutch, French, German, Russian and Italian, and shortly afterwards in Swedish, Polish and Danish.

J. Peretó (✉)
Departament de Bioquímica i Biologia Molecular, Institut de Biologia Integrativa de Sistemes I2SysBio (Universitat de València-CSIC), Universitat de València, Valencia, Spain
e-mail: juli.pereto@uv.es

J. Bertranpetit
Department of Medicine and Life Sciences (MELIS), Institut de Biologia Evolutiva IBE (Universitat Pompeu Fabra-CSIC), Universitat Pompeu Fabra, Barcelona, Spain
e-mail: jaume.bertranpetit@upf.edu

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_1

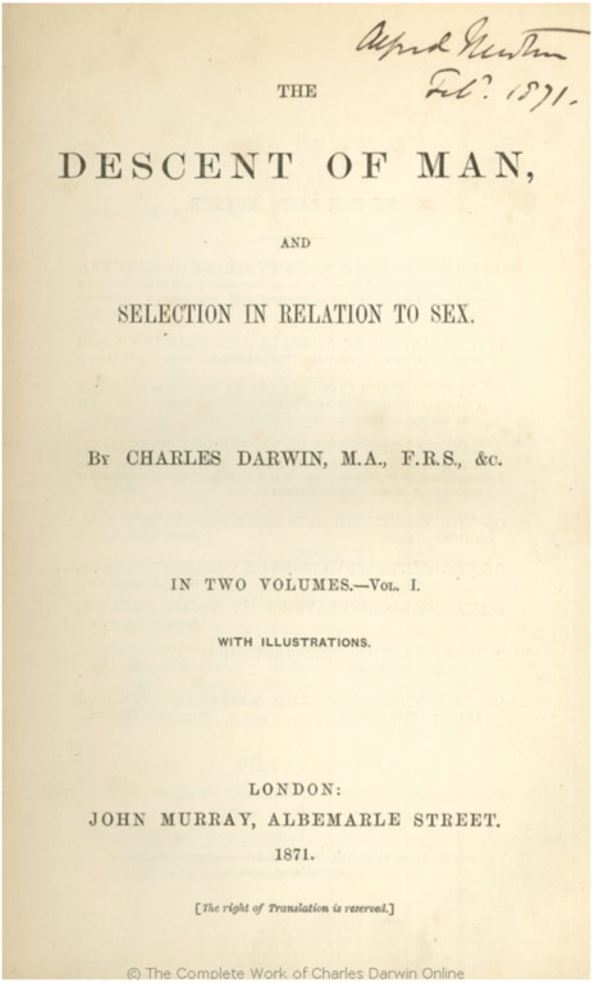

Fig. 1.1 Cover of the first edition of "The Origin of Man" (1871). Vol 1 http://darwin-online.org.uk/content/frameset?itemID=F937.1&viewtype=image&pageseq=1

Alfred Newton
Feb? 1871.

THE

DESCENT OF MAN,

AND

SELECTION IN RELATION TO SEX.

BY CHARLES DARWIN, M.A., F.R.S., &c.

IN TWO VOLUMES.—VOL. I.

WITH ILLUSTRATIONS.

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1871.

[*The right of Translation is reserved.*]

More than 11 years had passed since the publication of the first edition of *On the Origin of Species* (*Origin* from now on) and Darwin had been busy revising and expanding the reprints of this work and publishing two more books: on the fertilization of orchids (1862) and two thick volumes devoted to the domestication of plants and animals (1868). But he could no longer put off attacking a problem, that of the origin of humans in the context of his theory, mentioned laconically in *Origin*: "Light would be thrown on the origins of man and his history" (Darwin 1859, p. 488).[1] It was not for lack of study: in fact, he had been accumulating data and reflections on this question since the voyage of the *Beagle*, almost 40 years before.

---

[1] We have been inspired by this phrase to title this volume, which analyses the context of Darwin's work and opens up a panorama of current research on human evolution.

Darwin admits in his *Autobiography* that as soon as he was convinced, “in 1837 or 1838 [. . .] that species were mutable productions [. . .] I could not avoid the belief that man must come under the same law” (Barlow 1958). Nor was it because it did not seem to him a subject of capital importance: in a letter to Alfred Russel Wallace (in 1857), co-discoverer of natural selection, he told him that the origin of mankind seemed to him the “highest and most interesting question for the naturalist”. Simply put, as Janet Browne argues in her monumental biography of Darwin (Browne 2002), the time had come to storm “the citadel of the human mind and morality”: there was a scientific, academic, even social context receptive to a naturalistic explanation of our origins. “Darwinizing” about society was in vogue (Desmond and Moore 1991). Moreover, the racial and slave debate was raging and Darwin was far from indifferent (see Fradera, this volume). In the introduction to *Descent* the author confesses that his lack of interest in publishing ideas about the origin of man was so as not to “increase prejudice” about his views. However, “now [1871], the situation has changed”. Many naturalists, especially younger ones, accepted the fundamental evolutionary theses.

A series of events finally led him to publish his own vision of the problem. First, the appearance of a work by the geologist Charles Lyell on the antiquity of the human lineage, in which the author went further back in time than the archaeological findings of the time suggested. Secondly, the publication of a book on comparative primate anatomy that included humans, written by the zoologist Thomas Henry Huxley, Darwin’s well-known bulldog. But, above all, a text of 1869 by Wallace in which he disavowed one written 5 years earlier and denied, to Darwin’s scandal, any role of natural selection in the emergence of the human mind, replacing it with a spiritual intervention.

As Browne (2002) suggests, a letter from Wallace communicating his idea of natural selection was the spark that ignited in Darwin the urge to publish *Origin* and it was also he who, through his renunciation of a naturalistic explanation of the origin of humans, pushed him definitively to write *Descent*. Wallace was not just any author and his opinion could seriously damage the theory. Before reading Wallace’s text, Darwin, with horror, told him: “I hope you have not murdered too completely your own & my child”.[2] When he had the article in his hands, he left written in the margin a “No!!!” underlined three times. A well-argued demonstration that humans are an integral part of nature was thus urgently needed, as Darwin emphasizes in the introduction to *Descent*: “The sole object of this work is to consider, firstly, whether man, like every other species, is descended from some pre-existent form”. Wallace’s review of Darwin’s book was, however, generously complimentary, though without disguising the discrepancies. In fact, the general reaction was far from that “universal disapproval, if not execution” predicted by Darwin. It seemed to him that all this indicated the “increasing liberality of England” (Desmond and Moore 1991).

---

[2] Darwin to A. R. Wallace, 27 March [1869], Darwin Correspondence Project, letter no. DCP-LETT-6684.

Darwin's biographer says that *Descent* is the missing half of *Origin*, necessary to cross the final frontier of evolutionary theory. Actually, we should also add the monograph *The Expression of Emotions in Man and Animals* (henceforth *Expression*), published in 1872, originally intended as a chapter of *Descent* but finally embodied in a separate book. These two works form, in short, a unit of argument about the gradual origin of human mental faculties from those present in the animal world. And, together with *Origin*, "a coherent and harmonious trilogy" (Bellés 2017).

Descent, in the final version of 1877, consists of three parts (Darwin 1877). In the first (Chaps. 1–7), Darwin presents the anatomical and embryological arguments that relate humans to "lower forms", observations on mental capacities in animals and humans, the evolution of intellectual and moral faculties in human societies, as well as the question of races and their geographical distribution. A forced thematic transition leads us to the second part (Chaps. 8–18), where the author explains in great detail the action of sexual selection in animals, from invertebrates to mammals. The third part of the book (Chaps. 19–21) picks up the thread of the initial theme and contains the application of the principles of sexual selection to humans and a general summary with conclusions.

1.1 Victorian in Form and Substance

Browne (2002) argues that *Descent* shows us the most Victorian Darwin. Desmond and Moore (1991) go further, claiming that it contains not only the whole of Victorian life but the Darwin family history itself. We can say that it is a Victorian work, also in form. Darwin's style has been considered to be heir to the best qualities of the British literary tradition and indebted to Charles Dickens or Marian Evans (George Eliot), combined with a kindness and conciliatory politeness characteristic of his personal character. His ideas subverted many established beliefs, but he conveyed them with affability and prudence, without intimidation (Ros 2016). Darwin's masterful use of metaphors and ability to handle many simultaneous plot threads make Darwin's texts enduring works of art, as Browne (2002) described them. However, the structure of many sentences can be cloying and stilted for contemporary readers, an ill-flowing prose, even "soporific" in Quammen's eloquent expression (Quammen 2006). Especially when the author tries to respond, point by point, to his critics, sometimes with interminable paragraphs. Or when he presents an overwhelming enumeration of data and observations to support his argument, as happened with the domestication of plants and animals in *Origin* or with sexual selection in *Descent*. It is well known that, in this last book, his daughter Henrietta played the role of literary editor with great competence. The role of women as editors, private and hidden, was common at the time (Browne 2002). Darwin's wife Emma did so with *Origin* and other books. In this case, Henrietta assisted her father by structuring texts, rewriting passages to make them more intelligible, and correcting galley proofs. She helped not only to produce a “lucid and vigorous” style but to refine the reasoning, as the author himself acknowledged.

Darwin’s entire work, and especially his books on human evolution, cannot be understood in isolation from the idea of industrial progress and colonial rule of the Victorian era. For Darwin, Victorian Britain represents the pinnacle of cultural evolution and of the “civilized nations”, a way of life for which he seeks a biological explanation, naturalistic arguments that will later be a lever for unbridled extrapolations such as social Darwinism. In this sense, he is an author of his time, and his accounts of human origin and evolution reflect his own cultural and class prejudices. Darwin is also a representative author—perhaps the most representative—of the late nineteenth century ideal of the triumph of secular scientific progress over religious belief.

For Darwin, the human species was unique and races represented evolutionary stages towards perfection (Desmond and Moore 2009; Browne 2002; Ros 2009; Pelayo and Puig-Samper 2019). In *Expression* he emphasized that the universality of the expression of emotions in humans all over the world is “a new argument in favour of the several races being descended from a single parent-stock which must have been almost completely human [. . .] before the period at which the races diverged from each other” (Darwin 1872, p. 361). He recognized a racial hierarchy but he was not a racist in the current sense of the term (Saini 2019), much less a slaveholder. On the contrary, by family environment and by conviction accumulated from his experiences during the voyage of the Beagle, he was a firm abolitionist. Races, for him, did not reflect environmental adaptations, but were the result of sexual selection, preferences that resulted in morphological and cultural differences between the various human groups. A central role attributed to sexual selection was also a source of profound but amiable disagreement with Wallace. Darwin argued that among non-human animals, selection was usually made by the female, while in humans it is the male who takes the initiative: “the strongest and boldest men [. . .] in securing wives”. He thus offers an evolutionary basis for a prejudice deeply rooted in popular, patriarchal culture. And this detail fitted well with his notion of the evolution of women and men: men would have superior mental capacity and women would be “more tender and less selfish” and, in general, exhibit qualities of inferior civilizations. In any case, we should not take these middle-class white male prejudices out of their Victorian context, nor censor them by the standards of the present.

1.2 Evolution Without Fossils

Ros (2009) reasons that, in retrospect, Darwin’s work of synthesis on human evolution with the data and information available to him at the time is impressive. Just to focus on one aspect, Darwin’s evolutionary conviction about the origin of humans, based on the anatomical and embryological kinship with other primates—described by Huxley in his monograph *Evidence as to Man’s Place in Nature* (1862)—and the conjecture about our African origin could not have the support of palaeontology because the fossil remains of possible intermediate ancestors between humans and other primates had not yet been discovered. In fact, in 1864 Darwin had the opportunity to see the Neanderthal skull that had been found in Gibraltar in 1848 and, apparently, it left him rather cold (DeSilva 2021). Moreover, Huxley proposed that the other known Neanderthal skull, the one found in Feldhofer Cave in 1856, was still a peculiar human skull. Darwin, who fully trusted Huxley's judgement, regarded it as evidence of an extinct human race, and in *Descent* only once cites the "famous Neanderthal [skull]" in the context of the recent evolution of cranial volumetry in humans. He also refers to the jawbone found in La Naulette cave (now considered a Neanderthal fossil) in the discussion of the "reversion" of anatomical characters (in this case, the size of the canines) to primitive forms. In short, few fossils and poorly interpreted (for an analysis of the paleontological context in Darwin's time, see Pelayo and Puig-Samper 2019).

In *Origin* Darwin had already explicitly stated how aware he was of the imperfection of the fossil record. In *Descent* he draws on Lyell to state that the finding of fossils is an "extremely slow and fortuitous process". And that the regions where one would expect to find the remains that would connect humans to their extinct ancestors "have not as yet been searched by geologists". Despite the paleontological limitation, Darwin correctly predicted the place of origin of the human species. He applies here the vertical naturalistic thinking that worked so well for him in *Origin*, for example, in the discussion of extinct American mammals: there is a historical relationship of kinship between the present species inhabiting a certain geographical location and the extinct species buried metres below in that location. Thus, having established the undeniable anatomical, embryological and behavioural connection between humans and "Old World primates", "[i]t is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man's nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere" (Darwin 1877, p. 155).

1.3 A Well-Connected Author

Ros (2009) pointed out a very notable formal contrast between *Origin* and *Descent*, such as Darwin's use of bibliography. As is well known, *Origin* was the result of a radical change in Darwin's publication plan following the arrival in 1858 of Wallace's letter explaining his idea of natural selection (Costa and Peretó 2008). The risk of losing all priority in the statement of the theory of evolution led him to renounce the publication of a long series of volumes and concentrate on writing a more informative "summary", of "moderate size" according to the author (despite its good 400 pages) and without bibliographical apparatus. However, a book like *Descent*, which discussed such a serious and sensitive subject as human evolution, required the support of data and information from the widest possible spectrum of naturalists, anthropologists, anatomists, etc. and does so with a profusion of footnotes and documentary references. This demonstrates, as Ros (2009) points out, not only a deep and up-to-date knowledge of the literature, but also the vitality of the network of connections that Darwin had woven over the years with interlocutors around the world.

At first glance, it might seem surprising that a scholar in the middle of the English countryside, with the only company of his family and pets, could be so up to date with the scientific developments of his time. However, Darwin is a good example of the communicative habits of the naturalists of the time. Thus, despite living in a rural environment, he was well communicated with the capital, and visits from friends and colleagues frequented. Being an author of growing fame and impact, he was the recipient of numerous publications and books by authors from all over the world. However, as we have just mentioned, Darwin strategically established a diversity of epistolary connections not only with academics everywhere but with anyone who could supply relevant information, be they pigeon or dog breeders, orchid growers or museum curators. The Victorian postal service was considered the most efficient in the world and Darwin knew how to make the most of it.[3] Letters helped him to write and rewrite his works, as they channelled much of the criticism and reaction to his writings. All this, together with subscriptions to several scientific journals, made it possible that, from Down House, Darwin was aware of almost all the advances in the natural sciences of his time.

Many of the argumentative threads about human evolution that appear in *Descent* and *Expression* can be followed in the epistolary through Darwin's dialogue with relevant characters such as, for example, his cousin Francis Galton, the missionaries Thomas Staley and Waite Hock Stirling, the physician Guillaume Duchenne, the psychologist William Preyer, the psychiatrist James Crichton-Browne or the naturalist Ernst Haeckel, who had already dared with the evolutionary origin of humans. The questions and answers reflected in the letters are a representation of the usual topics of discussion in Victorian society: the unity of the human species and the glassy question of races, the superior position of European civilization and its role in the evolution of other societies (a subject closely linked to colonial ideology) or moral progress in humans and other animals. Certain correspondences were key in subjects that Darwin knew less about, such as the history of slavery or the incipient scientific studies on mental disorders.

---

[3] Today, more than 15,000 letters exchanged with more than 2000 interlocutors are preserved, many of them accessible online thanks to the *Darwin Correspondence Project* of the University of Cambridge (https://www.darwinproject.ac.uk/).

1.4 The Use of the Image (or Not) in Darwin's Work

Natural history has an intrinsic visual nature. The use of images in naturalist research and in the dissemination of the knowledge generated is an irreplaceable vehicle for transmitting reality to the recipients of this science. As Voss (2010) pointed out, Darwin's archive preserved by the Cambridge University Library gives an idea of how meticulously he collected images throughout his life and how important drawings, engravings or photographs were in his research and publications. Various representations of Darwin's ideas, both scientific ones, such as phylogenetic trees, and caricatures that appeared in satirical publications or on company logos (such as the famous *Anís del Mono* label), tell us about the explosive impact Darwin had on the academic world and on popular culture. A measure of the value that Darwin placed on images is the fact that, on more than one occasion and in the face of his editor's protests that the publication would become more expensive if figures were included, the author paid for the expense himself (Browne 2002).

Thus, a remarkable formal aspect in Darwin's work, well studied by historians, is the use he made of the image, but we could also look at those moments in which Darwin does not use a particular image. Undoubtedly, drawing had been a key tool in the documentation process during the voyage of the *Beagle*, and we have been left with many beautiful examples such as the watercolours of Conrad Martens. Darwin was not a good draftsman and in the *Autobiography* he acknowledges that many of the sketches he made during the voyage "proved almost useless" (Barlow 1958, p. 78). Therefore, the illustrations that we find in his work, with the exception of the geological diagrams for which he was gifted, are the result of the work of a variety of artists, engravers or photographers who collaborated with him. Thus, *Descent* incorporates engravings to document the characteristics relevant to sexual selection. And in the volume on the expression of emotions, the image already occupies a central position in the discourse, initiating the author in the scientific utility of photography, for example, through the mythical images provided by Duchenne of his experiments on the effect of electric shocks on facial expression or the expressive photography of Oscar Rejlander (Fig. 1.2). Photography was a resource that Darwin would later personally exploit very effectively in his botanical research. With the uses of images, we can follow in the work of the English naturalist a moment of transformation in the generation of knowledge and scientific communication in the late nineteenth century (Voss 2010).

But if there is an emblematic icon of evolution, it is the metaphor (or "simile" as Darwin calls it) of the tree of life. Thirteen handwritten drafts of phylogenetic trees survive, including the now famous diagram preceded by the statement "I think" in notebook B (1837–1838). However, in all of Darwin's published work, only one diagram appeared, which is, by the way, the only figure contained in *Origin*, and which is a representation of a theoretical genealogy of species. Quite possibly, the author, who had already used the image to good advantage in earlier works such as the account of the voyage of the *Beagle*, was under pressure to publish what he himself called "my abominable volume", and did not want to waste time choosing

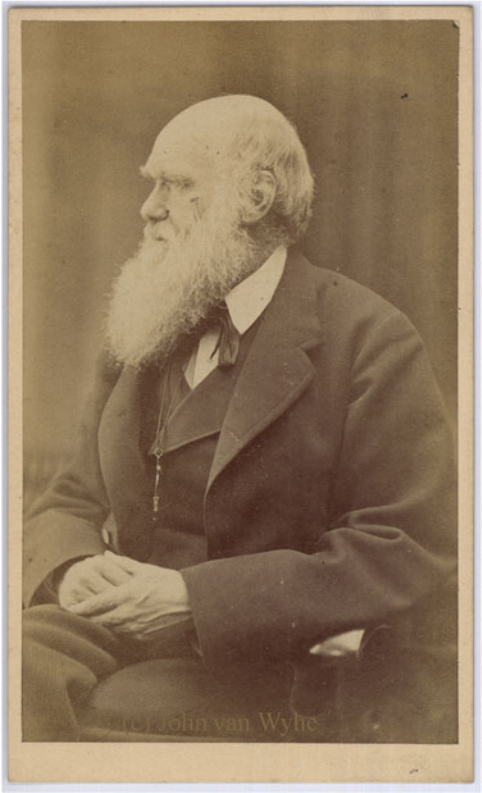

Fig. 1.2 Photograph of Charles Darwin taken by Oscar Rejlander in 1871. (Wikipedia) https://commons.wikimedia.org/wiki/File:Charles_Darwin_photograph_by_Oscar_Rejlander,_circa_1871.jpg#/media/File:Charles_Darwin_photograph_by_Oscar_Rejlander,_circa_1871.jpg

images. But why does a momentous book like *Descent* not incorporate any sketch of the evolutionary relationship between primates, such as the one the author sketched in 1868? A very simple pencil drawing of primate phylogeny, perhaps from the mid-1860s, survives, but the one dated 21 April 1868, analysed in great detail through successive amendments and corrections superimposed on the paper (Delisle 2007; Pietsch 2012; Archibald 2014), makes explicit the monophyly of the human genus (against polygenism) and its inclusion, as just another branch, within the primate tree. Humans share, in this picture, a distant common ancestor with a group formed by gorillas and chimpanzees, orangutans and gibbons (Fig. 1.3).

However, Darwin renounced the communicative power of the image and limited himself to verbalizing his ideas in *Descent*. The absence of this visual representation has also attracted the attention of historians. A recent case is that of Marianne Sommer who relates Darwin's decision to his full awareness of the limitations of arborescent iconography, such as the inability to simultaneously capture his strong conviction about the monophyly of the human species (Desmond and Moore 2009) and the racial hierarchies that, according to him, sexual selection had generated (Sommer 2021). In any case, it also seems credible, given his proverbial prudence in presenting the data, that Darwin decided not to include this scheme because he saw it

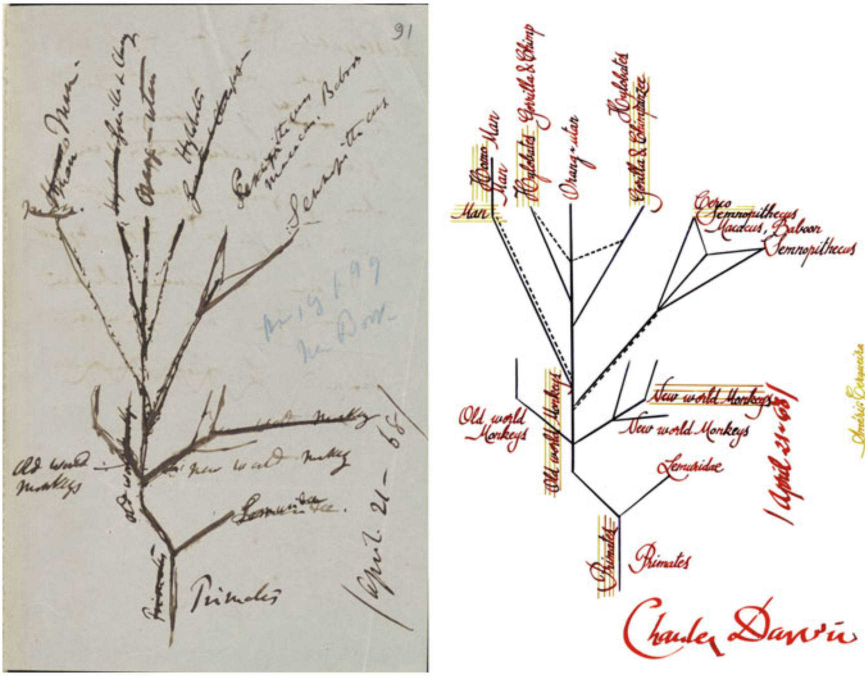

Fig. 1.3 Left, handwritten Darwin's phylogenetic tree of primates dated 21 April 1868 (manuscript DAR80.B91r reproduced by permission of the Cambridge University Library). Right, interpretation of the tree by Juan Luis Arsuaga and transcription by Américo Cerqueira; reproduced with permission of the author

as still too speculative. A bit like his ideas on the natural origin of life, which he never published (Peretó et al. 2009), Darwin would give up on making his argument about human evolution graphically explicit. In fact, the sketch was a way of ordering the taxonomic and phylogenetic ideas about the human genus put forward by other authors, such as Huxley, Wallace, Haeckel or Saint George Mivart. The key is given by Darwin himself in the handwritten note on the back of the scheme: "Disposition as far as I can understand by comparing the opinions of several naturalists on whose judgement much reliance may be placed - As for myself, I have no evidence to form an opinion" [the crossed-out words appear like this in Darwin's manuscript].

1.5 Human Evolution Partially Enlightened

> It has often and confidently been asserted, that man's origin can never be known: but ignorance more frequently begets confidence than does knowledge: it is those who know little, and not those who know much, who so positively assert that this or that problem will never be solved by science (*Descent*, Introduction, Darwin 1877, p. 2).

The aim of this collection of texts is to offer, on the one hand, a historical, sociological and philosophical context of *Descent*. On the other hand, we open a range of contemporary views on human evolution from disciplines as diverse as palaeontology, genomics, archaeology, linguistics, psychobiology or ethology. In homage to Darwin, we show what contemporary science illuminates, partially, about the origin and evolution of our species. Today we accept Darwin's main conclusion, that we are descended "from some form of lower organization", exhaustively documented by palaeoanthropology, ancient DNA and genomics of current human populations (Bergström et al. 2021), but we note that, as he himself feared, this may still be an "unpleasant" message for some people, 150 years later.

The collection begins with the text by Janet Browne, author of the most complete biography ever written about the English naturalist. In "The historical background to Darwin's *Descent of Man*" Browne places us in Victorian England and exposes the motivations that led the author to tackle the "highest and most interesting question" as a naturalist, logically continuing the discourse she had begun with *Origin*. The author shows how all the author's national and imperial, class, gender and racial prejudices are projected onto *Descent*. On the other hand, in "Modes of seeing the world: Darwin and the first Victorian generation", Josep Maria Fradera focuses on specific aspects of Darwin's reasons for tackling the question of humanity as a whole, his secular and naturalistic vision of the problem and, more specifically, how he managed the debate on slavery in the context of his ideas on the origin of races. For his part, Jesús Català follows in "The problem of design in the Darwinian proposal: A historical overview" an intellectual thread of Darwin with his polyhedral way of confronting the problem of design and the arguments of natural theology, as well as the scope of natural selection in the evolutionary process. Català provides an original look at little-known aspects of the tension between evolutionism and religion. The historical context block ends with the article by Marcos Morales and Martí Domínguez. In "Darwin under suspicion: The representation of Darwinism in the newspaper *ABC* (1909–1982)" the authors choose a conservative Spanish media to illustrate how the social and political environment throughout the twentieth century has imposed ideological biases, even censorship, on a scientific theory that is seen as a threat to the *status quo*, a stigma that already weighed in the Victorian England where Darwin lived.

A central aspect of *Descent* is the deployment of arguments in favour of evolutionary continuity in the appearance of the most complex and sophisticated mental capacities. In "*The Descent of Man*: Darwin and Psychology", Ester Desfilis details the psychological evidence presented by Darwin in *Descent* and delves into the not always friendly relations between evolutionism and psychology. The Darwinian approach to human behaviour has been and continues to be a fertile ground for the most acid controversies. Joana Rosselló, Liliana Tolchinsky and Carme Junyent review the evolutionary, developmental and linguistic arguments used by Darwin to deal with the origin of language ability in "Human evolution: The linguistic evidence". The authors reveal Darwin's profound knowledge of language, which led *Descent* to offer a very powerful conjecture on this complex and crucial question in his defence of the natural origin of human mental capacities.

As we have noted, Darwin argued for the evolution of humans without any significant paleontological evidence. The current situation is very different. María Martinón-Torres presents in "Human evolution in Eurasia: The fossils that Darwin did not know" an update of our knowledge on palaeoanthropology complemented with modern paleo-omics technologies that have changed our vision of the phylogeny of humans and their ancestors. The author also exposes the current debate on the multiple migrations of our species and its ancestors in the framework of the different versions of the "Out of Africa" model in which the expansions towards Asia are beginning to take centre stage. For their part, David Comas and Francesc Calafell offer us in "Human evolution: The genomic evidence" a careful description of the scope and limitations of the reading of the past inscribed in our genomes and in those recovered from extinct species. This exceptional evolutionary window offers views of the relationships between humans, Neanderthals, Denisovans, and perhaps other hominins that may have contributed to our current genomes. The technologies associated with ancient DNA not only allow us to recover our deepest history, such as the African origin of humanity, but also the most recent, represented by the migrations of human populations around the planet.

One of the pillars of Darwin's research on what makes us human was the anatomy compared to the rest of primates. In "The adaptations that made us human: Morphology" David M. Alba and Sergio Almécija update our knowledge about the most distinctive human characteristics such as habitual bipedalism, manipulation and the reduction of sexual dimorphism. Darwin had great intuitions, such as the proposal about our arboreal past, but the lack of fossils did not allow him to go further. Today we know that the appearance of most of the typically human morphological adaptations coincides with the origin of the genus *Homo*. For her part, Elena Bosch offers a review of evolutionary aspects that Darwin could never dream of in "The adaptations that have made us human: The genome". It is now possible to detect the imprint of natural selection in genomes and identify the adaptations, not only morphological but also physiological and metabolic, that have sculpted the human species.

In "How do we humans evolve?", Eudald Carbonell and Policarp Hortolà reflect on the processes that have made us human, such as how we obtain energy, how we exchange information and how we group together at various scales during socialization. The authors claim the need to build a robust theoretical framework to understand our evolution from the perspective that humanization is an unfinished process.

One subject that Darwin overlooked was the origin of art. However, in "Art as a human element", Inés Domingo Sanz argues that Darwinian thought is the great stage for the debates that have historically been held on the emergence of idiosyncratic human symbolic behaviour. As suggested in the article, the most recent of these debates is the discussion about the artistic capacity of Neanderthals.

As we have already mentioned, *Descent* has a very extensive central part devoted to sexual selection, an evolutionary mechanism that Darwin placed next to natural selection in his theoretical scheme. Roberto García-Roa and Pau Carazo argue in "Sexual selection: Following Darwin's legacy" that this part, sometimes underrated, of the Darwinian treatise is a major contribution to evolutionary biology and to biology in general, since sexual selection can be considered one of the most complex areas of the current study of evolution. On the other hand, Mauro Santos and Susana A. M. Varela analyse a fascinating aspect of sexual selection in “Genetic and cultural evolution of mate choice”, namely the component of cultural transmission added to the genetic determinants of mate choice behaviour.

Finally, the monograph closes with our article “How Past Shapes Future: The Biological Future of Humankind” in which we discuss to what extent the cultural and technological intervention of humans can influence their own evolutionary future.

1.6 Translations of *Descent* into Spanish and Catalan[4]

Five years after *Descent* was published, the first Spanish translation was published in Barcelona (“Imprenta de la Renaixensa”) by the poet, lecturer and journalist interested in the dissemination of science, Joaquim M. Bartrina (Gomis and Josa 2009b). Until then, Darwin had only circulated in Spanish with a chapter on geology in the “Manual de investigaciones científicas; dispuesta para el uso de los Oficiales de la Armada y viajeros en general” (Cadiz 1857) and an incomplete translation of *Origin* (Madrid 1872). Bartrina’s translation also corresponds only to a part of *Descent*, curiously, with the addition of texts by other authors. It should be noted that abridged versions of translated works were a common practice at the time and not to be underestimated as an informative resource. Between 1892 and 1897 “Trilla y Serra, editores” (Barcelona) reprinted Bartrina’s version. In 1885 José del Perojo and Enrique Camps translated the second English edition with the title “La descendencia del hombre y la selección en relación al sexo” (“Administración de la Revista de Medicina y Cirugía Prácticas”, Madrid), which can be considered the first complete translation of the work. The Editorial Sempere of Valencia (the printing house of El Pueblo, the newspaper founded by Blasco Ibáñez) will publish in 1902 the version by A. López White, which will be republished on several occasions during the following decades, already under the imprint of the Editorial Prometeo, of which Blasco was the editorial director. It should be noted that this translation, of which some 56,000 copies circulated (29,000 in Latin America) according to the publisher, is only the first part of Darwin’s book (Chaps. I to VII) and does not include the part on sexual selection or the final chapters (Fig. 1.4). Until the Spanish War, several translations, most of them partial, will circulate with a variety of titles: *The Origin of Man: Natural and Sexual Selection, The Past and Future of Mankind, The Struggle for Existence, Precursors and Descendants*, or *The Mental Faculties in Man and Animals*. They were published by publishers in Madrid, Barcelona, Granada and Valencia, linked to progressive and secular sectors. The translations

---

[4] For detailed and critical information on all editions of Darwin in Spanish and Catalan, see Gomis and Josa (2009a).

Fig. 1.4 Covers of the translations of "The Origin of Man" by López White (1902, 1920), Josep Egozcue (1984) and Joandomènec Ros (2009) (personal collection)

of Darwin's works during the nineteenth century have received the attention of philologists and specialists in translatology (see Pelayo and Puig-Samper 2019 and references cited). Thus, Carmen Acuña-Partal has investigated in detail Darwin's translations into Spanish and the cultural contexts in which they were produced. Darwin highly valued the dissemination of his work in other languages but, while he lived, he could hardly control the editorial strategies or ideological undercurrents behind the dissemination (or censorship) of his ideas (Acuña-Partal 2016). His work has always been fuel for manipulation.

Between 1933 and 1963, no translation of *Descent* was published again in Spain, but it reappeared in bookshops in the translation by Julián Aguirre for the publishing house Edaf (Madrid) with its characteristic blue plastic cover. This version will be reprinted several times up to the present day and, from 1980 onwards, will include a preliminary study by Faustino Cordón. Likewise, other publishers will release different translations during the following decades. Let us now take two examples, one of editorial neglect and the other of excellence. The first is the publication of the old translation of López White, from the beginning of the twentieth century, by the publishing house Alba (Alcobendas) at the end of the 1990s (and republished in 2000 and 2002) under the title "El origen de las especies" (sic). The quality counterpoint is the Spanish translation by Joandomènec Ros of the definitive edition of *Descent* (Darwin 1877). In this edition, Murray incorporated at the end an article by Darwin published in 1876 in *Nature* on sexual selection in primates. Ros's translation was published by Crítica (Barcelona) in 2009, the year of Darwin's bicentenary, and has been republished in 2021. This careful edition includes an introduction by José Manuel Sánchez Ron, director of the collection, a foreword by the translator and an epilogue by Carles Lalueza-Fox. Finally, in 2019, a large-format, 449-page volume with an extensive study by the historians Francisco Pelayo and Miguel Ángel Puig-Samper was added to the Biblioteca Darwiniana, directed by Rosaura Ruiz and published by Los Libros de la Catarata (Madrid). However, Darwin's text is not a current translation but the version of *Descent* made by Perojo and Camps 137 years ago!

In Catalan we only have one translation, the one published in 1984 by Edicions Científiques Catalanes in two volumes of the first edition of the book in a version by the late Josep Egozcue, with a foreword by Joan Rovira. If it is true that every generation should have a contemporary translation of the classics, we think it would be time to undertake a new translation into Catalan of Darwin's *The Origin of Man*.

References

Acuña-Partal C (2016) Notes on Charles Darwin's thoughts on translation and the publishing history of the European versions of [On] The origin of species. Perspectives 24:7–21

Archibald JD (2014) Aristotle's ladder, Darwin's tree: the evolution of visual metaphors for biological order. Columbia University Press, New York

Barlow N (ed) (1958) The autobiography of Charles Darwin 1809–1882. With the original omissions restored. Edited and with appendix and notes by his grand-daughter Nora Barlow. Collins, London

Bellés X (2017) Introducció. In: Darwin C (ed) L'expressió de les emocions en l'home i en els animals. Institut d'Estudis Catalans, Barcelona, pp IX–XII

Bergström A, Stringer C, Hajdinjak M et al (2021) Origins of modern human ancestry. Nature 590: 229–237

Browne J (2002) Darwin: the power of place. Knopf, New York

Costa M, Peretó J (2008) Introducció. In: Darwin CR, Wallace AR (eds) La lluita per la vida. Publicacions de la Universitat de València, València, pp 7–17

Darwin C (1859) On the origin of species: A facsimile of the first edition. Harvard University Press, Cambridge [1964]

Darwin C (1872) The expression of the emotions in man and animals. John Murray, London

Darwin C (1877) The descent of man, and selection in relation to sex, 2nd edn. John Murray, London

Delisle RG (2007) Debating humankind's place in nature 1860–2000. The nature of paleoanthropology. Routledge, Abingdon

DeSilva J (ed) (2021) A most interesting problem. What Darwin's Descent of Man got right and wrong about human evolution. Princeton University Press, Princeton

Desmond AJ, Moore JR (1991) Darwin. Penguin Books, London

Desmond AJ, Moore JR (2009) Darwin's Sacred Cause: race, slavery and the quest for human origins. Allen Lane, London, New York

Gomis A, Josa J (2009a) Bibliografía crítica ilustrada de las obras de Darwin en España (1857–2008). CSIC, Madrid

Gomis A, Josa J (2009b) Los primeros traductores de Darwin en España: Vizcarrondo, Bartrina y Godínez. Rev Hispan Filo 14:43–60

Pelayo F, Puig-Samper MA (2019) Estudio histórico. In: Darwin C (ed) El origen del hombre y la selección en relación al sexo. Los Libros de la Catarata, Madrid, pp xix–lvii

Peretó J, Bada JL, Lazcano A (2009) Charles Darwin and the origin of life. Orig Life Evol Biosph 39(5):395–406

Pietsch TW (2012) Trees of life. A visual history of evolution. Johns Hopkins University Press, Baltimore

Quammen D (2006) The reluctant Mr. Darwin. An intimate portrait of Charles Darwin and the making of his theory of evolution. WW Norton & Co, New York

Ros J (2009) Prólogo. In: Darwin C (ed) El origen del hombre. Editorial Crítica, Barcelona, pp XI–XXVII

Ros J (2016) Allò que Darwin no sabia. In: Ros J (ed) La saviesa combinada. Reflexions sobre ecologia i altres ciències. Edicions de la Universitat de Barcelona, Barcelona, Barcelona, pp 169–180

Saini A (2019) Superior. The return of race science. Beacon Press, Fourth Estate Books, Boston

Sommer M (2021) The meaning of absence: the primate tree that did not make it into Darwin's The Descent of Man. BJHS Themes, pp 1–17

Voss J (2010) Darwin's pictures: views of evolutionary theory, 1837–1874. Yale University Press, New Haven

Chapter 2
The Historical Background to Darwin's *Descent of Man*

Janet Browne

Abstract Darwin published *The Descent of Man, and Selection in Relation to Sex* in 1871 as a major contribution to the Victorian debate over the evolutionary origins of humankind. Much of that debate began after publication of Darwin's *Origin of Species* in 1859. Yet Darwin had deliberately excluded human beings from the *Origin*. The *Descent of Man* includes his longstanding research into the animal origins of human characteristics and several important new theories, including sexual selection. The theory of sexual selection lay at the heart of his proposed explanation of the diversification of human races. His reasons for publication are explored and the book is placed in contemporary nineteenth century social context.

Keywords Anthropology · Sexual selection · Human origins · History of biology · Victorian era

2.1 Introduction

In the *Descent of Man*, Charles Darwin dealt with what he called "the highest and most interesting problem for the naturalist". First published in English, in London, in the early weeks of 1871, *The Descent of Man, and Selection in Relation to Sex* was a comprehensive statement of Darwin's theory of evolution as it applied to human beings: in it he described what he knew about human origins in animals, the physical characteristics of different peoples, the emergence of language and the moral sense, the relations between the sexes in animals and in humans, and a host of similar topics that blurred the boundaries between ourselves and the non-human world. His aim was to demonstrate that human beings had gradually evolved from animals and that the differences were mainly of degree not kind. His conclusions were bold: "we must acknowledge, as it seems to me, that man, with all his noble qualities, with sympathy which feels for the most debased, with benevolence which extends not only to other

---

J. Browne (✉)
History of Science Department, Harvard University, Cambridge, MA, USA
e-mail: jbrowne@fas.harvard.edu

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_2

men but to the humblest living creature, with his god-like intellect which has penetrated into the movements and constitution of the solar system—with all these exalted powers—Man still bears in his bodily frame the indelible stamp of his lowly origin" (Darwin 1877, p. 619).

It had been a long process that brought Darwin to this point. Twelve years earlier, in the *Origin of Species* he had cautiously written that if his views were accepted, "light would be thrown on the origin of man and his history" (Darwin 1859, p. 488). In actuality, he had deliberately kept humankind out of the *Origin*—he had recognized from the very start of his researches that the topic would jeopardise calm consideration of his argument. Although increasing numbers of people in Britain and beyond rejected the literal truth of the biblical origin story, there were still enough Christian believers to make Darwin careful about what he wrote (Lightman 1987). The very definition of humanity in the West rested on a longstanding belief in the existence of a special moral sense bestowed on human beings by an assumed divine creator. As it turned out, the heated debates that followed publication of the *Origin* focussed explicitly on the question of human origins and the role of a divine force (Bowler 2007; Livingstone 2001). The controversy was just as intemperate as Darwin had feared.[1]

Why, then, did Darwin eventually decide to write a book like the *Descent of Man*? The archives indicate that he was deeply interested in the whole question of human origins and diversification from the time of the *Beagle* voyage, 1831–1836 (Hodge and Radick 2009; Barlow 1958).[2] On that voyage he had encountered several different indigenous groups and puzzled over their relationships to his own British society. Before the voyage, he expressed ardent support for anti-slavery movements underway in Britain, feeling that all human beings were the same under the skin (Desmond and Moore 2009). He clearly believed that humans were an essential part of the natural world and should be included in any interpretation of origins that he produced. Yet he deliberately drained humans from the text of the *Origin*. During the 1860s there were a number of contributary factors that perhaps helped to change his mind. Principally, Darwin felt the pressure of alternative stories mounting. The Duke of Argyll's creative evolutionism was gaining ground in the UK. Herbert Spencer's *Principles of Biology* and his *Essays: Scientific, Political and Speculative* integrated secular evolutionary concepts with political and social ideas that were already attractive to contemporaries. Ernst Haeckel was busy describing ape-ancestry to a German readership. Robert Chambers's anonymous transmutationist book *Vestiges of the Natural History of Creation*, first published in 1844, was still in active circulation, now including several European language translations (Greene 1959).

And Darwin's closest scientific friends were beginning to publish their own views about the evolution of mankind: Charles Lyell, Thomas Henry Huxley, and Alfred Russel Wallace each produced important studies that developed different aspects of

---

[1] Darwin's life and times are covered in Browne (1995, 2002).

[2] Two websites are valuable resources: Darwin Correspondence Project: http://www.darwinproject.ac.uk/ and The Complete Work of Charles Darwin Online: http://darwin-online.org.uk/

human ancestry. In 1863, Charles Lyell published the *Antiquity of Man*. In this book Lyell revealed the world of human geological history. Until then, the paucity of early human artefacts, such as worked flints and tools, had suggested that mankind was very recent in geological terms. The common assumption was that humans only appeared (or were created) when the earth arrived at its modern state, which was presumed to be after the glacial period—or for those who believed in the biblical flood, at the point when the floodwaters receded. Lyell pushed the origin of human beings back beyond this watery dividing line into the geological deep past. Although there were hardly any known human fossils to discuss, it was the first significant book after Darwin's *Origin of Species* to shake contemporary views of humanity.

Thomas Henry Huxley's *Evidence as to Man's Place in Nature* was published a few weeks after Lyell's book. Huxley did not fully adopt all of Darwin's ideas, but enthusiastically defended Darwin's right to propose naturalistic explanations for the living world. In this short polemical book, he showed how humankind must, on all biological grounds, be classified with the apes. The point was understood by readers but not necessarily accepted. One reviewer observed dryly "We are not yet obliged to be quite on all-fours with Professor Huxley".

Soon after was Alfred Russel Wallace, who had independently formulated the principle of evolution by natural selection. Wallace wrote two compelling articles on human evolution in the 1860s. In the first, he argued that natural selection was the primary force in changing apes into people. In the second article, published in 1869, in the magazine *Quarterly Review*, he backtracked and declared that natural selection seemed insufficient to explain humankind's extraordinary mental capacities. He agreed with Darwin that natural selection pushed apish ancestors to the threshold of humanity. But at that point, he thought perhaps physical evolution stopped and the power of mind took over. The human mind continued to advance, he argued, as cultural imperatives changed and developed.

Darwin was thoroughly taken aback. "I hope you have not murdered too completely your own and my child" he exclaimed to Wallace in surprise.[3] It was partly the alarm of seeing Wallace's article that encouraged him to express his own views fully in the *Descent of Man*. He could not agree with Wallace that some external force –Wallace believed it to be some spiritual power– had helped to make us what we are.

The moment at last seemed ripe to finalise his research on humankind and make it public. He had accumulated a large archive of information since his time on the *Beagle* voyage. He could also now call on the investigations of prominent anatomists and anthropologists who were favourably disposed towards a secular, biological view of humankind, such as Ernst Haeckel, Pierre Paul Broca, Jean Louis Armand de Quatrefages, Édouard Claparède, and Carl Vogt, and could consult colleagues like Francis Galton, John Lubbock, and Edward B. Tylor. His immense network of correspondents—generated during the *Origin of Species* years—could help locate

---

[3] Darwin to A. R. Wallace, 27 March [1869], Darwin Correspondence Project, letter no DCP-LETT-6684.

specialists to guide him through areas unfamiliar to him, such as the likely beginnings of human language. Late in the process, he asked his adult daughter Henrietta, aged 28, to act as copy editor, correcting his grammatical mistakes and helping with clarity. Soon Darwin had gathered so much material that he felt obliged to put some of it aside for another book. This additional material concerned the expression of emotions in animals and humans and was published in 1872, 1 year after *Descent of Man*, under the title, *The Expression of the Emotions in Man and Animals*. These two books represent Darwin's most important statements on the evolution and biology of humankind.

2.2 The *Descent of Man*

In its way, *Descent* can be regarded as the missing half of the *Origin of Species*. It was written in the same personal style as the *Origin,* with the same clarity, the same courteous modesty, the same inexhaustible piles of evidence, and the same rational integrity. Yet it is a book of its time that presents many problems for readers. The information now seems archaic, the two-volume format outmoded, and the social views utterly unacceptable today. Nevertheless, the central arguments have retained their power to inspire and invigorate. There are fascinating glimpses into Darwin's understanding of the biological basis of Victorian racial and social hierarchies, and gender relations. The word "evolution", first used in its modern sense, occurs in Volume 1, on page 2. Darwin also used the phrase "survival of the fittest" which he adopted from Herbert Spencer in 1868. Admittedly, the content of *Descent* is much more complex to understand than the arguments of the *Origin*. Nevertheless, *Descent* is an exceptional landmark publication in the story of human history that provides great insight into the depth and scale of the revolution in thought generated by evolutionary theory.

The book was printed in two volumes and published by John Murray, the London firm that had earlier published the *Origin of Species*. It was issued in 2500 copies in the first weeks of 1871 (Freeman 1977). Three further printings appeared during the same year, bringing the number of copies available to readers up to 8000. Darwin made small changes in the texts of each reprint. For bibliophiles, there are some interesting variants. Darwin's own copy, for example, was ready by December 1870 and has that date printed on its title page. A second edition was published in 1874 with corrections and emendations, including important material from Huxley on the brains of apes and mankind. In 1877 the English publishers recorded that they had issued a total of 12,000 copies. This edition of 1877 was the final one and all subsequent editions are printed from it. The American firm of D. Appleton and Co. simultaneously published the *Descent of Man* in New York in 1871, and continued to match the English editions pretty closely. In Europe, the Franco-Prussian war would seemingly have obliterated any prospect of foreign language editions and translations. Yet astonishingly, in view of the political situation during the siege of Paris and the dreadful events around the Commune, Darwin's book was translated into Dutch, French, German, Russian, and Italian in 1871, and into Swedish, Polish, and Danish shortly thereafter, a testimony to the fortitude of Darwin's European colleagues and general interest in evolutionary affairs.

The text was lengthy and, to modern eyes, meandering and verbose. It was divided into two parts. In Part 1, Darwin wished to connect animals and humans as closely as he could. He began by relating the many incontrovertible anatomical features common to both animals and mankind. Then he turned to the mental powers, stating decisively, "there is no fundamental difference between man and the higher mammals in their mental faculties" (Darwin 1877, p. 66). He went on to present instances of animal cognition, ranging from horses that knew the way home, to ants that defended their property, chimpanzees that used twigs as implements, bower-birds that admired the beauty of their nests, and household cats and dogs that apparently dreamed of catching their prey in their sleep. The domestic nature of Darwin's observations in this area, the large doses of willing anthropomorphism, inspired Frances Power Cobbe to call them "fairy tales of science", in a review published in 1872. These attractive anecdotes about mental activity in animals probably went a long way towards softening readers toward recognizing affinities between organic beings before being confronted with the shock of apes in the family tree.

Darwin subsequently moved on to cover language, religion, and the moral sense of humankind. The power of speech was obviously crucial since the possession of language was essential to all contemporary definitions of humankind and was at that time assumed to present an insuperable barrier. Darwin particularly wished to contest the widespread view that the ability to speak indicated a God's special gift to humans. The great linguist and scholar Friedrich Max Muller had said as much in the magazine *Nature* in 1870. Darwin came to believe that the ability to speak emerged quite differently, in a gradual fashion from the social vocalisations of apes and further developed in early human societies through the imitation of natural sounds.

He was similarly daring in proposing that religious belief was ultimately nothing more than a primitive urge to bestow an external cause on otherwise inexplicable natural events. At first, human dreams might have given rise to the idea of spirits, as the anthropologist Tylor suggested, or to animism, where plants and animals seem as if they are imbued with external forces. Darwin suggested that these beliefs could easily grow into a conviction about the existence of one or more gods who directed human affairs. He imagined that these views would develop as cultural sophistication increased. In his words, as societies progressively advanced in civilisation, ethical values would become attached to such ideas. Audaciously, he compared religious devotion to the "love of a dog for its master".

From religion it was but a small step to the moral world. Darwin argued that the higher human values, such as morality, emerged and spread as human civilisation progressed. He proposed that the phenomena of duty, self-sacrifice, virtue, altruism, and humanitarianism were acquired fairly late in human history and not equally by all tribes or groups. Some societies displayed these qualities more than others, he noted; and it is clear that he thought there had been a progressive advance of moral sentiment from “barbaric” societies, such as Ancient Greece or Rome, to the world of nineteenth century England that he inhabited. In this manner, he kept the English middling classes to the front of the minds of his readers as representative of all that was best in the nineteenth century culture. The higher moral values were, for him, self-evidently the values of his own class and nation.

Also in Part I Darwin discussed possible intermediaries between ape and human, and mapped out (in words) a provisional family tree, in which he took information mostly from fellow evolutionists like Haeckel and Huxley. In truth, Darwin found it difficult to give an actual evolutionary tree to humans. Although there were, by then, a few fragments of Neanderthal skulls available for study in European museums, these had not yet been conclusively confirmed as the remains of ancestral humans. Darwin tracked ancestry back to the Old World monkeys, saying that the human species must have diverged from an original monkey stock considerably earlier than the anthropoid apes, probably at a point close to now-extinct forms of Lemuridae. He further recognised the great apes as humanity’s nearest relatives. For the second edition of *Descent of Man* he asked Huxley to fill this gap with an up-to-date essay about fossil finds. Darwin could only guess at possible reasons for ancestral human forms to have abandoned the trees, to lose their hairy covering, and become bipedal. He relied on Haeckel’s work in this area to push the primate line back through Marsupials, Monotremes, Reptiles, Amphibians, and Fishes, ending up at the Ascidians, grandfathers of them all.

> The early progenitors of Man were no doubt once covered with hair, both sexes having beards; their ears were pointed and capable of movement; and their bodies were provided with a tail, having the proper muscles... The foot, judging from the condition of the great toe in the foetus, was then prehensile; and our progenitors, no doubt, were arboreal in their habits, frequenting some warm, forest-clad spot. The males were provided with great canine teeth, which served them as formidable weapons. (Darwin 1877, pp. 160–161)

2.3 Sexual Selection and Society

Part II covered Darwin’s idea of sexual selection. While mostly understood today as a feature of animal mating behaviour, Darwin believed this theory was his special contribution to understanding the evolution of humankind. It seems curious today that such a large part of the book was dedicated to this form of selection. Yet he claimed that it was a major force in the diversification of human beings into what were then considered to be separate races. “I do not intend to assert that sexual selection will account for all the differences between the races”, he wrote. Nonetheless, he felt certain that it was “the main agent in forming the races of man”. Sexual selection was “the most powerful means of changing the races of man that I know”.[4]

---

[4] Darwin to A. R. Wallace, 28 [May 1864], Darwin Correspondence Project, letter no. DCP-LETT-4510.

It was an idea he had been nurturing for many decades but brought to full sophistication for *Descent* (Richards 2017; Campbell 2006; Cronin 1991). He postulated that all animals, including humans, possess many trifling features that are developed and remain in a population solely because they contribute to reproductive success. These features were inheritable (as Darwin understood it) but carried no direct adaptive or survival value. The textbook example is the male peacock that develops large tail feathers to enhance its chances in the mating game even though the same feathers actively impede its ability to fly from predators. The peahen, argued Darwin, is attracted to large showy feathers, and if she can, will choose the most glamorous mate and thereby pass his characteristics on to the next generation. It was a system, he stressed, that depended on individual choice rather than survival value. He devoted nearly one-third of the book to establishing the existence of sexual selection in birds, mammals, and insects. In animals, he argued that the choice of mate was determined by the female: the peahen did the choosing. When he discussed humans he reversed that proposition and insisted that males mostly made the choices.

It was an important idea. Darwin used sexual selection to explain the divergence of early humans into the racial groups that then-contemporary physical anthropologists described. Preference for certain skin colours was, for him, a good example. He suggested that early men would choose women as mates according to localised ideas of beauty. The skin colour of an entire population could gradually shift as a consequence. "The strongest and most vigorous men … would generally have been able to select the more attractive women … who would rear on average a greater number of children" (Darwin 1877, p. 595). Different societies would have dissimilar ideas about what constituted attractiveness and so the physical features of various groups would gradually diverge through sexual selection alone.

He reinforced these views by insisting that sexual selection was not confined to physical attributes like hair or colour. According to Darwin, sexual selection among humans would also affect mental traits such as intelligence, maternal love, bravery, altruism, obedience, and the "ingenuity" of any given population; that is, human choice would go to work on the basic animal instincts and push them in particular directions.

Here, we encounter Darwin's bourgeois ideas about social hierarchies and gender differences among human beings. For example, he believed that sexual selection enhanced male superiority across the world. In early human societies, the necessities of survival, he argued, would result in men becoming physically stronger than women and that male intelligence and mental faculties would improve beyond those of women. It was self-evident to him that in civilised regimes men, because of their well-developed intellectual and entrepreneurial capacities, ruled the social order (Richards 1997).

> To avoid enemies, or to attack them with success, to capture wild animals, and to invent and fashion weapons, requires the aid of the higher mental faculties, namely, observation, reason, invention, or imagination. These various faculties will thus have been continually put to the test, and selected during manhood. [. . .] Thus man has ultimately become superior to woman (Darwin 1877, pp. 564–565).

In this way he made human culture an extension of biology and saw in every human society a "natural" basis for primacy of the male. After publication, feminists and suffragettes bitterly attacked this doctrine, feeling that women were being naturalised into a secondary, submissive role. They were right to feel aggrieved. Many medical men of the period assumed that women's brains were smaller than those of men and were eager to adopt Darwin's statement that women were biologically subordinate to men and altogether less evolutionarily developed. For many decades thereafter it was commonplace to assert that the "natural" function of women was to reproduce, not to think. Indeed, men in the medical profession thought that the female body was especially prone to disorders if the reproductive functions were denied. Something of this belief can be traced in Western culture through to the 1950s or so.

In the *Descent of Man* Darwin also made concrete his thoughts on human progress and society. We should not be surprised that Darwin held entirely conventional Victorian opinions. These were explained in the introduction to the second edition of 1874. A racial hierarchy, as Darwin saw it, ran from the most primitive tribes of mankind to the most civilised; and had emerged through competition, selection, and conquest. He thought that those tribes with little or no culture (as determined by Europeans) were likely to be overrun by bolder or more sophisticated populations. "All that we know about savages, or may infer from their traditions and from old monuments . . . show that from the remotest times successful tribes have supplanted other tribes" (Darwin 1877, p. 128). Darwin was certain that many of the peoples he called primitive would eventually be wiped out by Europeans: particularly the Tasmanian, Australian, and New Zealand aborigines. This was a playing out of the great law of "the preservation of favoured races in the struggle for life". His emphasis cast the notion of race into biologically determinist terms, reinforcing contemporary ideas of an inbuilt racial hierarchy and endorsing competitive imperial aggressions. Darwin made such activities "natural".

2.4 *Descent* in Victorian Context

Such words merged easily into contemporary ideologies of empire. The concept of natural selection as applied to mankind in *Descent of Man* seemed to vindicate harsh and continuing fights for territory, the subjugation of indigenous populations, and the expression of political power on the international scale. Indeed, formulated in this way, Darwin's concept of natural selection was a clear echo of the industrialised nation in which he lived. It comes as no surprise that, in turn, his views seemed to substantiate the leading political and economic commitments of his day. The success of white Europeans in conquering and settling in Tasmania, for example, seemed to make "natural" the whole-scale extermination of the original peoples. Conquest was deemed a necessary part of imperial progress.

Partly because of Darwin's endorsement and partly because of the influential writings of others, these views supported the high imperialism of the early twentieth century. Herbert Spencer's doctrine of "survival of the fittest", as used by Darwin, Wallace, and others, in *Descent of Man* and elsewhere, became a popular phrase in the development of social Darwinism (Hawkins 1997). Embedded in powerful class, racial and gender distinctions, social Darwinism used the prevailing ideas of competition and conquest to underpin and inform social and economic policies. Spencer's phrase "survival of the fittest" was well suited to encourage capitalist economic expansion, rapid adaptation to circumstance, territorial landgrabs, and settler colonisation. Karl Pearson, a committed Darwinian biologist based in London, expressed it starkly in 1900: he said, no-one should regret that "a capable and stalwart race of white men should replace a dark-skinned tribe which can neither utilise its land for the full benefit of mankind, nor contribute its quota to the common stock of human knowledge" (Pearson 1900, p. 360).

It is well known that Darwin's ideas were welcomed by many industrial entrepreneurs and manufacturers in Europe and North America, perhaps further afield as well. By the start of the twentieth century these commitments were being put into action by the businessmen, philanthropists, and business magnates who masterminded the development of North American industry, for example, J. D. Rockefeller and the railway tycoon James J. Hill who used "survival of the fittest" as a motivating slogan. In their view the strongest and most efficient company would naturally dominate the market and stimulate economic progress on the wider scale. Others, like Andrew Carnegie, the émigré Scotsman who created a vast fortune and spent the rest of his life giving it away, revered Herbert Spencer. These commitments were heavily biased towards the political right. Few such thinkers believed in state support for the poor. A welfare state or subsidised industry, it was assumed, would encourage idleness and permit an increasing number of unfit people or firms to survive, thereby undermining economic progress and national health.

Several of Darwin's remarks in *Descent of Man* captured anxieties that were soon made manifest in the eugenics movement. Darwin feared that what he called the "better" members of society were in danger of being numerically swamped by the "unfit". In this latter category Darwin included men and women of the streets, the ill, the physically disabled, indigents, alcoholics, and the mentally disturbed. He pointed out that medical aid and financial support through charitable undertakings for the sick and the poor ran against the fundamental principle of natural selection. Nevertheless, he suggested that it was the characteristic of a truly civilised country to aid the sick and help the weak.

In these passages Darwin anticipated many of the problems that his cousin Francis Galton would try to alleviate through the Eugenics movement. Galton was an enthusiastic convert to Darwin's theories and had little hesitation in applying the concept of natural selection to human populations. The "unfit", as Galton expressed it, tended to be more fecund than superior members of society. He campaigned tirelessly to reduce breeding rates among what he categorised as the poorer, irresponsible, sick, and profligate sectors of society. He recommended that the "more highly-gifted men" should have children and pass their attributes on to the next generation. Galton did not promote incarceration or sterilisation as ultimately adopted by the USA, nor did he conceive of the possibility of the whole-scale extermination of an entire people, as played out during World War II. However, he was a prominent advocate of taking human development into our own hands and the necessity of counteracting the likely deterioration of the human race—a resurgence of Thomas Robert Malthus's original ideas on the natural limits of population, now poured back into social and economic thought with a fully biological backing provided by Darwin (Chaplin and McMahon 2016). While Darwin's *Descent of Man* can hardly account for all the racial stereotyping, nationalist fervour and harshly expressed social prejudice found in years to come, there can be no denying the impact of Darwin's work in providing support for notions of racial superiority, reproductive constraints, gendered typologies, and class distinctions (Kevles 1985). History shows that *Descent* was a highly significant factor in the emergence of social Darwinism and eugenics—with all their terrible consequences.

2.5 Aftermath

Scholars nowadays agree that *Descent of Man* offered a far-reaching naturalistic account of human origins. Even so, few nineteenth century readers wished to place human beings on exactly the same level as beasts. The reviews in general pushed back. *Harper's Weekly* complained that, "Mr. Darwin insists on presenting Jocko as almost one of ourselves". An anonymous reviewer in *The World*, a New York literary magazine, said that, "Mr. Darwin, like the rest of his atheistic school, evidently rejects with contempt the idea of a spiritual God who creates and sustains the universe". The *Truth Seeker* called the book "hasty" and "fanciful". Another writer in the Catholic *Tablet* explained that human beings possessed rationality, a "perfectly distinct faculty from anything to be found in the brutes". The London *Times* deplored the book's publication, saying that "it is hard to see how, on Mr. Darwin's hypothesis, it is possible to ascribe to Man any other immortality or any other spiritual existence, than that possessed by the Brutes. To put them [these views] forward on such incomplete evidence, such cursory investigation, such hypothetical arguments as we have exposed, is more than unscientific—it is reckless". A correspondent in *The Guardian* summed them all up by appealing to the direct evidence of the Bible. "Holy Scripture plainly regards man's creation as a totally distinct class of operations from that of lower beings".

Others, nevertheless, welcomed Darwin's depth of learning, sincerity, and rationality. Questions about the animal–human boundary, the human soul and the divine origin of human morals had been topics of debate since Antiquity. Darwin's contribution to resolving these matters began with the *Origin of Species* and culminated with his *Descent of Man*. Immediately after publication, in an article on "Darwinism and Divinity" written in response to the *Descent,* the public intellectual (and father of the novelist Virginia Woolf) Leslie Stephen spoke for many of the coming generation by asking "What possible difference can it make to me whether I am sprung from an ape or an angel?" (Stephen 1872). In Stephen's eyes, the *Descent of Man* expressed an important new conviction that science was the place to look for answers about human origins. In a wider domain, the book obliged people to explore the implications of the very notion of what it meant to be human. In France, Germany, Italy, Spain, the Netherlands, Scandinavia, Russia, and North America, and progressively all over the globe, reaching China and Japan by the 1880s, people from every walk of life repositioned this controversial issue within their own cultural contexts. Such responses, evocative of the cultural diversity of the nineteenth and twentieth centuries, remind us that the introduction of new ideas is rarely straightforward and that the past histories of science have involved many different forms of publication, many different audiences, many different languages and intense personal effort as well as the lasting power of the ideas themselves.

References

Barlow, N (ed) (1958) The autobiography of Charles Darwin 1809–1882. With the original omissions restored. Edited and with appendix and notes by his grand-daughter. Collins, London

Bowler PJ (2007) Monkey trials and gorilla sermons: evolution and Christianity from Darwin to intelligent design. Harvard University Press, Cambridge, MA

Browne J (1995) Darwin: voyaging. Knopf, New York

Browne J (2002) Darwin: the power of place. Knopf, New York

Campbell BG (ed) (2006) Sexual selection and the descent of man: the Darwinian pivot. Aldine Transaction, New Brunswick

Chaplin J, McMahon DM (eds) (2016) Genealogies of genius. Palgrave Macmillan, New York

Cronin H (1991) The ant and the peacock: altruism and sexual selection from Darwin to today. University of Cambridge Press, Cambridge

Darwin CR (1859) On the origin of species: a facsimile of the first edition. Harvard University Press, Cambridge [1964]

Darwin CR (1877) The descent of man, and selection in relation to sex, Rev edn. John Murray, London

Desmond AJ, Moore JR (2009) Darwin's sacred cause: race, slavery and the quest for human origins. Allen Lane, London

Freeman RB (1977) The works of Charles Darwin: an annotated bibliographical handlist, 2nd edn. Dawson, Folkestone

Greene JC (1959) The death of Adam: evolution and its impact on Western thought. Iowa State University Press, Ames

Hawkins M (1997) Social Darwinism in European and American thought, 1860–1945: nature as model and nature as threat. Cambridge University Press, Cambridge

Hodge J, Radick G (eds) (2009) The Cambridge companion to Darwin, 2nd edn. Cambridge University Press, Cambridge

Kevles D (1985) In the name of eugenics: genetics and the uses of human heredity. Knopf, Random House, New York

Lightman B (1987) The origins of agnosticism: victorian unbelief and the limits of knowledge. Johns Hopkins University Press, Baltomore

Livingstone DN (2001) Darwin's forgotten defenders: the encounter between evangelical theology and evolutionary thought, 2nd edn. Regent College Pub, Vancouver

Pearson K (1900) The grammar of science, 2nd edn. Adam & Charles Black, London

Richards E (1997) Redrawing the boundaries: Darwinian science and Victorian women intellectuals. In: Lightman B (ed) Victorian science in context. University of Chicago Press, Chicago, pp 119–142

Richards E (2017) Darwin and the making of sexual selection. The University of Chicago Press, Chicago

Stephen L (1872) Darwinism and divinity. Pop Sci Monthly 1:188–202

Chapter 3
Ways of Seeing the World: Darwin and the First Victorian Generation

Josep M. Fradera

Abstract Charles Darwin's two great books of 1859 and 1871 are inseparably linked to the knowledge and mastery of the world by a few select European countries or countries formed by European descendants. That knowledge was, however, conditioned by contradictory problems and points of view, those of the time. The resolution of the question of slavery and the reinforcement of domination over the so-called aborigines, for example, were the obvious result of colonial expansion throughout the world. In one way or another, the concepts of species, subspecies or race were imbued with the ideas of progress and social hierarchy that the available information about the world seemed to confirm. Darwin was by no means oblivious to these questions, sometimes out of moral imperative and sometimes because of his discipline. Without ever betraying his task as a naturalist, his major works reflect the views and concerns of the science and culture of the Victorian generations.

Keywords Religion · Slavery · Abolitionism · Aborigines · Extinction · Race

Each era sees the world differently. It is the task of the present text to discuss the intellectual stimuli and limits that led Charles Darwin and his contemporaries to make a revolutionary turn in natural history. Indeed, it was the generation of the 1830s–1850s that first set out to break with the humanistic schema that the old English universities reproduced undeterred. It is difficult to imagine Darwin following the outline traced when he studied at Cambridge and ending up administering an ordinary Anglican parish. According to Charles Kingsley, the way to imagine that break with the previous culture could not be other than to place "the whole of

---

I am grateful for the kindness with which professors Alex Coello de la Rosa and Josep M. Salrach answered questions that are dealt with in this text. I would also like to thank Professor Jaume Bertranpetit for his invitation to participate in this book.

J. M. Fradera (✉)
Department of Humanities, Universitat Pompeu Fabra/ICREA, Barcelona, Spain
e-mail: josep.fradera@upf.edu

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_3

humanity" at the center of the concerns of science (Riskin 2020, p. 48). If anyone embodied this aspiration, it was the author of *The Origin of Species*, the naturalist who most consistently challenged the traditional idea of an external and unknowable force as the origin of everything.

It is common to refer to the key motivations in Darwin's life, his grandparents and parents and the social connections around him. The first was anti-slavery, practiced as a moral obligation by all branches of his family; the other was the religious crisis that spread among British and European enlightened circles. This second rupture came from the previous century but became wider and deeper during the lifetime of our character. It can be attributed both to the extraordinary increase in knowledge of natural history and to the simultaneous loss of the churches' ability to control society. However, less consideration is given to what the accumulation of knowledge about the natural environment and the diversity of the human species to Darwin and to the Victorian generations meant. This was not simply a circumstantial and cumulative expansion of biological or ethnographic data. It was about the impact on culture motivated by the exponential accumulation of information resulting from the appropriation of the entire world by a select club of European countries or countries formed by transplanted Europeans.

We begin with a fact that may seem merely anecdotal. In the first half of the 1850s, two British philanthropic bodies, the British and Foreign Anti-Slavery Society and the Aborigines Protection Society, joined forces. It is immediately apparent from their names alone that their aims were not identical. The first of those humanitarian societies was founded in 1787 to end human trafficking and slavery in the British colonies. The second, on the other hand, was formed half a century later to extend the idea of a humanitarian mandate to subjugated societies, whether or not slavery as institution was present. As we have said, both joined forces to protect populations mistreated as a result of European colonial expansion in the mid-nineteenth century. While the first had succeeded with the *Bill of Abolition* of 1833, the one formed in 1837 to protect Aboriginal people was just then beginning a campaign that would become increasingly complicated.

Even before Charles was born, the Darwin and Wedgwood families were deeply involved in the struggle against the slave trade and slavery as an institution. Abolitionism was neither a circumstantial nor a marginal impulse. During the 18th centuries and up to 1807–1808, when the Westminster Parliament abolished this infamous business for good, the British merchant navy had transported approximately one and a half million people from Africa to America. In the same year of abolition, some 750,000 slaves were still registered in the British colonies in the New World, a figure worthy of impressing the humanitarian sensibilities of many people. While the British were taking measures to put an end to the trade in human beings, they extended the end of slavery for another quarter of a century so as not to harm the interests of the West Indian planters. The former British colony that had been the USA abolished the traffic about the same time but on the condition, imposed by the southern states, of maintaining sine die and unfettered what was to become known as the "peculiar institution".

Fig. 3.1 Official medallion of the British Anti-Slavery Society with the motto: "Am I Not a Man and a Brother?". Josiah Wedgwood crafted the emblem in 1787 as a jasper cameo in his pottery factory. Although the artist who designed and engraved the seal is unknown, the cameo design is attributed to either William Hackwood or Henry Webber

The abolitionist movement brought together a group of people with very different motivations. When the first collections of signatures against the African slave trade were presented to Parliament, a coalition of forces began to take shape that would remain stable until the abolition of 1833 and even beyond, since the agreed and compensated formula of slavery allowed owners to keep their slaves for a few more years. This coalition included people from the Anglican world, such as its great spokesman William Wilberforce, very well placed in high British politics thanks to his friendship with the William Pitt the Younger, Prime Minister for 10 years. The abolitionist movement also included Quakers, Unitarians, Methodists, and other evangelicals. Many women also participated in it, who understood the offensive against slavery in parallel to the conquest of the political and social rights that were denied to them. The Darwin and Wedgwood families were part of the movement from the beginning. Josiah Wedgwood, great-uncle of the naturalist, had been a potter industrialist of great quality and very skilled in business. There is a famous anecdote that tells us about the involvement of Darwin's relatives in the anti-slavery campaigns. After a conversation with the great abolitionist apostle mentioned above, it occurred to Josiah Wedgwood to imagine an emblem that would mobilize the public opinion. To this end, he designed a medallion depicting a kneeling African with the slogan "Am I not a Man and a Brother?" (Fig. 3.1). The success of the initiative was so great that the motto became the most widely accepted symbol of the movement. It was used on clothing or in external and domestic decoration. The London group around Wilberforce, Grenville Sharp or Thomas Clarkson were known as the *Saints*, for their selflessness and dedication to the cause of ending slavery and its bastard child, the African slave trade. That crusade was experienced by the naturalist's grandparents and entire family as their own. Abolitionism was not just a political decision; it was above all a moral choice. The aversion to slavery and the mistreatment of human beings and animals persisted and conditioned Darwin's entire life.

The struggle against slavery provided first-hand information of what societies abused by Europeans were like. Josiah Wedgwood, for example, actively contributed to the publication of one of the most successful histories of the cruelty of the world of the slave trade and slavery itself. I refer to the autobiography of a supposed Nigerian prince, Eloudah Equiano (c. 1745–1797) published in 1789, a text that provided much data about the sufferings of specific individuals and entire subjugated populations. The second was the very expansion of information about how relations between Europeans and non-Europeans worked, something that depended too much on the moral view of the scourge of slavery. Africa and the Caribbean colonies talked about the evils of slavery on an unprecedented scale. However, it is necessary to understand what that flow of information meant. Briefly: the West African coast and slave societies in the New World were constituted by societies deformed or constructed by slavery, by the interaction between African and European societies, a history known for centuries (a classic by David Brion Davis discusses, from another point of view, the quality of information and the racial bias of European observers on Africa; Davis 1966, pp. 446–482). Darwin's own writings are an example of his familiarity with that institution. Darwin's *Voyage of the Beagle* (Darwin 1839), a book of his youth and a source of information, does not only record issues of an apprentice naturalist. The famous fragments that are usually quoted as testimony to the naturalist's aversion to that institution are more imbued with a moral rejection of it than with a strict desire for ethnological knowledge.

Darwin's first contact with slave labor came when the Beagle called at the Brazilian port of Salvador de Bahia in early 1832. In northern Brazil, Darwin saw firsthand what the abuse he had heard so much about in his family or in the abolitionist circles he frequented was all about. He saw on the ground that the revulsion was more than justified. He was equally shocked by the ship's captain Robert FitzRoy's defense of the institution (Barlow 1958, p. 74). Not all British people had the same views on slavery. Shortly thereafter, in Rio de Janeiro, he saw once again the aberrations that ownership of people entailed. On a visit to a plantation he observed how women and children from some 30 families were separated from their husbands and fathers to be sold mercilessly in the local market (Darwin 1839, p. 27). The way he narrates it reveals the sincere aversion that the naturalist had for an institution perfectly well known and debated by the British. The other place where the naturalist observed the workings of a slave society was at *Cape Colony*, but there, on his return, he could not spend enough time to confirm or qualify what he had seen before. One conclusion must be drawn: from the *Voyage of the Beagle* to the autobiographical fragments of his senescence -those that were manipulated or obliterated by his wife and son either for social or religious reasons—his aversion to slavery remained unchanged. It is necessary to take this into account in order to understand his work of maturity.

The question of slaved and forced labor haunted the naturalist throughout his life. By the time he had published *The Origin of Species* in 1859, two events of very different dimensions mobilized British society anew about slavery and the inevitable aftermath of abolition. The first was the American Civil War, a conflict that had at its heart the continued existence of servile labor. The human cost of the conflict was 600,000 dead. For historical, migratory and economic reasons, the British could not look at the war as a distant and alien event. The second event was domestic through and through, a conflict that accurately reflected the contradictions of the Victorian empire. We refer to the events of *Morant Bay*, a massacre of starving former slaves in the north of the island of Jamaica perpetrated by the island's authorities. The severity of the repression was enormous: 439 rebels were executed, 600 men and women were whipped and 1000 houses were burnt to the ground. To make it clear what law and order was all about, interim Governor Eyre decided to act against George William Gordon, the best-known advocate of the emancipated in the Jamaican assembly, with whom he had a long conflict over the so-called Tramway Scandal. The imprisonment did not seem sufficient to the governor, so Eyre took advantage of the situation to send him to the area where, thanks to the state of siege, he was able to execute him without mercy. This expeditious character provisionally occupied the post of governor as a result of the absence of a more qualified candidate. It was not that Eyre had no previous experience in colonial matters. He had been "protector of aborigines" in Australia, he had held a second-tier military post in New Zealand, and he had been "protector of indentured workers" in Trinidad (Hanford 2008). However, that the Jamaican office and deeds outweighed him was of such evidence that no great explanation was necessary.

An abuse of power of such magnitude, including a legal assassination of such cruelty, must necessarily raise a great stir in the metropolis (Olivier 1933; Semmel 1962; Heuman 1994). The repercussion and division in political and intellectual circles was enormous. At the forefront of those who supported the Jamaican authorities was Thomas Carlyle, the eccentric philosopher and writer with whom Darwin occasionally interacted. In his autobiographical recollections, the naturalist refers to the unclassifiable character of that influential polemicist, of whom the naturalist states that "his views on slavery are repulsive" (Barlow 1958, p. 113). Carlyle's aversion to ex-slaves was well known since the publication in *Fraser's Magazine* of the pamphlet *Occasional Discourse on the Negro Question* (1849). At the time of Morant Bay he republished that pamphlet of explicit racial hatred under the title *Shooting Niagara: and After?* (1867). The philosopher and economist John Stuart Mill was at the forefront of those who opposed Eyre and called for his prosecution. In short, the most prominent figures of the British intellectual world confronted each other as a consequence of events only apparently distant, mobilizing signatures for and against the prosecution of the governor who had already been dismissed. Despite the prudence with which Darwin always acted in public affairs, he signed in favor of demanding accountability, thus supporting the *Jamaica Committee* headed by Mill (Desmond and Moore 2009, pp. 349–350). The manifesto was signed by people as close to the naturalist as the great abolitionist Thomas Fowell Buxton—Wilberforce's most qualified heir—the naturalist T. H. Huxley, the

Quaker and radical politician John Bright, the sociologist Herbert Spencer and many others. It is very difficult to imagine Darwin remaining on the fringes of those who demanded justice.

However, when the dismissed governor arrived in Southampton, the local authorities and various personalities organized a lavish reception banquet for him. *The Times* published the individual financial contributions and the adhesions to the act of homage that had been programmed, a banquet with a *bouquet* of clear nostalgia for the good old times of slavery, of a clear hierarchy, to say the least. Darwin was enormously surprised to find that, among the names of those who supported the initiative, was one of his sons, William Erasmus. The naturalist saved the situation tactfully but at a very high and understandable personal cost.

When slavery seemed to be in retreat, the expansion of British settlers into *British North America* (Canada), New Zealand and *New South Wales* (future Australia), and *Cape Colony* (parent of the future Union of South Africa), introduced new characters into the picture of the moral conflicts with which British and Europeans viewed the territories acquired around the world. Unlike in the case of slavery, it was the land and not the labor that interested the European settlers in those places. There was not even an accepted term to name those populations that were to be fatally dispossessed, displaced and even extinguished. The French chose to speak of "indigènes," the British "aborigines," others preferred to call them "natives," pure etymological redundancies in either case. The *Aborigines Protection Society* was the first humanitarian entity that set out to defend those societies, fragile by definition. It is undeniable that the founding core of the new philanthropic enterprise—people like Thomas Fowell Buxton, Thomas Hodgkin (drafter with his brother of the first report to Parliament on the issue in 1837)—did not come out of nowhere. Most of them were earlier involved in abolitionist campaigns. Thus, a new classificatory map of human societies took shape. It was the first time that such an attempt was finally feasible. Previously, knowledge had been fragmentary, unsystematic and external, designed for centuries to contribute to various missionary enterprises and, later, during the eighteenth and nineteenth centuries, to justify the expansive dominion of the great imperial countries.

It is striking that the same Darwin who expressed his rejection and disgust in relation to slavery was so condescending to the condition and treatment of the "aborigines," as he observed during the voyage of the *Beagle*. Tierra de Fuego in America, and Australia and New Zealand in the Pacific, became privileged places of observation. The Fuegians had been of interest to the British administration even before the naturalist's voyage to South America. The Pacific had also been explored during the second half of the eighteenth century, an important enlightened and colonial preoccupation at the same time. The moment when the naturalist's views on those societies without political organization were most clearly expressed was during the *Beagle's* stay in Australia. It is known that Darwin took advantage of his passage through Sydney to visit the surrounding territory, something he would repeat in New Zealand. He passed a dark and implacable judgment on the Australian Aborigines, whom he nevertheless considered to be a step above the inhabitants of Tierra de Fuego he had previously observed. He referred to the local people as "black aborigines" (Darwin 1839, p. 519). It was the interrelationship between the British ability to develop the continent and the ability of the indigenous inhabitants that he reasoned with criteria that were both rational and charged with a thinly disguised ethnocentrism. This is demonstrated by the naturalist's dark premonition: "Besides these obvious causes of destruction, there seems to be a mysterious factor which is generally at work" (Darwin 1839, p. 520). The concept of *extinction* is decisive in the Darwinian conceptualization, valid for plants, animals and humans: "Extinction occurs mainly as a result of competition of one tribe with another and of one race with another" (Darwin 1877, p. 182). The epitaph that follows was clear enough.

Darwin's powers of observation were intertwined on more than one occasion with the circumstances and purposes that had shaped that diversity of societies. Three were more than obvious and served as a basis for analysis: the first was English society itself and by extension some select European societies, those that offered to the contemporaries no doubt of having raised civilization to the highest point; secondly, there were the societies with slavery, wrought by immoral and *unnatural* violence, doomed inevitably to be eliminated for social and moral reasons; and finally, there were the more remote places, where the 'aborigines' lived, those societies situated until the eighteenth century on the fringes of the great currents that shaped the world dominated by Europeans, for better and for worse. As the naturalist that he was, Darwin left out of that scheme the great societies of non-European roots with solid state organizations (such as those of South Asia or China) that he never visited and did not even think much about.

It is interesting to note how, despite the scientific vocation of some of the members of the humanitarian and social studies institutions of the time, the formulas for classifying human races that were put into circulation were based on criteria that were not so much homogeneous, alien to the regularity that science demands. The problem began already in the way in which the position of the Europeans, of the British in the first place, was thought from the second half of the XVIII century (an attempt to order these diverse elements can be found in Wolf 1982). Since Hume and the Scottish school, a classification in stages that no longer owed anything to divine providence was tried. At the top of an evolution that defined societies by their culture and complexity of social organization, Europeans were (some more than others) economically and socially diligent, Christian, white and sober and showed capacity to evolve in a direction that nobody hesitated to call "progress." Next to the Europeans, other complex societies could be registered, which were usually defined by the place that monotheistic religions occupied in them: Muslims, Jews or Israelis; Hindus and Buddhists. This was the scheme of Arthur de Gobineau, the first relevant theorist of a racial and consciously hierarchical classification.

Not everyone shared this nineteenth-century obsession. Alexis de Tocqueville, for example, disparaged the scheme of his protégé Gobineau by pointing out that he had a "horse trader's" mentality. Similarly, the German tradition starting with the Humboldt brothers was always very reticent about the idea of an inherent racial and social hierarchy that will last forever. There was a strong argument for this: not all those who belonged to the same group (often called "race") reached similar levels of

Fig. 3.2 The work The Taxidermist's Workshop (drawing from Viktor Mikhailovich Evstafiev, 1948) depicts an episode from Darwin's life while studying in Edinburgh and is kept in the State Darwin Museum in Moscow. His master taxidermist was John Edmonston, a freed black slave from Guiana who was brought to Scotland by the ornithologist Charles Waterton. Darwin describes him in his *Autobiography*: "By the way, a negro lived in Edinburgh, who had traveled with Waterton and gained his livelihood by stuffing birds, which he did excellently; he gave me lessons for payment, and I used often to sit with him, for he was a very pleasant and intelligent man" (Barlow 1958, p. 51). Reproduced with the permission of the State Darwin Museum, Moscow

development (see Bunzl 1996). Meanwhile, those with whom Europeans had had more frequent contact, the Africans, were defined as inhabitants of a lower stage and with a skin color that easily identified them. Slavery had not always been so consistently connoted by obvious phenotypic traits. This was not the distinction of the classical and medieval *servus* (Finley 1980). In any case, African societies had lived secularly constrained by a lack of self-initiative, trapped by a morally dubious but economically and socially viable institution as slavery of European origin (Fig. 3.2). Abolitionism had never questioned the possibility of labor and social progress of African "blacks", although it was necessary for them to demonstrate this capacity where the emancipation promoted by Europeans allowed them to do so. The results were rather disappointing from the point of view of many Europeans or Americans. They rarely wondered if anyone could progress economically with neither little or no land nor capital. Even taking this backwardness into account, there were other groups still below the societies built by Europeans by buying and selling human beings over centuries. Indeed, in Australia or Tierra del Fuego, Darwin himself and before him Louis Antoine de Bouganville or James Cook (with the botanist Joseph Banks as naturalist (see Musgrave 2020; Goodman 2020) had been able to observe the existence of very simple human groups during the voyages of circumnavigation. Australasia and the Pacific were the places where this observation was most easily to make. Darwin himself never hesitated to consider the Aborigines he had met as societies condemned by history. Meanwhile, contemporary descriptions of African 'Hottentots' or 'Eskimos' under the Hudson Bay Company had put Europeans on the trail of other simple and elementary social entities. When peoples from all corners of the empire were exhibited in their supposed natural habitat at the Great Exhibition in London in 1851, a cycle of universal discovery, in turn knowledge and possession, was closed (Stocking 1987; Pagden 2003).

The problem was that the formalization of that universal system of dominance, built with so much effort and violence as it will suffice to recall Cook's death in Hawaii in 1779 (Sahlins 1985; Obeyesekere 1997) was in no way based on homogeneous criteria. The idea of a common origin of Wallace and Darwin could not be indifferent to this hierarchy. The origins and nature of them was the greatest challenge to remake on scientific grounds the history of the species, the "common descent," "the long argument" that the naturalist pursued all his life (Mayr 1991). He himself could never deny the impression that the sight of the peoples of northern Brazil or the dances and behavior of the Fuegians at the southern tip of Tierra del Fuego, in the present-day Argentine Republic, had made on him. This group, that Darwin had portrayed as completely incapable of evolving for lack of social hierarchy and authorities of their own, will be almost annihilated by the wave of European herd owners that settle there.

The sum of all this set of classifications provided the idea of an entirely mapped world, despite the descriptive gaps that might still exist. The young Darwin himself had already pointed out: "the map of the world ceases to show gaps" (Darwin 1839, p. 607). All societies were, little or much, better or worse, known. The endless discussions about monogenism or polygenism, about interfertility and/or the possibility of reproduction with the risk of inevitable decadence, were all questions that referred again and again to the virtuality that could be granted to a hierarchy mended with various elements, often incongruent (Stocking 1968). The legacy that Darwin left to the natural and social sciences of the twentieth century referred again and again to the quality of that ordering scheme. Here is not the place to discuss what classification of human "races" within a single "species" was being attempted. The debate was rather oriented towards the definition and appreciation of the capacity of each of those groups to follow a process of adaptation to the most demanding patterns of civilization. The shift from descriptive ethnology to anthropology was oriented in this direction, accentuating the proximity within the species, or admitting an unbridgeable distance between parts of the species (Lorimer 2013, pp. 59–99). Charles Darwin left both doors open.

Earlier, in *The Descent of Man and Selection in Relation to Sex* (1871), a book of comparative naturalism between animal species and his own, he tried to unravel some of the great questions that he himself had put on the table, for which he had no solution. Briefly, to explain fertility between races, hybridization, extinction and inheritance, civilization and barbarism, as he did in the seventh chapter of the book, was beyond the reach of Darwin's generation. In short, without being able to determine the mechanisms and transmission of inheritance through the rules that fixed reproduction, the comparison between species was not enough. For this reason, it is difficult to define the book as that of a biologist or naturalist *tout court*. In this hard-hitting book, a set of issues between biology, psychology, culture, and social order combine to try to flesh out the explanatory shortcomings of the idea of natural selection. Issues, all of them, that I am not qualified to discuss. I am ready to admire, however, an effort of conceptualization of such ambition and transcendence.

References

Barlow, N (ed) (1958) The autobiography of Charles Darwin 1809–1882. With the original omissions restored. Edited and with appendix and notes by his grand-daughter. Collins, London

Bunzl M (1996) Franz Boas and the Humboldtian tradition: from Volksgeist and Nationalcharakter to an anthropological concept of culture. In: Stocking GW (ed) Volksgeist as method and ethic: essays on Boasian ethnography and the German anthropological tradition. University of Wisconsin Press, Madison, pp 17–79

Darwin CR (1839) Narrative of the surveying voyages of His Majesty's Ships Adventure and Beagle between the years 1826 and 1836, describing their examination of the southern shores of South America, and the Beagle's circumnavigation of the globe. Journal and remarks. 1832–1836. Henry Colburn, London

Darwin CR (1877) The descent of man, and selection in relation to sex, 2nd edn. John Murray, London

Davis DB (1966) The problem of slavery in western culture. Oxford University Press, Oxford

Desmond AJ, Moore JR (2009) Darwin's sacred cause: race, slavery and the quest for human origins. Penguin Group, London

Finley MI (1980) Ancient slavery and modern ideology. Penguin Books, Hardmonsworth

Goodman J (2020) Planting the world. Joseph Banks and his collectors: an adventurous history of botany. William Collins, London

Hanford P (2008) Edward John Eyre and the conflict of laws. Melbourne Univ Law Rev 32(26): 822–860

Heuman GJ (1994) The killing time: the Morant Bay rebellion in Jamaica. University of Tennessee Press, Knoxville

Lorimer DA (2013) Science, race relations and resistance. Manchester University Press, Manchester

Mayr E (1991) One long argument: Charles Darwin and the genesis of modern evolutionary thought. Harvard University Press, Cambridge

Musgrave T (2020) The multifarious Mr. Banks: from botany bay to Kew. The natural historian who shaped the world. Yale University Press, New Haven

Obeyesekere G (1997) The apotheosis of Captain Cook: European mythmaking in the Pacific. Princeton University Press, Princeton

Olivier S (1933) The myth of Governor Eyre. The Hogarth Press, London

Pagden A (2003) Peoples and empires: a short history of European migration, exploration, and conquest, from Greece to the present. Modern Library, New York

Riskin J (2020) Just use your thinking pump! Review of the scientific method: an evolution of thinking from Darwin to Dewey, by H. M. Cowles. NY Rev Books LXVII (11):48

Sahlins M (1985) Islands of history. University of Chicago Press, Chicago

Semmel B (1962) The Governor Eyre controversy. MacGibbon & Kee, London
Stocking GW (1968) The persistence of polygenist thought in post-Darwinian anthropology. University of Chicago Press, Chicago
Stocking GW (1987) Victorian anthropology. The Free Press, New York
Wolf ER (1982) Europe and the people without history. University of California Press, Berkeley

Chapter 4
The Problem of Design in the Darwinian Proposal: A Historical Overview

Jesús I. Català-Gorgues

Abstract Design was the subject of great controversy before and after the development of Darwinian theories. Deeply rooted in classical and Christian intellectual traditions, providential design had traditionally defined the way of interpreting the natural world as created by the divine hand. Questioning this claim was arguably the biggest problem in admitting Darwin's proposal, beyond discussions of evolution as fact. Despite his firm commitment to an alternative argument based on natural selection, Darwin himself showed his concern when confronted with the explanatory power of design. Some popularized views of Darwin's contribution have stimulated a misunderstanding of this problem, shaping a biased interpretation of Darwin's biography that reduces the historical accounts to a justificatory explanation of the dominant worldview of today.

Keywords Design · Teleology · Scientific biography · Science and religion · Nineteenth to twentieth centuries

4.1 Introduction

To say that Darwin changed the way we see ourselves as a species, and the way we see our species in this world, is possibly so commonplace that it has become a little less than banal. However, it is this commonplace that, among other reasons, justifies a text such as the present one and those that accompany it in this commemorative monograph. Having acknowledged, therefore, that contribution, we should ask where lies that sense of radical change regarding human nature that illuminated Darwinian theory. No doubt many people will evoke the provocative proclamation of an ape saga. It is not at all difficult to imagine how shocked many well-meaning, traditional minds were when, in the wake of Darwinism's growing popularity, depictions of humankind as descended from apes became commonplace. Later stories, aired by the mass media, and solidified by literature, the plastic arts,

---

J. I. Català-Gorgues (✉)
Universidad de Alcalá, Alcalá de Henares, Spain

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_4

music, and cinema, have done nothing but configure another commonplace, adventitious of the first: despite the weight of evidence that genetics, paleontology, ethology, and other sciences have accumulated over the last century and a half, there remains firm opposition to the attempt to make us very close relatives of chimpanzees or gorillas. The noisy presence of creationist groups is a constant reminder: the proposal to make human beings an evolutionary product of a non-human animal species is still, for many people, an unforgivable sin, the genesis of which must be attributed to Charles Robert Darwin.

This is probably true enough, but I doubt that it is as significant as it is often thought. First of all, we must remember that Darwin was not the introducer of the evolutionary conception of life. This is not the time to review the proposals that preceded Darwin, but we cannot forget that Darwin was born and grew up in an intellectual world that had already been discussing for some time the possibility that biological species were not fixed entities, but that they could have changed over the course of Earth's history. Extending this thought to the human species, of course, was a qualitative leap. More openly or more discreetly, however, there were already daring people who pointed to this possibility before Darwin. The same year of the English naturalist's birth, Lamarck wrote in his *Philosophie zoologique:*

> If man was only distinguished from the animals by his organisation, it could easily be shown that his special characters are all due to long-standing changes in his activities and in the habits which he has adopted and which have become peculiar to the individuals of his species (Lamarck 1809, I: p. 349).[1]

And then the French author goes into a series of hypotheses about the transformation of certain *quadrumans* (what we call primates) into genuine *bimans* (i.e., the human species).

These ideas immediately aroused controversy. In the thirties of the nineteenth century, when Darwin was living the great experience of the *Beagle* voyage, the fear of the bestialization of humanity was shared by many authors. It was precisely in Great Britain, where Lamarck had found a notorious echo, especially in radical ideological environments, that important debates on the issue took place, which stimulated the young anatomist Richard Owen to devote an important research effort in the osteology of chimpanzees and orangutans to refute Lamarckist proposals (Desmond 1989). The controversies, however, were not confined to the scholarly cenacles. An 1844 book published anonymously and aimed at non-scholarly readers, *Vestiges of the natural history of creation*, achieved formidable success. The scientific knowledge of its author, later revealed to be the journalist Robert Chambers, was not exactly excellent. Quite a few of the reviews insisted on the serious basic errors contained in the book. The editions, however, went out of print one after the other, and the shudder that the *bestseller* caused is the most sensational proof of how, in Victorian society, evolution—not yet the so-called—was already a subject of popular interest. Needless to say, humans were within the general evolutionary scheme being expounded. The surviving handwritten notes of some readers of the

---

[1] I quote from the English translation by Hugh Elliot (Lamarck 1963, pp. 169–170).

time show how they disagreed with human origins in apes, but at the same time, they did not find it an original or unexpected idea either (Secord 2000).

The waves of scandal that Chambers provoked had a double impact on Darwin. Firstly, because it was clear how far someone could beat him to the publication of a theory on the transmutation of living species in a short period of time. And, secondly, and even more startlingly, because many negative reactions to the book, from important authors, confirmed Darwin's fear of becoming a source of public controversy and confrontation if he finally published his theory. Darwin rightly thought that *Vestiges's* geology and zoology were quite bad. But this did not lead him to believe that, however much he might exhibit a much higher level of expertise, the detractors of evolution would be more benevolent towards him (Browne 2003a). Considering that it would still be 15 years before the publication of *On the origin of species* (*Origin* from now on), it seems that the second blow penetrated deeply into Darwin's mind. In any case, the book, significantly, avoids any approach to human evolution, although everyone interpreted it as extensible to the origins of humanity.

4.2 The Design Argument

There is no doubt: talking about the evolution of non-human living beings has never been anywhere near as controversial as talking about the evolution of the human species, and this was already very clear in Darwin's own time. So why did *Origin* provoke such an intense and polarized reaction? It is true that not Darwin, but other authors, disciples of his, such as Thomas Henry Huxley, were quick to bring out their own contributions and applied the Darwinian scheme to the origin of mankind. This added controversy, obviously. But the direct reaction against Darwin's book had occurred immediately upon its publication, without waiting for these derivative contributions. It seems, then, that the evolution *of living beings as a whole* was, in any case, a reason for a harsh and even aggressive debate. But the subject, nevertheless, was not new. Darwin's theory must have involved something else, some addition to the schemes of evolution had to be introduced, which explains so much animosity.

The diversity of life has fascinated thought since ancient times. All the great cultures faced the question of how numerous, different, very often beautiful, and always admirably adapted living beings are and remain. Countless naturalist vocations, including Darwin's, were born of that fascination. We should, however, go much further back in history to find the first theories that strove to find a reason. Greek thought, of course, generated a large body of ideas that, in one way or another, explained the existence of species and how they related to the environment. The most common explanation was based on the argument of design, which dominated our conception of life and nature as a whole until Darwin put forward the theory of natural selection.

Our claim to rationally explain the world leads us to accept that it is ordered. This order is what we try to systematize when we construct an explanatory theory. One of the clearest examples of this order is manifested in the adaptations of living beings to their living conditions. These adaptations entail anatomical and morphological solutions, behavioural patterns, distribution areas, etc. We observe, for example, a cat hunting mouse; we quickly think that those retractable claws, those sharp teeth, the silent steps with which it moves or the eurythmic condition of its stalking body, are, as a whole, conceived or designed for the predatory function that defines the cat in its feeding habits. Here lies the argument of design, which quickly extends from particular individuals and concrete species, to the whole of the mutual relations between living beings, and of these with their environment. An immense web of purposes and ends governs, therefore, the natural world. A design, in short, is based on an *arrangement* of elements with a *purpose* or *aim*. There are many Greek authors who argued about design. Aristotle, with his discourse on final causes, is usually considered the most systematic of such an argument. He was not, in any case, the only one; and despite dissent such as that of the Atomists and Epicureans, the majority current ended up building a sense of nature governed by design and finalism (Glacken 1967; Depew 2008).

The idea of design, it is easy to see, combined very well with the belief in a creative intelligence. Christianity, which after all established its theological frameworks on philosophical substrata with Greek roots, thus found in design a comfortable argument to explain the action of the Creator. A design is also a plan. And it was the divine plan, after all, that was the focal point to which adaptive diversity led. According to the Christian worldview, moreover, all of this was subordinated to the preeminent place of humans as the culmination of divine creation. The ultimate reason for the whole web of design that sustained nature was none other than to guarantee our existence.

Naturalistic studies did not propose alternatives to this assumption for many centuries. So much so that in the mid-eighteenth century Carl von Linné, the great Swedish taxonomist, spoke of an *economy of nature* as a programme for the study of the harmonious relationships between all species. Linné, known above all for his proposal of biological nomenclature—the basis of which we still accept—and his system of classification, assumed, like Aristotle, the fixity of species. It is tempting to think that science would have been better off without species finalism, design or fixity, and there are those who still make such historical judgements, with an attitude that ultimately denies the history of science its ability to understand contextually the ideas about nature in the past; the ideas and, it must be added, the cultural practices surrounding science, as defining of science as those. After all, nature, conceived as a sacred entity because it was a divine work, sacralized the one who studied it, who came to have a moral consideration superior to that of the common people (Shapin 2008). This, of course, has not been a minor factor in the legitimation and in the very demarcation and definition of studies on the natural world, which has maintained a presence until more recent times than we think, especially if we consider certain rhetorics of the task of scientists at the service of society.

But we must not lose focus. It is true that the conceptual edifice that was maintained right up to the eighteenth-century associated finalist design with fixism. But the explanatory power was in the former. In that sense, assuming a transformist or evolutionist explanation was a problem; but it was more problematic to fight against the argument of design, because fixism needed design, but not the other way around. And, hypothetically, one can conceive of a transformative creation, interpretations of the Bible aside (and, please, let no one think that a literal reading of scripture has been the most common attitude throughout the history of Christian thought). It is very difficult, however, to conceive of it, creation, without end, design or plan.

Darwin knew a lot about this. It was not for nothing that he failed as a medical student in that nest of sceptics that was Edinburgh, while he obtained a *Bachelor of Arts* with good grades in the traditional and punctilious Cambridge. To obtain this degree, necessary to continue his studies to become an Anglican clergyman, he had to master the treatises on natural theology that so inspired the doctrine of the Church of England at that time. Biographers agree in presenting Darwin as a young man convinced of the explanatory power of design in the work of God, a crucial element in that theological current. His fondness for insects or geology led him, he thought, to a deep appreciation of creative action. He too, most likely, would feel that nature studies morally strengthened its practitioners. At Cambridge, in fact, there was an atmosphere, not of concord between science and religion, but almost, as Browne (2003a, p. 129) points out, of a conviction that "science, in a sense, *was* religion." So Darwin, beyond all suspicion, was a firm believer in design when he embarked on the *Beagle*. He was less so, it is true, when he returned. And this was accentuated when he began to conceive of a mechanism for the genesis of species that seemed to obliterate the design argument.

4.3 The Danger of Projecting Our Obsessions

According to Ghiselin (1972, p. 134), natural selection allowed evolution to act blindly and without rational cause, generating adaptations contingent on circumstances, making it "antithetical to design," constituting, at the historical moment of *Origin's* publication, "a devastating argument against the prevailing conceptions of adaptation." It could not be said more clearly. And what this entailed, in the eyes of many of Darwin's contemporaries, was a comprehensive redefinition of how the diversity of living things had been interpreted. Since the design argument had been linked to divine action, voices were soon raised that, for different interests, assumed that Darwin was expelling God from the stage of life.

What was Darwin really thinking? The answer is far from simple. According to the version of events that he himself constructed in his autobiography, when he was writing *Origin* he felt "compelled to look to a First Cause having an intelligent mind in some degree analogous to that of man," and all because of "the extreme difficulty or rather impossibility of conceiving this immense and wonderful universe, including man [...] as the result of blind chance or necessity." From then on, that impulse would fade away until he recognized himself as "agnostic" (Barlow 1958, pp. 92–94). To what extent things were really so is a recurrently revisited question, and an exhaustive study of the bibliography would take time, effort and space that we cannot afford. The details are very interesting when it comes to figuring out Darwin's religious positions, evidently. It is worth remembering, in any case, that even minds considered genius—always a suspicious consideration, it must be said—have the right to doubt, to modify their positions and to negotiate culturally, socially and sentimentally—and not only, nor primarily, intellectually—their beliefs. Darwin's intention when, in the last paragraph of *Origin,* he spoke of the greatness of the vision of life that he had expounded over almost 500 pages, of a life "originally breathed into a few forms or into one" (Darwin 1859, p. 490), continues to be wonderfully mysterious. And it is even more so after the addition of "breathed by the Creator" from the second edition onwards. Did Darwin really believe that life had been animated at its origin by a creator? Or was the formula just a way of appearing religiously orthodox? Or, more subtly, was he trying to acknowledge how ignorant he was and was being about the origin of life? (Ospovat 1980). Each reader can interpret as he or she wishes. The words, once written, are no longer the exclusive patrimony of the author. But we must be careful if we intend to make categorical judgments on such questions. Those who, when the book was published, stoked the fire against the obvious impiety of its author, interpreted those words in the second sense. They coincided, then, with the representatives of the opposite extreme, those who made Darwin an icon of irreligiousness.

After all, one thing is what a reading arouses in each person, and another is whether it corresponds to the author's true intention. This is not a problem when we are reading a poem. But it is more annoying if it is a scientific work. We are so unaccustomed to confusing the ideal of objectivity with the annulment of the margin of opinion, that we continue to believe, with complete stupidity, that science has the obligation to offer incontrovertible answers. And neither science, much less its practitioners, are there for that. The history of science, for that matter, even less so. And we do not have an incontrovertible answer to the question of what Darwin's religious position was at every moment of his existence, but we do have plenty of evidence of how he was not at all interested in actively combating the Christian faith with his theory, unlike what some of his followers, such as Ernst Haeckel, did, conditioning the way Darwinism was received and interpreted (Richards 2008, 2017). Incidentally, it is very nice to consider ourselves, as we are Darwinists, Darwin's intellectual children or grandchildren. That is why we celebrate his memory. But we are perhaps less fond of seeing ourselves as Haeckel's children, or grandchildren, or simply nephews and nieces. It is the case that the more militantly secularist versions within evolutionism exhibit historical roots that are rather more Haeckelian than Darwinian (in the sense of "dependence on," not so much "doctrine of"). Besides, Haeckel conditioned so much the way Darwin was disseminated and spread, that it would not be a bad thing to be cautious before proclaiming ourselves heirs of any legacy.

4.4 Is It Really Over with Finalism?

Darwin's legacy is that of a revolutionary. For some time now, however, historians of science have been questioning the canonical accounts of the so-called scientific revolutions, which makes some philosophers uncomfortable and irritates more than a few scientists. Part of this irritation stems from the loss of a comfortable and welcoming reference to the identity of the very science that is practiced today. It sounds very nice to say that current biology was born with Darwin, because it allows us to live comfortably under the legitimizing shelter of genius; and in a field that continues to be conflictive in the eyes of some people, it helps to delimit very well the sides, a resource very dear to many people obsessed with affiliations and labels. The problem is that we can hardly take Darwin out of a centuries-old tradition of knowledge, natural history, to make him suddenly military as a biologist. This, in any case, is not the most important thing. What is really decisive about questioning the pious narratives around the great changes in the theories and practices of science is that, unfortunately for some, they show in a stark way the negotiations that lead to innovation. Negotiations, no more and no less, that are established with ideas, attitudes, and behaviors that today we consider "a thing of the past," but that were an unavoidable "present situation" at the precise biographical moment of the so-called revolutionaries. At the time of inscribing modern physics in the register of birth, papa Newton was still, *velis nolis*, an alchemist and a theologian. And his alchemy, and especially his theology, are crucial in the genesis of his mechanical proposal, which nobody fails to recognize as capital, fundamental and defining of another way of conceiving nature the influence of which extends to the present day, but which in no way was conceived with today's assumptions. For Newton, and for most of his contemporaries, it was reasonable to negotiate with theology, something that is not reasonable today when we do physics. The point is that Newton *could not do* physics as we understand it, but practiced a natural philosophy that was culturally dialogical with theology.

In Darwin's case, the question is not solved just by acknowledging, as I have already tried to explain, that he knew the design argument well from his studies at Cambridge, so defined at the time by the stream of natural theology, the Reverend William Paley and the influential *Bridgewater Treatises*.[2] Darwin did not simply know the design argument, as one who knows the enemy in order to defeat him. Rather, Darwin negotiated with the design argument. It is that negotiation that allowed him to find an alternative mechanism to God's designing action, and not an a priori rejection of anything. Certain observations, especially during the voyage of the *Beagle*, and subsequent ponderings, are what finally convinced him of the inadequacy of the classical design argument. But the fact is that important parts of it remained in the new explanatory scheme, especially as a rhetorical construction.

---

[2] Some of these treatises, expressing Anglican orthodoxy in relation to science, were written by Darwin's own teachers, such as Adam Sedgwick, an important man in his training.

We have seen that the argument for design was teleological or, more simply put, finalistic. Design must obey a purpose, an intention, a finality. And that purpose is prescribed, once Greek finalism is associated with Christianity, by the provident action of the creative divinity. This is a key aspect, naturally, in the argument of the natural theology that Darwin knew so well and admired so much when he was a student. As this same Darwin, a little older, found that the argument of design based on the directing action of the Creator was not explanatory, neither of the diversity of species nor of their adaptations, there are those who automatically deduced that Darwin had suppressed the teleology or finalism of biology. An example is given by the American theologian Charles Hodge. It was 1874 when, after nearly 200 pages of arguments, he concluded that the blunt question that gave the title to his book, *What is Darwinism?* deserved an even blunter answer: "It is Atheism." Hodge, who was by no means a literalist and who knew a lot of philosophy, was subtle enough to say that evolution and natural selection were constituent, but not distinctive, elements of Darwinism. What, according to Hodge, distinguished Darwinism was that natural selection acted without design, driven by unintelligent causes. Explicitly, he said that "Darwin rejects all teleology, or the doctrine of final causes. He denies design in any of the organisms in the vegetable or animal world" (quoted in Livingstone 1984, p. 332). In reality, things were a bit more complicated.

Darwin, it is true, was contesting the idea of provident design in 1859 and later. But, as is very well manifested in the memorable epistolary exchange with Asa Gray in 1860–1861, he was also incapable of thinking that the world was the result of chance, which is in principle the alternative that seems to us the most logical *from the conditions of our time*. He also, equally explicitly, declared to Gray that he had no intention "to write atheistically" (quoted in Browne 2003b, p. 176). To be sure, Hodge found that the consequence of rejecting design was to embrace atheism, but that was not Darwin's intention. Why must this be insisted upon? Because if we approach Darwin's biography from the present consequences of his contribution—which for many evolutionists is the same as for an anti-Darwinist like Hodge, atheism (Stamos 2008)—we do not understand the character.

On the other hand, there is a temptation to think that the abandonment of the design argument entails the renunciation of any teleological explanation, as Hodge argued. Precisely when the exchange of letters we have mentioned was taking place, Darwin was gathering materials for his book *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing*, popularly known as *The Fertilisation of Orchids,* the first edition of 1862 and the second of 1877. The book was conceived to provide evidence for the action of natural selection in the interaction between species (orchids are fertilized by insects, and with a very high degree of specificity); and many such arguments can be found:

> The labellum is developed into a long nectary in order to attract Lepidoptera, and we shall presently give reasons for suspecting that the nectar is purposely so lodged that it can be sucked only slowly (very differently from what occurs in most other plants), in order to give time for the viscid matter on the under side of the saddle [of the viscid disc] to set hard and dry (Darwin 1877, p. 23).

Those “in order to” and “purposely” inevitably sound like finalistic or teleological argumentation. Darwin did not abandon that kind of argument. What he did abandon is the kind of providential teleology that was embodied in the design argument. Unlike physics, which leaves no room for questions that ask for explanations dependent on future events (for example, saying that the purpose of the energetic processes that define the Sun and its distance from the Earth is to provide suitable conditions for life), biology can employ a teleological discourse when it wants to figure out, say, the functions of the floral structures of orchids. Hodge may have thought that no teleology other than divine design was possible; for him, and for the most influential anti-Darwinists, this was in fact, and not evolution or natural selection, the main cause of the rejection of the content of *Origin* and the works that followed it. However, Darwin’s postulate of a mechanism of slow and continuous modification, contingently adjusted to selective pressures exerted by a changing environment, and operating on variability that is generated spontaneously, not deliberately, is for the purpose of survival, and this is a true final cause (Lennox 1993). There are those who would like to eliminate teleology from biological arguments, and perhaps that would be good. It should not be forgotten, however, that conceptual negotiations also involve terminological negotiations. Language in general, and words in particular, have histories as interesting as those of the people who use them, and the language of science does not escape historical contingencies either. As Michael Ruse (2000) has argued, in the case of teleological expressions these also involve very powerful metaphors. Metaphors are rhetorical resources, expressions to make oneself understood, but they are also tied to the theoretical structure of science itself, so removing them can have serious consequences for the theories themselves. Has the good reader stopped to think about the power of metaphor in the expression “natural selection”? Is there selection, in any case, without a certain purpose?

4.5 Conclusion

The very powerful and metaphorical natural selection projected Darwin to a particular place in the history not only of science, but of universal culture. But there were complex negotiations, with himself, with his environment, and with the ideas and uses of language in force, in order for the concept to come to fruition. And this, because of the immense historical and cultural weight that the providential design had. The strategy did not go through a general blasting, as it is often said in a not very nuanced way. Darwin, after having publicly established the concept in 1859, did not leave it fixed at that point. Precisely in the work that we commemorate in 2021, the work that he devoted to what is usually considered the most controversial aspect of his program, human evolution, Darwin (1871) showed how he had perhaps relied too much on the potential of natural selection; how he had then chosen to limit its scope; and how, at the time of writing *The descent of man,* he went round and round about the presence of organic structures that did not seem useful. How to make an alternative mechanism to design acceptable, when it was not able to explain an aspect that this same design did not count? Darwin succeeded thanks, among other things, to his insightful analysis of homologies. But the touchstone was the old argument of design, by no means the fixity of species.

Darwin was building his theory, from the founding programme expressed in *Origin*, to the development of that programme in his later works. Consequently, it makes no sense to take Darwin as a one-piece, static and solidified figure. If we want that, we might as well admire the statue of Joseph Boehm in the *Natural History Museum* in London and forget about his biography. Nor does it make much sense to resort to Darwin's biography to justify what is today the theory of evolution. Biographical moments are very relevant in understanding how people do science, but they say little about how the science done by those people ends up being understood, applied, developed or extended. A good example is how, despite Darwin himself, some rushed to make natural selection, as an explanation of the origin of the human species, a justification for certain social, political and economic programs quite regrettable, if we take into account their historical consequences, and with serious consequences for the public assessment of evolutionism (Tort 2008). We ourselves, with the best of intentions, can apply Darwinist principles to combat the anthropocentric residues that are still present in many interpretations of natural reality. Perhaps this was more sympathetic to him, but the truth is that Darwin kept the problem of the differential condition of humans with respect to other animals in a very central situation (Muñoz-Rubio 2003). There is no doubt that proclaiming an evolutionary continuity between animals and humans was a key step, but it is very doubtful that Darwin raised it as a bet against anthropocentrism.

I do not know if the history of science in general, and biographies of scientists in particular, serve any purpose; if they have, let's put it this way, no *purpose* at all. But if the commemoration of a scientific work moves us to wonder about its genesis, and this leads us to review the biography of its author, let it be for the *purpose of* understanding, as Darwin's best biographer says, "the relationship between this prolific inner world of the mind and the private and public lives that he created for himself" (Browne 2003b, p. 7).

References

Barlow N (ed) (1958) The autobiography of Charles Darwin 1809–1882. With the original omissions restored. Edited and with appendix and notes by his grand-daughter Nora Barlow. Collins, London

Browne J (2003a) Charles Darwin: voyaging. Pimlico, London

Browne J (2003b) Charles Darwin: the power of place. Pimlico, London

Darwin CR (1859) On the origin of species: a facsimile of the first edition. Harvard University Press, Cambridge [1964]

Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London

Darwin C (1877) The various contrivances by which orchids are fertilised by insects, 2nd edn. John Murray, London

Depew DJ (2008) Consequence etiology and biological teleology in Aristotle and Darwin. Stud Hist Phil Biol Biomed Sci 39:379–390. https://doi.org/10.1016/j.shpsc.2008.09.001

Desmond A (1989) The politics of evolution: morphology, medicine, and reform in radical London. University of Chicago Press, Chicago

Ghiselin MT (1972) The triumph of the Darwinian method. University of California Press, Berkeley

Glacken CJ (1967) Traces on the Rhodian shore: nature and culture in Western thought from ancient times to the end of the eighteenth century. University of California Press, Berkeley

Lamarck JBPA (1809) Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des Animaux; à la diversité de leur organisation et des facultés qu'ils en obtenennent; aux causes physiques qui maintiennent en eux la vie et donnent lieu aux mouvements qu'ils exécutent; enfin, à celles qui produisent, les unes le sentiment, et les autres l'intelligence de ceux qui en sont doués. Dentu, Paris

Lamarck JB (1963) Zoological philosophy. An exposition with regard to the natural history of animals (trans: Elliot H). Hafner, New York

Lennox JG (1993) Darwin was a teleologist. Biol Phil 8:409–421

Livingstone DN (1984) The idea of design: the vicissitudes of a key concept in the Princeton response to Darwin. Scot J Theol 37:329–357

Muñoz-Rubio J (2003) Charles Darwin: continuity, teleology and ideology. Sci Cult 12:303–339. https://doi.org/10.1080/09505430309011

Ospovat D (1980) God and natural selection: the Darwinian idea of design. J Hist Biol 13:169–194

Richards RJ (2008) The tragic sense of life: Ernst Haeckel and the struggle over evolutionary thought. University of Chicago Press, Chicago

Richards RJ (2017) The role of biography in intellectual history. Know 1:295–318. https://doi.org/10.1086/693727

Ruse M (2000) Teleology: yesterday, today, and tomorrow? Stud Hist Phil Biol Biomed Sci 31: 213–232

Secord JA (2000) Victorian sensation: the extraordinary publication, reception, and secret authorship of vestiges of the natural history of creation. University of Chicago Press, Chicago

Shapin S (2008) The scientific life: a moral history of a late modern vocation. University of Chicago Press, Chicago

Stamos DN (2008) Evolution and the big questions: sex, race, and other matters. Blackwell, Malden, MA

Tort P (2008) L'effet Darwin. Sélection naturelle et naissance de la civilisation. Seuil, Paris

Chapter 5
Darwin Under Suspicion: The Representation of Darwinism in the Newspaper *ABC* (1909–1982)

Marcos Morales and Martí Domínguez

Abstract Since its introduction in Spain, Darwinism has been a source of controversy between the most liberal and conservative sectors of society, according to historians. This movement has suffered especially restrictive periods, such as Franco's dictatorship, where it was subjected to strong censorship. This work presents a set of articles from the newspaper *ABC*, published from 1909 to 1982—centenary of the birth and death of the naturalist—whose analysis shows how the socio-political conditions have influenced the representation of Darwinism.

Keywords Darwin · ABC · Spain · Twentieth century · Franco dictatorship

5.1 Introduction

The representation that the written press provides of different scientific events is a magnificent tool for analysis. It not only contextualizes these processes in the political, social, and legislative conditions in which they took place, but also shows how these factors conditioned their transmission (Fernández 2014). Of these scientific events, the Darwinian controversy was one of those that had the greatest repercussion in the British press at the time of its communication (Ellegård 1990, pp. 1859–1872).

With regard to the monitoring of this controversy in the Spanish press, different authors have carried out general studies. Among these we can highlight: Glick's *Darwin in Spain* (2010, originally published in 1982) and the two works by Núñez (1969, 1982).

M. Morales
Professor of Biology and Geology, Conselleria d'Educació, Cultura i Esport (GVA), IES Ramon Cid, Benicarló, Spain

M. Domínguez (✉)
Department of Language Theory and Communication Sciences, Faculty of Philology, Translation and Communication, University of Valencia, Valencia, Spain
e-mail: Marti.Dominguez@uv.es

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_5

In addition, with the celebration of the second centenary of Darwin's birth, several articles analyzed how the media had transmitted the figure of the scientist. Some worth mentioning are: *Darwin in the press: what the Spanish dailies said about the 200th anniversary of Charles Darwin's birth* (Díez et al. 2009), *Darwin as news: Darwin's image through the media on the bicentenary of his birth* (Moreno and Lujan 2009) and *Spanish Darwinian iconography: Darwin and evolutionism portrayed in Spanish press cartoons* (Domínguez and Mateu 2012).

Finally, it is worth mentioning two Master's Final Projects that made an extensive approach to the representation of Darwinism in different Spanish newspapers. The first of these was carried out by Clara Florensa with the title *Study of the treatment of the theory of evolution in* La Vanguardia Española *between 1939 and 1978* (Florensa 2010). The second one was elaborated by Marcos Morales and supervised by Martí Domínguez: *Study of the treatment of the Theory of Evolution in the* ABC *newspaper between 1909 and 1982* (Morales 2017).

5.2 Contextualization: A Brief History of Darwinism in Spain

The history of Darwinism in Spain is a story burdened by controversy since its reception during The six revolutionary years (1868–1874). Enveloped by a hot socio-political context, Darwinism was quickly polarized, with defenders in the liberal sector and detractors in the conservative one (Glick 2010, p. 13). This polarization was largely related to the socioeconomic situation of the country, persistent illiteracy and the presence of a powerful church allied with conservative forces (Blázquez 2007).

In spite of this, at the end of the nineteenth century this confrontation was losing strength as the years went by and the different sectors took refuge in their respective institutions—scientific and medical faculties versus theological and philosophical institutions. However, an unprecedented act would rekindle the flame of the original confrontations in 1909. Encouraged by the motivation of the students of the Faculty of Medicine of the University of Valencia, the tribute to Darwin on the centenary of his birth awakened the old confrontations between the different sectors. According to Miguel de Unamuno, at that time: "the Faculty of Medicine of Valencia was the main Spanish nucleus of Darwinism" (López-Piñero 2008, p. 189).

During the following years there were different positions on Darwinism, ranging from anti-evolutionism supported by clerical institutions to the defense by different naturalists of the time. Some of them were Odón de Buen y del Cos (1863–1945) or Ignacio Bolívar (1850–1944). In addition, during this period, different evolutionary conceptions coexisted in Spain, such as mutationism, neo-Lamarckism or orthogenesis (Blázquez 2009b).

In the first half of the twentieth century, two names are of obligatory mention for their contribution to the foundation of evolutionary ideas. The first of these is

Antonio de Zulueta (1885–1971), who introduced in his line of study the ideas of Mendelian inheritance in Spain (Pelayo 2009). The other outstanding biologist is Jaume Pujiula (1869–1958), who followed the work of the entomologist Erich Wasmann (Peretó and Català 2016).

With the defeat of the Second Republic, Darwin and his ideas were classified as materialistic and atheistic biology by the new institutional forces. This fact would cause most evolutionary scientists to be exiled from the country or marginalized.

During the first decade of the post-war period, no works by Darwin would be published, with only two exceptions: *Narrative of the surveying voyages of His Majesty's Ships Adventure and Beagle between the years 1826 and 1836, describing their examination of the southern shores of South America, and the Beagle's circumnavigation of the globe* (Darwin 1839) and *On the Origin of Species* (Darwin 1859). It would take until 1963 for finding Darwin's works again with some normality in bookstores. It would be during this decade when the new Darwinism of modern synthesis would begin to be introduced in Spanish universities, and some of them would even be allowed to carry out tributes on the centenary of the publication of *On the Origin of Species (*Blázquez 2009a).

Spain would experience a period of scientific marginalization in the evolutionary field during these decades (Blázquez 2001). From this environment of scientific marginalization, new proposals would appear that would attempt to reconcile the theory of evolution with Catholic doctrine. A notable author of this movement would be the paleontologist Miquel Crusafont Pairó (1910–1983), who acquired certain relevance in the national and international scientific sphere (Acosta 2013). Crusafont became the maximum disseminator of the ideas of the French Jesuit paleontologist Teilhard de Chardin (1881–1955) and the American paleontologist George Gaylord Simpson (1902–1984) at state level (Blázquez 2001). The publication of *Evolution* by Crusafont et al. (1966), a collective book in the *Biblioteca de Autores Cristianos* coordinated by Miquel Crusafont, Bermudo Meléndez, and Emiliano Aguirre—exponents of Teilhard's followers in Spain—marked a milestone in the efforts of Catholic scientists to negotiate with the theory of evolution.

Another decisive disseminator at this time was the popular naturalist Félix Rodríguez de la Fuente (1928–1980), who with his television program *Blue Planet* helped to transmit evolutionist ideas (Acosta 2008). During the last years of the twentieth century, evolutionism was once again normalized in the academic and research sphere.

In this paper, we present a selection of the most representative articles published in the *ABC* between 1909 and 1982, where the figure of Darwin or his ideas are reflected, and which show the socio-political conditioning of the time, as well as the participation of the most prominent figures of the time.

5.3 Darwin in the *ABC*: 1909–1982

As already mentioned, the newspaper *ABC* followed up the tribute to Darwin held at the Faculty of Medicine of the University of Valencia, on the occasion of the first centenary of the birth of the English naturalist. The newspaper published two articles, on 19 and 23 February 1909. The first, under the heading *Homage to Darwin*, stated:

> Invitations have been circulated for the school tribute to Darwin, to be held next Monday in the auditorium of the University. The Dean of the Faculty of Medicine, Mr. Casanova, will preside, and lectures will be delivered by the professors Messrs. Bartual, Boscá and Unamuno, who will arrive Sunday for this purpose.

The second article, after the celebration of the tribute, told how the event had developed, and the figure of Miguel de Unamuno was especially highlighted, claiming that "the speech of the wise professor, always original and entertaining, at times instructive, and sometimes paradoxical, was received with great curiosity and applauded at the end with enthusiasm."

Despite this, the newspaper would not take long to present clear examples of how the debate on the theory of evolution continued to be present in society. Without any doubt, the most evident case would be Doctor Tomás Maestre Pérez (1857–1936)—professor of legal medicine and psychiatry at the Central University—and the Reverend Father Zacarías Martínez-Núñez (1864–1933)—a priest of the Order of Saint Augustine in El Escorial. A total of 20 open letters written by these individuals between December 5, 1910, and January 26, 1911, involved a public debate on the theory of evolution and how the theory and religious institutions should influence education (Morales and Domínguez 2017).

Within this set of letters, the last one published by the priest, on January 11, 1911, where he criticizes the convictions of the professor, is especially noteworthy:

> But to affirm, as you do, so simply and with such good faith, that the colloid substance is life, and that it gave origin to the primordial cell, there in the depths of the Ocean, and that today it is also manufactured in our laboratories, [...] that, believe me, my friend, is not experimentally demonstrated; although supporters of evolution affirm it, there is no biological, philosophical or paleontological proof.

On the other hand, Azorín would also expose his doubts about Darwinist ideas in articles such as *Independencia*, published on December 18th, 1909, or *Tradicionalismo positivista*, published on June 4, 1910. In spite of this, perhaps the article where Azorín most explicitly argues his concerns would be *Social Pessimism*, published on April 8, 1912:

> From this application of Darwinism to politics, a multitude of errors and harmful illusions arose; a multitude of excesses, injustices and iniquities were justified by the doctrine of social Darwinism.

This anguish regarding the repercussions of social Darwinism would be a recurring theme in the articles of the time, as shown by *Words to the wind... sentimental crime* de Manuel Bueno Bengoechea, published on April 8, 1925, through the intervention of Sofia (a character from a play by Marcel Prévost):

> Sofia's sentimental Darwinism, according to which the strong have the right to sacrifice the weak in order to be happy, sounds to us like a sinister irony, because there is nothing so dramatic or so sad as the contradiction of our philosophy with our temperament [...]. Neither Sophia nor Antony deserve to be classified in that zoological variety which has made selfishness a weapon of combat and cruelty a rule of conduct.

Despite this fear of the application of Darwinist ideas in the social sphere, the Spanish press respected the right to transmit them as long as they were based on scientific fact. This is how Enrique Gómez Carrillo explains it, in the article *Darwinian dogma,* published on September 24, 1925, where he wants to "protest against the Yankee judges who shortly condemned the professor who explained evolutionist theories in a University of Dayton," justifying that he did so only because "seeing that, in the name of the Protestant dogma, a scientific theory was prevented from being freely professed, I could not contain my indignation. But not then, nor ever, did it occur to me to declare myself a supporter of Darwinism." Even so, the author does not miss the opportunity to demonstrate his disagreement with these evolutionist ideas and he bases his ideas on the work *The transformist dogma* by Joseph Grasset, affirming that there are shortcomings such as "the lack of the intermediary creature between man and chimpanzee" and denying ideas such as "a slow evolution converts the molecular mass into vegetable and animal beings animated by living cells. Passing through the monkey, man comes from the initial fly."

The debate was served, and Darwinism flooded society, finding that year, 1925, one of the most important pieces of evidence of the time. The William Fox company presented the film *Darwin was right*, which appeared repeatedly advertised in the newspapers of the time and we can see transcribed by M. White in the Sunday supplement *Blanco y Negro* of November 22, 1925. *Darwin was right* recounts the experiences of Dr. Linaza, "a passionate enthusiast of Darwinism and the doctrines of the author of 'The Origin of Species by Means of Natural Selection'." The film revolves around a phrase of the doctor, who exclaims: "Darwin was right! The ancestors of our ancestors were monkeys, and what monkeys! in ancient, remote times..."

During the following decade, different evolutionary theories were frequently presented in the newspaper, and we can find examples such as José Rocamora's *Hearts without firmness*, published on April 4, 1930, where he proposed that ontogeny compiles phylogeny:

> It has been said that every animal reflects in its embryonic evolution the organisms which are inferior to them, and it has been asserted that the various stages of development of the heart show us that it does not arrive at its highest organization except by passing transitorily through forms which have remained as definitive for the subordinate animal classes.

Embryonic development and the inheritance of acquired characters were two disciplines that were of special concern to the scientists of the time, and this is demonstrated by *Genetic vulgarization. Inheritance of acquired traits* by José Vázquez Sánchez, published on 13 October 1930:

> In view of the above, Weismann's theory, support of those who deny the hereditary transmission of acquired characters, is quite affected. This inheritance was admitted long ago, based on the theory of Lamarck first, and Darwin later, but since the year 1888, in which Weismann made public his theory of "continuity of germ-plasm," denying the inheritance of these characters, the first two fell into disuse and the new theory was admitted as true.

It is curious to note that this author mentions the "illustrious director of the Biology Laboratory of Sarriá, Reverend Father Pujiula," who affirmed that "there are no biological units of a permanent and unalterable character, but centers modifiable by association, dissociation and chemical changes, which if by force or number predominate over some others in the act of fecundation, the characters caused by them appear in the new being."

Another of the protagonists of the time would appear a short time later in the news of the National Academy of Pharmacy of March 8, 1933, which announced the conference of "Don Antonio de Zulueta, head of the Laboratory of Biology of the National Museum of Natural Sciences, on the subject 'Evolution of organisms'." In this conference, Antonio de Zulueta spoke of the doctrines of Lamarck, Darwin and Wallace, and "noted that while there is near unanimity among biologists, as to the fact of evolution, there is, on the contrary, great indecision as to how it is verified and the causes behind it."

The biological sciences are in a splendid moment of dissemination and acceptance, so much so that we can even observe articles that allude to genetic studies from abroad, as in *Around rational seed selection* by Vicente Roceta Duran, published on May 3, 1935, where it is reported that "in a small garden of the Augustinian Abbey of Brünn (Czechoslovakia), and around 1856–1863" the Augustinian Gregory Mendel had made the discovery "which was to influence the concept of 'selection' in the most transcendental way." The author not only explains the conclusions of the religious man, but also concludes: "'Natural selection' and 'mutations' (the appearance of new forms or characteristics in a living being, without apparent justified cause), can be said to have been the only means that Providence used to create, in time and space, the immense majority of the races that existed at that time."

Despite the latent optimism towards Darwinism and associated scientific theories, the proximity of the outbreak of the Civil War would show a new trend of criticism towards evolutionism. José Mª Salaverria wrote on May 13, 1936, in his article entitled *In the drunkenness of victory*, that "[...] the pagan and realistic doctrine of Machiavelli: it is the materialistic and energetic doctrine of Nietzsche, of Darwin, of the struggle for life, of the exploitation of the weak by the strong." With the establishment of Franco's dictatorship, the discourse against Darwinist ideas became more radical, and on 29 October 1939, Felipe Sassone published *The charming friend*, in which the author argues that "man" is the only species that can take a walk and plays sports, and is totally opposed to Darwin, to the point of cursing his memory:

> Man and monkey, his imitator, and not his ancestor, as Darwin wanted. I take this opportunity to curse Darwin's memory, as well as Freud's and Karl Marx's.

He would not be the only author to criticize the ideas of the English scientist. The writer and founder of Falange, Eugenio Montes, *On Chile's national holiday. My toast*, published on September 19, 1944, would express an even more grotesque opinion:

> But I think of Darwin. There is no evolution in nature, I say to myself. That he said about going little by little, of a smooth and continuous transit, of life as a slow progress, all this corresponds to English nature, but not to the physical truth of the cosmos. The Englishman's nature is progressive, but that which God made in the world is not so.

On August 16, 1947, *The island of wolves* was published. In the book, Agustín de Foxá talks about the islands in general, and the Galapagos in particular, stating the following: "[...] where the blond Charles Darwin, studying his tortoises and iguanas, fabricated the Theory of evolution, which tried to replace the pink Adam with the hairy gorilla."

With the arrival of the new decade, the dictatorship's restrictions on Darwin relaxed somewhat, and this is also reflected in the articles that deal with him. One of the first examples is found on August 9, 1953, in the text *Civilization and civilizations* by Ramón Pérez de Ayala, where the author talks about the theory of diffusionism and highlights one idea:

> Lately, Soviet scholars claim to have found aboriginal specimens of wild cereals on Russian territory. So, the first civilization originated in Russia; as well as the last and definitive degree of civilization; according to them, the one reached by Russia; because Marx was also an evolutionist, if a somewhat simplistic one, since he dogmatically assures the definitive finality of evolution or historical dialectics.

Another even more surprising example can be found on July 20, 1957, in *A physiological discovery now serves to achieve "spontaneous confessions,"* by Richard Gibson, where he states:

> And after the 19th century and Darwin, biology has accumulated a multitude of proofs that the human being, far from being an exceptional creature, halfway between the beast and the angel, is simply an animal that dominates others thanks to the complexity of its nervous system.

At the end of the decade, several articles appeared, glossing the centenary of the publication of *The Origin of Species*, where the articles written by Ramón Pérez de Ayala on 3 September and 26 November 1959 were particularly noteworthy.

The reconciliation of the theory of evolution with the Catholic Church would be a recurring theme during the following decade, as we can see in *Eppur si muove*, by Juan José López Ibor, published on 29 December 1964:

> The second trend is the evolutionist one, which was born with Darwin's thesis on the origin of the species, which motivated an enormous, century-long metaphysical and religious scandal—until the work of Teilhard de Chardin and the recent council—motivated by the undue linking of the idea of creation with the fixity of species, and of the connection of man's spirituality with Cartesian philosophy.

Another protagonist of the time, Félix Rodríguez de la Fuente, would also spread Darwinist ideas with the article *The cunning and intelligence of the baboons*, published on June 29, 1968:

> Mutations, natural selection, the environment and food resources have made the baboons very different from their carnal cousins the colobus monkeys, which have never left the treetops.

The conservative Spanish society was reconciled with the English scientist, who once again had the approval of the editors of *ABC*, as is the case of *The history of France on the most beautiful stamps in the world*, written by Pedro González Rábago and published on October 16, 1970:

> All this, lest anyone should think that he would want to say that scientific atrocity that 'man descended from apes', which some ill-intentioned person attributed to Darwin, who never said it, as all his writings prove, where it can be verified by anyone who wishes to do so. Darwin was deeply religious and only confirmed the fact of evolution, perfectly proven and today admitted even by the Catholic Church itself. It is not, therefore, a theory, but scientific fact.

As the end of the dictatorship approaches, evolution appears more evidently in the articles of the newspaper, and the fear of the old Francoist censorship is lost, as in the news *Oparin, Calvin and Urey—three Nobel Prize winners, protagonists in a meeting that begins in Barcelona on Monday*, published on June 23, 1973, and signed by C.D.:

> What does this mean?" wondered Miller. After a careful analysis, he observed that with his experiment he had achieved the synthesis of organic compounds, amino acids among them, the fundamental basis of proteins and, ultimately, of life. Oparin's hypotheses were definitely confirmed.

Already established in the new democracy, authors like Cándido—pseudonym of Carlos Luís Álvarez—in *The couple*, published on September 17, 1978, even dared to criticize how Darwin's image had been treated during Franco's regime:

> I could say that there was some Darwinism in my explanations, but since Darwin was considered a Red, and even a Republican, a few years ago, he made some concessions to transcendence after all.

But the Darwinist year par excellence would be 1982, a date that for many historians is the moment when the democratic transition truly began with the victory of PSOE in the national election. This year, moreover, coincides with the centenary of Darwin's death, a fact that will be widely represented in the media. Particularly noteworthy is the newspaper published on March 28, 1982, where Darwin's image appears on the front page. In this issue, the newspaper reflects on the life and work of the scientist:

> Charles Darwin is one of those men of science who, like Copernicus or Galileo, made a historic turning point in our understanding of the world. His findings on the evolution of life and the origin of man overturned the knowledge of his time. As the commemorations of the first centenary of his death begin, *ABC* starts a review of his work, analyzed by Spanish authors Rof Carballo, Pinillos and Schwarts, and by François Jacob, winner of the Nobel Prize for Medicine. The 'Cándido' column, an editorial representation and a few pages of

documentation complete this vision of the great and controversial figure of the English naturalist.

5.4 Conclusions

Media analysis offers us a faithful representation of the relationship between the advance of science and its socio-political context. In the case of Charles Darwin, we can affirm that both his figure and his ideas have been a point of dispute between conservative and liberal sectors in Spain for much of the twentieth century. Moreover, we can state that the prohibition and marginalization of the figure of the English naturalist by Franco's dictatorship had an immediate repercussion in the newspaper *ABC*, which clearly underestimated him for a good part of those years. On the other hand, the analysis of this newspaper also allows us to understand how the arrival of new scientific theories was transmitted to society and the social repercussion they had, generating different currents of opinion.

References

Acosta C (2008) La teoría de la evolución y la censura en TVE. Entre el fijismo, el finalismo ¿y el neodarwinismo? Act Hist Ciència Tècnica 1:271–277

Acosta C (2013) Un pie en el cielo y otro en la ciencia. Las interacciones productivas de Miquel Crussafont (1910–1983). Dynamis 33:321–342

Blázquez F (2001) La teoría sintética de la evolución en España. Primeros encuentros y desencuentros. Llull 24:289–313

Blázquez F (2007) Notas sobre el debate evolucionista en España (1900-1936). Rev Hispan Fil 12: 23–44

Blázquez F (2009a) Breve historia del darwinismo en España. Ambio 1:23–29

Blázquez F (2009b) La recepción del darwinismo en la universidad española (1939-1999). Anu Hist Iglesia 18:55–68

Crusafont M, Meléndez B, Aguirre E (1966) La evolución. Biblioteca de Autores Cristianos, Madrid

Darwin CR (1839) Narrative of the surveying voyages of His Majesty's Ships Adventure and Beagle between the years 1826 and 1836, describing their examination of the southern shores of South America, and the Beagle's circumnavigation of the globe. Henry Colburn, London

Darwin C (1859) On the origin of species: a facsimile of the first edition. Harvard University Press, Cambridge

Díez E, Mateu A, Domínguez M (2009) Darwin in the press: what the Spanish dailies said about the 200th anniversary of Charles Darwin's birth. Contrib Sci 5:193–198

Domínguez M, Mateu A (2012) Spanish Darwinian iconography: Darwin and evolutionism portrayed in Spanish press cartoons. Public Underst Sci 22:999–1010

Ellegård A (1990) Darwin and the general reader: the Reception of Darwin's theory of evolution in the British periodical press, 1859–1872. Original publication 1958. University of Chicago Press, Chicago

Fernández D (2014) La polémica del Darwinismo en la España en el siglo XIX y sus repercusiones culturales y pedagógicas. Master Thesis, Universidad de Cantabria

Florensa C. (2010) Estudi del tractament de la teoria de l'evolució a La Vanguardia Española entre 1939 i el 1978. Master Thesis, Universitat Autònoma de Barcelona-Universitat de Barcelona
Glick T (2010) Darwin en España. Publicacions de la Universitat de València, València
López-Piñero J M (2008) El darwinismo valenciano del siglo XIX y su fundamento histórico. Consell Valencià de Cultura, València
Morales M (2017) Estudi del tractament de la teoria de l'evolució al diari ABC en el 1909 i el 1982. Master Thesis, Universitat de València
Morales M, Domínguez M (2017) La evolución a carta abierta. Seguimiento de la polémica entre el Doctor Tomás Maestre y el Padre Zacarías en el diario ABC a principios del s. XX. eVOLUCIÓN 12(2):39–44
Moreno C, Lujan JL (2009) Darwin como noticia: La imagen de Darwin a través de los medios de comunicación en el bicentenario de su nacimiento. Ludus Vitalis 17:259–279
Núñez D (1969) El darwinismo en España. Editorial Castalia, Madrid
Núñez D (1982) La muerte de Darwin en la prensa española de la época. Triunfo 89:76–93
Pelayo F (2009) Debatiendo sobre Darwin en España: antidarwinismo, teorías evolucionistas alternativas y síntesis modernas. Asclepio 61(2):101–128
Peretó J, Català J (2016) A reconciliation with Darwin? Erich Wasmann and Jaime Pujiula's divergent views on evolutionism: biologists and Jesuits. Metode Sci Stud J 7:87–93

Primary Bibliography[1]

Azorín (1909) Independence. ABC, p 4
Azorín (1910) Positivist traditionalism. ABC, pp 7–8
Azorín (1912) Social pessimism ABC, pp 5–6
Bueno M (1925) Words to the wind... Sentimental crime. ABC, pp 7–8
Candide (1978) The bride and groom. ABC, p 15
CD (1973) Oparin, Calvin and Urey -three Nobel Prize winners-, protagonists of a meeting that begins on Monday in Barcelona. ABC, pp 75–76
Darwin, 1882–1982 (1982) ABC, p 1
De Foxá A (1947) The island of wolves. ABC, p 3
Gibson R (1957) A physiological discovery now serves to achieve "spontaneous confessions". Blanco y Negro, pp 114–115
Gómez E (1925) The Darwinian dogma. ABC, p 7
González Rábago P (1970) The history of France in the most beautiful stamps of the world. ABC, pp 13–15
Homage to Darwin in Valencia by telephone from our private service (1909). ABC, p 9
López Ibor JJ (1964) Eppur si muove. ABC, p 3
Martinez Z (1911) Last letter. Addressed to Dr. Maestre. ABC, p 5
Montes E (1944) On Chile's national holiday. My toast. ABC, p 3
National Academy of Pharmacy (1933) ABC, p 38
Pérez de Ayala R (1953) Civilization and civilizations. ABC, p 3
Pérez de Ayala R (1959a) Humanities. Classical spirit and scientific mentality. ABC, p 3
Pérez de Ayala R (1959b) Journey to Patagonia. Repellent and horrifying names. ABC, p 3
Rocamora J (1930) Hearts without firmness. ABC, p 6
Roceta V (1935) On the rational selection of seeds. ABC, pp 12–14
Rodríguez de la Fuente F (1968) The intelligence of the baboons. Blanco y Negro, pp 92–97
Salaverria JM (1936) In the drunkenness of victory. ABC, p 3

---

[1] Note that the newspaper headlines have been translated.

Sassone F (1939) The charming friend. ABC, p 3
Valencia by telephone from our private service (1909) ABC, p 10
Vázquez J (1930) Genetic vulgarization. ABC, pp 11–14
White M (1925) Darwin was right. Blanco y Negro, pp 24–28

Chapter 6
The Descent of Man: Darwin and Psychology

Ester Desfilis

Abstract The aim of this article is to review the psychological evidence presented by Darwin in *The Descent of Man, and Selection in Relation to Sex*, as well as the complex reciprocal relationships between evolutionism and psychology. The theory of evolution by natural selection has been, is, and will be fundamental for psychology, since it allows us to better understand the behavior and psychological processes of humans and other animals. The influence of the theory of evolution on psychology has been very diverse. On the one hand, the recognition of the similarities between humans and other animals due to biological continuity has encouraged experimental studies to understand the causal mechanisms of behavior, justifying the use of laboratory animals as models to study the basis of human psychological processes. On the other hand, the idea of continuity in the psychological capacities of all animals gave rise to animal psychology and comparative psychology, which study the similarities and differences between the psychological processes and behaviors of different species. The recent incorporation of the evolutionary perspective for understanding the design of the human mind by evolutionary psychology deserves a separate mention. Darwinian approaches to the study of human behavior are a source of much controversy and have given rise to conflicting positions ranging from euphoric acceptance to furious rejection.

Keywords Psychology · Mind evolution · Psychobiology · Evolutionary psychology · Theory of mind

---

E. Desfilis (✉)
Departament de Medicina Experimental, Facultat d'Educació, Psicologia i Treball Social, Universitat de Lleida, Institut de Recerca Biomèdica de Lleida Fundació Dr. Pifarré (IRBLleida), Lleida, Spain
e-mail: ester.desfilis@udl.cat

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_6

6.1 Introduction

Darwin's contribution to biology is indisputable, his theory revolutionized the discipline and laid the foundations for transforming it into a science; however, his influence on psychology is not as well known, nor as accepted, although it is a subject on which many articles have been published. Already in 1909, to celebrate the centenary of Darwin's birth, the journal *Psychological Review* published a special issue on the influence of Darwinism on psychology, sociology, and philosophy. The same happened in 2009, when countless activities were organized around the world to commemorate the bicentenary of Darwin's birth and the sesquicentenary of the publication of *On the origin of species* (*Origin* henceforth). From the perspective of psychology, the nine articles published in a special issue of *American Psychologist* (Dewsbury 2009), the official academic journal of the American Psychological Association,[1] should be highlighted. However, it is no easy task to assess the impact of Darwinism in psychology, because the positions on the subject are radically opposed depending on the psychological subdiscipline and the theoretical and/or political positioning of the authors, and because it is such a broad topic that it would be enough for a book (or several).

When I re-read Darwin's *The descent of man, and selection in relation to sex* (*Descent* from now on) to write this essay, I was struck (to the point of making me feel uncomfortable) by how old-fashioned his ideas about human races or class and gender differences are, which obviously cannot be properly assessed without taking into account their historical and social context (Shields and Bhatia 2009 make a very interesting analysis of this issue), but I was also surprised by how modern some of his ideas about the behavior and mental processes of animals (including humans) are and how many of the debates and controversies of that time are still alive.

6.2 *Origin*: From Species to Man

In *Origin* the word "man" appears 56 times, but practically all of them speak of man as the agent that selects, not as the object of the selection process. Darwin makes lavish use of the analogy between the mechanism of natural selection and the "artificial" selection exercised, consciously or unconsciously, by humans on domesticated species of animals and plants, favoring the survival and reproduction of individuals with the desired characteristics. However, Darwin was perfectly aware that humans were the product of evolution and should be included, along with the rest of living beings, in any explanation of their origin. In fact, the last chapter of the book, in which he presents the final conclusions, includes the only paragraph

---

[1] Incidentally, the British Psychological Society did not see fit to devote a special issue, or even an article, to Darwin in the *British Journal of Psychology*. In fact, it is curious that no article containing the word Darwin in the title has ever been published in the journal.

dedicated to human evolution, in which he also anticipates the implications of the theory of evolution for psychology:

> In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history (Darwin 1859, p. 488).

The end of this paragraph is one of the most quoted sentences in Darwin's work and he himself quotes it in the introduction to *Descent* (Darwin 1871). In this book Darwin fully immerses himself in the implications that the theory of evolution by natural selection has for understanding human nature and the origin of our species, and delves into the mechanism of sexual selection. Darwin knew that his theory would generate much controversy and opposition, it had taken him two decades to put in order all the data that supported it and decide to publish them in *Origin*, and including the evidence on human evolution could generate even greater social rejection. He was not wrong. The fact that he did not explicitly leave humans out of the scope of his theory (quite the contrary, as the quoted sentence of the conclusions indicates), was interpreted by many of his detractors as a tacit support for the origin of man from other animals. It is curious to see how some of the critical reviews of *Origin* go so far as to claim that Darwin said what he did not dare to say:

> Mr. Darwin boldly traces out the genealogy of man, and affirms that the monkey is his brother, and the horse his cousin, and the oyster his remote ancestor. The human body, in his view, is only a slowly developed zoöphyte, out of which it has grown by a process as natural and uniform as that by which a calf becomes a cow; and, by a parallel advancement, the human mind has become what it is out of a developed instinct (Anonym 1860, p. 475)

What had changed in 1871 to lead Darwin to publish a whole book devoted to human evolution? As Darwin himself acknowledges, what encouraged him to publish it was the good reception that the theory of evolution was having among most naturalists, but also the fact that several works had been published that provided evidence of evolutionary continuity between our species and the great apes, for example, those written by Thomas H. Huxley or Ernst Haeckel, the latter so appreciated by Darwin that he claimed that if he had read it before starting to write *Descent* he would never have written it, which is surely more a polite comment than a reality.

A criticism repeated at that time by many detractors of the idea of the origin of man from other animals was that, although similar in anatomy, humans possessed unique mental capacities and moral faculties incomparable to those of any other species, which highlighted the fact that we had been created in the image of a superior being. Even some naturalists and thinkers who accepted that the rest of living beings could have evolved by natural selection doubted that this mechanism could explain the origin of our species or our mental capacities. To Darwin's surprise, Alfred R. Wallace himself, co-discoverer of the theory of evolution by natural selection, considered that the human mind was too complex to have evolved gradually and that we should accept an evolutionary discontinuity between the mere sensitivity present in other animals and human rational intelligence. Darwin admits that man possesses mental capacities superior to those of other animals, but he considers that the differences are of degree. For him there are no exclusively human mental capacities; indeed, the existence of similar mental capacities between man and other primates is a clear proof of their evolutionary continuity.

In *Descent*, Darwin devotes two chapters to presenting evidence that "there is no fundamental difference between man and the higher mammals in their mental faculties" (Darwin 1871, p. 35). In the first of the chapters, he practically takes for granted that we share the same senses, that we have a few instincts in common related to survival and reproduction (in the next chapter he deals at length with the social instinct) and that we experience the same emotions (he does not elaborate much this point to which he will devote his next book *The expression of the emotions in man and animals*, Darwin 1872, *Expression* from now on). However, he devotes most of this chapter and the whole of the following chapter to providing examples of the existence in different animals of the "more intellectual faculties and emotions," which he considers basic to the development of the "higher" mental faculties, and to demonstrating that those faculties that were considered exclusively human were not such. He concludes that both the complex emotions (including wonder and curiosity) and the more intellectual faculties (imitation, attention, memory, imagination, and reason) are present in all vertebrate animals (especially primates), although to different degrees, and that within each species there is inter-individual variation (on which natural or sexual selection can act). One by one, he dismantles the assertions made by different authors about the insurmountable differences between human capacities and those of other animals. The use of tools, the capacity for abstraction, self-awareness, language, the sense of beauty, and human religiosity would have precursors in more rudimentary mental abilities present in other animals. Special mention deserves for Darwin the moral sense, which he relates to the origin of sociability, and to which he devotes a whole chapter and part of another. The chapter begins with the following sentence:

> I fully subscribe to the judgment of those writers who maintain that of all the differences between man and the lower animals, the moral sense or conscience is by far the most important. (Darwin 1871, p. 70)

It is interesting how he begins by underlining his agreement with the statement, and then goes on to expose as highly probable that any animal endowed with strong social instincts and advanced mental capacities should inevitably possess a sense of morality.[2] Social instincts, such as the urge to help our fellows and compassion (empathy), along with the importance we attach to the approval and disapproval of our actions by others would have served as the impetus and guide for basic rules of right and wrong, from which the moral sense would have evolved. Life in society

---

[2] Throughout the book Darwin uses this resource on numerous occasions: claiming to agree with a socially accepted idea, to then generate doubts about it or directly provide evidence that contradicts it.

would not only have driven the evolution of morality, but also of human[3] intellectual faculties, aspects that are addressed in Chap. 5, concluding that in man these faculties would have been gradually perfected through natural selection acting on individuals or groups (tribes).

> It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection (Darwin 1871, p. 166)

It is evident that Darwin was particularly concerned with the evolution of morality and social instinct, and he devotes a third of the first part of the book to this subject. *Origin*'s main message emphasized competitive relationships, mainly between individuals of the same species.[4] Natural selection favors selfish individuals over altruistic ones. The problem is that in nature there are numerous examples of cooperative behavior and apparent altruism in social species of zoological groups as diverse as insects, birds, and mammals. Darwin was aware of the problem, and many of his detractors had used it to attack his theory. Even today the evolution of cooperation and altruism in social species is a topic of great interest and controversy among behavioral scholars, ethologists, and psychologists alike. Interestingly, although theories have been refined and evidence has accumulated to support them, all the mechanisms proposed by Darwin to answer this problem continue to be the subject of study and debate by different disciplines. In *Descent* Darwin puts much emphasis on the psychological causal mechanisms ("proximate" causes in the sense of Mayr 1961) that would drive social animals to behave altruistically, such as empathy or compassion[5] (a key component of his idea of social instinct) and feelings of satisfaction or remorse (depending on whether one acts following the instinct or not), aspects that still arouse considerable interest from psychologists (Jensen 2016). In different chapters, Darwin introduces, sometimes without much emphasis, explanations related to most of the "ultimate" causes (Mayr 1961) that are still considered relevant today, such as kin selection, reciprocity, reputation and intergroup selection, the latter being the most controversial today (West et al. 2007; Kurzban et al. 2015). Darwin was also concerned about the philosophical, social and political implications

---

[3] Many cognitive psychologists now agree that the main driver of the evolution of intelligence was the social environment. The effective management of the demands of the social environment would have driven the evolution of the brain and intelligence in different species of social animals (Byrne and Whiten 1988; Dunbar and Shultz 2007).

[4] Although in the popular imagination natural selection is often associated with examples of evolutionary pressures exerted by individuals of one species on another (e.g., predator-prey or parasite-host relationships), it was clear to Darwin that the greatest competition was between individuals of the same population.

[5] "Sympathy" in the original.

of his theory, which both Wallace and some of his most fervent followers had already pointed out. At stake was to understand the origin of our goodness and hence perhaps the emphasis on the importance of social instinct and morality as central elements to what makes us human. For Darwin, human nature includes competitive tendencies, but also prosocial ones, the latter being the highest, the most genuinely human.

6.3 Acceptance of the Theory of Evolution and Its Impact on the Beginnings of Psychology

The theory of evolution received important criticism from theologians, philosophers, and naturalists, but it was well received by the psychologists of the time (Angell 1909). In the nineteenth century, psychology is in the process of independence from its philosophical matrix, to become a scientific discipline. Several decades before the publication of *Descent*, psychology had already begun its transformation into an experimental science and aspired to explain mental processes from their physiological mechanisms, to which the studies of various authors with training in medicine and physiology had contributed. The experimental work of Hermann L. F. von Helmholtz, Ernst H. Weber, and Gustav T. Fechner, the fathers of psychophysics, had provided quantifiable data on the relationship between the mental (sensory experiences) and the material (external reality in the form of stimuli varying in controlled characteristics). On the other hand, observational studies on the effects of acquired brain damage in humans by authors such as Paul Broca, who is considered the father of neuropsychology, had demonstrated the association between areas of the brain and specific cognitive functions. Broca was a fervent Darwinist and the recognition was mutual (Broca is cited 14 times in the second edition of *Descent*).

Among the first to apply the theory of evolution to psychology we find Herbert Spencer who in several of his publications and especially in his *The principles of psychology* (1855) defends the continuity of all mental phenomena from the contractions of a polyp to the evolution of thought and the need to consider mental processes as adaptations to the environment. The book is written before the publication of *Origin* and in it he sets out his own ideas about evolution based on Lamarck. For Spencer, complex mental phenomena arise from the association of simple phenomena such as sensations and this association occurs because organisms are in a process of progressive adaptation to the environment, adjusting the subjective experience to the environment; these adjustments could be passed on to offspring (Young 2000). For Spencer the laws of evolution are universal, the processes of integration and differentiation generate changes that affect different levels of organization from the solar system to human societies, through the Earth, climate, plants, and animals. Spencer will apply his laws of evolution not only to psychology, but to many other disciplines such as philosophy, education, biology, sociology, and ethics (Holmes 1994). Although Spencer is considered the father of social

Darwinism, his view of evolution was more Lamarckian than Darwinian, as evidenced by his strong defense of the inheritance of acquired characters in his writings and his criticism of natural selection to which he devotes the text "The inadequacy of natural selection" (Spencer 1893). Spencer was the one who formulated the phrase "survival of the fittest," which Darwin incorporated in the fifth edition of *Origin*. Spencer's work had a great influence on Darwin, who quotes him nine times in the second edition of *Descent* and prompted him to include the possibility that some modifications in morphological characters or habits acquired throughout life could become hereditary (Darwin 1871).

The definitive impulse to experimental psychology came from the hand of Wilhelm M. Wundt with the publication in 1874 of his book entitled *Grundzüge der physiologischen Psychologie* (*Principles of Physiological Psychology*) and the creation of his psychological research laboratory in 1879. One of his disciples Edward Tichener is considered the founder of the structuralism school, whose aim was to identify the basic elements or structures of psychological experience through introspection, and on which Darwinism had little impact beyond assuming our kinship with the rest of living beings and placing psychology within the natural sciences. Darwinism had a much greater impact on functionalism, a theoretical current that arose in the USA at the end of the nineteenth century and which stated that the aim of psychology was to understand the function of mental processes, their adaptive value. In 1890, William James published *Principles of Psychology*, one of the most important books of psychology, with a clear influence of the work of Spencer and Darwin. In his book, James argues that mental processes such as emotions, selective attention, and consciousness are adaptations of the mind that have evolved by natural selection. These processes allow organisms to process information about the environment helping them to generate adaptive behaviors that contribute to their survival and reproduction (Ludden Jr 2019). James drove the development of the American school of psychology, which came of age in 1892, with the founding of the American Psychological Association (APA).

For much of the twentieth century, the predominant theoretical approach in the study of behavioral mechanisms was behaviorism, led by American psychologists John B. Watson and Burrhus F. Skinner, influenced by the reflexology of Russian researchers Ivan M. Séchenov and Ivan P. Pavlov. For the behaviorists, introspection, which had been the preferred methodological approach of 19th century psychologists, did not provide reliable data. The only possible scientific approach was the objective observation and quantification of changes in behavior in response to different stimuli or environmental modifications, in controlled experiments. Behaviorists are evolutionists, but they consider that the evolutionary process would have generated a reduced repertoire of basic and innate mental abilities that would include the most elementary sensory processing and a few general rules for learning and reasoning. According to their approach, heredity and instincts would not be important in explaining human behavior (a view opposed to Galton's, which we will discuss later); what we are and what we do is a consequence of our experiences, which shape our behavior in response to positive or negative reinforcement. Human behavior, personality and intellect would be the result of culture and the nurturing environment.

6.4 The Theory of Evolution and the Psychological Disciplines

Beyond his influence on the theoretical currents of the young psychology, Darwin's work had an important impact on the origin of several of the disciplines that constitute the field of study of psychology, and one of them is developmental psychology. William T. Preyer's pioneering studies on the psychological development of the child (*Die Seele des Kindes*, *The Soul of the Child*; Preyer, 1882) were inspired by the observations on the development of the psychological capacities of his children that Darwin had published in *Descent*, *Expression* and above all in a scientific article based on the annotations on his firstborn son that he published in the recently founded psychology journal *Mind* (Darwin 1877), and which is considered the first systematic study of developmental psychology. Darwin was methodologically innovative, applying to infant behavior the same systematic observation and structured description (detailing the exact time of appearance or disappearance of each behavior) that he used for the study of nature; a method copied by later psychologists (Lorch and Hellal 2010). However, Darwin's theoretical contribution to developmental psychology is more controversial, with some authors arguing that Darwinism was highly influential, while others argue that his contribution was very partial and mostly erroneous (Vidal et al. 1983; Charlesworth 1992). At the end of the decade of 1890, some psychologists bet on introducing the evolutionary approach in its full extent to the studies of human psychological development, naming this new approach evolutionary developmental psychology (Geary and Bjorklund 2000; Hernández-Blasi et al. 2008).

Darwinism had a decisive influence on the origin of another discipline of psychology: differential psychology (Mukiur 2009). Francis Galton, Darwin's cousin, is considered the father of this discipline, which studies the psychological differences between individuals or groups. After reading *Origin*, Galton was very impressed by the explanatory power of natural selection to understand the evolution of living beings and aspired to apply its principles to the study and advancement of our species. For natural (or artificial) selection to act on a character, two conditions had to be met: it had to vary between individuals and this variation had to be heritable. Galton set out to demonstrate that human psychological capacities fulfilled these two premises, using quantitative measures of psychological traits (based on questionnaires) and developing statistical techniques that were very advanced for his time. He was the first to carry out studies on heritability, to demonstrate the relative influence of heredity and environment ("nature" *vs.* "nurture"), based on genealogy studies and comparing twins. His methodological contributions were very important, but Galton's ideas were burdened by the classism and racism of the time, which led him to conclude that the fittest individuals, i.e. those endowed with better qualities, belonged mostly to distinguished families, i.e. the wealthier social classes. Furthermore, he concluded that intelligence and other psychological characteristics were mostly inherited (innate) and that the environment was of little importance. Therefore, the abilities of our species could be improved by techniques of "artificial selection" or eugenics. Eugenic ideas were very well accepted, especially among the ruling social classes, but also among the emerging middle class across the political spectrum. Many philosophers and thinkers supported it. Galton proposed a positive eugenics (favoring the reproduction of the most intelligent), but many theorists and politicians of the late nineteenth century and much of the twentieth century opted to apply a negative eugenics (sterilization or elimination of individuals carrying "undesirable" characteristics).[6] Those considered unfit for reproduction included criminals, people with physical or mental disabilities, and members of disadvantaged social groups (the poor, immigrants, and ethnic minorities). From the second half of the twentieth century, eugenics went from being considered morally desirable[7] to ethically unacceptable, partly because of the horror generated by the Nazi extermination camps. The rejection of eugenics and its consequences has led many psychologists to overlook Galton's contributions to psychology (some articles and books on the history of psychology do not even mention him). Darwin himself did not support eugenics, although he thought that the relaxation of natural selection on our species could harm it; he did not consider acceptable the intervention of the state on reproduction, nor the withdrawal of help to the weakest ("which would deteriorate the noblest part of our nature" in Darwin's own words) (Paul 2003). Darwinism has been used to defend the most diverse political and social causes, which has generated an atmosphere hostile to the application of Darwin's ideas to the scientific study of human societies. In fact, it is among social psychologists where we find the most radically anti-Darwinist positions.

One of the fields in which evolutionary thought has most influenced is the study of animal behavior, which has traditionally been addressed by two disciplines: ethology and animal psychology. Within the latter, comparative psychology is the current in which the evolutionary perspective has been more present (Colmenares 1996; Burghardt 2009). Comparative psychology would have its genesis in the descriptions of the behavior of various animal species made by Darwin in the chapter on instinct of the *Origin*, but especially in *Descent* and *Expression* (Gottlieb 1979). Following the path initiated by Darwin, George J. Romanes aimed to demonstrate the continuity in psychological processes between animals and man, as well as their phylogenetic origins, by collecting information on the maximum number of species,

---

[6] Although forced sterilization is now a legally and socially rejected practice, it is still applied in many countries to specific population groups, as reflected in the report of the joint statement that the World Health Organization (2014) on the elimination of forced sterilization. https://www.who.int/reproductivehealth/publications/gender_rights/eliminating-forced-sterilization/en/.

[7] "Since the object of all social morality is the good of the human race, and since eugenics also has no other end in view except the improvement of the human race, it is plain that social morality and eugenics are indissolubly connected," p. 26 of the article published by Inge (1909).

analogously to what was being done in comparative anatomy. He published three books on the subject: *Animal Intelligence* (1882), *Mental Evolution in Animals* (1883), and *Mental Evolution in Man* (1888). In them he compares the behavior of several animal species with human behavior and elaborates a theory on the evolution of intelligence. Between Darwin and Romanes there was a deep friendship and mutual recognition. *Mental Evolution in Animals* includes as an appendix a posthumous text by Darwin, which he wrote as part of the chapter on the instinct of the *Origin* instinct and did not finally include.

Later comparative psychologists, concerned with applying maximum objectivity to the study of animal behavior, criticized Darwin's and Romanes' contributions for basing their proposals on anecdotal observations, for their mentalistic approach and their anthropomorphic interpretations (Angell 1909; Fitzpatrick and Goodrich 2017). One of the most incisive critics was C. Lloyd Morgan, who laid the foundation for the application of rigorous methods to the study of comparative psychology. In order to avoid errors in the interpretation of animal behavior, he proposed the principle known as "Morgan's canon," published in his *Introduction to Comparative Psychology* (1894). Humans tend to attribute mental states, thoughts, feelings, and intentions to other human beings. This ability is now called Theory of Mind (Premack and Woodruff 1978) and is considered to be of great adaptive value in allowing us to predict the behavior of others and act accordingly. However, this tendency to mentalize the actions of others is not limited to individuals of our species, but we apply it to other living beings or even inanimate objects. The problem is that it can lead us to attribute to animals capabilities that they do not possess. This error is called anthropomorphism and is what Morgan's canon aims to avoid by applying the principle that an action should not be interpreted as the result of a higher psychic faculty, if it can be interpreted as the result of a lower one in the psychological scale. Although Morgan accepts that all living beings are genealogically related, he considers that the differences that separate human beings from the rest of nature cannot be ignored. In one branch of a phylogenetic tree, novelties may appear that do not appear in others, so that a shared genealogy does not imply that there are no qualitative differences between the traits of related species. Morgan does not exclude the possibility of interpreting animal behavior as the result of higher mental processes, but to accept this hypothesis requires empirical evidence of the existence of these psychological processes in that species and this evidence could only be obtained through the application of rigorous experimental methods (Colmenares 2015; Fitzpatrick and Goodrich 2017). Morgan's work directly inspired Thorndike's experimental studies on animal learning and was an important stimulus for the behaviorist movement.

Compliance with the dictates of Morgan's canon is still considered a fundamental requirement when investigating animal minds (Shettleworth 2010; Colmenares 2015; Fitzpatrick and Goodrich 2017). However, there are more and more critical voices with its postulates. We find them among philosophers of science (for example, Daniel Dennet, Elliot Sober and Simon Fitzpatrick), but also among biologists and psychologists studying comparative animal cognition (Frans de Waal, Gordon Burghardt, Kristin Andrews, and Marc Bekoff, among others). Some authors have argued that the application of a "critical" anthropomorphism would not only not be a mistake to avoid, but could help us to better understand animal behavior and to generate useful hypotheses for subsequent experimental testing (Burghardt 1991; de Waal 1999). A frequent criticism is that the application of the canon can avoid overestimating the mental complexity of animals, but it can also underestimate it, and it would be as bad to attribute cognitive abilities to animals that do not have them, as not recognizing them in animals that do have them (de Waal 1999; Sober 2005; Andrews and Huss 2014). Also, it has been criticized the lack of clear criteria to consider a mental ability as superior or inferior to another, and that this classification would rely on an anthropocentric view (Sober 2005). These criticisms have been countered by other authors, such as Wynne (2004, 2007), who defend the validity of Morgan's canon against the risk of falling into a folk psychology. Although all comparative psychologists assume that there are very large differences between humans and other primates in cognitive abilities, some agree with Darwin in considering that they are of degree, i.e. quantitative, while others consider that the differences are qualitative and represent a clear discontinuity between humans and other animals (Premack and Woodruff 1978; Colmenares 2015).

6.5 Evolutionary Psychology: A New Theoretical Approach

In the last decade of the twentieth century, a new psychological current emerged with force, which calls itself evolutionary psychology and has as its main objective to discover and understand the design of the human mind and its adaptations. The principles on which it is based can be summarized in the following statement: our neural circuits are the result of an evolutionary process and have been "designed" by natural selection to solve the problems that our ancestors have faced throughout our evolutionary history. Evolutionary psychologists believe that our brains are made up of cognitive modules, highly specialized mental algorithms, which have evolved independently to appropriately solve the problems our ancestors faced: finding a mate, finding food, defending themselves from enemies, raising children, etc. The anthropologist John Tooby and the psychologist Leda Cosmides were the main theorists of this perspective and they propose that in order to understand our behavior in the present, we have to take into account that it is generated by information processing mechanisms that exist because they solved adaptive problems in the past, in the ancestral environments in which the first humans evolved and, therefore, could be neutral or maladaptive in the present (Tooby and Cosmides 1990, 2005). An important novelty of this theoretical approach with respect to other evolutionary approaches to psychology is that it does not emphasize the continuity between humans and other animals, but rather the adaptive value of human behavior and mental processes.

Although the foundations of evolutionary psychology go back to Darwin's theory of natural selection, its most recent antecedents are to be found in the sociobiology of Edward O. Wilson. The publication of his book *Sociobiology: The new synthesis* in

1975 marked the beginning of a "resurgence" of interest in applying the evolutionary perspective to the study of human behavior. In this context, different approaches emerged within biology, anthropology and psychology that received different names: sociobiology or biosociology, human ethology, dual inheritance theory, cultural evolution, ecology of human behavior, evolutionary (or Darwinian) anthropology, and evolutionary (or Darwinian) psychology. Some of these names are synonymous, but others represent different approaches, with different emphases and methodologies, that were originally at odds with each other (e.g., human behavioral ecology and evolutionary psychology). In fact, these different evolutionary approaches to human behavior have much in common, since they coincide in the main adaptive problems that humans must solve to survive and reproduce and, therefore, in their research topics (e.g., obtaining food, avoiding danger, reproductive strategies, mate choice, childcare, task division, cooperation, etc.). They also agree on the potential of evolutionary theory to blur the boundaries between academic disciplines that study different aspects of human behavior (Desfilis 2009).

During the first decade of the twenty-first century, a great effort of integration was made to include the different approaches and methodologies in a common theoretical framework (Dunbar and Barrett 2007). This broad view of evolutionary psychology proposes that in order to understand human behavior and the human mind, it is necessary to consider functional issues (related to the adaptive value of a trait in the present or in the past), mechanisms (cognitive and neurobiological), and ontogeny (the complex interactions between genes and environment during development). In addition, it is essential to recognize the importance of culture and complex social relationships as factors responsible for our behavior (Desfilis 2009). To date, this process of convergence has not been completed, although many bridges have been built between different disciplines and approaches (Brown and Richerson 2014).

Despite its youth, evolutionary psychology has generated an enormous social interest that goes beyond the scientific field, giving rise to conflicting positions, philias, and phobias. Many scientific articles of original research have been published, but also theoretical and review articles, manuals for university teaching, popular science books, and journalistic articles. In addition, documentaries and television programs have been made on some of its research topics. Criticism of evolutionary psychology by scientists from different specialties has been numerous and diverse (Curry 2003; Neher 2006; Bolhuis et al. 2011). It has been criticized for assuming an extreme adaptationism, for the excessive specialization of the mental modules it proposes, for a conception of the environment of evolutionary adaptation that is too strict and too distant in the past, and for not adequately considering neural mechanisms, nor the complexity of the interactions between genes and environment during development. Many of these criticisms have been made by proponents of applying the evolutionary approach to the study of human behavior and mind; thus, they do not deny the interest of the approach, but criticize the more restrictive versions of evolutionary psychology. However, evolutionary psychology has also received amendments to the whole, especially from some sectors of the social sciences, which consider that culture is the only valid causal explanation for our behavior, and that biology has nothing to contribute. Feminist sociologist of science

Hilary Rose and neuroscientist Steven Rose are among the most radical critics. Their arguments are that evolutionary psychology is more a fashionable ideology (with political objectives) than a science, because it promotes simplistic, socially irresponsible and culturally pernicious explanations of human behavior that justify conservative and anti-feminist prejudices and political positions (Rose and Rose 2000; Curry 2003).

6.6 Darwin and Twenty-First Century Psychology

As we have seen throughout the chapter, since the publication of *Descent* the application of the evolutionary perspective to the human mind has generated and still generates a lot of rejection; most probably because it concerns our beliefs about our place in the world, our deep intuition that we are special. In fact, all human societies have some story about the origin of man, which includes the idea of our uniqueness; we are unique and exceptional, different from the rest of the beings that inhabit the planet. When psychology refers to the uniqueness of humans, it invokes qualities, capacities, and/or abilities that would be exclusively human and that would represent a clear discontinuity with other species. Psychologists have devoted much effort to investigating what human uniqueness consists of.

Darwinism in its more modern approaches has much to contribute to the twenty-first century psychology, and psychobiology is the discipline that bears the responsibility for incorporating this perspective, as it is the discipline that applies a biological approach to the understanding of behavior and mental processes. However, in a review of the history of the concept of psychobiology, Donald Dewsbury (1991) concludes that by the end of the twentieth century psychobiology had adopted an overly reductionist approach, in which the term biology is used as a synonym for physiology. In general, psychobiological disciplines interested in understanding the neural mechanisms of behavior, such as physiological psychology, psychopharmacology, neuropsychology, or psychophysiology, although they assume that the brain and neural mechanisms are the result of the evolutionary process, consider that to understand how these mechanisms work, the evolutionary pressures that have sculpted them are not relevant. Very few textbooks in these disciplines include a view on the ultimate causes or evolutionary function, i.e. on the adaptive value of psychological mechanisms (an interesting exception is Striedter 2016).

It is time to apply the broader conception of psychobiology, which was proposed by Dewsbury (1991) himself and has been subsequently elaborated by other authors (Colmenares 2015). Among other things, this broad conception incorporates the evolutionary perspective and pays attention to both proximate and ultimate causal explanations (Colmenares 2015). In this context, it is important for all psychology students to learn the basic concepts of evolutionary biology and behavioral ecology, so that they can adequately understand evolution and contribute to the future integration of evolutionary approaches into mainstream psychology (Burke 2014).

References

Andrews K, Huss B (2014) Anthropomorphism, anthropectomy, and the null hypothesis. Biol Philos 29(5):711–729

Angell JR (1909) The influence of Darwin on psychology. Psychol Rev 16(3):152–169

Anonym (1860) On the origin of species, by means of natural selection. Charles Darwin. Living Age 66(848):474–506

Bolhuis JJ, Brown GR, Richardson RC, Laland KN (2011) Darwin in mind: new opportunities for evolutionary psychology. PLoS Biol 9(7):e1001109

Brown GR, Richerson PJ (2014) Applying evolutionary theory to human behaviour: past differences and current debates. J Bioecon 16(2):105–128

Burghardt GM (1991) Cognitive ethology and critical anthropomorphism: a snake with two heads and hognose snakes that play dead. In: Ristau CA (ed) Cognitive ethology: the minds of other animals: essays in honor of Donald R. Griffin. Lawrence Erlbaum Associates, Hillsdale, pp 53–90

Burghardt GM (2009) Darwin's legacy to comparative psychology and ethology. Am Psychol 64(2):102–110

Burke D (2014) Why isn't everyone an evolutionary psychologist? Front Psychol 5:910

Byrne RW, Whiten A (eds) (1988) Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans. Oxford University Press, Oxford

Charlesworth WR (1992) Darwin and developmental psychology: past and present. Dev Psychol 28(1):5–16

Colmenares F (ed) (1996) Etología, psicología comparada y comportamiento animal. Editorial Síntesis, Madrid

Colmenares F (2015) Fundamentos de psicobiología, Vol. II: Comportamiento y procesos psicológicos en contexto evolutivo. Editorial Síntesis, Madrid

Curry O (2003) Evolutionary psychology: "fashionable ideology" or "new foundation"? Hum Nat Rev 3:81–92

Darwin CR (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life, 1st edn. John Murray, London

Darwin CR (1871) The descent of man, and selection in relation to sex. John Murray, London

Darwin CR (1872) The expression of the emotions in man and animals. John Murray, London

Darwin CR (1877) A biographical sketch of an infant. Mind Quart Rev Psychol Phil 2(7):285–294

de Waal F (1999) Anthropomorphism and anthropodenial: consistency in our thinking about humans and other animals. Philos Top 27:255–280

Desfilis E (2009) Comportamiento humano y evolución. In: Colmenares F (ed) Bases Biológicas de la Conducta (I). Centro de Estudios Financieros. UDIMA, Madrid, pp 95–118

Dewsbury DA (1991) Psychobiology. Am Psychol 46(3):198–205

Dewsbury DA (2009) Charles Darwin and psychology at the bicentennial and sesquicentennial: an introduction. Am Psychol 64(2):67–74

Dunbar RIM, Barrett L (eds) (2007) The Oxford handbook of evolutionary psychology. Oxford University Press, Oxford

Dunbar RI, Shultz S (2007) Evolution in the social brain. Science 317(5843):1344–1347

Fitzpatrick S, Goodrich G (2017) Building a science of animal minds: Lloyd Morgan, experimentation, and Morgan's Canon. J Hist Biol 50:525–569

Geary DC, Bjorklund DF (2000) Evolutionary developmental psychology. Child Dev 71(1):57–65

Gottlieb G (1979) Comparative psychology and ethology. In the first century of experimental psychology, 1st edn. Routledge, pp 147–176

Hernández-Blasi CH, Gardiner AK, Bjorklund DF (2008) When development matters: from evolutionary psychology to evolutionary developmental psychology. Anu Psicol 39(2):177–191

Holmes B (1994) Herbert spencer. Prospects 24(3):533–554

Inge WR (1909) Some moral aspects of eugenics. Eugen Rev 1(1):26–36

Jensen K (2016) Prosociality. Curr Biol 26(16):748–752

Kurzban R, Burton-Chellew MN, West SA (2015) The evolution of altruism in humans. Annu Rev Psychol 66:575–599

Lorch M, Hellal P (2010) Darwin's "natural science of babies". J Hist Neurosci 19(2):140–157

Ludden DC Jr (2019) A history of modern psychology: the quest for a science of the mind. SAGE Publications, New York

Mayr E (1961) Cause and effect in biology. Science 134(3489):1501–1506

Mukiur RM (2009) La influencia de Charles Darwin en el estudio de las diferencias individuales de Francis Galton. Rev Hist Psicol 30(2):215–222

Neher A (2006) Evolutionary psychology: its programs, prospects, and pitfalls. Am J Psychol 119(4):517–566

Paul DB (2003) Darwin, social Darwinism and eugenics. In: Hodge J, Radick G (eds) The Cambridge companion to Darwin. Cambridge University Press, New York, pp 214–239

Premack D, Woodruff G (1978) Does the chimpanzee have a theory of mind? Behav Brain Sci 1(4): 515–526

Rose H, Rose S (eds) (2000) Alas poor Darwin: arguments against evolutionary psychology. Harmony Books, New York

Shettleworth SJ (2010) Clever animals and killjoy explanations in comparative psychology. Trends Cogn Sci 14(11):477–481

Shields SA, Bhatia S (2009) Darwin on race, gender, and culture. Am Psychol 64(2):111

Sober E (2005) Comparative psychology meets evolutionary biology: Morgan's canon and cladistics parsimony. In: Daston L, Mitman G (eds) Thinking with animals: new perspectives on anthropomorphism. Columbia University Press, New York, pp 85–99

Spencer H (1893) The inadequacy of "natural selection". Contemp Rev 63:153–166

Striedter GF (2016) Neurobiology: a functional approach. Oxford University Press, New York

Tooby J, Cosmides L (1990) The past explains the present: emotional adaptations and the structure of ancestral environments. Ethol Sociobiol 11(4-5):375–424

Tooby J, Cosmides L (2005) Conceptual foundations of evolutionary psychology. In: Buss DM (ed) The handbook of evolutionary psychology. Wiley, New York, pp 5–67

Vidal F, Buscaglia M, Vonèche JJ (1983) Darwinism and developmental psychology. J Hist Behav Sci 19(1):81–94

West SA, Griffin AS, Gardner A (2007) Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J Evol Biol 20(2):415–432

World Health Organization (2014) Eliminating forced, coercive and otherwise involuntary sterilization: an interagency statement, OHCHR, UN Women, UNAIDS, UNDP, UNFPA, UNICEF and WHO

Wynne CDL (2004) The perils of anthropomorphism. Nature 428:606

Wynne CD (2007) What are animals? Why anthropomorphism is still not a scientific approach to behavior. Comp Cogn Behav Rev 2(1):125–135

Young RM (2000) The development of Herbert Spencer's concept of evolution. In: Offer J (ed) Herbert spencer: critical assessments, vol 2. Routledge, London, pp 378–383

Chapter 7
Human Evolution: The Linguistic Evidence

Joana Rosselló, Liliana Tolchinsky, and Carme Junyent

Abstract In *The Descent of Man* (1871), Darwin substantiates the idea that our species originated by natural selection, including the mind. Consequently, he meets the challenge of Max Müller, for whom the capacity for language in particular cannot be explained as a result of natural selection. Darwin overcomes the challenge with a conjecture about the evolution of language that is less well known but more suggestive and powerful, complete and integrated than others currently in force; moreover, by focusing on articulate speech, it is more biologically plausible. The power of his proposal stems from a deep knowledge of language. Here too, Darwin studies phylogeny with an eye to ontogeny; glossogeny, that is, linguistic change, does not escape him either. Phylogeny, ontogeny, and glossogeny constitute, in this order, the three parts of this article.

Keywords Darwin · Speech · Vocal production learning · Evolution of language · Language acquisition · Glossogeny

7.1 Phylogeny

The Descent of Man, and selection in relation to sex (*Descent* henceforth) (Darwin 1871) is an extensive argument to demonstrate that our species has evolved by natural selection. Darwin, consequently, had to build in a selectionist explanation of the origin of language. Only in this way could he counter very widespread adverse positions embodied, for example, by the naturalist Alfred R. Wallace and the linguist Max Müller. The former, co-discoverer with Darwin of the theory of natural selection, denied that it was applicable to the human mind, and the latter considered that language establishes an impassable frontier between humans and animals. In *Descent*, the section specifically devoted to tackling the challenge of language consists of only ten dense paragraphs, which deserve to be read and reread for the

J. Rosselló (✉) · L. Tolchinsky · C. Junyent
Department of Catalan Philology and General Linguistics, University of Barcelona, Barcelona, Spain
e-mail: joana.rossello@ub.edu

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_7

cautious boldness, completeness and scope of the evolutionary conjecture they present. It is also worth reading them to know firsthand what Darwin said. It should be borne in mind that the Darwinian proposal has long been ignored (Fitch 2010, p. 474) and that, once rediscovered, it is often presented in part, as the precursor of what is now referred to as "musical proto-language" (Fitch 2013a, b; Tallerman 2013). At the same time or separately, it is fairly widely held that the proposal is limited to a conjecture about the origin of speech rather than language (Lorenzo 2006; Bolhuis et al. 2014). Speech, in turn, is considered secondary in the otherwise antagonistic approaches dominant today, namely constructionism (Tomasello) and nativism (Chomsky).

Contrary to these dominant views, by contextualizing and scrutinizing Darwin's argument, it can be affirmed that the now called musical proto-language is an important piece of a complete and integrated evolutionary view of language in which speech is central. Completeness and integration are the two principles that Darwin never abandons in reconstructing the evolution of language; evolutionary continuity is presupposed. Completeness is especially evident in the fact that Darwin differentiates the notions of language, speech, and tongue (a particular language) and uses them accordingly. Moreover, to a certain extent he takes into account the signed modality. He treats the signs used by the deaf as a manifestation of language, something that took a long time to be accepted in linguistics. When necessary he goes even further and adds *articulate* (articulate language, articulate speech). His careful use of terms contrasts with what is observed today. Darwin, for example, never uses "speech and language." Such a phrase, on the other hand, has become a common fixed expression in many articles (42,600,000 entries in *Google,* January 2021) where one thing is not differentiated from the other, thus contributing to the conceptual confusion prevailing in the language sciences. Moved by the principle of integration, at the antipodes of dichotomous and essentialist thinking, Darwin reconciles concepts normally considered antagonistic. Thus, the innate (instinct) and the learned (art), communication and thought, use and knowledge interact rather than oppose each other. The reader will be able to appreciate this below, in the reproduction of the story line of the section *Language*, in Chap. 3.

Chapter 3 of *Descent* is the first chapter devoted to human and lower animal mental powers. On a documented empirical basis, sometimes anecdotal, Darwin reasons that incipient stages of capacities supposedly exclusive to man can be observed or inferred in other animals. This would be the case with the ability to progressively improve, to make tools or handle fire, abstraction, and self-consciousness, etc. Also, of course, with respect to language, which in the corresponding section is examined with more attention than the others by the fact that "this faculty has been considered precisely as one of the most important differences between man and the lower animals." Moreover, according to our author, it is the case that language may well be the cause of other human peculiarities. Let us see it. Darwin, at the end of the fourth chapter of the second edition (definitive version of the text, Darwin 1877a), begins by saying that "the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" (Darwin 1877a, p. 126); he summarily reviews the data that support the assertion in question and, finally, with the caution that he occasionally intersperses with his boldness, he reasons thus:

> If it could be proved that certain high mental powers, such as the formation of general concepts, self-consciousness, etc., were absolutely peculiar to man, which seems extremely doubtful, it is not improbable that these qualities are merely the incidental results of other highly-advanced intellectual faculties; and these again mainly the result of the continued use of a perfect language (Darwin 1877a, p. 126)

It should be noted that the possibility pointed out in the quote, rightly called plan B by Bickerton (2014), only makes sense if it can be shown that language does not escape natural selection. And no, it does not escape it since, as Darwin remarks—with an example of integration of opposites—language being "half-art, half-instinct [. . .] still bears the stamp of its gradual evolution." Of note is that it is not on the basis of being a half-instinct that language falls under the sphere of action of natural selection. Also the half-art does. Such an integration is at the heart of the brilliant argument deployed in the ten paragraphs of Chap. 3 (Darwin 1877a); an argument to be followed carefully.

Paragraph 1. Other animals have language. Darwin, a redoubtable master in the art of introducing into his discourse quotations from others, puts into the mouth of the archbishop and "very competent judge" Whately that man "is not the only animal that can make use of language to express what is passing in his mind, and can understand, more or less, what is so expressed by another" (Darwin 1877a, p. 84). Darwin, even with the Archbishop's support, is not content with anecdotes about how monkeys, dogs, or birds understand each other vocally.

Paragraph 2. The use of articulate language is unique to man. Unlike animals, man possesses an *articulate* language in addition to using, like other animals, [non-articulate] cries, *gestures and facial movements*—note the integration of the spoken modality with gesture and facial expression. But be careful, this exclusive use cannot be confused neither with the understanding of articulated sounds, something that dogs are capable of; nor with the mere production/articulation of such sounds, as parrots and other birds can do; nor with the ability to connect sounds with defined ideas in the production, a milestone within the reach of trained parrots. What truly differentiates us from the rest of animals is the "almost infinitely larger power [of man] of associating together the most diversified sounds and ideas; and this obviously depends on the high development of his mental powers" (Darwin 1877a, pp. 85–86).

Paragraph 3. Art or instinct: could language be an art, similar in this respect to brewing or baking, as some philologists seem to believe? Writing, perhaps yes, Darwin answers, but not language. Nor does language seem to be a pure instinct insofar as languages have to be learned. Still less would it be a pure art "since man has an instinctive tendency to speak, as we can see in the babbling of our little ones." Languages, moreover, cannot be considered deliberate inventions in whole; they have been formed slowly and, unconsciously, through numerous steps. For that reason, *the closest analogy* to language is to be found in the *sounds of songbirds*, who exercise their ability instinctively but have to learn the song from parents or tutors. Songs as such are thus as little innate as languages. Ontogenetic parallels between the development of speech and song in birds, transmission of learned songs belonging to another species, glossogenetic parallels between the dialectal differences in the song of a single species according to geographical distribution and the dialects of languages; because of that and some other details Darwin concludes that "an instinctive tendency to acquire an art is not peculiar to man" (Darwin 1877a, p. 86). In a clear but subtle way, it is formulated what much later Marler (1991) would call "instinct to learn," the quintessence of the principle of integration. The nature *vs.* culture dichotomy is called into question. The half-art, half-instinct combination is not a partial product of natural selection operating on the half-instinct: it is the two halves that fall under its effect.

Paragraph 4. Origin. Familiar with linguists of contrary opinions like Schleicher and Müller, Darwin proposes his own view, namely that language originated by *imitation* and modification by means of *articulated sounds* of various natural sounds with the help also of signs and gestures. At an ancestral stage, the voice must have been used for *singing*, as among primates is observed in gibbons. In these animals, as in birds, singing has a primary function related to courtship and mating, which makes it an object of *sexual selection*, and is thus used for competitive purposes and territorial defense. With the capacity for vocal imitation in place and given the existence of different predator alarm cries in various species of monkeys and birds, could it not be that a particularly clever ape imitated the grunt of a predator to alert its conspecifics to the kind of danger that was approaching? "This would have been a first step in the formation of a language" (Darwin 1877a, p. 87).

Paragraph 5. The effects of the continued use of language on the brain are more important than the refinement of the organs of speech. Darwin argues that the mental powers of our ancestors had to be far superior to those of the present apes before the most imperfect form of speech was given. Now, once speech is installed, its *continued use* and consequent refinement must have impacted *the mind by* enabling and impelling it to carry out *long sequences of thought*: "An extended series of thoughts cannot be done without the aid of words, any more than an extended calculation can be done without the use of numbers or algebra." The connection between the "faculty of speech" and the brain is furthermore beyond doubt as shown by brain diseases affecting "speech" (Darwin 1877a, p. 88).

Paragraph 6. Against Max Müller, concepts pre-exist words. The linguist argued that having words entailed being able to form general concepts and, thus, that without words no animal can have these concepts: an insurmountable barrier would thus separate humans from the rest. Darwin, for his part, insists here that he has already shown how other animals have the ability to form concepts, albeit rudimentarily. He also adds that it would not be understood how it is possible for children under one year old to connect sounds and ideas if these ideas are not already in their minds.

Paragraph 7. Primacy of speech. Darwin recognizes that, although the use of the fingers to translate speech shows that signing, as we would now say, is perfectly efficient, the fact that the hands cannot be used for other purposes while signing is a serious drawback. On the other hand, vocal communication has many precedents in other animals.

Paragraph 8. Glossogenetic parallels. See Sect. 7.3.

Paragraph 9. Complex languages in barbarian peoples. See Sect. 7.3.

Paragraph 10. Brief conclusion. Just as the complexities and refinements of the barbarian languages are not proof that they were the object of a special act of creation—the content of paragraph 9—so neither does "the faculty of articulate speech" in itself present an insuperable objection to the belief that man originated from lower forms.

It would be difficult to find a proposal on the evolution of language as precise and nonrestrictive at once. Because of being generally precise, it is easy to detect its weak points. Given the importance of the specification *articulate*, for example, an explicit characterization of the term is missing. Fitch (2013a) interprets articulate vocalization as an augmented vocalization thanks to more fine-grained control of lip and tongue movements. No doubt that would be a condition for achieving articulate character but the concept of articulate goes beyond that. It can mean discrete, on the basis of a reduced and combinable inventory of segments/sounds, with a phonological basis in short. A related problematic point is the Lamarckian appeal to the inherited effects of use that appears repeatedly in *Descent*: it would be through such effects that articulate speech or language would come into being (Darwin 1877a, p. 48; and in the original paragraph 5 and 7, pp. 88 and 89, respectively). Better known perhaps is the error of attributing a high capacity for imitation to monkeys (original paragraph 4: Darwin 1877a, b, p. 87), which perhaps still dominates public opinion.

Although Darwin's proposal—see paragraph 3 *above*—can only please advocates (Marler 1976; Nottebohm 1975; Jarvis 2019) of the central role of *vocal production learning* (VPL) (modification of one's own vocalization as an imitative response to experience with the vocalizations of others) in the evolution of language, it is a probably wrong overstatement to claim (*pace* Fitch 2013a) that this notion is already in Darwin's proposal. In paragraph 7 we have proof of this. It turns out that there the great apes' inability to speak is attributed to insufficient intelligence and not to the constitution of their vocal organs. The possession of vocal organs which by continued practice could have been used for speech is assimilated to the case of nightingales and crows, which, though having a similar disposition of vocal organs, are in the former case excellent singers, but not so in the latter. Reasoning by analogy fails here. It fails because crows should be the birds that excel with their songs given their superior intelligence, as we know today; we also know today that, in spite of the difference in their singing, both species are *vocal production learners.* This leads to separate vocal imitation from intelligence (see Searcy and Nowicki 2019) and associate the former instead with VPL, a relatively uncommon evolutionary feature resulting from the duplication of an older neural *pathway* for motor learning (Jarvis 2019), at the base of which there would be a deep homology (Fitch 2013b).

With VPL at the basis of speech, the importance of vocal imitation increases. Without vocal imitation (or its manual substitute in the signed modality) words could not be acquired in ontogeny and without words, no language; moreover, as Darwin rightly says, no possible or at least controllable sequences of thought either. Taking a little further what he said in the paragraph 5 summarized above, Darwin presents language as the mechanism that "excites trains of thought which would never arise from the mere impression of the senses, or if they did arise could not be followed out" (Darwin 1877a, p. 610). Without words, how would we voluntarily access concepts (Bickerton 2014) and cease to be solely subject to mere sense impressions? How, in turn, could we produce these words in silent mental successions, i.e. do with syntax complex thought, if we could not also produce speech internally, if we were not *vocal production learners*? Our species is that of ancestors who invented "articulate language [and words with it] if, indeed, the word *invented* can be applied to a process, completed by innumerable steps, half-consciously made" (Darwin 1872, p. 60). Darwin's suggestion is that speech, syntax, and thought would be inextricably linked, as Lieberman (2006) has always defended without resorting, however, to the biological substrate provided by VPL. The Darwinian proposal is complete, not partial; central, not peripheral.

The instinct to learn, which Darwin understood so well and before anyone else—see paragraph 3 *above*—is extremely important. How without language, learned with the instinct of *vocal production learners*, could we, humans, learn as much as we learn? The enormous limitations posed by the absence of language in the so-called non-verbal autism are in this sense very illustrative. This notwithstanding, the fundamental and primary character of this instinct to learn goes unnoticed. As a recent example, take *How we learn. Why brains learn better than any machine... for now* by Dehaene (2020). This book does not even mention that the learning of words requires a vocal imitation ability which is based in VPL. There is still a long way to go before Darwin's view of language evolution in particular, with the corresponding (corrective) updates, gets the place it deserves in today's cognitive science.

7.2 Ontogeny

Darwin records the behavior of his first-born son from his birth on 27 December 1839 until the age of 11 with the same thoroughness with which he had recorded the behavior of giant tortoises and marine iguanas, mockingbirds, and finches. Here are some examples from Darwin (1877b):

> – After 64 days he made some little meaningless noises to please himself (p. 292).
>
> – At 4 months the first indications of imitation of sounds appear, at 7 months the emission of the first sounds without meaning, but with affective value (p. 291).
>
> – When he was exactly 1-year old, he made the great progress of inventing a word for food, "mum" (p. 293).
>
> Darwin does not limit himself to observing what his child does spontaneously, but tests the child's reactions to his intrusions: he intentionally touches the sole of the newborn's foot, strokes his cheek or puts his finger in his mouth to check the precision of his reflex

> movements, makes sounds to see if the baby looks at the place from which they are produced. This is a guided observation, aimed at testing hypotheses.

Why does Darwin devote himself to explore his child's behavior so thoroughly? What hypotheses guide his exploration? In the first place, Darwin turns to the study of human newborns to look for empirical evidence of phylogenetic continuity; evidence that there would not be a qualitative leap between the mental faculties of man and higher mammals, nor between these and other species. He looks for indicators of phylogenetic continuity in his child's behavior not only for language but also for reflexes, different emotions, and intelligence in general.

While recognizing the "immense interval" between the cognitive and communicative abilities of infants (humans) and those of other species, he maintains that this interval is covered with innumerable gradations. It is these gradations that Darwin seeks, both phylogenetically and ontogenetically; discovering them will lead him to demonstrate that, indeed, there is no qualitative difference between man and other species.

Be that as it may, it is clear to Darwin that the emergence of language in the individual (and in the species) marks an important difference, a milestone that requires an explanation. The second reason for observing his son is to explain the emergence, the appearance of a fundamentally different function in development. This explanation is provided by his interpretation of his own child's behavior: novelty in development arises from the growth and fusion of early (more primitive) functions. In the specific case of the child, some psychological functions appear in a rudimentary form, develop in parallel and then merge to give rise to a new function: in the plan of action, from reflexes one moves to an incipient intentionality, in the plan of emotions, from a diffuse and reactive discomfort one evolves to a wide range of emotional responses, and in the plan of reasoning one progresses from associations to the anticipation of one event from another. The three evolved functions, intentional action, emotional expression, and anticipation, merge to give way to the first signs of language. Thus, Darwin advances one of his general evolutionary principles: new functions—in this case language—emerge from more primitive functions. There is no creation, only evolution.

Finally, Darwin's decision to scrupulously record his son's behavior is to support his anti-creationist stance. Indeed, from creationist positions, it does not make much sense to observe children, given that human beings are created as adults. Nor is it justified to observe development if we assume, as empiricists do, that human beings are a direct result of their environment. According to nativism, the introspective study of the adult would be sufficient. An interactionist position such as Darwin's invites to study specific subjects in specific contexts in order to understand how their individual characteristics interact with the specific circumstances in which they have grown up (Gruber 1981).

The influence of the Darwinian enterprise and its interactionist stance on the study and conceptualization of language development is enormous. His observations established the empirical basis for research in developmental psycholinguistics (Cole and Cole 1996) and for one of the most widely used methods at the dawn of the scientific study of language: the observation of particular cases. In this research methodology, a small number of subjects—sometimes only one—are observed in natural contexts and their behavior is carefully recorded.

Moreover, many of Darwin's descriptions of his son's first utterances made it possible to identify evolutionary peculiarities and some fundamental characteristics of ontogenetic development. For example, the fact that in early infant language an expression can have many meanings, as he points out:

> At exactly the age of a year, he made the great step of inventing a word for food, namely *mum* [...] he used this word in a demonstrative manner or as a verb, meaning 'Give me food'. [...] But he also used *mum* as a substantive of wide signification; thus he called sugar *shu-mum*, and a little later after he had learned the word 'black', he called liquorice *black-shu-mum*, black sugar-food (Darwin 1877b, p. 293).

More than a century later, psycholinguists wonder about the scope and meaning of this evolutionary feature.

Darwin detects that his son understands many more expressions than he is able to produce. Today we know that the number of expressions that young children understand usually doubles the number that they are able to produce. He also clearly points out the notable acceleration that occurs around 20 months in the acquisition of lexical items, a phenomenon that is currently called "lexical explosion" whose neurological correlate has been demonstrated (Pujol et al. 2006). Finally, Darwin stops to point out very precisely the variations in intonation that he notices in his son's first utterances and which correspond to different sentence modalities: "I was particularly struck with the fact that when asking for food by the word *mum* he gave to it (I will copy the words written at the time) 'a most strongly marked interrogatory sound at the end'" (Darwin 1877b, p. 293). Consistent with his fundamental phylogenetic hypothesis, Darwin does not interpret varieties in intonation in relation to a linguistic phenomenon, as a possible expression of modality, but as a rhythmic phenomenon, "musical pitch," which serves him to argue for phylogenetic continuity.

Language is, for Darwin, fundamentally a means of communication, of expression of emotions and of reasoning. Although in his own reflections he shows familiarity with different grammatical aspects, particularly morphological ones, which serve to compare different languages in his observations of children's behavior, none of these features is even mentioned. His descriptions focus on the occurrence, increase and precision of the meaning of words, and he does not seem to attach any special importance to the fact that he understands words or sentences. Much more striking, for Darwin, is the difference in the speed with which children learn new words or the capacity for imitation they have, as opposed to dogs; much more striking than the ability to combine words present in the former and absent in the latter.

From the current emergentist positions on language development, many of Darwin's interactionist ideas have been recovered and, fundamentally, his notion of ontogenesis as growth and fusion of previous functions that give rise to new functions and that in a very succinct manner Elizabeth Bates subscribes to: language is “a new machine made of old parts” (Bates et al. 1991, p. 35).

7.3 Glossogeny

When discussing Darwin’s view of language diversity and linguistic change, it is necessary to distinguish ideological interpretations impregnated with a misnamed Darwinism from the Darwinian position itself. The former justifies inequalities as the “natural” result of evolution and translate into the idea that some languages are more advanced than others, or that the development of languages corresponds to the development of the peoples who speak them. Darwin could not be further from these ideas, so where did this confusion originate? Simplifying considerably, we could say that in an interpretation of his thought based on considerations such as those found in the eighth paragraph of the section devoted to language and ignoring what the author says in the ninth, penultimate, paragraph.

The eighth paragraph begins with the observation that there is evidence that both languages and species have formed gradually. Indeed, as Alter (1992) has documented, Darwin repeatedly argued, partly as *captatio benevolentia*, that his evolutionary ideas had been reinforced by contact with linguistics and ethnology. It should be borne in mind that in Darwin’s time it had already been shown that linguistic change operates largely by modification and diversification from a predecessor language (homology). It is not surprising, therefore, that our author had a great interest and considerably high technical knowledge of glossogeny and established several biological-linguistic parallels. Thus, in the eighth paragraph, in addition to the homology referred to, he mentions that in the relations among languages one can see the application of the same formation processes (analogy). The dominant languages and dialects (*sic*) would spread everywhere and lead to the extinction of the others. A language is considered either as a species or as an organism. As a species, a language cannot be born in two different places or reappear once extinct—ideas that Darwin attributes to Lyell; as an organism it can be classified by its ancestry or other characters. Other possible parallels go down to the scale of words. One of them reproduces a fragment from Max Müller that goes like this: “A struggle for life is constantly going on amongst the words and grammatical forms in each language. The better, the shorter, the easier forms are constantly gaining the upper hand, and they owe their success to their own inherent virtue” (Darwin 1877a, p. 91). That the author of the quotation is Müller, an anti-selectionist, and not Schleicher, the ultra-Darwinian who crossed the border of similes to assume literally that languages are organisms, is not without irony and shows to what extent Darwin’s influence on linguistic conceptualization was as great or greater than the other way round.

The ninth paragraph contrasts with the previous one. An argument is presented there against the idea that there are some languages more perfect than others. “With respect to perfection,” he says, “a naturalist does not consider an animal [with perfect symmetry in radiating lines] more perfect than a bilateral one with comparatively few parts, and with none of those parts alike, excepting on the opposite sides of the body." (Darwin 1877a, p. 91). So it is with languages. As if this were not enough, it turns out that the *leitmotif* of this analogy is Friedrich Schlegel's observation—to whom he alludes and quotes indirectly—that languages corresponding to "the lowest grade of intellectual culture"—a dictum that Schlegel himself exemplifies with "the Basque and the Lapponian, and many of the Amerindian languages"—show "a very high and elaborate degree of art in their grammatical structure." In other words, neither a path of perfection nor a correspondence between degree of artifice and "high civilization." In the end, the fact remains that many popular ideas about languages are still steeped in the ideology exuded by the eighth paragraph rather than the rigor of the ninth.

References

Alter SG (1992) Darwinism and the linguistic image. The Johns Hopkins University Press, Baltimore

Bates EA et al (1991) Symbols and syntax: a Darwinian approach to language development. In: Krasnegor NA, Rumbaugh DM, Schiefelbusch RL (eds) Biological and behavioral determinants of language development. Erlbaum, Hilldale, pp 29–66

Bickerton D (2014) More than nature needs Language, mind and evolution. Harvard University Press, Cambridge

Bolhuis JJ, Tattersall I, Chomsky N et al (2014) How could language have evolved? PLoS Biol 12(8):e1001934

Cole M, Cole SR (1996) The development of children. Macmillan, New York

Darwin C (1871) The descent of man, and selection in relation to sex, vol 2. John Murray, London

Darwin C (1872) The expression of the emotions in man and animals. John Murray, London

Darwin C (1877a) The descent of man, and selection in relation to sex, 2nd edn. John Murray, London

Darwin C (1877b) A biographical sketch of an infant. Mind Quart Rev Psychol Philos 2(7):285–294

Dehaene S (2020) How we learn. Why brains learn better than any machine… for now. Viking, New York

Fitch WT (2010) The evolution of language. Cambridge University Press, Cambridge

Fitch WT (2013a) Musical protolanguage: Darwin's theory of language evolution revisited. In: Bolhuis JJ, Everaert M (eds) Birdsong, speech and language exploring the evolution of mind and brain. MIT Press, Cambridge, pp 489–504

Fitch WT (2013b) Convergence and deep homology in the evolution of spoken Language. In: Bolhuis JJ, Everaert M (eds) Birdsong, speech and language exploring the evolution of mind and brain. MIT Press, Cambridge, pp 45–62

Gruber H (1981) Darwin on man. University of Chicago Press, Chicago

Jarvis ED (2019) Evolution of vocal learning and spoken language. Science 366:50–54

Lieberman P (2006) Toward an evolutionary biology of language. Harvard University Press, Cambridge

Lorenzo G (2006) El vacío sexual, la tautología natural y la promesa minimalista. Antonio Machado Libros, Madrid

Marler P (1976) An ethological theory of the origin of vocal learning. Ann N Y Acad Sci 280:386–395

Marler P (1991) The instinct to learn. In: Carey S, Gelman R (eds) The epigenesis of mind: essays on biology and cognition. Lawrence Erlbaum Associates, Hillsdale, pp 212–231

Nottebohm F (1975) A zoologist's view of some language phenomena, with particular emphasis on vocal learning. In: Lenneberg EH, Lenneberg E (eds) Foundations of language development. Academic Press, New York, pp 61–103

Pujol J et al (2006) Myelination of language-related areas in the developing brain. Neurology 66: 339–343

Searcy WA, Nowicki S (2019) Birdsong learning, avian cognition and the evolution of language. Anim Behav 151:217–227

Tallerman M (2013) Join the dots a musical interlude in the evolution of language. J Ling 49:455–487

Chapter 8
Human Evolution in Eurasia: The Fossils that Darwin Did Not Know

María Martinón-Torres

Abstract During the last decade, we have witnessed a significant increase in human fossils whose analysis has forced us to redefine the evolutionary landscape of the genus *Homo*. The findings of the last 10 years have complicated and enriched our interpretation of the "human bush" by highlighting (1) the great morphological variability of the fossil record during the Pleistocene and (2) a greater role of the Asian continent in the reconstruction of our origin. This article presents a general review of the human fossils found or reanalyzed in the last decade and whose study has caused a change in the current paradigm in human evolution. Our analysis forces us to reconsider many of the basic premises of models such as "Out of Africa 1" and "Out of Africa 2," especially those that explain human evolution and hominin dispersals as unidirectional, linear, and demographically simple processes. Our review emphasizes the role that Asia plays in the reconstruction of our origin during the Pleistocene, including critical stages for the emergence of our own species.

Keywords Neanderthal · Denisovan · Paleogenomics · Paleoproteomics · Out of Africa

8.1 Introduction

Over the last decade, we have witnessed a significant increase in the number of human fossils whose analysis has forced us to redefine the evolutionary landscape of the genus *Homo*. Despite the importance and impact that the advent of molecular techniques has on the study of our origins, fossils are and will continue to be the primary and essential evidence to advance in the study of our ancestors. Hard evidence remains the primary source of information—even for molecular data—about the time, place and manner in which hominins evolved. Charles Darwin's

---

M. Martinón-Torres (✉)
CENIEH (National Research Center on Human Evolution), Burgos, Spain

Anthropology Department, UCL, London, UK
e-mail: maria.martinon@cenieh.es

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_8

astuteness is astonishing for having been able to come up with the theory of evolution by natural selection without relying on what today constitutes a fundamental piece of paleoanthropology: fossils. In *The descent of man, and selection in relation to sex* (Darwin 1871) Darwin himself highlighted the absence of fossils, a type of evidence that, in time, would prove him right:

> With respect to the absence of fossil remains, serving to connect man with his ape-like progenitors, no one will lay much stress on this fact, who will read Sir C. Lyell's discussion, in which he shews that in all the vertebrate classes the discovery of fossil remains has been an extremely slow and fortuitous process. Nor should it be forgotten that those regions which are the most likely to afford remains connecting man with some extinct ape-like creature, have not as yet been searched by geologists (Darwin 1871, p. 201).

The findings of the last 10 years have complicated and enriched our interpretation of the "human bush" by highlighting: (1) the great morphological variability of the fossil record during the Pleistocene and (2) a greater prominence of the Asian continent in the reconstruction of our origin.

This article presents a general review of the human fossils found or reanalyzed in the last decade and whose study has caused a change in the current paradigm in human evolution. This paper does not intend to make an exhaustive review of all the fossils found recently, but to focus on those that have had the greatest impact on the reformulation of the models that explain the origin and early dispersals of both our genus and our own species, colloquially known as "Out of Africa 1" and "Out of Africa 2." This review will place particular emphasis on dental data, as they are the most abundant and the best-preserved skeletal element in all periods and geographic locations, allowing for a broader and deeper assessment of the variability of hominins during the Pleistocene. In addition, dental morphology is highly heritable and therefore represents a valuable source for investigating phylogenetic relationships between extant and extinct human groups.

8.2 Revisiting "Out of Africa 1"

Until now, the preponderant idea within the scientific community is that practically all the hominin species found in Eurasia, respond to a variable number of dispersals out of Africa promoted by climatic, environmental, ecological or demographic changes (Agustí et al. 2009; Bar-Yosef and Belfer-Cohen 2001). The fossil evidence of the first of these dispersals is found in the site of Dmanisi (Georgia), where the remains of up to five individuals dated to around 1.77 Ma (millions of years), have been found (Lordkipanidze et al. 2013). The taxonomy of these fossils (see Fig. 8.1) is still under debate and they have been assigned to *Homo erectus* (Gabunia and Vekua 1995), *H.* sp. *indet* (*aff. ergaster*) (Rosas and Bermúdez de Castro 1998) and *H. georgicus* (Gabunia et al. 2002). Analysis of the dentition suggests that the Georgian hominins show a mosaic of primitive characters, present in *Australopithecus* and *H. habilis*, and other derived features that bring them closer to the classical Asian *H. erectus* populations (Martinón-Torres et al. 2008). Thus, the

Fig. 8.1 The first hominins outside Africa. Image of skull D2700 and mandible D2735 from the Dmanisi site (Georgia)

Dmanisi hominins would be close to the node from which the Asian and African populations of the Early Pleistocene originated (Martinón-Torres et al. 2008) (the early Pleistocene is situated between 2588 Ma and 781 ka [thousands of years]). Based on the dentognathic and cranial evidence, and considering their biogeographical framework, we cannot rule out the possibility that the ancestors of Asian *H. erectus* and *H. ergaster* evolved in Eurasia, not in Africa (Dennell and Roebroeks 2005; Rightmire et al. 2006). Following this line of evidence, the presence outside Africa of a hominin with similar characteristics to *H. habilis* or even more primitive than this one, would be compatible with the hypothesis that the first departure from the African continent may have happened even earlier, 2.4–2.6 Ma ago, coinciding with the oldest evidence of lithic industry (Sahnouni et al. 2018) or even 3.0–3.5 Ma ago, when the barrier of the Arabian desert did not yet exist and, therefore, did not represent the obstacle that it represented for the faunal movement between continents—including hominins—since 1 Ma ago. In this situation, the first migratory hominin could have been any of the species recognized in the African record at the end of the Pliocene or beginning of the Early Pleistocene (about 2588 Ma ago): *H. rudolfensis*, *H. habilis*, *H. erectus* or even a representative of the genus *Australopithecus*. The recent discovery of the species *H. luzonensis*, which lived in the island of Luzon 50–67 ka ago. leaves open the possibility that the protagonist of the first Eurasian excursion was a species prior to *H. erectus* origins. *H. luzonensis*, found in the Callao Cave (Philippines) and with signs of insular dwarfism, displays a series of anatomical features that are absent or rare in the genus *Homo* and can be found with higher frequencies in *Australopithecus*. Thus, *H. luzonensis* could represent the relict of a population that left Africa before the appearance of *H. erectus*.

8.2.1 "Out of Asia" and the Settlement of Europe

The imbalance between the intensity of paleontological work in Africa and Eurasia has undoubtedly had an impact on the reconstruction of the current paradigm. The discovery of new Eurasian fossils has led to a reconsideration of the weight that Africa has had in the human settlement of Europe (Dennell and Roebroeks 2005; Martinón-Torres et al. 2007). Similarities between European and Asian hominins suggest that they may have shared a closer common ancestor with each other than with African populations (Martinón-Torres et al. 2007). In addition, we now know that traits typically found in Neanderthals and modern humans were present in human populations from about 1 Ma ago (Martinón-Torres et al. 2007; Bermudez de Castro et al. 1997; Bermúdez de Castro et al. 2012). In particular, *H. antecessor* from Gran Dolina-TD6 (Atapuerca, Spain) has been proposed as the last common ancestor (LCA) of *H. sapiens* and *H. neanderthalensis* based on the expression of a unique combination of features, a primitive dentition and the earliest known expression of a modern-like face (Fig. 8.2) (Bermudez de Castro et al. 1997). The recent analysis of the dental proteome of *H. antecessor* (Welker et al. 2020) confirms its phylogenetic position at the base of the clade including *H. sapiens*,

Fig. 8.2 The first hominins of Europe. Digital reconstruction from computed axial microtomography of the ATD6-69 maxilla of the species *Homo antecessor*, highlighting the modern aspect of its facial topography. Credits: Laura Martín-Francés

H. neanderthalensis and the Denisovans. Thus, molecular biology points to *H. antecessor* being *at* or *near* the node of divergence of Neanderthals and modern humans, ratifying the hypotheses proposed from the fossil evidence (Bermudez de Castro et al. 1997; Bermúdez de Castro et al. 2017; Martinón-Torres et al. 2019). In this context, the Gran Dolina hominins could represent a lateral branch that preceded the origin of Neanderthals and modern humans. However, several researchers have pointed out that the midfacial anatomy of Chinese fossils such as Yunxian (Quyuan) and Tangshan (Nanjing) is similar to *H. antecessor* (Vialet et al. 2010). This evidence is compatible with an Asian-European connection during the Early Pleistocene or early Middle Pleistocene and the possibility of a Eurasian origin for the LCA (Bermúdez de Castro and Martinón-Torres 2013). This proposal has long been criticized for its apparent incompatibility with the genetic data, which suggested an earlier divergence for *H. sapiens* and *H. neanderthalensis* (Mounier and Mirazón Lahr 2016). However, the analysis of nuclear DNA obtained from the population of the Sima de los Huesos de Atapuerca, dated to 430 ka, suggests that the separation between the two lineages occurred between 550 and 765 ka (Meyer et al. 2016). These dates would be compatible with the search for the LCA at the end of the Early Pleistocene.

If we consider the possibility that *H. antecessor* was the LCA, two main scenarios emerge regarding its origin. In the first one, *H. antecessor* could have originated in Africa. A branch of that ancestral population would have evolved into *H. sapiens* about 300 ka ago as suggested by fossils from the Jebel Irhoud site (Hublin et al. 2017). If this idea is correct, we should find in the African fossil record features that would later be characteristic of Middle Pleistocene hominins, such as those of the Sima de los Huesos and *H. neanderthalensis.* Another alternative is the proposal that Southwest Asia, especially the area of the Levantine corridor, was the place of settlement and evolution of a mother population that would have occupied this region more or less continuously given the stability of favorable environmental conditions (Almogi-Labin 2011). Moreover, this region is considered a hotspot of biodiversity and, therefore, of phylogenetic diversity. This hypothesis implies the movement of populations towards Europe, Asia, and Africa in a discontinuous way, when environmental conditions and biogeographical barriers allowed it. The mother population would continue to evolve in an area that we have called "Central Area of Dispersals of Eurasia" (CADE), in Southwest Asia, so that the daughter populations, in each of these migrations, would carry the phenotypic novelties of the mother. This scenario would explain: (1) the morphological diversity of human populations in Europe during the Middle Pleistocene (Dennell et al. 2011; MacDonald et al. 2012), (2) the probable origin of Neanderthals in this region, and (3) the presence of derived characters shared between *H. antecessor* and the Middle Pleistocene populations of Africa, Asia, and Europe, such as the midfacial topography (Freidline et al. 2013; Lacruz et al. 2013; Vialet et al. 2010), some dental and mandibular traits (Martinón-Torres et al. 2007) and postcranial features (Bermúdez de Castro et al. 2012). Although these populations share traits because of the common origin, each group will develop its own distinctive traits. This scenario would explain why *H. antecessor* displays obvious differences from classic *H. erectus despite* their common heritage (see Xing et al. 2018). Increasingly, Southwest Asia is presented as an essential area in all models being developed to explain the colonization of Eurasia by different hominin species, including our own (Bergström et al. 2021; Bretzke and Conard 2017).

The first Europeans, currently represented by the fossils from Orce (Toro-Moyano et al. 2013) and from Sima del Elefante site in Atapuerca, dated at around 1.2–1.4 Ma (Carbonell et al. 2008) could be related to the first dispersal out of Africa, currently represented by the Dmanisi hominins, and not necessarily respond to a new dispersal around the Jaramillo magnetic reversal, between 1.07 Ma and 990 ka ago.

8.3 Revisiting "Out of Africa 2"

Genetic evidence has been a key piece in abandoning linear, anagenetic narratives to explain human evolution outside Africa. In addition to classic *H. erectus* (Xing et al. 2018). Asia has witnessed the arrival and/or evolution of *H. sapiens* (Liu et al. 2015; Shang et al. 2007), the Denisovans (Krause et al. 2010; Sawyer et al. 2015) and some human populations without clear taxonomic assignment (Liu et al. 2013; Wu and Bruner 2016; Xing et al. 2019). The Denisovans have been described primarily by their genome and are identified as an extinct type of human that shares a common ancestor with modern humans and Neanderthals, although they are closer to Neanderthals (Krause et al. 2010; Sawyer et al. 2015) from whom they would have diverged some 640 ka ago and whose DNA can be found in some current populations of Melanesia and Australia. Paradoxically, in contrast to the abundance of molecular data, the scarcity of fossils that can be attributed to the Denisovans stands out: three teeth, a phalanx (Krause et al. 2010; Sawyer et al. 2015) and the fragment of a hemimandible from the Tibetan site of Xiahe (Chen et al. 2019) identified as "Denisovan" by palaeoprotein analysis. Thus, it is unclear whether Denisovans deserve a species-level distinction or whether they are perhaps already represented in many of the Asian fossils we already know, especially those of less clear taxonomic assignment such as the samples from Xuchang, Maba, Xujiayao, Panxian Dadong or Hualong (Liu et al. 2013; Wu et al. 2019; Wu and Bruner 2016; Xing et al. 2015). Our characterization of the dental fossil record has led to the identification of a group that we have called "non-H. *erectus* Middle Pleistocene" hominins from Asia, among which the Denisovans could possibly be found. These groups are characterized by the lack of potentially autopomorphic features for *H. erectus* such as the dentine crenulations on the occlusal surface of molars and labial surface of incisors (Xing et al. 2018) and the presence of derived traits more typical of late *Homo* populations, in particular *H. neanderthalensis* (Wu and Bruner 2016; Xing et al. 2015).

Molecular data suggest that Denisovans hybridized with modern humans, Neanderthals, and a third archaic lineage whose identity remains unknown (Sawyer et al. 2015). The paucity of data on the phenotypic expression of hybridization adds an element of difficulty to interpret the morphological variability of the fossil record (Ackermann et al. 2016). This problem also affects the identification of the earliest populations of modern humans found outside Africa.

The "Out of Africa 2" is a model that delineates the first departure of our species from Africa around 50 ka, and postulates that *H. sapiens* replaced all existing human forms on that great journey without hybridizing with them. The fact that introgression has been identified in the genomes of current populations forces us to rethink the original formulation of "Out of Africa 2." In addition to the discovery that our species interbred with other hominin lineages, there is a growing body of evidence that questions the date of 50 ka for the first departure of modern humans outside Africa.

The identification of one of the Apidima skulls as *H. sapiens* would imply the presence of our species in Eurasia 210 ka ago (Harvati et al. 2019) and, therefore, much earlier than admitted so far. However, both the identification and the dating are controversial, as this skull has been found literally next to another one assigned to *H. neanderthalensis* and dated at 170 ka (Harvati et al. 2019). Furthermore, the diagnosis of this specimen as *H. sapiens* is not based on the identification of *sapiens* apomorphies but on the absence of some characteristically Neanderthal features. This fact may simply be due to intrapopulational variability, as is the case with the skulls from the Sima de los Huesos where not all skulls show the full range of Neanderthal characters. Another of the earliest modern specimens is the maxilla from Misliya (Israel) (Herhkovitz et al. 2018) which together with Qafzeh and Skhul would establish the presence of *H. sapiens* in the Near East about 100 ka ago earlier than previously thought. However, these sites at the gates of Africa are considered to provide limited information when it comes to assessing the ability of dispersal and adaptation of our species to other ecosystems or, ultimately, to a real "exit" from Africa.

There are now more than 40 localities in China belonging to the Late Pleistocene, some of which have yielded fossils that can be confidently assigned to *H. sapiens* (Boivin et al. 2013; Dennell et al. 2020). Until recently, the earliest evidence east of Arabia documenting the presence of *H. sapiens* was from the sites of Tianyuan (China), Niah Cave (Borneo), Tam Pa Ling (Laos), and Lake Mungo (Australia), all dated to between 40 and 50 ka (Demeter et al. 2012; Shang et al. 2007). The 47 teeth from Fuyan Cave in Daoxian (southern China) (Liu et al. 2015) and the jawbone and teeth from the Zhirendong locality (southern China), recently dated at 110 ka (Cai et al. 2017) have revived the hypothesis that *H. sapiens* was out of Africa between 30 and 60 ka earlier than predicted by the recent "Out of Africa" hypothesis (Fig. 8.3). Other fossils such as the 85 ka human phalanx from Al-Wusta (Arabia) and the dental specimens recovered at Lida Ajer in Sumatra (Westaway et al. 2017), Luna Cave, Gaqian (Tubo), and Huanglong in China (Shen et al. 2001).

The amount of data in other domains (archaeological, environmental, chronological, and genetic) compatible with this model is also increasing (Boivin et al. 2013; Reyes-Centeno et al. 2014). However, the critics to this proposal are still present. Some authors have expressed their skepticism when it comes to accepting the evidence that points to an early presence of *H. sapiens* in Eurasia. The main

Fig. 8.3 Early *Homo sapiens* in Asia. Image of 47 teeth found in Fuyan Cave (Daoxian), southern China, dated between 80 and 120 ka

criticisms are focused on the chronological analysis, demanding more data, including direct dating of fossils, to ratify the dates obtained (Hublin 2021; Michel et al. 2016). However, the importance of a precise date and a solid chronostratigraphic context is universal to all archaeological and paleontological findings, not only to those of the Asian continent, and the same standards must be used when accepting or not the new pieces of the puzzle. Of particular note is a recent study in which Sun and his colleagues question the chronology of five sites in southern China where the presence of *H. sapiens* before the 45–50 ka limit is claimed (Sun et al. 2021). To do so, they perform genetic analysis and direct AMS ^{14}C dating (carbon-14 analyzed with accelerator mass spectrometry) on several faunal and "human" samples recovered from these localities. Among these samples there are several faunal remains and two "human" teeth collected by Sun and his team at the Fuyan site, without the supervision of the team that excavated the site, and which they attribute to the same sample published by Liu et al. (2015). Sun et al. (2021) conclude that all these samples are Holocene, obtaining dates around 9 ka for the two "human" teeth from Fuyan. Surprisingly, one of the two teeth dated and from which human DNA has been extracted belongs to an herbivore, questioning all admissible quality standards for a scientific study (Martinón-Torres et al. 2021). The ^{14}C analysis is also inadequate for samples of that potential antiquity and the parameters obtained, including the C/N ratio of the samples, point to contamination and/or probable post-depositional alteration (Martinón-Torres et al. 2021). In this sense, the work of Sun et al. (2021) does not provide sufficient data to question the hypothesis of the early presence of *H. sapiens* in China. Although we agree on the importance of continuing to improve the quality of the data we handle, the same quality is necessary to be able to refute hypotheses.

In particular, the Fuyan sample has been dated to between 80 and 120 ka by a multidisciplinary approach involving Uranium series analyses of speleothems and stalagmites sealing the fossil deposit, paleomagnetism, and examination of associated fauna (Liu et al. 2015). Specifically, ^{14}C analysis was attempted on three fossils: a human tooth and two faunal remains. Due to the lack of collagen, results were only obtained in one of them, the fragment of a long animal bone, which yielded a date greater than 43 ka cal BP (dating in calibrated years), which is the limit of carbon dating in the laboratory of the University of Beijing.

The study of dental and cranial evidence from China (e.g., Liu et al. 2015; Wu et al. 2014; Xing et al. 2015) reveals differences in the geographical distribution of sites with *H. sapiens* remains. Those early Late Pleistocene localities with fossil teeth that can be attributed with reasonable confidence to our species (e.g. Luna Cave, Fuyan Cave, Zhiren Cave) tend to be restricted to southern China (Liu et al. 2015). However, the age of *H. sapiens* fossils found in the north tend to be no older than 40–45 ka. This suggests that, during the same period, continental Asia was inhabited by at least two different populations, more derived in lower latitudes and more primitive in the north. This pattern could be traced back to the Middle Pleistocene. Fossils from Panxian Dadong in the south (Liu et al. 2013) are more derived than other Middle Pleistocene groups found in higher latitudes, such as Zhoukoudian, Hexian, Yiyuan or Xujiayao (Xing et al. 2018; Xing et al. 2015). These data would support the possibility of a southern route, more favorable for the early dispersal(s) of our species. This early dispersal would have had a minor genetic impact on current populations, but fossils are an increasingly strong evidence to prove this possibility. This variability is relevant for studying the routes of these migrations and the isolation or interactions between these human groups. Climatic instability and the varying extension of the deserts could have favored a pattern of fragmentation, intermittent contacts in some regions and predominantly isolation between northern and southern China (Boivin et al. 2013; Dennell et al. 2020) but also complex patterns within each area. The markedly derived character of fossils from Fuyan (Daoxian) with an age greater than 80 ka, while samples such as those from the Dushan site in southern China, 15 ka old, show markedly archaic traits despite their assignment to *H. sapiens* are good examples of this complexity (Liao et al. 2019). The combined study of fossil and molecular evidence could help elucidate whether the presence of these primitive characters is interpreted as (1) the survival in isolation of one of the first *H. sapiens* to enter China, (2) evidence of introgression of a primitive group into the region, or (3) regional variation. Any of the three options points to a complex demographic history in this region.

8.4 Final Conclusion

This review highlights the importance of fossils in reconstructing our origins, including the "recent" history of our own species. The analysis of the fossil record yields fundamental data on the variability observed in different periods, and is the key evidence to trigger new questions about the past. Even in this new era of molecular methodology, it is compulsory and crucial to continue carrying out fieldwork and excavations, a demanding and arduous activity, which requires dedication and time, not always successful, and not always recognized, but without which paleontology could not progress. New fossil discoveries in less explored areas or the consideration of certain samples, especially from Asia, in the construction of the paradigm, have led to important changes the interpretation of our past, giving the Asian continent a decisively greater role in the origin and evolution of hominin species, including our own. The real advances in our field will undoubtedly come from an effective collaboration and integration between fossil and molecular data. This collaboration is indispensable to delve into new challenges in paleoanthropology, such as the identification of hybrids in the fossil record and the taxonomic characterization of new specimens that do not fit into the hominin species defined so far.

On the 150th anniversary of the publication of *The descent of man, and selection in relation to sex*, we cannot help but wonder how far Darwin would have come if he had known the extraordinary fossils we study today.

Acknowledgments The research reported in this paper has received support from the Dirección General de Investigación del Ministerio de Ciencia, Innovación y Universidades (PID2021-122355NB-C33), the Consejería de Cultura y Turismo de la Junta de Castilla y León, the Fundación Atapuerca, British Academy (International Partnership and Mobility Scheme PM160019) and The Leakey Foundation through the personal support of Gordon Getty (2013) and Dub Crook (2014–2022). The microtomography image of ATD6-69 was obtained in the ICTS-CENIEH microscopy laboratory in collaboration with CENIEH staff.

References

Ackermann RR, Mackay A, Arnold ML (2016) The hybrid origin of "modern" humans. Evol Biol 43(1):1–11

Agustí J, Blain H-A, Cuenca-Bescós G et al (2009) Climate forcing of first hominid dispersal in Western Europe. J Hum Evol 57:815–821

Almogi-Labin A (2011) The paleoclimate of the Eastern Mediterranean during the transition from early to mid Pleistocene (900 to 700 ka) based on marine and non-marine records: an integrated overview. J Hum Evol 60(4):428–436

Bar-Yosef O, Belfer-Cohen A (2001) From Africa to Eurasia - early dispersals. Quat Int 75(1): 19–28

Bergström A, Stringer C, Hajdinjak M et al (2021) Origins of modern human ancestry. Nature 590: 229–237

Bermúdez de Castro JM, Martinón-Torres M (2013) A new model for the evolution of the human Pleistocene populations of Europe. Quat Int 295:102–112

Bermudez de Castro JM, Arsuaga JL, Carbonell E et al (1997) A hominid from the lower pleistocene of atapuerca, Spain: possible Ancestor to Neandertals and modern humans. Science 276(5317):1392–1395

Bermúdez de Castro JM, Carretero JM, García-González R et al (2012) Early pleistocene human humeri from the gran dolina-TD6 site (sierra de atapuerca, spain). Am J Phys Anthropol 147(4): 604–617

Bermúdez de Castro JM, Martinón-Torres M, Arsuaga JL et al (2017) Twentieth anniversary of *Homo antecessor* (1997-2017): a review. Evol Anthropol 26(4):151–171

Boivin N, Fuller DQ, Dennell R et al (2013) Human dispersal across diverse environments of Asia during the Upper Pleistocene. Quat Int 300:32–47

Bretzke K, Conard NJ (2017) Not just a crossroad: population dynamics and changing material cutlrue in southwestern Asia during the Late Pleistocene. Curr Anthropol 58:S449–S462

Cai Y, Qiang X, Wang X et al (2017) The age of human remains and associated fauna from Zhiren Cave in Guangxi, southern China. Quat Int 434:84–91

Carbonell E, Bermúdez de Castro JM, Parés JM et al (2008) The first hominin of Europe. Nature 452:465–469

Chen F, Welker F, Shen C-C et al (2019) A late Middle Pleistocene Denisovan mandible from the Tibetan Plateau. Nature 569(7756):409–412

Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London

Demeter F, Shackelford LL, Bacon A-M et al (2012) Anatomically modern human in Southeast Asia (Laos) by 46 ka. Proc Natl Acad Sci 109(36):14375–14380

Dennell R, Roebroeks W (2005) An Asian perspective on early human dispersal from Africa. Nature 438:1099–1104

Dennell R, Martinón-Torres M, Bermúdez de Castro JM (2011) Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. Quat Sci Rev 30:1511–1524

Dennell R, Martinón-Torres M, Bermúdez de Castro JM et al (2020) A demographic history of Late Pleistocene China. Quat Int 559:4–13

Freidline SE, Gunz P, Harvati K et al (2013) Evaluating developmental shape changes in Homo antecessor subadult facial morphology. J Hum Evol 65(4):404–423

Gabunia L, Vekua A (1995) A Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. Nature 373(6514):509–512

Gabunia L, de Lumley M-A, Vekua A et al (2002) Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). C R Palevol 1:243–253

Harvati K, Röding C, Bosman AM et al (2019) Apidima cave fossils provide earliest evidence of *Homo sapiens* in Eurasia. Nature 571:500–504

Herhkovitz I, Weber GW, Quam RM et al (2018) The earliest modern humans outside Africa. Science 359:456–459

Hublin JJ (2021) How old are the oldest *Homo sapiens* in Far East Asia? Proc Natl Acad Sci 118: 2101173118

Hublin JJ, Ben-Ncer A, Bailey SE et al (2017) New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. Nature 546:289–292

Krause J, Fu Q, Good JM et al (2010) The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. Nature 464(7290):894–897

Lacruz RS, Bermúdez de Castro JM, Martinón-Torres M et al (2013) Facial morphogenesis of the earliest Europeans. PLoS One 8:1–7

Liao W, Xing S, Li D et al (2019) Mosaic dental morphology ina terminal Pleistocene hominin from Dushan Cave in southern China. Sci Rep 9:1–14

Liu W, Schepartz LA, Xing S et al (2013) Late middle Pleistocene hominin teeth from Panxian Dadong, South China. J Hum Evol 64(5):337–355

Liu W, Martinon-Torres M, Cai Y-J et al (2015) The earliest unequivocally modern humans in southern China. Nature 526(7575):696–699

Lordkipanidze D, Ponce de León MS, Margvelashvili A et al (2013) A complete skull from Dmanisi, Georgia, and the evolutionary biology of early homo. Science 342(6156):326–331

MacDonald K, Martinón-Torres M, Dennell RW et al (2012) Discontinuity in the record for hominin occupation in south-western Europe: implications for occupation of the middle latitudes of Europe. Quat Int 271:84–97

Martinón-Torres M, Bermúdez de Castro JM, Gómez-Robles A et al (2007) Dental evidence on the hominin dispersals during the Pleistocene. Proc Natl Acad Sci 104(33):13279–13282

Martinón-Torres M, Bermúdez de Castro JM, Gómez-Robles A et al (2008) Dental remains from Dmanisi (Republic of Georgia): morphological analysis and comparative study. J Hum Evol 55(2):249–273

Martinón-Torres M, Bermúdez de Castro JM, de Pinillos M (2019) New permanent teeth from Gran Dolina-TD6 (Sierra de Atapuerca). The bearing of *Homo antecessor* on the evolutionary scenario of Early and Middle Pleistocene Europe. J Hum Evol 127:93–117

Martinón-Torres M, Cai Y, Tong H et al (2021) On the misidentification and unreliable context of the new “human teeth” from Fuyan Cave (China). Proc Natl Acad Sci 118:32102961118

Meyer M, Arsuaga JL, Filippo CD (2016) Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. Nature 531:504–507

Michel V, Valladas H, Shen G et al (2016) The earliest modern Homo sapiens in China? J Hum Evol 101:101–104

Mounier A, Mirazón Lahr M (2016) Virtual ancestor reconstruction: revealing the ancestor of modern humans and Neandertals. J Hum Evol 91:57–72

Reyes-Centeno H, Ghirotto S, Détroit F et al (2014) Genomic and cranial phenotype data support multiple modern human dispersals from Africa and a southern route into Asia. Proc Natl Acad Sci 111:7248–7253

Rightmire GP, Lordkipanidze D, Vekua A (2006) Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. J Hum Evol 50:115–141

Rosas A, Bermúdez de Castro JM (1998) On the taxonomic affinities of the dmanisi mandible (Georgia). Am J Phys Anthropol 107:145–162

Sahnouni M, Parés JM, Duval M et al (2018) 1.9-million- and 2.4-million year-old artifacts and stone tool-cutmarked bones from Ain Boucherit, Alferia. Science 362:1297–1301

Sawyer S, Renaud G, Viola B (2015) Nuclear and mitochondrial DNA sequences from two Denisovan individuals. Proc Natl Acad Sci 112:15696–15700

Shang H, Tong H, Zhang S et al (2007) An early modern human from Tianyuan Cave, Zhoukoudian, China. Proc Natl Acad Sci 104(16):6573–6578

Shen GJ, Wang W, Wang Q et al (2001) U-series dating of hominid site Ganqian Cave at Tubo, Liujiang, Guangxi in South China. Acta Anthropol Sin 20:238–244

Sun S-F, Wen S-Q, Lu C-Q et al (2021) Ancient DNA multimethod dating confirm the late arrival of anatomically modern humans in southern China. Proc Natl Acad Sci 23:e158118

Toro-Moyano I, Martínez-Navarro B, Agustí J et al (2013) The oldest human fossil in Europe, from Orce (Spain). J Hum Evol 65:1–9

Vialet A, Guipert G, Jianing H et al (2010) Homo erectus from the Yunxian and Nankin Chinese sites: anthropological insights using 3D virtual imaging techniques. C R Palevol 9(6–7): 331–339

Welker F, Ramos-Madrigal J, Gutenbrunner P et al (2020) The dental proteome of *Homo antecessor*. Nature 580:235–238

Westaway K, Louys J, Awe R et al (2017) An early modern human presence in Sumatra 73,000–63,000 years ago. Nature 548:322–325

Wu X, Bruner E (2016) The endocranial anatomy of Maba 1. Am J Phys Anthropol 160:633–643

Wu XJ, Crevecoeur I, Liu W et al (2014) The temporal labyrinths of Eastern Eurasian Pleistocene humans. Proc Natl Acad Sci 111:10509–10513

Wu X-J, Pei S-W, Cai Y-J et al (2019) Archaic human remains from Hualongdong, China, and middle Pleistocene human continuity and variation. Proc Natl Acad Sci 116(20):9820–9824

Xing S, Martinón-Torres M, Bermúdez de Castro JM et al (2015) Hominin teeth from the early Late Pleistocene site of Xujiayao, Northern China. Am J Phys Anthropol 156(2):224–240

Xing S, Martinón-Torres M, Bermúdez de Castro JM (2018) The fossil teeth of the Peking Man. Sci Rep 8:1–11

Xing S, Martinón-Torres M, Bermúdez de Castro JM (2019) Late middle Pleistocene hominin teeth from Tongzi, southern China. J Hum Evol 130:96–108

Chapter 9
Human Evolution: The Genomic Evidence

David Comas and Francesc Calafell

Abstract Since Darwin, we understand the process that generates biological diversity, including human diversity, as a genealogical tree that relates all individuals and all species. Within this framework of analysis, and by comparing genomes at different scales (between individuals of the same or different populations or species) we can reconstruct this process, that is, we can know the history of humans as a species or as a group of populations. We will see how, beyond the present moment, the analysis of ancient DNA has allowed a diachronic perspective in which we no longer see only the tips of the branches, but the entire branches. We will illustrate this perspective with the vertical and horizontal relationships between humans, Neanderthals and Denisovans (and other hominins that may have contributed to our current genomes). Within our species, we will give examples from the deepest history, such as the African origin of humanity, but also from more recent history, such as the reconstruction of the Roma diaspora.

Keywords Anatomically modern humans · Neanderthals · Denisovans · Introgression · Genomes

9.1 The Family Tree of Humankind

The core of the Darwinian theory of evolution is often summarized as the sum of two ideas: inheritance with modification plus differential survival according to the inheritance received. In this chapter we will see how the first idea (the combination of genealogy and mutation) has allowed us to understand the origin of humans as a species and their subsequent development, while we kindly refer the reader to the chapter by Elena Bosch in this same monograph, where she explores how the second idea, natural selection as read in the genome, gives us clues as to what makes us human, or at least what has allowed us to survive to the present day.

D. Comas · F. Calafell (✉)
Institute of Evolutionary Biology (CSIC-UPF) and Department of Medicine and LifeSciences, Pompeu Fabra University, Barcelona, Spain
e-mail: Francesc.calafell@upf.edu

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_9

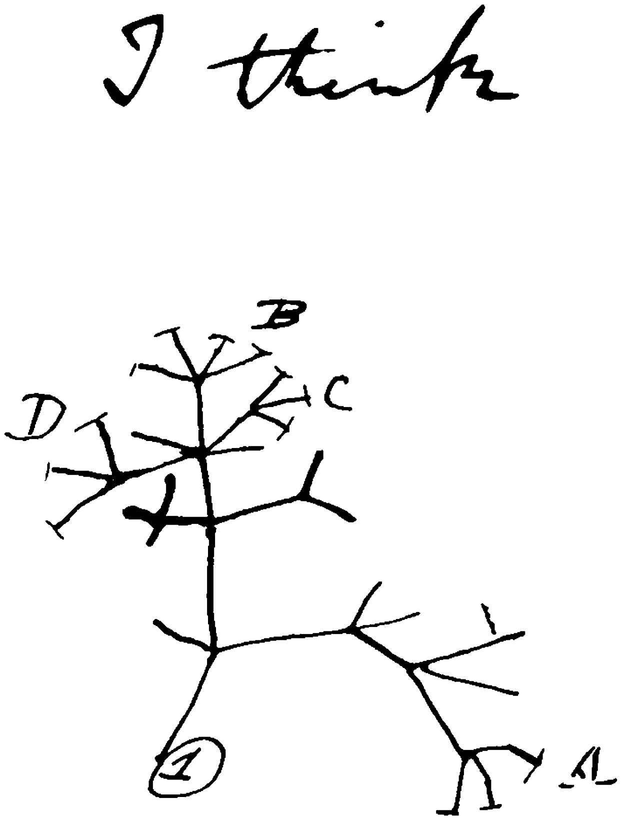

Fig. 9.1 Diagram of the phylogenetic tree that Darwin Drew in 1837 in notebook B of the series on the transmutation of species. By the way, this notebook is missing, possibly stolen, since 2001. In March 2022 it has been anonymously returned to the Cambridge Library in perfect state

In 1837, in notebook B of the series on the transmutation of species, Darwin drew the basic scheme of any phylogenetic tree (Fig. 9.1), as a genealogical relationship between species, in an image that has become iconic but that also bequeathed us a framework on how to think about the origin of species and the accumulation of the variation they contain. It is on this idea that current phylogenetics is based.

Any genome of any living being is the result of the accumulation of variation along the genealogical history that leads from the origin of life to the present. But the path that leads from the beginning to each organism is specific to each individual: it is its genealogy. It is from this tree that genomic[1] variation accumulates in its

---

[1] Obviously, there is a blatant exception in horizontal gene transfer, which can occur at many scales, between distant species such as bacteria, or in situations that can make us rethink the very frame of reference of what we consider different species, as in the case of the introgression of archaic humans, which we will discuss in this chapter.

multiple forms: single nucleotide polymorphisms, or changes in the structure of the genome itself at scales ranging from a few bases in whole chromosomes, or jumps of elements that are, or had been, or look like viruses. Each of these events plants a flag on a branch of the tree: all the descendants of that branch will carry this new state in their genomes (unless a mutation occurs that reverts the genome to its original state, which is very unlikely). Comparing different genomes allows us to find these shared signals and reconstruct the family tree of our object of study.

But trees are also a magnificent example of fractals, one of the basic forms we find in living beings, as systematized and understood by the late Jorge Wagensberg. A unique feature of fractals is their scale invariance, which also applies to phylogenetic trees. Let us imagine a family searching for one of its members among those buried in the mass graves of the Spanish Civil War: it will be necessary to compare their genomes (or a small part of them) with that of a promising corpse to verify whether the genetic genealogy that links them to the corpse coincides with the family genealogy. Somehow, although it is necessary to adapt the techniques, the same logic is used to decide which tree best explains the most basic relationships of life, such as the one that can bind this family of *Homo sapiens* with the daisies, chrysanthemums, fungi and bacteria that have contributed to decompose the corpse or the archaea that could have lived in the intestine of the deceased. We will dedicate this chapter, however, to the trees that link humans to each other and to their closest dead relatives, Neanderthals and Denisovans.

However, the accumulation of diversity provides us with more than the shape of the tree. Because we know the speed with which this variation accumulates, we can give this tree a time scale that the shape of the tree itself, as we have seen, does not reveal. We have, then, a molecular clock, although perhaps it would work better, given its diversity, to compare it with a set of metronomes that mark very different rhythms. We know how to set the molecular clock in different ways, depending on the case. Basically, we can observe mutation live in microorganisms, counting mutations and dividing by the elapsed time; we can even adapt this strategy for certain forms of variation in the human genome, where we can see and count mutations by looking at hundreds or thousands of meiosis, either by comparing parents and offspring or by analyzing well-documented pedigrees such as those in Iceland or Flanders. But most mutations are too slow to be observed live, so we must turn to paleontology to calibrate the molecular clock. If the fossil record provides us a more or less clear date for the separation between two species, then the number of cumulative changes between the two divided by the elapsed time gives us the rate of substitution.[2]

At the current stage of technological development, a large number of complete human genomes can be generated with a reasonable budget. We have thousands of genomes sequenced at a high quality, with projects that ensure an adequate geographical representation of the human species. In addition, we have even more

---

[2] Which is not the same as the mutation rate, since there may have been parallel mutations, or backmutations, that do not provide observable changes when comparing two species.

information available thanks to strategies that give us an approximation to nucleotide diversity, such as SNP (single nucleotide polymorphism) *array* genotyping, in which up to 1–2 million positions scattered throughout the genome are interrogated, or exome sequencing, in which the sequence of the vast majority of the protein-coding regions of the genome is produced. The result is that we have a huge number of genomes characterized in one way or another. This has allowed us to move from analyses based on a single locus (a single gene, the Y chromosome, mitochondrial DNA) or even a single position, to understanding variation simultaneously across the entire genome. By comparing many genomes of diverse population origins, we are able to recognize partial sequences (haplotypes) that are more frequent in some populations than in others. This allows us to quantify gene flow between populations, or, for a certain individual, to paint the chromosomes as a mosaic of different population origins. And beyond gene flow between current populations, we are also able to recognize regions of the genome introgressed from archaic humans, as we will explain later. Thus, we are also able to unfold the family tree of humans in space (and we call that *phylogeography*), and to recognize each of our genomes as a palimpsest of multiple origins and connections.

The other great pillar that buttresses the current understanding of human evolution is the availability of a large number of ancient genomes.[3] This has been an incredible technological feat that, with great difficulty, has allowed us to do what not so many years ago seemed impossible: to have ancient genomes of humans and our closest relatives, with a geographical coverage that spans all five continents. It should be noted, however, that, either because of the ease of preservation of DNA in colder climates, or because of Eurocentric interest or the availability of anthropologists, archaeologists, and geneticists in the field, Europe is also overrepresented in the field of ancient DNA. If by ancient DNA we mean DNA from a deceased person, we have a broad temporal representation, from 50,000 years ago to recent historical epochs. Therefore, it is now possible to make a diachronic reconstruction of human evolution, as Olalde et al. (2019) do in the case of the Iberian Peninsula, from the Mesolithic to the Muslims. Therefore, while the observation of contemporary diversity has allowed us to reconstruct the history of human populations, this approach can now be considered as a source for generating hypotheses that we can often (but not always) verify by turning to the DNA of our ancestors.

Beyond our species in the strictest sense, the availability of Neanderthal and Denisovan genomes has revealed the family tree that links us, as well as the lateral contribution or introgression of other human genomes into our own. However, undoubtedly, the ability we now have to locate real rather than inferred genomes, in the inner branches of phylogenetic trees is a spectacular and irrefutable proof of human evolution.

---

[3] We use here *genomes* in the sense of partially characterized human genome sequences, either by sequencing at low coverage or by capturing thousands of SNPs across the entire genome.

9.2 The Tangled Bank of Human Evolution

In this section we will see how we were able to reconstruct the recent tree of human evolution, and how we discovered that, actually, recent human evolution is more a bush of intertwined branches than a succession of fissions that give rise to watertight branches between them. Both the first published Neanderthal mitochondrial DNA sequence, from a fossil from Vindija (Croatia) 38,000 years ago (Green et al. 2008), and the first whole genome, from a sample from Altai (Siberia) 50,000 years ago (Green et al. 2010; Prüfer et al. 2014) gave clear results: the lineages of Neanderthals and anatomically modern humans diverged about 500,000 years ago. This is the last fork in the tree of life leading to us.

But as early as the first draft of the Neanderthal genome, the authors noticed an unexpected fact: Neanderthals shared more derived alleles with modern-day Europeans and Asians than with Africans. When comparing human, Neanderthal and chimpanzee sequences, Europeans, Asians, and Neanderthals often carried the same allele, which was different from that of Africans and chimpanzees. It could be that there were mutations that reverted to the ancestral state, or that they occurred in parallel in the Neanderthal branch and in the branch leading to Europeans and Asians. But there is no reason why these reversions or parallel mutations did not also occur, and to the same extent, in Africans. The authors propose a different explanation: there was introgression between Neanderthals and anatomically modern humans; the ancestors of present-day Europeans and Asians and Neanderthals met, interbred and had fertile offspring about 50,000 years ago, probably in the Near East, where there is archeological evidence of the presence of anatomically modern humans and Neanderthals in close time frames.

Introgression causes an exception in a rigid phylogenetic model: depending on which regions of the genome we look at, we will obtain different phylogenetic trees. However, these are exceptions, and, from the majority of the genome, we can obtain a clear consensus tree (which is precisely what allows us to detect these divergences that we interpret as a result of introgression). But, in itself, Neanderthal introgression is not a rarity, and numerous examples have been described in other groups of closely related species,[4] such as between chimpanzees and bonobos (De Manuel et al. 2016). See Gokcumen (2019) for a review on introgression between archaic and modern humans.

The introgressed sequences undergo a series of processes that alter their fate. First, recombination causes introgressed haplotypes to become progressively shorter as they recombine with sequences from anatomically modern humans. This process can be used to date introgression and to distinguish possible independent introgression events. For example, given the proportion of Neanderthal DNA it contains and the length of the fragments, some remains found in Peştera cu Oase, Romania, and which morphologically appear intermediate, are estimated to correspond to a human

---

[4] In fact, introgression makes the very concept of species more vague and imprecise.

who had a Neanderthal great-great-grandfather, while the rest of his ancestors were anatomically modern.

But the most important factor for the survival of introgressed sequences is, as Darwin knew very well, the effect on the survival of the carriers. These effects can run the gamut of possibilities, from being incompatible with life to giving a selective advantage to pure neutrality. Thus, neither Neanderthal Y chromosomes nor mitochondrial genomes (mtDNA) have been found in humans. The lack of recombination and the small effective population size of these genomic regions may explain the loss purely by drift, or by any mismatch at any Y or mtDNA locus. However, mapping Neanderthal introgressed regions in humans shows a significant deficit on the X chromosome, which would suggest some sort of partial reproductive incompatibility between humans and Neanderthals. In general, Neanderthal sequences are less frequent in coding and regulatory regions of the human genome, and it is inferred that introgression may have altered the epistatic interactions within each species. Neutral introgressed variation, by definition, has followed the same path as properly human variation, changing in frequency, or even becoming extinct, with the same probability. But there are also examples of introgressed variation that turned out to be adaptive in humans; the most spectacular example, which we will see below, however, comes from the Denisovans. Most cases of adaptive introgression involve the immune system (HLA haplotypes) and interaction with pathogens such as RNA viruses, including SARS-CoV-2!

9.3 The Faceless Human

The ability to describe the genetic diversity existing in a genome from ancient remains and to compare it in a phylogenetic context (i.e., within a family tree) has allowed the discovery of a new group of humans, the Denisovans. The Denisova cave in Siberia contains some skeletal remains that are anatomically Neanderthal, and others that are too small to identify with certainty. Sequencing of mtDNA extracted from a finger bone dated 50–80,000 years ago provided a major surprise: it did not fall within known Neanderthal variation, but had diverged from Neanderthals and humans a million years ago (Krause et al. 2010). Analysis of the complete nuclear genome, which was published shortly thereafter (Reich et al. 2010), clarified that Denisovans are phylogenetically closer to Neanderthals, which diverged about 600,000 years ago, while the ancestors of humans diverged from the Neanderthal-Denisovan branch 800,000 years ago (and not 500,000 years ago as inferred by comparing only humans and Neanderthals). In the same article, a molar found in the same cave was genetically confirmed as Denisovan. Given the scarcity of bone remains available, the definition of a Denisovan was based primarily on its genome; for the first time, a mammal species[5] was defined not on the basis of morphology or

---

[5] Svante Pääbo, who led this research, prefers not to speak of a species but of a "group of hominins."

behavior, but on the basis of its genome. And this has been the only criterion available to us for identifying Denisovan remains; beyond other bone fragments from the Denisova cave itself, the only Denisovan specimen found is the Xiahe mandible, in Tibet, although the identification is based not on the genome itself but on the protein composition of the collagen extracted from the mandible, and on the presence of Denisovan DNA sequences in environmental samples from the Xiahe cave (see the chapter by María Martinón-Torres in this same volume). Methylation patterns in a set of genes related to development and craniofacial morphology have provided more information about the appearance of the Denisovans than the few skeletal remains that can be attributed to them.

Denisovans also interbred with humans and Neanderthals; in the latter case, one of the bones found at Denisova corresponded to a 13-year-old girl, whose genome indicates a Denisovan father and a Neanderthal mother. In the case of humans, the presence of Denisovan sequences is greatest in Southeast Asia and especially among Melanesians; it is possible that the first anatomically modern humans encountered Denisovans in their colonization of Southeast Asia and Sahul. We owe the Denisovans a spectacular example of adaptive introgression: modern Tibetans carry a Denisovan haplotype of the *EPAS1* gene (a hypoxia-inducible transcription factor) that allows them to adapt to altitude.

9.4 Ghosts of the Past

We have just seen how, from very little biological material, we can infer the presence of a new species. We have gone a step further: in several cases, we recognize archaic humans through the imprint they have left in our genomes, without being able to attribute these archaic genomes to any specific biological remains. And all this is possible thanks to the theoretical framework bequeathed to us by Darwin, basically by reconstructing the phylogenetic paths that our genomes have followed. Indeed, we can propose hypothetical models for the reconstruction of the history that has generated human diversity. These models include the sequence of fissions and fusions (introgression, gene flow), the times at which these events occurred and the size of the populations involved. We can propose alternative models, which, for example, may or may not include the presence and contribution of unknown archaic humans (ghost populations). To decide between different models, we implement them in the form of simulations and count how many times they give us results reasonably similar to the actual diversity, described by a set of statistics. The model that most often comes closest to the actual diversity will most likely be the one that actually occurred. This approach, called approximate Bayesian computation (ABC), depends on a multitude of parameters and involves making a large number of arbitrary a priori decisions; thus, Mondal et al. (2019) coupled deep learning to ABC and inferred that an unknown and distinct archaic population of Neanderthals and Denisovans contributed to the current genomes of South Asian populations. It should be noted, however, that ABC can tell us whether model A is better than model B, but it does not guarantee that model A is correct; we are limited by our imagination and by what we think is plausible in elucidating what processes and what species, tangible or phantom, may have been involved.

The presence of haplotypes highly divergent from the rest of the genome is also interpreted as a sign of archaic introgression, although these haplotypes have not been described in any known ancient genome. This method was also employed in some of the studies detecting archaic introgression of unknown origin in present-day Africans, with a divergence time located between 0.5 and 2 million years (Lorente-Galdos et al. 2019; Durvasula and Sankararaman 2020). However, several possible confounding factors must be taken into account, such as the action of balancing selection or the population structure of the group of humans that, in Africa, originated modern humans. These factors could also partially explain the presence of divergent sequences in present-day Africans.

9.5 Answers on Human Evolution Inscribed in the Genome

Leaving aside the phylogenetic relationships of humans with other species, even the closest but extinct ones such as Neanderthals and Denisovans, the evolution of humans has left traces in our genome as a result of demographic[6] processes. We can reconstruct migrations, population mixing, isolations, and expansions of human groups through population analysis and comparison of genomes of current human individuals and even including data from extinct humans. This type of analysis allows us to reconstruct the evolution of humans, our history, at different time scales. We can reconstruct the most recent history of an individual, of their relationships in the last generations, through the analysis focused on disciplines such as forensic genetics or genealogy. But we can also reconstruct much older and global events, such as the origin of our species or the settlement of large territories and continents. On an intermediate time scale between the examples above, we can clarify what demographic processes have affected specific population groups and how local geographic regions have been colonized. To give examples of some of these processes, we introduce below a set of cases that have allowed us to reconstruct human history at different time scales with the help of data from other disciplines such as paleontology, linguistics, or archeology, among many others. As we will see, the analysis of genomes allows us to confirm or reject hypotheses about the recent and ancient history of human populations, or to propose new ones.

---

[6] As we mentioned at the beginning of this article, the adaptive events that also leave traces in the genome are dealt with in the work of Elena Bosch in this monograph.

9.5.1 The African Origin of the Human Species

Since the late twentieth century a broad consensus has prevailed on the African and recent origin of our species. Palaeoanthropological, archeological, genetic, and even linguistic data confirm the origin of humans in Africa some 200,000 years ago. The first genetic evidence of the African origin of humanity comes from the analysis of mtDNA which shows that the most differentiated and basal mitochondrial genomes of current populations are those present in African populations and that the rest of the genomes are a small fraction of the diversity found in Africa. The African origin of the current human populations was also confirmed with the analysis of the paternal lineages, through sequences of the Y chromosome. In any case, it must be taken into account that both mtDNA and Y chromosome lineages (the uniparental genomes) represent only a small fraction of our genomes and are more affected by genetic drift than the rest of the genome due to their smaller effective size. Therefore, other parts of the genome must be analyzed to be able to provide conclusions about our origins that will be all the more robust the larger the fraction of the genome analyzed. In this sense, all autosomal genetic analyses, from the analysis of a few markers to the complete genome sequence (Auton et al. 2015; Mallick et al. 2016), show more diversity in African populations due to our African origin, but also because African populations have maintained a larger effective size that has allowed them to accumulate more variation. The fact that our species arose in Africa and for thousands of years diversified on the African continent before colonizing the rest of the planet allowed more genetic variants to accumulate there compared to other human populations. Non-African humans represent a subset of the genetic diversity of African populations due to the bottleneck, a drastic reduction of individuals, that they suffered during the African exit between 45,000 and 60,000 years[7] ago.

Despite the consensus on the African origin of humans, current genetic data do not allow to state conclusively which was the geographical region within the continent where our species appeared. Some genomic data point to the east of the continent (Tishkoff et al. 2009) or to southern Khoisan-language populations (Henn et al. 2011), and even uniparental data suggesting the presence of basal lineages in West Africa (Mendez et al. 2013; Lipson et al. 2020). The fact that current populations are not representative of the geographic area where they currently live due to multiple migrations over tens of millennia and the possible disappearance of human populations makes it difficult to precisely locate the origin of humans. This lack of certainty in the local origin within Africa could support the hypothesis of a possible multi-regional origin of our species within the African continent. The compilation of more genomic data, including complete genomes of extant and extinct individuals, and the analysis of complex demographic models will allow us

---

[7] This departure of our species from Africa is known as Out of Africa (OOA) in reference to the novel of the same name published in 1937 by the Danish writer Karen Blixen. A good review of the genetic data confirming this Out of Africa of humans can be found in (Henn et al. 2012). See also the current state of the subject in the chapter by María Martinón in this book.

to refine and contrast the different hypotheses on the local origin of humans within Africa.

9.5.2 The Forgotten Diaspora: The Origins of the Roma People

Genomic data, together with data from other disciplines, have made it possible to carefully reconstruct the history and demography of humans at the continental and macro-geographical level. Within the intracontinental sphere, some human migrations and diasporas have been genetically documented, such as the case of the expansion of the Bantu peoples in sub-Saharan Africa, the Jewish diaspora, or the expansion of Tupi-Guarani languages in South America. However, many questions at a more local geographic and population-specific scale remain unknown and that genomic data are helping to resolve. One of these local histories is the diaspora of the Roma people, also known as Gypsies, which has been the focus of some of our research. Despite being the largest[8] transnational ethnic minority in Europe, few genetic studies have focused on the origin of the Roma people. Historical records show that the Romani people have been marginalized and socially persecuted at different times and in different regions of Europe. Linguistic data suggest an origin of the Roma in the Indian subcontinent, since the Romani language belongs to the Indo-Aryan branch of the Indo-Iranian linguistic family, related to languages such as Sanskrit, Nepali, Gujarati, Hindi, or Punjabi. The first genetic studies that pointed to the Indian subcontinent as the origin of the Roma people focused on the analysis of Mendelian diseases characteristic of the Roma, where mutations shared with current populations of India and Pakistan were described (Kalaydjieva et al. 2001).

The analysis of uniparental genomes showed that the genetic composition of the Romani people is extremely heterogeneous, with a mixture of lineages from the Indian subcontinent and typically European lineages, some of which are lineages with a small number of founders. This genetic composition is compatible with a diaspora of Roma ancestors from the Indian subcontinent to Europe characterized by multiple founder effects, population bottlenecks, and differential gene flow between males and females with European populations (Gresham et al. 2001; Martínez-Cruz et al. 2015; García-Fernández et al. 2020). As we have mentioned above, uniparental lineages represent a small part of our genome, but the analysis of autosomal markers and whole genomes has confirmed and refined uniparental data by applying complex demographic models (Mendizabal et al. 2012; Font-Porterias et al. 2019; Bianco et al. 2020). The origin of the Roma people according to autosomal data can be traced to northwestern India, around present-day Punjab, about 1500 years ago, when the ancestors of today's Roma underwent a strong bottleneck and migration

---

[8] There are no precise statistics on the number of Roma in Europe, and approximations point to a population of around 10 million.

across the Middle East to Europe about 900 years ago. Thereafter they dispersed rapidly across the European continent mixing with local populations in heterogeneous ways depending on the Roma group. For example, genomic data show more admixture with local European populations in Roma groups on the Iberian Peninsula than in the Balkans.

Despite efforts to make the Roma people visible in the European genetic landscape, although we have few studies and little data, and given the heterogeneity of Roma groups, much of their genetic diversity and history is still unknown, especially those small groups that have not been studied or the components of the second great Roma diaspora to the Americas.

9.5.3 Europe's Prehistory Reconstructed from Ancient DNA

The examples given above reconstruct the history of human populations through the genetic study of current populations. By analyzing the genetic diversity that we observe at the present time, we try to reconstruct what the past has been like. In other words, we take a look at the past from the present. But thanks to technological advances in the recovery of ancient biological material, we can reconstruct past history in a different way, by directly observing what past populations were like through the genetic analysis of ancient individuals. This approach has become widespread in the last decade and a plethora of ancient DNA data from human populations has been produced, in spite of the fact that it is very expensive and depends on the state of conservation of the sample to be analyzed, since DNA degrades easily.

In the race to obtain DNA from ancient humans in Europe, the first milestone was set by Svante Pääbo's group by recovering the mtDNA of a mummified individual in the Tyrolean Alps about 5000 years old, whose entire genome was later sequenced and a population analysis was carried out (Handt et al. 1994). Since then, DNA has been recovered from hundreds of ancient remains on the European continent from different eras: Paleolithic hunter-gatherers, early Neolithic farmers and herders, individuals from the Metal Ages, to individuals from more recent European history, including historical figures such as Richard III of England or the last Tsar of Russia (Ivanov et al. 1996; King et al. 2014). Early compilations of genomic data from different ages in Europe and comparison with genomic data from current Europeans showed that current populations are the result of population admixtures and replacements that have taken place since the first occupation of the continent by hunter-gatherer populations from the Middle East. These genetic studies help to resolve the long-standing debate across different scientific disciplines questioning the role of early Paleolithic hunter-gatherers to Neolithic farmers and herders in the current composition of Europeans. A debate ensued between the supporters of a substitution and extinction of the Paleolithic individuals and the supporters of a cultural replacement without demographic change. The ancient genomic data in Europe point to a hybrid model where Paleolithic and Neolithic populations interbred and even later populations arriving from the Central European steppes contributed to the current European genetic pool in a very heterogeneous way.

But the study of ancient DNA in Europeans provided us with a surprise: beyond the dichotomy between local Mesolithic and Neolithic newcomers from the Middle East, among the current European ancestors we find, in the same proportion as the two previous ones, individuals coming from the Eurasian steppe, the descendants of which arrived in Central and Western Europe with the Bronze Age. In particular, the genetic turnover was much more intense on the Y chromosomes: between 50 and almost 100% of the Y chromosomes of Western Europeans belong to a lineage, R1b-M269, which is not found in the ancient DNA record before the bronze age and which clearly comes from the East of the continent.

Currently, ancient DNA studies in Europe address more local aspects such as population movements in the Iberian Peninsula in the last eight thousand years through the analysis of hundreds of ancient genomes, the influence of agriculture in southeastern Europe, the genetic composition and migrations in ancient imperial Rome or the influence of eastern Mediterranean populations on the westernmost islands, to give a few examples (Mathieson et al. 2018; Antonio et al. 2019; Fernandes et al. 2020). These studies show that the availability of more ancient genomes will allow in the near future to resolve increasingly recent historical processes in Europe and other geographical regions.

Thanks to Darwin's work, we have the tools to reconstruct our evolution as a species, both in relation to the closest hominins and within humans. But, as the table of contents of this work you are reading shows, the reconstruction of our past is a complex task where each discipline contributes a piece of this mosaic and where a collective effort will be needed to make them fit together.

References

Antonio ML, Gao Z, Moots HM et al (2019) Ancient Rome: a genetic crossroads of Europe and the Mediterranean. Science 366:708–714

Auton A, Abecasis GR, Altshuler DM et al (2015) A global reference for human genetic variation. Nature 526:68–74

Bianco E, Laval G, Font-Porterias N et al (2020) Recent common origin, reduced population size, and marked admixture have shaped European Roma genomes. Mol Biol Evol 37:3175–3187

De Manuel M, Kuhlwilm M, Frandsen P et al (2016) Chimpanzee genomic diversity reveals ancient admixture with bonobos. Science 354:477–481

Durvasula A, Sankararaman S (2020) Recovering signals of ghost archaic introgression in African populations. Sci Adv 6:5097

Fernandes DM, Mittnik A, Olalde I et al (2020) The spread of steppe and Iranian-related ancestry in the islands of the western Mediterranean. Nat Ecol Evol 4:334–345

Font-Porterias N, Arauna LR, Poveda A et al (2019) European Roma groups show complex West Eurasian admixture footprints and a common South Asian genetic origin. PLoS Genet 15: e1008417

García-Fernández C, Font-Porterias N, Kučinskas V et al (2020) Sex-biased patterns shaped the genetic history of Roma. Sci Rep 10:18142

Gokcumen O (2019) Archaic hominin introgression into modern human genomes. Am J Phys Anthropol 171(Suppl 70):60–73

Green RE, Malaspinas AS, Krause J et al (2008) A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing. Cell 134:416–426

Green RE, Krause J, Briggs AW et al (2010) A draft sequence of the Neandertal genome. Science 328:710–722

Gresham D, Morar B, Underhill PAA et al (2001) Origins and divergence of the Roma (gypsies). Am J Hum Genet 69:1314–1331

Handt O, Richards M, Trommsdorff M et al (1994) Molecular genetic analysis of the Tyrolean Ice Man. Science 264:1775–1778

Henn BM, Gignoux CR, Jobin M et al (2011) Hunter-Gatherer genomic diversity suggests a Southern African origin for modern humans. Proc Natl Acad Sci 108:5154–5162

Henn BM, Cavalli-Sforza LL, Feldman MW (2012) The great human expansion. Proc Natl Acad Sci 109:17758–17764

Ivanov PL, Wadhams MJ, Roby RK et al (1996) Mitochondrial DNA sequence heteroplasmy in the Grand Duke of Russia Georgij Romanov establishes the authenticity of the remains of Tsar Nicholas II. Nat Genet 12:417–420

Kalaydjieva L, Gresham D, Calafell F (2001) Genetic studies of the Roma (Gypsies): a review. BMC Med Genet 2:5

King TE, Fortes GG, Balaresque P et al (2014) Identification of the remains of King Richard III. Nat Commun 5:5631

Krause J, Fu Q, Good JM et al (2010) The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. Nature 464:894–897

Lipson M, Ribot I, Mallick S et al (2020) Ancient West African foragers in the context of African population history. Nature 577:665–670

Lorente-Galdos B, Lao O, Serra-Vidal G et al (2019) Whole-genome sequence analysis of a Pan African set of samples reveals archaic gene flow from an extinct basal population of modern humans into sub-Saharan populations. Genome Biol 20:77

Mallick S, Li H, Lipson M et al (2016) The Simons genome diversity project: 300 genomes from 142 diverse populations. Nature 538:201–206

Martínez-Cruz B, Mendizabal I, Harmant C et al (2015) Origins, admixture and founder lineages in European Roma. Eur J Hum Genet 24:937–943

Mathieson I, Alpaslan-Roodenberg S, Posth C et al (2018) The genomic history of southeastern Europe. Nature 555:197–203

Mendez FL, Krahn T, Schrack B et al (2013) An African American paternal lineage adds an extremely ancient root to the human Y chromosome phylogenetic tree. Am J Hum Genet 92: 454–459

Mendizabal I, Lao O, Marigorta UM et al (2012) Reconstructing the population history of European Romani from genome-wide data. Curr Biol 22:2342–2349

Mondal M, Bertranpetit J, Lao O (2019) Approximate Bayesian computation with deep learning supports a third archaic introgression in Asia and Oceania. Nat Commun 10:246

Olalde I, Mallick S, Patterson N et al (2019) The genomic history of the Iberian Peninsula over the past 8000 years. Science 363:1230–1234

Prüfer K, Racimo F, Patterson N et al (2014) The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505:43–49

Reich D, Green RE, Kircher M et al (2010) Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468:1053–1060

Tishkoff SA, Reed FA, Friedlaender FR et al (2009) The genetic structure and history of Africans and African Americans. Science 324:1035–1044

Chapter 10
The Adaptations That Made Us Human: Morphology

David M. Alba and Sergio Almécija

Abstract Humans share many morphological features with living great apes but also display unique characteristics related to habitual bipedalism, manipulation, cognition, diet, and sociosexual behavior. Darwin inferred that all these features were interrelated but could not determine their order of appearance. Since then, molecular data have revealed that humans and chimpanzees diverged from their last common ancestor (LCA) approximately 9–7 million years ago. Understanding the nature of this LCA is essential to elucidate the first evolutionary steps of the human lineage. However, it is impossible to reconstruct it without the aid of the fossil record. A review of all currently available evidence suggests that this ancestor was arboreal and possessed an orthograde body plan, hand length proportions similar to humans', and chimpanzee-like intelligence and culture. The earliest adaptations of the human lineage are related to bipedalism, manipulation, and a reduction of sexual dimorphism. However, most adaptations to habitual bipedalism do not appear until later in australopiths. It is not until the origin of *Homo* that most adaptations of modern humans appear, being related to habitual purposive stone tool use and tool-making, meat consumption, and more advanced cognition and complex social behaviors.

Keywords Human evolution · Hominins · Paleoanthropology · Adaptation · Comparative anatomy

---

D. M. Alba (✉)
Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain
e-mail: david.alba@icp.cat

S. Almécija
Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain

Division of Anthropology, American Museum of Natural History, New York, NY, USA

New York Consortium in Evolutionary Primatology, New York, NY, USA
e-mail: salmecija@amnh.org

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_10

10.1 Introduction

> [T]he difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind. [...] At what age does the new-born infant possess the power of abstraction, or become self-conscious and reflect on its own existence? We cannot answer; nor can we answer in regard to the ascending organic scale (Darwin 1871, pp. 105–106).

10.1.1 The Concept of Adaptation

The concept of "adaptation" is often applied to any trait that performs a given function and confers an evolutionary advantage, being thus inferred to have evolved by means of natural selection. This excludes ecophenotypic features (plastic responses that are not genetically determined), characters evolved by genetic drift, and by-products of selection upon other features (Gould 2002). However, performing a certain role is not a sufficient condition to refer to adaptation (Gould 2002): we distinguish between adaptations (selected to carry out their current function) and exaptations (originated because of another reason and subsequently co-opted for their current role). Even when we can determine the current function of a given feature, it is difficult to identify adaptations, because during evolution structures often acquire new functions.

10.1.2 The Relationship Between Form and Function

Functional morphology aims to discern the relationship between form and function in anatomical structures, which is quite challenging. Comparative anatomy among extant groups represents a first approach that, combined with phylogenetic data, enables the inference of ancestral morphotypes. However, behavioral, physiological, and biomechanical studies are required to test morphofunctional hypotheses and, thus, be able to propose adaptive hypotheses about the original selection pressures. Only this way we can reasonably argue that a given trait is an adaptation for a particular function.

10.1.3 Paleobiology

Extant organisms provide only partial knowledge of evolutionary history and often do not allow us to distinguish adaptations from exaptations. To do so, one must recourse to the fossil record, which despite its numerous limitations uniquely provides direct access to deep time. To validate adaptive hypotheses in the fossil record, there needs to be historical concordance between a given character and the function attributed to it. Often, the fossil record indicates that certain characteristics arose to perform different functions from their current ones. Below, we review the main characteristics of modern humans and, with the aid of the fossil record, try to discern what are the main morphological adaptations throughout human evolution.

10.2 The Human Primates

10.2.1 Separating the Wheat From the Chaff

Human beings (*Homo sapiens*) are the result of a long evolutionary process and, hence, a mosaic of morphological features that appeared at different times in the history of life. Some are shared with all vertebrates, mammals, primates, and so on, successively up to our closest relatives, the great apes (orangutans, gorillas, and chimpanzees). Both primitive traits shared with distant relatives and those shared only with extinct members of the human lineage may be adaptations. Nevertheless, when we wonder what makes us human, we are referring to derived traits that distinguish us from our closest relatives and represent unique adaptations of the human lineage.

10.2.2 Humans' Closest Relatives

The phylogenetic relationships between humans and extant great apes were controversial for a long time. Initially, Darwin refrained from discussing human origins, but over 150 years ago he devoted a whole book to the subject (Darwin 1871). For more than a century, paleontological remains did not settle this question, and for a long time it was considered that gorillas and chimpanzees were more closely related to one another than to humans. However, molecular studies have confirmed that humans and chimpanzees shared a last common ancestor (LCA) during the Late Miocene, between 9 and 7 million years ago (Ma) (Moorjani et al. 2016). Currently, most authors (e.g., Alba 2012) classify humans and great apes in a single family (hominids s.l.; Fig. 10.1) within the superfamily hominoids. They further distinguish the African great ape and human lineage (subfamily hominines) and, among them, the human lineage (tribe hominins). Finally, the term "humans" refers to any species of the genus *Homo*.

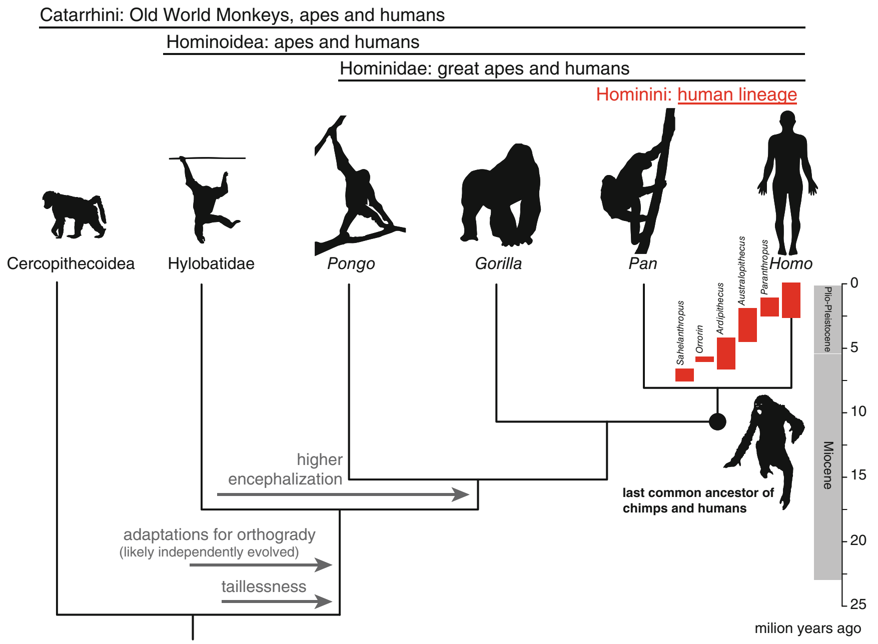

Fig. 10.1 Schematic phylogenetic tree of extant hominoid primates and approximate chronostratigraphic range of hominin genera. The lack of external tail and an orthograde boy plan are some of the characteristics (among many others) that humans share with our closest living relatives

10.2.3 The Last Common Ancestor of Chimpanzees and Humans

The LCA between chimpanzees and humans represents the starting point of human (and chimpanzee) evolution. Hence, it is essential to reconstruct it to understand the early adaptations of the human lineage. Some authors consider that chimpanzees represent a good approximation to the ancestral morphotype (Wrangham and Pilbeam 2001), so that bipedalism would have evolved from a semi-terrestrial knuckle-walking ancestor. Unfortunately, the fossil record of African great apes is virtually non-existent, but the fossil record of Miocene apes shows unequivocally that ancestral morphotypes cannot be reconstructed from living species alone because numerous features have evolved in parallel (e.g., Alba 2012). This might be the case for knuckle-walking in gorillas and chimpanzees, so rather than assuming that chimpanzees are "time machines" (Wrangham and Pilbeam 2001), it is preferable to consider all available information from both Miocene apes and hominins.

10.3 Main Adaptations of the Human Lineage

We may group the main adaptations of humans into five morphofunctional complexes: bipedal locomotion; refined manipulation; high encephalization with advanced cognitive and cultural abilities; reduced masticatory apparatus and omnivorous diet; and reduced sexual dimorphism related to sociosexual behavior. Darwin (1871) concluded that bipedalism would have originated within the framework of an adaptive complex that would also include high encephalization, tool-making, and reduced canines. Bipedalism would have freed the hands, and this would have enabled tool use and tool-making, which would have replaced the canines as a weapon, leading to a feedback loop that would have led to human culture and, ultimately, civilization. Nonetheless, the order of appearance and, in particular, the original adaptive value of these features has been widely discussed. In the following, we focus on the information provided by the fossil record (Fig. 10.1), and especially the earliest putative hominins from the Late Miocene—*Sahelanthropus* (~7 Ma), *Orrorin* (~6 Ma) and *Ardipithecus* (~5.8–4.4 Ma; Fig. 10.2c)—which preceded the

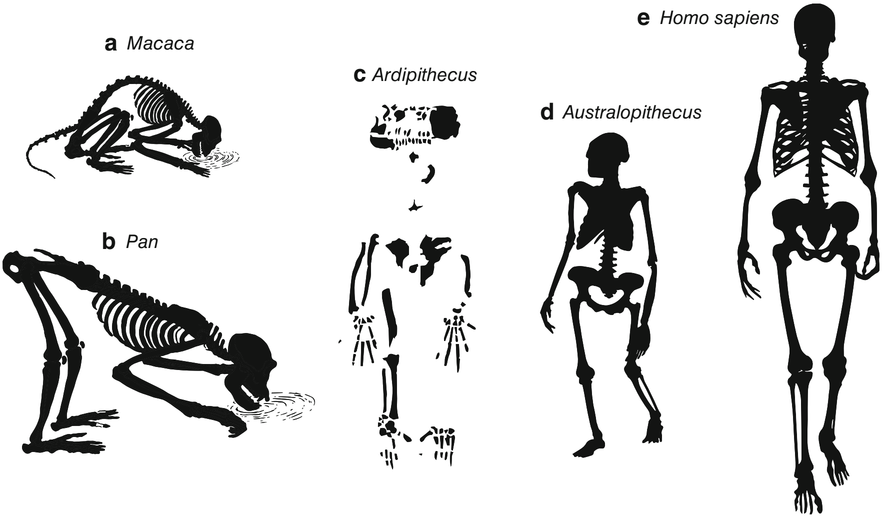

Fig. 10.2 (**a**, **b**) Skeletal silhouettes of a macaque (**a**) and a chimpanzee (**b**) displaying a similar posture to illustrate the differences between the prograde and orthograde body plan, respectively; redrawn from figure 28 of Schultz (1969). (**c**–**e**) Silhouettes of the skeleton of *Ardipithecus ramidus* ((**c**) ARA-VP-6/500, attributed to a female), the skeletal reconstruction of *Australopithecus afarensis* ((**b**) AL 288-1, "Lucy"), and a modern human (**c**). All skeletons are drawn at approximately the same scale. The orthograde body plan, characteristic of all extant hominoids, is characterized by a wider and shallower thorax and a shorter and stiffer lumbar region, among other features. It is probably an adaptation for vertical climbing, which was subsequently co-opted for other types of locomotor behaviors, including bipedalism. *Ardipithecus* was probably orthograde and displays some features indicative of bipedalism, but lacks most adaptations for habitual terrestrial bipedalism. These are present in australopiths, which nevertheless retain, unlike humans, characters indicative of some degree of arboreal locomotion

later appearance of australopiths (*Australopithecus* and *Paranthropus*; Fig. 10.2d) and, finally, humans (*Homo*; Fig. 10.2e).

10.3.1 Locomotion

Like the rest of extant hominoids, human beings are, above all, peculiar erect and tailless simians. In anthropoids, two main types of locomotor behaviors may be distinguished: pronograde, in (sub)horizontal supports with the trunk held approximately horizontal and the limbs under compression; and orthograde (or antipronograde), with the trunk verticalized and the limbs often under tension. All extant hominoids possess an orthograde body plan—suitable for performing antipronograde behaviors (vertical climbing, suspension, knuckle-walking, and bipedalism)—in addition to lacking an external tail and displaying specialized elbow and wrist features (Ward 2015). Thus, living forms suggest that the hominoid LCA would be an orthograde climbing and suspensory primate. However, the fact that all extant apes display to some extent both climbing and suspensory behaviors precludes discerning whether orthogrady originated as an adaptation to one behavior or the other. Instead, the fossil record indicates that the evolution of the locomotor apparatus occurred in a mosaic fashion, and that the loss of the tail (Fig. 10.1) was among the first features to evolve (Kelley 1997; Ward 2015). Furthermore, the fossil record shows unequivocally that orthogrady would have evolved several times in parallel, being an adaptation for vertical climbing that was subsequently co-opted for suspension along various lineages (e.g., Alba 2012; Ward 2015).

Despite the scarce evidence available, Late Miocene hominins are generally considered as occasional bipeds (e.g., Harcourt-Smith 2015). The anterior position of the foramen magnum in *Sahelanthropus* has been interpreted as an adaptation to bipedalism, but postcranial evidence suggests otherwise (Macchiarelli et al. 2020). In turn, the postcranial remains of *Ardipithecus kadabba* (5.8–5.2 Ma) are too scanty to draw definitive conclusions (Harcourt-Smith 2015). Instead, the femur of *Orrorin* suggests that it would have been a habitual biped despite the retention of climbing abilities (Senut et al. 2001; Almécija et al. 2013). In *Ardipithecus ramidus* (4.4 Ma; Fig. 10.2d), the morphology of the pelvis and the foot further indicates an incipient adaptation to bipedalism (White et al. 2009; Harcourt-Smith 2015), albeit more primitive than that of australopiths (with the big toe still abducted). Furthermore, the hands of *Ardipithecus* suggest that bipedalism would not have evolved from a semi-terrestrial knuckle-walking ancestor, but from an essentially arboreal one (White et al. 2009). There is no reason to think that *Ardipithecus* was not an orthograde climber (Harcourt-Smith 2015), which in trees would have employed both orthograde and pronograde postures, similarly to Miocene great apes such as *Pierolapithecus* (Alba 2012).

It is thus likely that the LCA possessed an orthograde body plan, later co-opted for knuckle-walking (and specialized below-branch suspension) in chimpanzees and bipedal walking in hominins. These types of locomotion are adaptations for exploiting the environment in new ways: the former is a compromise between specialized arboreal locomotion and terrestrial quadrupedalism, whereas bipedalism represents a greater orthograde specialization in terrestriality to exploit trophic resources in more open forest environments. The evolution of either type of locomotion is harder to explain starting from a pronograde ancestor. Instead, given the functional similarities between climbing and bipedalism, a climbing orthograde ape would not have required many anatomical changes to move bipedally on the ground. Despite orthogrady would not be an adaptation (but an exaptation) for bipedalism, multiple bipedal adaptations would have been subsequently superimposed throughout hominin evolution (Harcourt-Smith 2015), such as the big toe aligned with the rest of the toes or the knee located closer to the center of gravity. Many of these features are already well documented shortly before 4 Ma in the genus *Australopithecus*, which would have already been a habitual terrestrial biped (Ward 2015) despite retaining primitive features indicative of arboreal locomotion (Harcourt-Smith 2015). However, an almost obligate terrestrial bipedalism is not found until the appearance of *Homo erectus* s.l. in Africa slightly before 2 Ma (Harcourt-Smith 2015).

10.3.2 Manipulation

Adaptation to habitual terrestrial bipedalism involved the specialization of the foot as a propulsive organ and the progressive freeing of the hand from locomotor functions. Humans have a shorter hand, with less curved phalanges and a relatively longer and stouter thumb, than chimpanzees (Almécija et al. 2015; Fig. 10.3). While the long

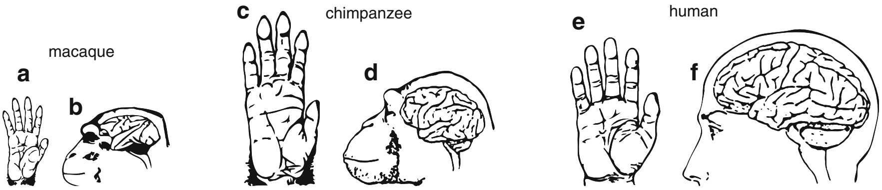

Fig. 10.3 Hand proportions (**a**, **c**, **e**) and brain size (**b**, **d**, **f**). The hands have been redrawn from figure 5 of Schultz (1968), while the heads with brains have been redrawn from figure 1 of Huble (1979). All figures are at approximately the same scale. The proportions of the chimpanzee hand (with a relatively short thumb and elongate fingers), which do not allow for pulp-to-pulp precision grasping (see Fig. 10.4), are probably derived relative to the condition of their last common ancestor (LCA) with humans. Modern humans display length proportions closer to the inferred condition for the LCA. Hence, they might not represent an adaptation, but an exaptation, for the manufacture of lithic industry. The most primitive hominins show some adaptations for refined manipulation due to the release of the locomotor functions of the hand, whereas the remaining adaptations for purposeful stone tool-making did not evolve until the acquisition of more advanced cognitive abilities in early humans. In fact, stone tool-making is as much, if not more, related to cognitive abilities than to manipulative skills. Chimpanzees, like all other extant great apes, possess larger brains (relative to body size) and higher cognitive abilities than monkeys, but far less than humans

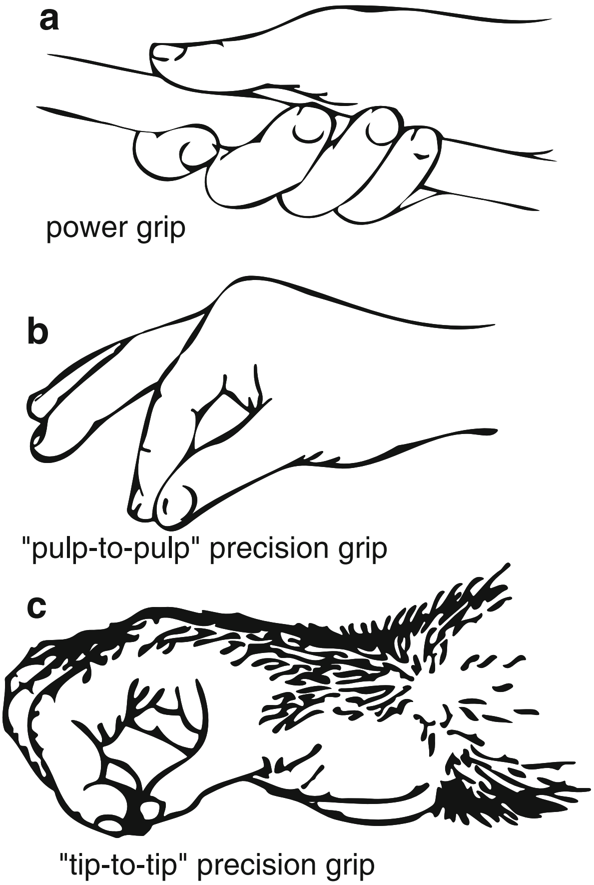

Fig. 10.4 Human power grip (**a**) and precision grip (**b**) compared to a precision grip performed by a chimpanzee (**c**). The possession of a long thumb relative to the rest of the fingers allows humans to perform a pulp-to-pulp precision grip (**b**). In contrast, the comparatively short thumb (relative to the rest of the fingers) of chimpanzees necessitates other types of precision grips (e.g., tip-to-tip) that are less effective (**c**). The first two panels (**a**, **b**) have been redrawn from figures 28a and 24 of Napier (1993), while the third panel (**c**) has been redrawn from figure 6 of Christel (1993). The images are not at the same scale

hand of chimpanzees functions as a grasping hook that facilitates vertical climbing and below-branch suspension, the proportions of the human hand facilitate 'pulp-to-pulp' precision grasping between the thumb and the remaining fingers (Napier 1993; Alba et al. 2003; Almécija et al. 2010; Almécija and Sherwood 2017; Fig. 10.4). It is highly unlikely that precision grasping is an adaptation to stone tool-making, because australopiths from 3.3 Ma already possessed modern human-like hand proportions (Alba et al. 2003; Almécija and Sherwood 2017) prior to the oldest record of undisputed lithic tools about 2.6 Ma. It is uncertain whether these stone tools were produced by australopiths, but the systematic manufacture of lithic industry did not become widespread until about 2 Ma (Panger et al. 2002), after the emergence of the genus *Homo*.

Once the locomotor selection pressures on the hand were relaxed, due to the progressive adaptation to terrestrial bipedalism, natural selection would have optimized hand anatomy for manipulation (Alba et al. 2003). However, both *Ardipithecus* and gorilla hand proportions (more similar to those of humans) suggest that the LCA, like most Miocene apes, would have displayed, as compared to modern chimpanzees, shorter fingers with a relatively longer thumb (Almécija et al. 2015). The long hand of chimpanzees and orangutans would have emerged independently as an adaptation for specialized suspensory behaviors (Almécija et al. 2015). Hence, the possession of a relatively long thumb would not be an adaptation, but an exaptation, for stone tool-making. However, unlike Miocene great apes, both *Orrorin* and *Australopithecus* already display a distal thumb phalanx morphology related to pulp-to-pulp precision grasping (Almécija et al. 2010; Almécija and Sherwood 2017). Thus, the adoption of terrestrial bipedalism, even if incipient, would have already prompted the acquisition of certain adaptations for refined manipulation in the earliest hominins (Almécija et al. 2010). This could have allowed australopiths to manufacture tools with organic materials (Panger et al. 2002) or even to occasionally make stone tools. Regardless, it would not have been until the origin of the genus *Homo*, with the adoption of committed terrestrial bipedalism, that other characteristics of the human hand (thumb and finger joint robusticity) would have appeared as an adaptation to stone tool-making.

10.3.3 Cognition and Life History

Purposive tool-making is also related to the possession of certain cognitive capacities, reflected in the huge size of our brain (Fig. 10.4)—especially the neocortex (Almécija and Sherwood 2017)—and entailing the possession of a disproportionately large braincase. The fossil record shows a remarkable increase in cranial capacity over time, especially during the evolution of the genus *Homo* since 2 Ma. A larger brain is advantageous for processing more information, but also metabolically very expensive to maintain (Aiello and Wheeler 1995). Thus, throughout evolution, a trade-off is established between the energetic constraints and the cognitive requirements of a given ecological niche. A simple brain/body size ratio is inadequate to describe the relationship between the two variables because larger species have smaller brains in relative terms. However, there are mathematical procedures to adequately compare relative brain size (or “encephalization”) among species. Encephalization is highly correlated with the cognitive abilities of various primate groups; in particular, extant great apes are more encephalized than monkeys and lesser apes, in agreement with the enhanced cognitive abilities of the former (Alba 2010). Studies of encephalization in fossil hominoids further indicate that Late Miocene great apes were already as encephalized as living ones, such that the hominid LCA would have already displayed more advanced cognitive abilities than earlier hominoids (Alba 2010). The higher encephalization and intelligence of great apes has been related to their particularly slow life history, and paleohistological data indicate that Miocene hominoids already possessed, like hylobatids, a slower life history than living monkeys (Kelley 1997). All this suggests that the encephalization increase of great apes was preceded by (and probably required) the prior acquisition of a particularly slow life history.

Ardipithecus would not be more encephalized than extant great apes, while australopiths may display a slight increase in encephalization (Alba 2010), perhaps related to more advanced cognitive abilities and cultural capacities. However, the most important encephalization increase would not have occurred until the emergence of the genus *Homo*, followed by subsequent increases in several human species during the Pleistocene (Alba 2010). It is difficult to determine which cognitive abilities were the target of natural selection, but there is a tight temporal relationship between encephalization increments and technological advances. In turn, the morphology of braincase endocasts suggests that australopiths already showed a significant cortical reorganization prior to the encephalization increase linked to *Homo* (Almécija and Sherwood 2017). In contrast, frontal lobe reorganization is not found until earliest *Homo* species, and it is not until *H. erectus* that we find a modern human-like endocranial configuration. Modern humans possess a peculiar life history characterized by slow maturation with early weaning and prolonged brain growth well beyond the end of childhood (Kelley and Bolter 2013). Tooth palaeohistological analyses suggest that australopiths, despite a possible increase in encephalization, still displayed a life history like that of extant great apes (Kelley and Bolter 2013). In contrast, *H. erectus* appears more similar to modern humans, and since 1 Ma extinct human species seemingly display a dental developmental pattern as slow as modern humans (Kelley and Bolter 2013). The fact that successive increases in encephalization predated the acquisition of a human-like maturation pattern suggests that enhanced cognitive abilities would have led (through reduced mortality) to a readjustment of life history, and not the other way around.

10.3.4 Diet

The skull of modern humans is not only highly derived due to the reorganization of the basicranium (related to bipedalism) and a disproportionate increase of the neurocranium (owing to high encephalization), but also because of the reduction of the masticatory apparatus (in relation to diet). *Ardipithecus* has a slightly more derived facial configuration than great apes and a generalized dental morphology, suggesting a diet less specialized in ripe fruit consumption than that of chimpanzees (White et al. 2009). In contrast, the masticatory apparatus of australopiths is characterized by the possession of robust mandibles, thick enamel, and disproportionately large postcanine teeth (Grine and Daegling 2017). The masticatory apparatus morphology of australopiths (especially *Paranthropus*) seems better adapted than that of *Ardipithecus* to the consumption of hard, tough, and/or abrasive food items (Grine and Daegling 2017). However, often there is no close correspondence between dental morphology and diet (Grine and Daegling 2017). Therefore, to make palaeodietary inferences, studies of microwear and enamel isotope composition, which allow us to infer what a species actually ate, are required. According to these data, *Ardipithecus* would have consumed a broader spectrum of trophic resources than chimpanzees (White et al. 2009), while the oldest *Australopithecus* do not significantly differ from *Ardipithecus* or African great apes (Grine and Daegling 2017). It is not since 3.5 Ma that a greater dietary diversity is found among hominins, which would have allowed australopiths to successfully exploit more open and arid environments than chimpanzees (Grine and Daegling 2017).

In contrast, the smaller teeth of *Homo* may be related to an increase in extraoral food processing thanks to the manufacture of lithic industry, so that the earliest representatives of the genus *Homo* would have exploited a wider range of trophic resources, including the consumption of meat and marrow (Thompson et al. 2019). In fact, *H. erectus* already displays a suite of anatomical changes (larger body size and higher encephalization) that have been linked to increased meat consumption (Milton 1999). This dietary change would have released the energetic constraints that previously prevented the maintenance of such a large brain (Aiello and Wheeler 1995; Milton 1999), not necessarily through the consumption of more energetic foods, but more nutritive and easier to digest (Milton 1999). From *H. erectus* onward, meat consumption would have secured protein and micronutrient demand, and at the same time allowed maximizing the consumption of high-energy plant items such as ripe fruit (Milton 1999). This would have prompted an encephalization increase, leading to a new positive feedback loop between intelligence, material culture, and reduced mortality.

10.3.5 Sociosexual Behavior

The most defining hominin features include decreased canine size and sexual dimorphism, with the concomitant loss of the upper canine honing complex (White et al. 2009; Plavcan 2012). Sexual dimorphism is related to social system and mating type (Plavcan 2012), as already noted by Darwin (1871), who attributed it to sexual selection. In female primates, sexual selection occurs mainly through mate choice, whereas agonistic behaviours related to mate competition are more relevant in males, albeit depending on the social structure (Plavcan 2012). Monogamous and polyandrous species would be expected to lack canine or body size dimorphism, whereas polygynous species should in principle display the highest levels. However, a given degree of dimorphism cannot be unequivocally associated with a particular social system and/or mating type, because dimorphism also depends on differential selection on males and females separately (Plavcan 2012). The pattern of sexual dimorphism in modern humans is unique among primates, combining many secondary sexual characters (e.g., swollen breasts in females, and greater skeletal robusticity and more developed musculature in males) with a low canine and body size dimorphism. The selective basis for such a pattern is unclear. Most secondary sexual characters might be due to mate choice by both sexes, whereas differences in body size and musculature might be related to male competition for access to females. This would agree with the fact that, despite the establishment of pair bonds, the most frequent mating system across human societies is a serial monogamy with some degree of polygyny (Plavcan 2012).

The fossil record indicates that canine size may have started to decrease very early in human evolution (Senut et al. 2001; Brunet et al. 2002; White et al. 2009). Indeed, in *Ar. ramidus* the upper canine is almost monomorphic and incisiviform, as in australopiths, and the canine honing complex has already been lost (White et al. 2009). Canine reduction would indicate low levels of male competition; however, based on the apparently low degree of body size dimorphism, it has also been hypothesized that *Ardipithecus* would exhibit a monogamous mating system with pair bonding (White et al. 2009). This is highly debatable, because male competition levels, rather than mating system, are the most important factor determining canine dimorphism (Plavcan 2012), and some promiscuous and polygynous species also show little dimorphism. Paradoxically, australopiths (despite lacking canine dimorphism) are highly dimorphic in body size, whereas a modern human-like degree of dimorphism is not found until *H. erectus* or later species (Plavcan 2012). The combination of marked body size dimorphism and reduced canine dimorphism might indicate the evolution of a more polygynous social system with greater competition among males in australopiths—given that, once the honing complex was lost, it would not have been feasible to select for larger canines in males. Therefore, the establishment of pair bonds between males and females might not have evolved until *H. erectus* or even later species of the genus *Homo*.

10.4 Discussion and Conclusions

Over 150 years after the publication of Darwin's (1871) *The Descent of Man*, comparative morphology and palaeobiological studies have established solid foundations to discuss adaptive hypotheses about the distinctive features of the human lineage (Table 10.1). In fact, we currently have much more information on the origin of humans than on the origin of chimpanzees—which have been shown to be inadequate models for reconstructing the LCA of chimpanzees and humans. Current evidence suggests that this LCA was an arboreal primate with an orthograde body plan adapted for vertical climbing; manipulative abilities greater than those of extant chimpanzees but lesser than humans'; chimp-like intelligence, life history and cultural capacity; a frugivorous diet less specialized in soft fruit consumption than in chimpanzees; and sociosexual behavior characterized by a moderate degree of male competition. From this LCA, the hominin and chimpanzee lineages would have responded differently to the environmental changes that, during the Late Miocene and Plio-Pleistocene, progressively caused the reduction and fragmentation of rainforest habitats. The acquisition of semi-terrestrial knuckle-walking locomotion would have allowed chimpanzees to continue exploiting arboreal trophic resources despite the absence of a continuous forest cover. In hominins, the acquisition of increasingly habitual bipedalism would have allowed the exploitation of new trophic resources in increasingly more open environments.

Table 10.1 The main adaptations of humans (genus *Homo*), australopiths (genera *Australopithecus* and *Paranthropus*) and early hominins (*Ardipithecus* and *Orrorin*) are synthetically summarized and compared with the features inferred for the last common ancestor between chimpanzees and humans (inherited from Miocene great apes). Functional interpretations of morphological features are indicated within parentheses, being distributed into five morphofunctional complexes: locomotion (L), manipulation (M), cognition (C), diet (D), and sociosexual behavior (S)

Last common ancestor of chimpanzees and humans (>9–7 Ma)	
L	Orthograde body plan (vertical climbing and arboreal quadrupedism without knuckle-walking)
M	Short hand with relatively long thumb (powerful grasping capabilities)
C	Great ape-like encephalization (culture [learned social traditions] with possible use of unmodified stones and manufacture of organic tools)
D	Digestive and masticatory apparatus less specialized than in chimpanzees (generalist frugivorous diet)
S	Marked body size and canine sexual dimorphism (male competition for access to females)
Earliest hominins (~7–4 Ma)	
L	Femur/pelvis with incipient adaptations for bipedalism; e.g., long femoral neck (facultative terrestrial bipedalism with orthograde arboreal locomotion)
M	Thumb with adaptations for refined manipulation (pulp-to-pulp precision grasping)
D	Dental morphology less specialized than in chimpanzees (generalist frugivorous diet based on forest trophic resources)
S	Reduced dimorphism, loss of canine honing complex (low competition among males)
Australopiths (~4–2 Ma)	
L	Foot, knee, pelvis, etc. with adaptations for habitual bipedalism; e.g., presence of foot arches (terrestrial bipedalism with some degree of arboreal locomotion)
C	Slightly higher encephalization than great apes and important cortical reorganization (greater cognitive and cultural capacities?, greater visuospatial and sensorimotor integration, sporadic stone tool-making?)
D	(Hyper)megadont molars, thick enamel, specialized masticatory apparatus (consumption of trophic resources from more open environments)
S	Marked body size dimorphism but low canine dimorphism (increased male competition, polygynous social structure?)
Humans (from *Homo erectus* ~2 Ma)	
L	Further adaptations for bipedalism; e.g., shorter toes (committed terrestrial bipedalism)
M	Further adaptations for refined manipulation; e.g., more robust thumb and finger joints (systematic manufacture of lithic industry)
C	Encephalization much higher and greater cortical reorganization than in great apes (more elaborate cognitive, cultural, symbolic and technological capacities)
D	Reduced masticatory apparatus (extra-oral food processing and regular meat consumption)
S	Low canine and body size sexual dimorphism but abundant secondary sexual characteristics (pair bonding [serial monogamy with some polygyny], mate choice by both males and females)

Broadly speaking, we may distinguish three main types of hominins (Table 10.1): the earliest representatives, from about 7 Ma onward; australopiths, beginning at about 4 Ma; and humans, since about 2.5 Ma. The fossil record indicates that some derived characteristics of the human lineage were already present in Late Miocene hominins, including not only some traits of the cranial base and the facial skeleton, but also some adaptations to facultative bipedalism (in *Orrorin* and *Ardipithecus*) and more refined manipulation. These adaptations would have been possible thanks to the possession, in the LCA, of an orthograde body plan and hand proportions more similar to those of humans than to those of chimpanzees. This would be due to ancestral adaptations for vertical climbing that, in early hominins, would have been co-opted for new locomotor and manipulative functions. Simultaneously, changes in sociosexual behaviors would have led to a progressive reduction in canine size and the loss of the honing complex, without relevant concomitant changes in diet or cognitive abilities. More numerous adaptations to habitual terrestrial bipedalism would not have emerged until the evolution of australopiths, when new types of trophic resources characteristic of more open environments were exploited. Australopiths may also have acquired more advanced cognitive and cultural abilities, as well as greater body size (but not canine) dimorphism, possibly due to the evolution of a more polygynous social system. Then, between approximately 2.5 and 2.0 Ma, the earliest species of the genus *Homo* would have appeared, occupying ecological niches probably not very different from those of australopiths. However, regular mean consumption, thanks to the systematic and purposeful manufacture of lithic industry, would have allowed a more substantial increase in encephalization. Ultimately, this would have led, around 2–1.5 Ma, to the emergence of a new adaptive type of primate—*H. erectus*—characterized by committed terrestrial bipedal locomotion, enhanced cognitive abilities, more refined manipulative skills clearly related to stone tool-making, a diet including the regular consumption of large prey meat, and decreased body size sexual dimorphism (possibly linked to pair bonding). Probably, these changes would not have been possible without the co-optation of some ancestral locomotor and manipulative adaptations for tool-making once cognitive and cultural capabilities allowed.

Darwin (1871) concluded that bipedalism, tool-making, increased encephalization and reduced canines would have constituted a feedback loop leading to human culture and, ultimately, civilization. One hundred and fifty years later, both the fossil record and the study of our closest relatives have taught us that these characteristics did not evolve all at once in concert. Some of them, such as a higher level of intelligence, certain cultural skills, and even human hand proportions, were already present to a large extent in the LCA. Others, such as bipedalism, further adaptations to refined manipulation, and reduced canine sexual dimorphism, date back at least incipiently to the earliest hominins from the Late Miocene, and would have become well established more than one million years before the origin of the genus *Homo*. The knowledge acquired since Darwin's time has vindicated a close relationship between the evolution of bipedalism and manipulative abilities, but not between the latter and tool-making, which more strongly relies on cognitive abilities than hand anatomy. Once a certain encephalization threshold was trespassed, stone tool-making (thanks to the co-optation of ancestral cognitive, cultural, and manipulative abilities) and associated meat consumption would have led to the evolution of the genus *Homo*. Regularly including meat in the diet, even if in low proportion, would have satisfied micronutrient requirements and, in this way, enabled an increased consumption of more energetic foods, thus releasing the metabolic constraints that until then had prevented a further increase in intelligence. This way, a feedback loop would have been established between cognitive abilities and technology, possibly mediated by reduced mortality rates, and since *H. erectus* human evolution would have become more determined by cultural evolution than ever before. In other words, from about 2 Ma onward, technology would have changed the rules of evolution, because artificial selection (on ourselves) would have taken a role as important as (if not more than) natural and sexual selection (Taylor 2010). Technology would not only be part of us, but what has made us what we are—an 'artificial' primate specifically adapted to adapt the environment for our own convenience. Humans, in short, would have fallen into a "technological trap" that, due to overpopulation and natural resources depletion, would have ended up driving the biosphere to a point of no return. Will we be able to get out of this trap? In a literal sense, the solution is no longer in our hands, because technology has largely transcended anatomy. And yet, it could be within our reach if we heed the following definition of technology (Taylor 2010): "the know-how to shape things to achieve ends that appear impossible."

Acknowledgments This work has been funded by the Agencia Estatal de Investigación (CGL2016-76431-P and CGL2017-82654-P, AEI/FEDER EU; PID2020-117289GB-I00 and PID2020-116908GB-I00, MCIN/AEI) and the Generalitat de Catalunya (CERCA Programme and consolidated research group 2017 SGR 116 GR).

References

Aiello LC, Wheeler P (1995) The expensive-tissue hypothesis. The brain and the digestive system in human and primate evolution. Curr Anthropol 36:199–221

Alba DM (2010) Cognitive inferences in fossil apes (Primates: Hominoidea): does encephalization reflect intelligence? J Anthropol Sci 88:11–48

Alba DM (2012) Fossil apes from the Vallès-Penedès Basin. Evol Anthropol 21:254–269

Alba DM, Moyà-Solà S, Köhler M (2003) Morphological affinities of the *Australopithecus afarensis* hand on the basis of manual proportions and relative thumb length. J Hum Evol 44: 225–254

Almécija S, Sherwood CC (2017) Hands, brains, and precision grips: origins of tool use behaviors. In: Kaas J (ed) Evolution of nervous systems, vol 3, 2nd edn. Academic Press, Amsterdam, pp 299–315

Almécija S, Moyà-Solà S, Alba DM (2010) Early origin for human-like precision grasping: a comparative study of pollical distal phalanges in fossil hominins. PLoS ONE 5:e11727

Almécija S, Tallman M, Alba DM et al (2013) The femur of *Orrorin tugenensis* exhibits morphometric affinities with both Miocene apes and later hominins. Nat Commun 4:2888

Almécija S, Smaers JB, Jungers WL (2015) The evolution of human and ape hand proportions. Nat Commun 6:7717

Brunet M, Guy F, Pilbeam D et al (2002) A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418:145–151

Christel M (1993) Grasping techniques and hand preferences in Hominoidea. In: Preuschoft H, Chivers DJ (eds) Hands of primates. Springer, Vienna, pp 91–108

Darwin CR (1871) The descent of man, and selection in relation to sex, vol 2. John Murray, London

Gould SJ (2002) The structure of evolutionary theory. The Belknap Press of Harvard University Press, Cambridge

Grine FE, Daegling DJ (2017) Functional morphology, biomechanics and the retrodiction of early hominin diets. C R Palevol 16:613–631

Harcourt-Smith WEH (2015) The origins of bipedal locomotion. In: Henke W, Tattersall I (eds) Handbook of paleoanthropology, 2nd edn. Springer, Heidelberg, pp 1919–1959

Huble DH (1979) The brain. In: Flanagan D (ed) The brain. W. H. Freeman and Co, San Francisco, pp 3–10

Kelley J (1997) Paleobiological and phylogenetic significance of life history in Miocene hominoids. In: Begun DR, Ward CV, Rose MD (eds) Function, phylogeny and fossils: Miocene hominoid evolution and adaptation. Plenum Press, New York, pp 173–208

Kelley J, Bolter D (2013) Growth, development, and life history in hominin evolution. In: Begun DR (ed) A companion to paleoanthropology. Blackwell Publishing, Chichester, pp 97–117

Macchiarelli R, Bergeret-Medina A, Marchi D et al (2020) Nature and relationships of *Sahelanthropus tchadensis*. J Hum Evol 149:102898

Milton K (1999) A hypothesis to explain the role of meat-eating in human evolution. Evol Anthropol 8:11–21

Moorjani P, Amorim CEG, Arndt PF et al (2016) Variation in the molecular clock of primates. Proc Natl Acad Sci 113:10607–10612

Napier J (1993) Hands. Princeton University Press, Princeton

Panger MA, Brooks AS, Richmond BG et al (2002) Older than the Oldowan? Rethinking the emergence of hominin tool use. Evol Anthropol 11:235–245

Plavcan JM (2012) Sexual size dimorphism, canine dimorphism, and male-male competition in primates. Where do humans fit in? Hum Nat 23:45–67

Schultz A (1968) Form und Funktion der Primatenhände. In: Rentsch B (ed) Handgebrauch und Verständigung bei Affen und Frühmenschen. Verlag Hans Huber, Bern, pp 9–30

Schultz AH (1969) The life of primates. Unwin Bros, Woking

Senut B, Pickford M, Gommery D, Mein P et al (2001) First hominid from the Miocene (Lukeino Formation, Kenya). C R Acad Sci 332:127–144

Taylor T (2010) The artificial ape: how technology changed the course of human evolution. St. Martin's Press, New York

Thompson JC, Carvalho S, Marean CW et al (2019) Origins of the human predatory pattern. The transition to large-animal exploitation by early hominins. Curr Anthropol 60:1–23

Ward C (2015) Postcranial and locomotor adaptations of hominoids. In: Henke W, Tattersall I (eds) Handbook of paleoanthropology, 2nd edn. Springer, Heidelberg, pp 1363–1386

White TD, Asfaw B, Beyene Y et al (2009) *Ardipithecus ramidus* and the paleobiology of early hominids. Science 326:75–86

Wrangham R, Pilbeam D (2001) African apes as time machines. In: Galdikas BMF, Briggs NE, Sheeran LK et al (eds) All apes great and small, vol. 1: African apes. Kluwer Academic Publishers, New York, pp 5–17

Chapter 11
The Adaptations That Have Made Us Human: The Genome

Elena Bosch

Abstract Identifying what makes us humans and understanding the genetic basis of our uniqueness are issues of interest and debate in biology. By analyzing genomic data we can detect and use the footprints that adaptive (positive) natural selection leaves in our genome to identify human adaptations at different timescales, as well as the resulting phenotypical traits that in current populations define us as humans. Although genomics has allowed us to recognize some of these adaptations from the pattern of variation expected under the classical or hard selective sweep model, the field starts to address novel approaches. These new strategies include not only methods to identify polygenic adaptations but also multidisciplinary procedures to understand the relationship between the genomic footprints of selection, the underlying functional genetic variants, the adaptive phenotype they determine, and the selective pressure that has driven each adaptation.

Keywords Human adaptation · Natural selection · Positive selection · Selective sweep · Polygenic selection

11.1 Introduction

Natural selection refers to the gradual, nonrandom process of accumulation of beneficial and heritable characteristics that we observe generation after generation in populations as a result of the existence of heritable variation in the reproductive success and/or survival of individuals. The concept, proposed simultaneously by Charles Darwin and Alfred R. Wallace (Darwin and Wallace 1858), is one of the main mechanisms that explain evolutionary change, but above all it is the only evolutionary force that facilitates the adaptation of populations and species to their changing environments.

E. Bosch (✉)
Department of Medicine and Life Sciences, Institute of Evolutionary Biology (UPF-CSIC), Universitat Pompeu Fabra, Barcelona, Spain
e-mail: elena.bosch@upf.edu

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_11

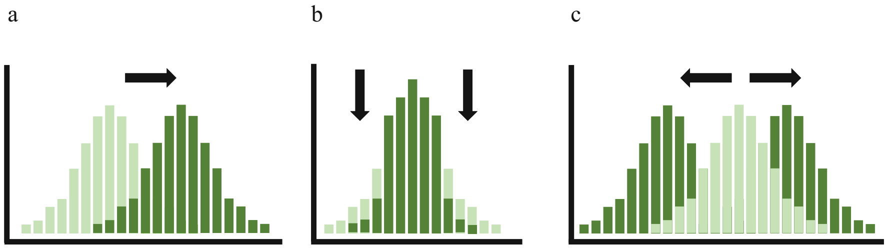

Fig. 11.1 Types of natural selection. (**a**) Directional (positive or Darwinian) selection. This is a type of selection in which the individuals of the population presenting the features of one of the extremes of the phenotypic distribution for a biological trait are favored. Consequently, the phenotypic distribution of the population will move towards the extreme with the most favored phenotypes. (**b**) Stabilizing (purifying or negative) selection. The extremes of the distribution of a particular phenotype are selected against when a particular range of values in the distribution is favored. Thus, the phenotypic distribution becomes narrowed. (**c**) Disruptive or balancing selection. A type of selection in which the individuals from the two extremes of the phenotypic distribution in the population are favored. Consequently, those individuals with intermediate phenotypic features disappear from the population and the distribution splits into two (or more) peaks that will represent the contrasting phenotypes simultaneously favored in that given environment

Thanks to the development of different high-throughput genotyping and sequencing platforms during the last decades and the subsequent abundance of genomic data from different human populations, we can easily test which specific regions of our genome show patterns of variation compatible with different types of natural selection (Fig. 11.1). Moreover, we can do this search without any a priori assumption about which genes or biological functions have facilitated our adaptation to different environments. However, once these candidate regions with patterns of variation compatible with the action of natural selection are recognized, we will then need to identify the true underlying adaptive variants, the adaptive phenotype they determine, as well as the selective pressure that has driven each adaptation. In this review I will present the main strategies for identifying the footprint of adaptive natural selection (also called Darwinian, positive or directional selection; Fig. 11.1a), some examples of well-characterized human adaptations identified with these methods, and the main limitations in the interpretation and understanding of these footprints.

Depending on the evolutionary timeframe in which we want to interrogate the action of natural selection, we will use strategies based on comparing genomes: between the human genome and that of other primate species, between different human populations (and this is the level at which most methods are more robust), or even between particular human populations and different extinct hominids, thanks to the recent availability of the genomes of several Neanderthal and Denisovan individuals. In this way, we will be able to infer species-specific adaptations, selective events geographically restricted in particular human populations, or even adaptive introgressions received from archaic humans.

11.2 Cross-Species Comparisons

Selection tests based on cross-species comparisons allow us to identify substitutions and genomic changes that are specific to our lineage and that may potentially have contributed to our divergence. Therefore, they allow us to explore adaptations that occurred millions of years ago (for example, about six million years ago when we compare the human genome with that of the chimpanzee) and that characterize us as a species. In this case, one of the most commonly used strategies to identify the footprint of positive selection between species is the comparison of nucleotide substitution rates. Given a region of DNA coding for a protein, we can compare the proportion of nonsynonymous changes (nucleotide changes that imply an amino acid change in the protein) to the proportion of synonymous changes (nucleotide changes that do not imply an amino acid change) between the genomes of two species to calculate the ratio Ka/Ks, also referred to as dN/dS or w depending on the context. Assuming that synonymous changes are neutral (not affected by natural selection), the ratio between the two types of substitutions will measure the possible accumulation of deleterious or beneficial mutations, in a coding region. Usually, mutations at the DNA level that change an amino acid are not well received by natural selection, as they may compromise the function or structure of the encoded protein; therefore, most genes in our genome have a Ka/Ks ratio well below 1. In contrast, values above 1 are exceptional and are interpreted to occur when the accumulation of amino acid changes in a protein has been favored as these changes could represent evolutionary novelties and therefore be potentially adaptive in one of the compared lineages. Moreover, other related methods have been adapted to explore the Ka/Ks ratio in particular lineages or branches in a given phylogenetic tree, as well as, in particular codons or within particular protein domains (Yang and Nielsen 2002; Zhang et al. 2005). In general, while the aforementioned comparative analyses have limited power to detect selection on individual genes, they are powerful strategies to identify which biological functions have changed most significantly in our lineage relative to that of the chimpanzee or other nonhuman primates.

The great sequence similarity found between the human and chimpanzee genomes, and the fact that our proteins are virtually identical, has led us to explore other types of variation in our genomes to identify other possible biological innovations in our lineage. For example, the use of comparative genomic hybridization techniques with cDNA (complementary DNA) probes in *arrays* (Marques-Bonet et al. 2009) and more recently also, the analysis of read coverage (*coverage* or number of unique reads that include a given nucleotide in the reconstructed DNA sequence) differences across genomes after their massively parallel sequencing (Kronenberg et al. 2018) allows to identify human-specific gene duplications and expansions that could represent evolutionary novelties in our lineage, especially when these changes can be related to particular changes in function or to actual differential expression patterns between the compared species.

11.3 Tests Based on Intraspecific Variation

Tests based on the intraspecific variation of our genome (or human polymorphism) will allow to identify adaptations that occurred more recently in our lineage, from a few tens of thousands of years ago to more ancient adaptations depending on the signature they interrogate. Thus, we can study the human adaptative response to the particular selective pressures we experienced during different key points in our evolutionary history such as during the human expansion out of Africa and subsequent colonization of new territories, where the climatic conditions were very different from our ancestral savannah, or after the introduction of farming and pastoralism as a form of subsistence in the Neolithic (Sabeti et al. 2006). In this case, most genome-wide searches (*genome scans*) for positive selection in humans have focused on detecting the footprints of the so-called hard selective sweep model. The model assumes the appearance of a new allele in a given genomic region that provides a selective advantage to its carriers. Consequently, generation after generation, the new allele is expected to rapidly increase its frequency towards fixation, sweeping with it the immediate surrounding alleles in the original chromosome where it arose by mutation and thus eliminating the remaining allele combinations of the population not carrying that new adaptive allele (Fig. 11.2a). We have different statistical tests that allow us to capture different key features of the pattern of variation resulting from this classical or hard selective sweep: (a) frequency spectrum-based methods, which allow us to detect a reduction of diversity, an excess of high-frequency derived alleles and/or a tendency towards an excess of rare alleles; (b) linkage disequilibrium extension-based methods that detect unusually long haplotypes relative to their frequencies in the population; and (c) methods based on population differentiation that capture allelic variants with high levels of population differentiation and that are therefore highly informative when the selective events and subsequent genetic adaptations are geographically restricted.

11.3.1 Tests Based on Frequency Spectrum

According to the classical sweep model, when, in a given genomic region, an adaptive variant becomes fixed sweeping with it the immediate genomic surrounding variation, we will expect to find a drastic reduction of its diversity when compared to other regions of the genome evolving under neutrality, which are expected to present both recent and much older (and more frequent) polymorphisms in the population. Thus, we initially expect a significant loss of diversity around positively selected regions of the genome. Over time, new alleles will appear by mutation, but for these new alleles, probably being most likely neutral, it will take a long time to increase their frequencies and evenly restore the initial diversity. Under this scenario, in the pattern of variation of the genomic regions under positive selection, we expect to find a characteristic signature of low overall genetic diversity and some excess of

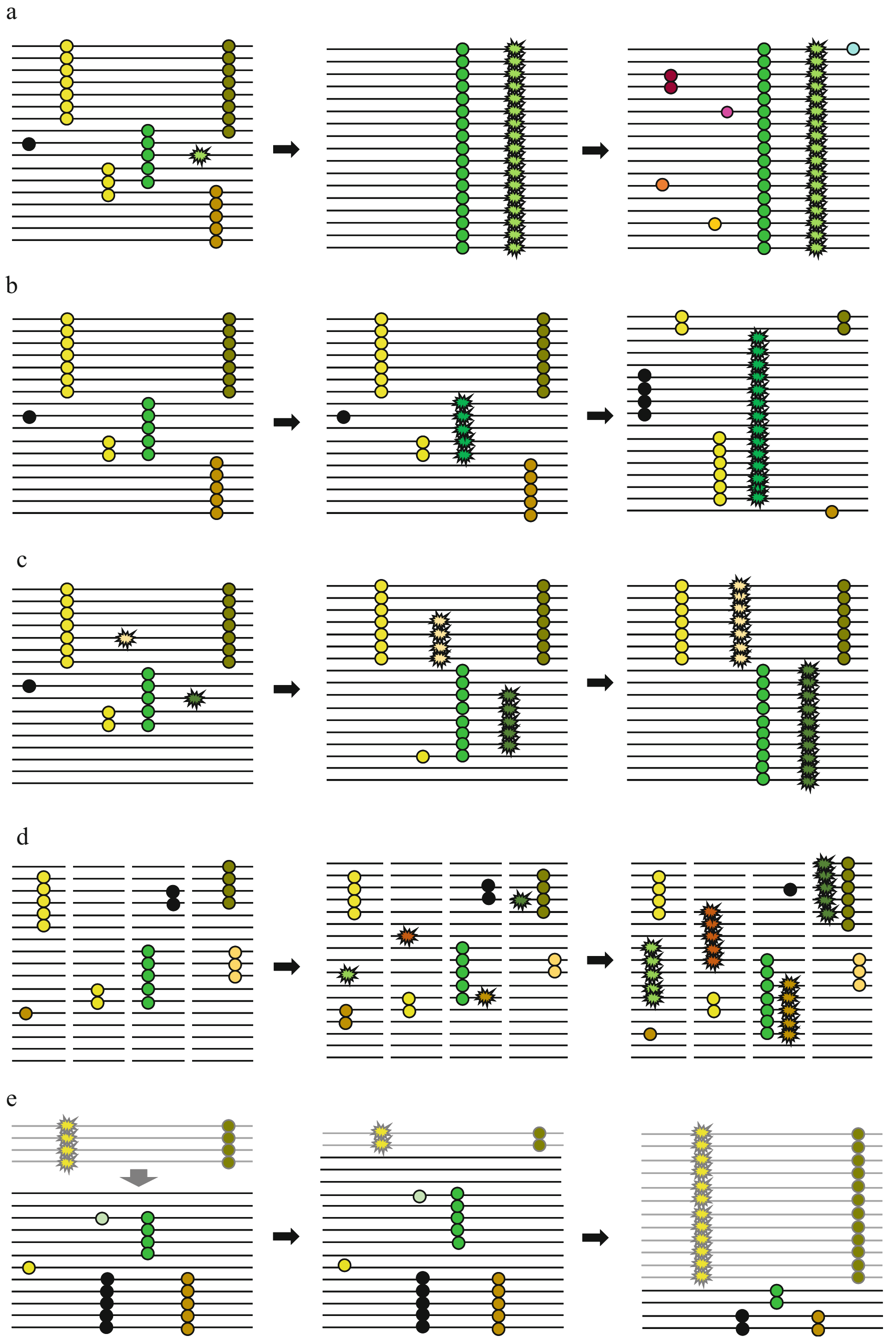

Fig. 11.2 Molecular footprints of positive natural selection or Darwinian selection. (**a**) Classical or hard sweep. (**b**) Soft sweep from pre-existing neutral variation in the population that becomes adaptive to an environmental change. (**c**) Soft sweep from the appearance of more than one adaptive

rare alleles once mutation starts to introduce new variation. The most commonly used tests that allow us to detect this type of deviation in the frequency spectrum are the Tajima's D test (Tajima 1989), and other related neutrality test statistics such as Fu and Li′s D (Fu and Li 1993) and Fu's F (Fu 1997).

Derived alleles (i.e., nonancestral alleles) arise by mutation and generally tend to have lower allele frequencies than the ancestral ones. In a selective sweep, however, the derived alleles linked to the beneficial allele can be swept at high frequency in the so-called *hitchhiking effect*. Since many of these derived alleles will not reach complete fixation (as a result of an incomplete sweep or due to the occurrence of a recombination event between their genomic position and the selected allele), positive selection can create another feature in the pattern of variation of the genomic regions under positive selection consisting of an excess of derived alleles at high frequency with respect to neutrality. The most common approaches used to detect this excess are the Fay and Wu H test (Fay and Wu 2000) and the direct search for a high proportion of SNPs (single nucleotide polymorphisms) with a given derived allele frequency threshold, such as above 80% (Walsh et al. 2006).

11.3.2 Tests Based on Population Differentiation

In humans, the levels of population differentiation are mostly determined by genetic drift and migration. However, local adaptation (i.e., that adaptation specific to a given geographical area) can accentuate the levels of differentiation of particular loci in our genome. For example, while the O allele of the *Duffy* blood group is virtually absent outside Africa, the same allele presents very high frequencies in some African populations where it has been locally selected because it confers resistance to malaria. Other known cases of local genetic adaptations identified from unusual patterns of population differentiation include several variants that determine lighter skin pigmentation outside Africa, as well as other genetic variants that confer protection against malaria in Africa. We can quantify the extreme allele frequency differences observed in the *Duffy* system calculating the F_{ST} statistic (the most commonly used population differentiation measure) between African and non-African populations and using all SNPs in the human genome as a reference.

Other related strategies, such as the *Population Branch Statistic* (PBS) (Yi et al. 2010), use the values of F_{ST} obtained among three populations to identify which genomic positions exhibit extreme differentiations along each of the branches of the corresponding three-population tree. This design has been particularly informative for identifying loci involved in local adaptations to extreme conditions such as the artic climate or high altitude by comparing two recently diverged populations but

Fig. 11.2 (continued) variant at the same locus. (**d**) Polygenic selection or selection on a complex trait. (**e**) Adaptive introgression living under clearly contrasting local selective pressures (extreme cold or hypoxia, respectively, in the two previous cases, compared to normal conditions) with a third population with a deeper divergence time as reference (Yi et al. 2010; Fumagalli et al. 2015; Amorim et al. 2017).

11.3.3 Tests Based on Unusual Haplotype Extension or Linkage Disequilibrium

Selective sweeps create a distinctive footprint in the patterns of linkage disequilibrium that it is not expected under neutrality. When a new allele is favored by positive selection, it increases its frequency rapidly enough for recombination not to have time to break the initial association of the new favored allele with the remaining neighboring alleles on the ancestral chromosome where it appeared by mutation. Thus, recent positive selection produces an unusual combination of alleles at high frequencies that have long-range associations (or linkage disequilibrium) with other alleles present on the same chromosome. We will detect these long-range associations in the form of a haplotype or a particular combination of alleles (where the selected allele originally appeared) as long as recombination does not substantially erase these associations (which will eventually happen with time). On the contrary, since neutral alleles will require a long time to reach high population frequencies by genetic drift (if this is the case), they will never simultaneously present high frequency and associations over long distances. Thus, we have different tests for the detection of recent positive selection events (less than 30,000 years) that explore the relationship between allele frequency and the extent of linkage disequilibrium by directly comparing the length of haplotypes associated with different allele variants in each candidate region or the extent of haplotypic homozygosity.

The iHS (*integrated Haplotype Score*) and XP-EHH (*Cross-Population Extended Haplotype Homozygosity*) are the most commonly used linkage-based statistics. While iHS compares the extent of haplotypic homozygosity between the alleles of a given SNP in a population and is particularly informative for identifying variants under positive selection that have not yet reached fixation, i.e., detecting incomplete or ongoing selective sweeps (Voight et al. 2006), XP-EHH compares the extent of haplotypic homozygosity between populations and it is especially useful for detecting recently selected variants after a complete (or almost complete) selective sweep in a given population (Sabeti et al. 2007).

11.4 Verifying the Statistical Significance

The statistical tests described above allow to distinguish the pattern of genetic variation expected under positive natural selection from neutrality. However, particular events in the demographic history of each population (such as bottlenecks and population expansions) may create patterns of variation similar to those expected under positive selection. Thus, the direct inference of a selection event sometimes is complicated, especially when only a small number of loci are studied. However, since demographic events influence the entire genome more or less equally but adaptive events only act on the pattern of variation in the genomic regions under selection, it is possible to identify cases of positive selection by using genome-wide data and determining which regions of the genome have the most extreme deviations from neutrality using any of the statistics described. From the empirical distribution of the statistics values across the whole genome, either calculated by polymorphic position or by overlapping windows comprising several SNPs, we can easily identify which loci (or genomic regions) present extreme values in each distribution and consider them as the most likely candidates to have suffered strong selection pressures (Akey 2009). Although in this type of empirical approach we may obtain false positives, the subsequent identification of functional variants in these candidate regions and the complete understanding of their relationship with an adaptive phenotype and underlying selective pressure may help to convincingly identify new true adaptive cases. In turn, we must be also aware that we are likely to obtain many false negatives due to lack of power when focusing only on the topmost extreme signals of classical selective sweeps.

Through simulations we could improve the identification of *outliers* by applying a neutral model and/or considering different selection models incorporating, when appropriate, the specific demography of the populations used, the genome recombination map, and/or possible biases in the type of variation analyzed either by the use of SNP genotyping data or by the use of sequencing data with low coverage. Undoubtedly, if the neutral variation of the genome were perfectly modeled in these simulated scenarios, we could simply identify the variants that are more extreme in comparison with this neutral distribution as candidates for selection or we could even test whether they match a particular simulated selection regime given according to a particular demography and a given selection coefficient. However, we often do not know the real shape of this neutral distribution, neither how it has been affected by the particular demographic histories of human populations. On the other hand, and especially for populations with complex admixture histories in their past, when genomic information from several populations is available, the use of *admixture* plots has also proven to be a quite effective strategy to identify strong selection events and to be able to associate these to changes in allele frequencies in particular branches of their corresponding tree (Refoyo-Martínez et al. 2019). Similarly, estimating genome-wide genealogies for thousands of samples at a time can now be effectively used to estimate the dispersal rate of a given lineage relative to alternative lineages over a given time period and to investigate different forms of selection (Speidel et al. 2019).

Finally, other approaches employ composite strategies to try to combine the specific footprints that each statistic detects in order to obtain greater sensitivity in the selection analysis, to directly identify the specific variants under selection or even to be able to classify the regions detected under selection according to whether they have been affected by recent/old and incomplete/complete selective sweeps in different human populations (Grossman et al. 2010; Pybus et al. 2015; Szpak et al. 2018). Since each selection statistic captures different aspects of the selective sweep, composite strategies help to avoid the particular false positives of individual statistics and provide greater statistical power to detect selection.

11.5 Beyond the Classic Selective Sweep

Although most studies of positive selection in humans have focused on capturing the footprints of classical selective sweeps, other models of selection such as polygenic selection (where multiple loci contribute to a given adaptive phenotype) and so-called soft selective sweeps (when different novel variants at a particular loci are selected at the same time or when selection favors a pre-existing polymorphic variant in the population that becomes adaptive due to a change in the environment) may have contributed equally to human adaptation (Pritchard et al. 2010). In these cases, the footprints that appear in the pattern of variation in regions under selection are clearly more subtle and difficult to capture with the standard methods developed to detect the so-called hard or classical selective sweeps (Fig. 11.2).

In soft sweeps, since the favored variants will be present in different haplotypes or chromosome types (Fig. 11.2b, c), when these increase in frequency and become fixed, we will not be able to detect the strong signatures of classical selective sweep, where a single variant that has just appeared by mutation in a single haplotype is selected. In this case, statistics such as nSL (Ferrer-Admetlla et al. 2014), H12 and H2/H1 (Garud and Rosenberg 2015), or SDS (Field et al. 2016) have been proposed as strategies that would improve the detection of these type of weaker signatures. Similar to iHS, the nSL statistic was designed to capture the increase in haplotypic homozygosity that positive selection creates when favoring a given segregating variant in the population. In this case, nSL measures the extent of homozygosity from the number of segregating sites with shared alleles across the haplotypes that accompany the corresponding ancestral and derived alleles of a given polymorphic position without requiring a genetic map (Ferrer-Admetlla et al. 2014). On the other hand, the H12 and H2/H1 statistics, also based on haplotypic homozygosity, allow considering, depending on the case, all the haplotypes of the population, the most abundant haplotype or the two most frequent haplotypes present in the sample to capture and distinguish, thanks to their combination, both hard (where we expect a unique major haplotype favored) and soft (with two or more haplotypes selected at the same time) sweeps (Garud and Rosenberg 2015). The SDS statistic (*Singleton*

Density Score; Field et al. 2016) uses whole genome sequence data to infer changes in SNP allele frequencies from the distortion that recent selection creates on the genealogies of the sampled haplotypes, resulting in shorter terminal branches in the case of favored alleles. The method allows the detection of both classical sweeps and cases of recent positive selection from previously pre-existing neutral variation.

In the case of polygenic selection (Fig. 11.2d), the resulting genomic footprints may only involve very subtle coordinated changes of allele frequencies at the multiple loci involved in each particular adaptive function or trait. As most human phenotypes are likely to have a complex genetic architecture and are not the result of just one or a few strong effect variants, several approaches and strategies are being devised to recognize the molecular footprint of polygenic adaptation. Although the footprints of selection on each of the genes involved in these complex phenotypes may often not be sufficient to stand out individually in a genome-wide context, an efficient approach to capture this type of scenario is to compare the evidence of adaptation across the entire set of genes associated with particular phenotypes or complex traits at once (Daub et al. 2013). However, it is often the case that a complete knowledge of all the genes involved in a complex phenotype is not always available, nor it is easy to model the really small effects that some of these loci have on these complex traits. Especially in native populations, usually not considered in large association studies or GWAS consortia, the use of *polygenic risk scores* based on reference populations to model the effects of each of these loci could be problematic. Other approaches to detect the more subtle adaptive patterns expected in the case of polygenic selection focus on correlating allele frequency changes with different environmental variables, such as temperature, humidity, solar radiation, or nutrient availability, among others. In this case, it is important to correct for the genetic structure of the populations used in the analysis, but when using sequencing data, the resulting environmental associations identified allow to directly relate specific adaptive genetic variants with a causal selective pressure. This strategy has successfully identified functional human polymorphisms associated with tolerance to cold, radiation, and pigmentation (Hancock et al. 2011).

Finally, genetic introgression from close species could, in exceptional cases, facilitate our adaptation through a pre-existing adaptive variant in these other species (Fig. 11.2e). Different specific statistical approaches are available to detect introgression which have allowed to describe several examples of adaptive variants that different human populations would have acquired from introgression with Neanderthals or Denisovans (Racimo et al. 2015). This is the case, for instance, of the TLR6-TLR1-TLR10 receptors involved in the recognition of external pathogens in European populations (Dannemann et al. 2016) or of the *EPAS1* gene in Tibetan populations, where it would facilitate their adaptation to hypoxia (Huerta-Sánchez et al. 2014).

11.6 Limitations and Future of Selection Studies

Regardless of the mode of selection operating, once any signature of positive selection has been identified in the genome, we need to understand its biological relevance as a case of human genetic adaptation. We need to go from the putative genotype under selection to the adaptive phenotype. This includes not only deciphering the molecular action and underlying adaptive phenotype of the selected variants, but also identifying the selective pressure at play in each case. Although the number of fully characterized cases of positive selection is still limited (Rees et al. 2020), they have allowed us to identify and understand different human adaptations that have undoubtedly contributed to our survival and colonizing success as a species (see examples related to our defense against pathogens, diet and nutrient availability, ultraviolet radiation, and altitude in Table 11.1). The bottleneck in the studies of positive selection is not the identification of the candidate regions per se but precisely the huge difficulty we have in understanding, without a priori hypothesis or the appropriate experimental design to investigate particular selective pressures, the relationship between the genotypes of the candidate regions found under selection and the corresponding adaptive phenotypes these determine.

The first examples of successfully characterized cases of selection began with prior knowledge of an adaptive phenotype, for which genetic evidence for selection

Table 11.1 Examples of genetic adaptations in humans

Adaptation	Genes	Population or geographic region
Language	*FOXP2*	Human lineage
Malaria	*HBB*, *HBA*, *HPA*, *GYPA*, *GYPB*, *GYPC*, *G6PD*, *FY*	Sub-Saharan Africa
Trypanosoma	*APOL1*	Africa
Flagellated bacteria	*TLR5*	Africa
General immune response	*TLR1-TLR6-TLR10*, *HLA* group, *CD5*	Multiple populations
UV radiation	*SLC24A5*, *SLC45A2*, *OCA2*, *MCR1*, *TYRP1*, *DCT*	European, Asian
Hair morphology	*WWTP*	Asian
Altitude	*EPAS1*, *ELGN1*, *PPARA*	Tibetans
	VAV3, *CBARA1*, *ARNT2*	Ethiopian Highlands
	ELGN1, *EDNRA*, *NOS2A*, *BRINP3*	Andean Population
Lactase persistence	*TBI*	European and African
Diet—Zinc	*SLC30A*, *SLC39A8*	East Asia and Africa
Diet—Selenium	*DI2*, *GPX1*, *GPX3*, *CELF1*, *SPS2*, *SEPSECS*	China
Diet—Iron	*HFE*	Europeans
High-fat diet	*FADS*	Inuit, Native Americans
Arsenic toxicity	*AS3MT*	Argentina

was subsequently identified, usually targeting plausible candidate genes (Vitti et al. 2013). The search of footprints of selection at the genomic level has the great potential to allow us to infer new hypotheses to test new cases of selection without any bias or prior assumption regarding which genomic regions might facilitate adaptation in each selective context. However, we should be aware that most of these genome-wide searches often provide lists of candidate adaptive regions with no indication of the possible functional variation or specific adaptive phenotypes that these regions might have facilitated. Thus, their interpretation and understanding are not straightforward and follow-up functional studies are usually required to validate the potential adaptive variants and phenotypes of each case in relation to particular selective pressures. Moreover, most signatures of positive selection usually span large regions of the genome, including multiple functional variants, and many different genes often with more than one function each and thus potentially affecting many different phenotypes. The work by Wang et al. (2020) illustrates the difficulty in identifying the variants and adaptive phenotypes behind a candidate region when investigating one of the strongest footprints of positive selection detected in humans: the 2p21.3 locus. The locus contains the lactase gene and the selection signals found in European populations have been associated with the derived allele of a regulatory variant that allows the persistence of lactase in adulthood and therefore the digestion of milk. In this case, it was classically inferred that, in populations where fresh milk is used as a food resource, carriers of the allele variant that facilitates the persistence of lactase would have increased their survival chances in past episodes of famine. However, by investigating the genomic content of the entire region under selection, as well as some of the phenotypes associated with the region in other species, the authors identified a microRNA (miR-128-1) in the European favored haplotype, directly involved in metabolic processes of energy expenditure that could also represent an adaptation to periods of famine in our past.

Those genomic scans of positive selection based on the comparison of populations living in different environments, or even in extreme conditions, have allowed to infer with some success a more direct causal relationship between the potential selective forces considered a priori and the candidate regions for selection identified in the genome. This type of design applied to diverse human populations living at high altitude in the mountains of Tibet, the Andes, or in Ethiopia has allowed to identify, for example, different human genetic adaptations, some of them convergent, related to hypoxia (Yi et al. 2010; Huerta-Sánchez et al. 2013; Borda et al. 2020). In other cases, combining genome-wide genetic data with phenotypic data related to the adaptive hypothesis also provides a promising strategy when trying to identify the footprints of positive selection related to particular adaptive phenotypes, such as short stature in pygmy populations from Africa (Jarvis et al. 2012; Mendizabal et al. 2012) or the Andaman Islands (Mondal et al. 2016).

Undoubtedly, the growing number of functional annotations in the coding and regulatory regions of the human genome, the increasing availability of genome-wide association studies for several complex phenotypes, together with the adoption of new experimental strategies to interrogate the relationship between genotype and phenotype, and the incorporation of other selection models will not only improve our understanding of the various adaptations that have occurred in our evolutionary history and thus define us as humans, but also identify functional variants in our genome with potential biomedical relevance.

Acknowledgments This review has been possible thanks to the support of the "Dirección General de Investigación, Generalidad de Cataluña" (2017SGR702), the "Ministerio de Ciencia e Innovación," and the "Agencia Estatal de Investigación (AEI)" through the project PID2019-110933GB-E00/AEI/10.13039/501100011033 and the "Unidad de Excelencia María de Maeztu" funded by the MCIN and the AEI (Doi: 10.13039/501100011033; Ref: CEX2018-000792-M).

References

Akey JM (2009) Constructing genomic maps of positive selection in humans: where do we go from here? Genome Res 19:711–722

Amorim G, Nunes CE, Meyer K et al (2017) Genetic signature of natural selection in first Americans. Proc Natl Acad Sci U S A 114:2195–2199

Borda V, Alvim I, Mendes M et al (2020) The genetic structure and adaptation of Andean highlanders and Amazonians are influenced by the interplay between geography and culture. Proc Natl Acad Sci U S A 117:32557–32565

Dannemann M, Andrés AM, Kelso J (2016) Introgression of Neandertal- and Denisovan-like haplotypes contributes to adaptive variation in human toll-like receptors. Am J Hum Genet 98:22–33

Darwin C, Wallace A (1858) On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. J Proc Linn Soc London Zool 3:45–62

Daub JT, Hofer T, Cutivet E et al (2013) Evidence for polygenic adaptation to pathogens in the human genome. Mol Biol Evol 30:1544–1558

Fay JC, Wu C (2000) Hitchhiking under positive Darwinian selection. Genetics 155:1405–1413

Ferrer-Admetlla A, Liang M, Korneliussen T, Nielsen R (2014) On detecting incomplete soft or hard selective sweeps using haplotype structure. Mol Biol Evol 31:1275–1291

Field Y, Boyle EA, Telis N et al (2016) Detection of human adaptation during the past 2000 years. Science 354:760–764

Fu YX (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925

Fu YX, Li WH (1993) Statistical tests of neutrality of mutations. Genetics 133:693–709

Fumagalli M, Moltke I, Grarup N et al (2015) Greenlandic Inuit show genetic signatures of diet and climate adaptation. Science 349:1343–1347

Garud NR, Rosenberg NA (2015) Enhancing the mathematical properties of new haplotype homozygosity statistics for the detection of selective sweeps. Theor Popul Biol 102:94–101

Grossman SR, Shlyakhter I, Shylakhter I et al (2010) A composite of multiple signals distinguishes causal variants in regions of positive selection. Science 327:883–886

Hancock AM, Witonsky DB, Alkorta-Aranburu G et al (2011) Adaptations to climate-mediated selective pressures in humans. PLoS Genet 7:e1001375

Huerta-Sánchez E, DeGiorgio M, Pagani L et al (2013) Genetic signatures reveal high-altitude adaptation in a set of Ethiopian populations. Mol Biol Evol 30:1877–1888

Huerta-Sánchez E, Jin X, Asan et al (2014) Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. Nature 512:194–197

Jarvis JP, Scheinfeldt LB, Soi S et al (2012) Patterns of ancestry, signatures of natural selection, and genetic association with stature in Western African pygmies. PLoS Genet 8:e1002641

Kronenberg ZN, Fiddes IT, Gordon D et al (2018) High-resolution comparative analysis of great ape genomes. Science 360:eaar6343

Marques-Bonet T, Kidd JM, Ventura M et al (2009) A burst of segmental duplications in the genome of the African great ape ancestor. Nature 457:877–881

Mendizabal I, Marigorta UM, Lao O, Comas D (2012) Adaptive evolution of loci covarying with the human African pygmy phenotype. Hum Genet 131:1305–1317

Mondal M, Casals F, Xu T et al (2016) Genomic analysis of Andamanese provides insights into ancient human migration into Asia and adaptation. Nat Genet 48:1066–1070

Pritchard JK, Pickrell JK, Coop G (2010) The genetics of human adaptation: hard sweeps, soft sweeps, and polygenic adaptation. Curr Biol 20:R208–R215

Pybus M, Luisi P, Dall'Olio GM et al (2015) Hierarchical boosting: a machine-learning framework to detect and classify hard selective sweeps in human populations. Bioinformatics 31:3946–3952

Racimo F, Sankararaman S, Nielsen R, Huerta-Sánchez E (2015) Evidence for archaic adaptive introgression in humans. Nat Rev Genet 16:359–371

Rees JS, Castellano S, Andrés AM (2020) The genomics of human local adaptation. Trends Genet 36:415–428

Refoyo-Martínez A, Da Fonseca RR, Halldórsdóttir K et al (2019) Identifying loci under positive selection in complex population histories. Genome Res 29:1506–1520

Sabeti PC, Schaffner SF, Fry B et al (2006) Positive natural selection in the human lineage. Science 312:1614–1620

Sabeti PC, Varilly P, Fry B et al (2007) Genome-wide detection and characterization of positive selection in human populations. Nature 449:913–918

Speidel L, Forest M, Shi S, Myers SR (2019) A method for genome-wide genealogy estimation for thousands of samples. Nat Genet 51:1321–1329

Szpak M, Mezzavilla M, Ayub Q et al (2018) FineMAV: prioritizing candidate genetic variants driving local adaptations in human populations. Genome Biol 19:5

Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595

Vitti JJ, Grossman SR, Sabeti PC (2013) Detecting natural selection in genomic data. Annu Rev Genet 47:97–120

Voight BF, Kudaravalli S, Wen X, Pritchard JK (2006) A map of recent positive selection in the human genome. PLoS Biol 4:e72

Walsh EC, Sabete P, Hutcheson HB et al (2006) Searching for signals of evolutionary selection in 168 genes related to immune function. Hum Genet 119:92–102

Wang L, Sinnott-Armstrong N, Wagschal A et al (2020) A MicroRNA linking human positive selection and metabolic disorders. Cell 183:684–701

Yang Z, Nielsen R (2002) Codon-substitution models for detecting molecular adaptation at individual sites along specific lineages. Mol Biol Evol 19:908–917

Yi X, Liang Y, Huerta-Sanchez E et al (2010) Sequencing of 50 human exomes reveals adaptation to high altitude. Science 329:75–78

Zhang J, Nielsen R, Yang Z (2005) Evaluation of an improved branch-site likelihood method for detecting positive selection at the molecular level. Mol Biol Evol 22:2472–2479

Chapter 12
How Do We Humans Evolve?

Eudald Carbonell and Policarp Hortolà

Abstract How do we humans evolve? This is probably the most important question to answer as a self-aware animal species. The question that arises is whether Darwin and Wallace theory of natural selection serves to explain human evolution. The three processes that humanize us, differentiating us from the rest of the animal kingdom, are: (a) the way we obtain energy from the environment (production), (b) the way we pass information to each other (communication), and (c) the way we group ourselves into aggregations of different sizes (socialization). Critical consciousness is a consequence of the operative intelligence that has led us to operative consciousness. Our species needs responsible evolution and conscious progress. But this will only be viable if we socialize the critical consciousness of our species. It is necessary to reflect on how this knowledge and approaches of the theory of social evolution can be applied to the current and future practice of the species. And, as a consequence, we have to continue building a theoretical body that allows us to understand our evolutionary process from within the human specificity itself. We are not yet fully "human," but we are in the process of becoming human, because we still depend in part on chance. We will be fully human when we depend only on logic.

Keywords Human evolution · Behavior · Socialization · Anthropological prospective · Epistemology

12.1 Introduction

How do we humans evolve? This is probably the most important question we have to answer as a self-aware animal species. In the mid-nineteenth century, the figure of Charles Darwin burst onto the scientific scene with force by posing diversity in terms of natural selection, as did Alfred Russel Wallace, so that evolutionary biology culminates the revolution against metaphysics (Hortolà and Carbonell 2007). In the

---

E. Carbonell · P. Hortolà (✉)
Rovira i Virgili University (URV), and The Catalan Institute of Human Paleoecology and Social Evolution (IPHES-CERCA), Tarragona, Catalonia, Spain
e-mail: eudald.carbonell@urv.cat; policarp.hortola@urv.cat

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_12

same way that those naturalists instituted a theory of biological evolution, this theory had to be completed by a theory of social evolution by the scientists and philosophers of the twenty-first century. Darwin and Wallace are our inspiration to start this task. Just 150 years ago, one of the most influential works that concerns us was published. Just as the long title of the foundational work of evolutionism has been popularized as simply *The Origin of Species* (Darwin 1859), the work we refer to here is usually called *The Descent of Man* or, more succinctly, *Descent* (Darwin 1871).

It seems obvious that Darwin and Wallace theory of natural selection was responsible for beginning to give consistency to the study of human evolution. But the answer is not sufficiently complete, and can only be posed and constructed from a transdisciplinary approach. All living beings are subject to natural selection and mutation processes. Therefore, from this point of view of explanatory effectiveness, the theory of evolution is impeccable. But, in our case, we have to clearly distinguish "hominization" from "humanization" (Carbonell and Hortolà 2020). Consequently, we must inquire if the theory of evolution, as it is conceived for living beings in general, is accurate enough to explain not only hominization but also humanization, our uniqueness. We are referring to whether there is a complementary theory to what evolutionists have already contrasted regarding the survival and reproduction of our genus, the genus *Homo*. The question we ask ourselves is whether the laws of natural selection and the implementations that have been made with the synthetic theory of evolution in the twentieth century can explain how it is possible that an animal singularity like ours has arisen (Gould 2002).

We cannot understand human evolution as a normal evolutionary process, but as an epiphenomenon. This is why here we expose the foundations of a theory of human evolution where induction and deduction are part of it. Both approaches help us to face a major challenge of our humanity. Without problematizing there is no scientific progress. And this is precisely what we want to do with this explanatory proposal of species.

12.2 A Theoretical Approach to a Central Hypothesis on Humanization

The life and earth sciences, in convergence with the social sciences, have brought us resilience as a species. This has been through the methods and techniques developed to be able to contrast theories. To arrive at this form of practical knowledge, we have also used the methods of philosophy, psychology, and sociology. Field and laboratory work have been essential in order to have evidence that explains the processes proposed as essential to the main theoretical *corpus*. Without this redundant practical knowledge, it would not be possible to have proposed the structures that support humanization. We know and have documented the anatomical, genetic, and biochemical changes. But also the economic and technological ones and, therefore, social and behavioral changes.

Acquisitions “fossilize” in the sense that they are fixed. The enlargement of the encephalon can be known by the enlargement of the cranium, at the same time that we can also know how certain parts of the brain have evolved. The genetic structure in nuclear and mitochondrial DNA and changes in the position of nucleotides have fossilized in the preserved organic material, the climate in the pollen and crystals in the stems. Many tools, whether lithic or osseous, have also been preserved and, as a consequence, we have been able to follow the increase of their complexity. The organization of domestic space and the techniques of hunting and consumption, and later those of agriculture and livestock, have also fossilized. Nature is the laboratory that allows us to see the experiment that has built our humanization. The fossilization of biocenosis is the great ally of evolutionists committed to field work. And reverse engineering, a safe method to test and contrast evolutionary hypotheses.

Evolution is, in reality, a biobehavioral integration in constant feedback (Boyd et al. 2011). Therefore, we have to understand humanization as both an adaptation and an alternative to such an adaptation; that is to say, a progressive form of change. Alternative because, in many cases, it accelerates evolution and helps to break the parsimony of natural systems. The appearance of the singularity of the human system arises precisely from this acceleration or hierarchization of behavior and culture above the biological system.

First of all, we must consider the concepts that explain the processes and that can allow us to know the mechanisms of social evolution. Obviously, always within the framework of the theory of biological evolution. As Darwin literally says in Chap. IV of *Descent*, “[…] the social instincts lead an animal to take pleasure in the society of its fellows, to feel a certain amount of sympathy with them, and to perform various services for them. The services may be of a definite and evidently instinctive nature; or there may be only a wish and readiness, as with most of the higher social animals, to aid their fellows in certain general ways. But these feelings and services are by no means extended to all the individuals of the same species, only to those of the same association.” In the case of the human being, what is most relevant is how the theoretical-practical elements of science are used, understood as praxis; that is, the concrete method that allows us to apprehend the facts through hypotheses that, in turn, have been generated within the framework of classifications and universal knowledge, experimentation as relevant evidence, etc. (Hortolà and Carbonell 2006). From our perspective, the constituent processes are three: production, communication, and socialization. We cannot understand cultural selection if it is not within the framework of natural selection. In our view, it is not a matter of co-evolution, but of “integrated” evolution. This is the first question that one must clarify in order to break with a false dichotomy fed by an unsynthetic and partial vision (Lumsden and Wilson 2005 [1981]). The fundamental body is demarcated by those three interconnected properties (production, communication, and socialization, see Fig. 12.1). This is what has made us human. The way these three processes are structured and their progression is what has given us the uniqueness we enjoy as a species. Understanding the interrelationship and how these processes work can allow us to formulate what properties we have brought out as humans. Probably, first unconsciously and then consciously and reflexively, our adaptive behavior has been

Fig. 12.1 The three interconnected processes that have made us human: production, communication, and socialization

completing the synthesis of the human system through biological, social, and cultural acquisitions.

Ultimately, what we want is to simplify the complexity of the evolutionary process so that we can understand and explain it, answering the question “what makes us human.” The three properties, previously stated by Pettersson (1996), form an explanatory triad that can underpin our theoretical approach.

12.2.1 Production

The way we obtain energy from the environment differentiates us from the rest of the animal kingdom. In the production, the most important thing that has intervened has been the technique, and now the technology. Obtaining food for biological reproduction is fundamental for biotic systems. In the human system, obtaining food has been a process of adaptation through a series of continuous acquisitions in space and time that have become universalized. Food is obtained, processed, elaborated and, in many cases, preserved. This means that obtaining them has become increasingly complex as we have perfected the way of obtaining, storing, and transporting them. This has generated a high neuromotor capacity, accompanied by a quantitative growth of the size of the brain, but also, and above all, of the qualitative change of some functional areas, such as the prefrontal and parietal lobes.

The production of morphological codes (tools) requires technical training, both in planning and execution. Knowledge of the environment is essential for the selection of raw materials. Planning to acquire them is also very important, but what is more substantial are the methods and techniques to carry out the transformation of the materials, thanks to operational schemes. The ability to plan and sequence is essential in humanization. Without this neuro-operative capacity it would not have been possible to develop the other capacities. The way we acquire energy conditions or determines the way we communicate and also the way we group ourselves. Technology and its amplification through science have been fundamental for humanization. It has been one of the fundamental acquisitions on the road to becoming human and ending up being an evolutionary singularity.

Technology requires theory, abstraction, knowledge, quantification, and complex planning. From the aforementioned approaches, methods and protocols arise for the creation of the devices and appliances that allow us to live. There is a great leap between technique as a direct constructive element and technology as an element derived from theory. In order to make this leap, an important resocialization of the species has been necessary.

12.2.2 Communication

The great capacity to pass information among us, among the individuals of the species (intraspecific communication), determines the increase of complexity of the human system through its efficiency in the resolution of situations at all levels. Selection, in the long run, always acts in the direction of the most well-adapted and efficient in communication. Language is the tool that enables us to learn, and also for an education of the species: cultural, technological, and social learning.

With a high probability, articulated language has allowed the development of abstraction and symbolic thought, which in turn has exponentially increased our complexity (Corballis 2003). There is much scientific debate about the origin of language (Pinker 2007; see Chap. 7 of this book). There is indirect empirical evidence for the existence of language at least 400,000 years ago in *Sima de los Huesos* at Atapuerca archeological and paleontological sites: the study of the middle ear and cranial reconstruction has shown that in this chronology humans heard in broadband like *Homo sapiens* (Martínez et al. 2004). This would be in agreement with the theory of language innatism, but probably not only of species as it had been postulated (Chomsky 1975), but of genus. It is very likely that language also works with a series of structures that are universal. Not only is there a language that ends up being articulated, but also the nonarticulated forms of communication have a very important specific weight: gestural language, facial language, mathematical language, etc.

From an initial structure, humans have been building a network of languages all over the planet that have served to unite populations and facilitate their continuity by increasing the behavioral diversity of our genus. A conglomerate of languages aimed at increasing sociability.

12.2.3 Socialization

As a consequence of our own nature as social animals, the way we group ourselves in aggregations of different sizes generates interdependent networks that, at the same time as they intercommunicate, maintain diversity. Indeed, the genus *Homo* and, fundamentally, our species, has built a diversity of aggregations that have been basic to increase our complexity. Cooperation has been one of the important engines of socialization (Axelrod 1984). By constituting themselves in organized and conscious cooperative groups, they qualify natural selection thanks to cultural selection. We could say that they generate an evolutionary form based on an encapsulated but interdependent social integration. It is here where we can infer human sexual complementarity as an evolutionary basis, without which true species cooperation would not be possible and, as a consequence, stable aggregations emerge, both reproductively and socially. The consequence is the appearance of territories populated by units ranging from millions of specimens to groups of a few tens, domestic, urban and rural structures. It has been an experimentation that has allowed us to have a perspective of ourselves as a phenomenon and evolutionary singularity.

The increase of sociability allows the increase of complexity and the resocialization of the human system. The increase of complexity is only possible with successive resocializations. It is in this way that socialization, passed through technology and thanks to the possibility of transmission through communication, makes us human (Carbonell et al. 2008). Evolutionary rhythms are marked by the existence of a temporal distance between the emergence or discovery of a new acquisition and its socialization. To the extent that the time of discovery or innovation in the human system is shortened, history accelerates. All this can be contrasted empirically. An example we always use is the domestication of fire and its socialization, to make an analogy with the mobile phone. While fire is an innovation of a million years ago, its generalization or socialization becomes effective and universal after 600,000 years. It took only 40 ears to move from the landline to the mobile phone, and it took only 5 years to move from 4G (high speed) technology to the development of 5G (universal wifi).

Can we have evolved as a human singularity without the convergence of the three processes we have developed in the central body? That is to say, is humanization possible without a sophisticated and progressive way of producing food as well as the development of a language and a progressive socialization of the acquisitions that allow us to adapt? This is the question we have to contrast and see if the central body has an answer. Observing the evolution of humanity, it is difficult to understand an evolution without the parameters that we have hierarchized. Even admitting biocultural evolution as a manifestation of the human system, the behavior and culture transmitted from generation to generation have made it possible that the diversity of memory of the system has allowed human survival. The hypothesis is reinforced if we can contrast throughout history a tendency of all these processes towards the generation of diversity. If there is a loss of diversity, does our survival jeopardize?

Critical consciousness is a consequence of operative intelligence that has led us to operative consciousness. A change of phase that has been possible thanks to the continuous resocializations through which the genus *Homo* and specifically our species has gone through, which has made the exponential leap towards humanization and then towards post-humanization (Carbonell 2018).

12.3 Conclusion

The three processes that humanize us (production, communication, socialization) are included in the same consideration of the dynamic law of projection of the future of the species. All of them are necessary so that they can feed back on each other. All of them can be conceptualized. All of them are based on a progression towards complexity. All of them are universal. As a consequence, the three processes explain what a theory of the social evolution of life, especially the life and history of humanity, can be based on. These three elements explain how the process of cultural selection has ridden over natural selection. Genes and memes have allied to establish a form of evolutionary singularity that we do not share so far with any other known animal. Our uniqueness has been built as emergences have been socialized faster and faster. This means that, as new acquisitions have caused us to draw energy from the environment and to communicate differently, human populations have evolved in such a way that the processes of increasing complexity have never stopped.

We may call "gender resocialization" the progressive process of incorporating acquisitions and their impact. Resocialization is the way in which biocultural selection acts to evolve the genus *Homo*. Indeed, if in biological evolution the fittest is the one that adapts best, in social evolution the population that is most likely to survive is the one that shortens the time between the emergence or new acquisitions and their socialization. This is the population that has the greatest capacity to survive and also to grow demographically. Biological transmission, now profoundly modified by biotechnology and cultural transmission, is still the mechanism of the species. But at this time in an accelerated way. This cultural transmission must be done from the capacity of knowledge transmission. We have to use social networks to further increase our sociability. We have to do it to break the randomness and randomness of human processes. We have to give them a species logic in which the part of cultural selection weighs more than the biological one.

As a consequence of the implementation of science in society, technology has spiked dramatically. This determines that, in human social relations, communication will become even more necessary. The social relations of production are more and more determined by technological increase. If predictions are well made, our species will come to shorten the time between the emergence of acquisitions so much that our spatial and temporal singularity will synchronize. The tendency towards globalization and, as a consequence, uniformity, is a strategic error of the species. We have to know that a social theory of evolution can predict it. Therefore, we can apply, to the functioning of the species, the formulation we have made. Our species needs responsible evolution and conscious progress. But this will only be viable if we socialize the critical consciousness of our species.

It is necessary to reflect on how this knowledge and approaches of the theory of social evolution can be applied in the current and future practice of the species. And, as a consequence, we must continue to build a theoretical body that allows us to understand our evolutionary process from within the human specificity itself. We are not yet fully "human." We are simply in the process of becoming human, because we still depend in part on chance. We will be fully human when we depend only on logic.

References

Axelrod R (1984) The evolution of cooperation. Basic Books, New York

Boyd R, Richerson P, Henrich J (2011) The cultural niche: why social learning is essential for human adaptation. Proc Natl Acad Sci U S A 108(suppl 2):10918–10925

Carbonell E (2018) Elogio del futuro. Arpa Editores, Barcelona

Carbonell E, Hortolà P (2020) From past unaware hominization to future conscious humanization: social evolution in retrospect and prospect. In: Grinin LE, Korotayev AV (eds) Evolution. Evolutionary aspects: stars, primates, and religion. 'Uchitel' Publishing House, Volgograd, pp 164–185

Carbonell E, Mosquera M, Rodríguez XP et al (2008) Eurasian gates: the earliest human dispersals. J Anthropol Res 64:195–228

Chomsky N (1975) Reflections on language. Random House, New York

Corballis MC (2003) From hand to mouth. Princeton University Press, Princeton

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London

Gould SJ (2002) The structure of evolutionary theory. Harvard University Press, Cambridge, MA

Hortolà P, Carbonell E (2006) Ciencia paradigmática y paradigma científico: una prospectiva para el nuevo milenio. Elementos 63:9–13

Hortolà P, Carbonell E (2007) Creación *versus* evolución: del *Origen de las especies* al diseño inteligente. Asclepio 59:261–274

Lumsden CJ, Wilson EO (2005 [1981]) Genes, mind, and culture [25th anniversary edition]. World Scientific Publishing, Singapore

Martínez I, Rosa M, Arsuaga J-L et al (2004) Auditory capacities in middle Pleistocene humans from the sierra de Atapuerca in Spain. Proc Natl Acad Sci U S A 101:9976–9981

Pettersson M (1996) Complexity and evolution. Cambridge University Press, Cambridge

Pinker S (2007) The language instinct. HarperCollins Publishers, New York

Chapter 13
Art as a Human Element

Inés Domingo

Abstract 150 years ago, when Charles Darwin wrote his revolutionary book *The Descent of Man and Selection in Relation to Sex*, there was no reason to believe that research into the origins of art and symbolic behavior would end up playing a key role in the debates on the emergence of modern human behavior. Especially since, as discussed in this chapter, none of these unique aspects of human behavior called his attention. Interestingly, though, his theories on human evolution are behind two of the great controversies in prehistoric art research that have divided the international scientific community: the authenticity of the Altamira paintings and their prehistoric chronology, back in 1879, and the current controversy over the artistic and symbolic capacity of Neanderthals. In this chapter, we will reflect on these two issues by summarizing where the main debates on the origins of art and symbolic behavior are today.

Keywords Prehistoric art · Origins · Artistic capacity · Symbolic behavior · Neanderthal

13.1 Introduction

The birth of art and the origins of symbolic behavior are today considered two of the great milestones of human evolution and two of the indicators of the emergence of modern human behavior (d'Errico et al. 2003; Villaverde 2020).

Since the discovery of the art, the debates about the chronology, the identity of the authors, or the type of archaeological evidence announcing the existence of creative thought and symbolic behavior in prehistoric times have caused strong divisions in the international scientific community. Two of these debates, separated by almost a hundred years and perhaps the most controversial in research on prehistoric art and, why not, also on human evolution, are related to very unique finds challenging

---

I. Domingo (✉)
Department of History and Archaeology, ICREA/University of Barcelona/SERP, University of Barcelona, Barcelona, Spain
e-mail: ines.domingo@ub.edu

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_13

preconceived ideas. In the first place, we refer to the discovery of prehistoric art in Altamira in 1879, received with skepticism by the intellectuals of the time, both evolutionists and creationists, and which unleashed a major controversy about the authenticity (for a synthesis of this controversy see Lewis-Williams 2002, among others). Second is the recent attribution of several samples of rock art to Neanderthals (Pike et al. 2012; Hoffmann et al. 2018) which has added to the debates raising the possibility that they had already developed behaviors until then considered exclusive to Anatomically Modern Humans (henceforth Modern Humans), such as abstract thought, language, or art (d'Errico et al. 2003). The genesis of both controversies is, in my opinion, the same. They both question deep-rooted approaches to human evolution and the definitions we have been constructing about ourselves and our intellectual superiority compared to other human groups, both present and past. In the first case, we are talking about the late 19th and early twentieth century view that classified humans based on evolutionary stages (as described by Lubbock in his 1865 book *Prehistoric Times*), and advocating our supposed superiority over humans who lived in prehistoric times, and also over any contemporary human group with a hunter-gatherer way of life. At that time, all these populations were systematically described as barbaric, primitive, rooted in the stone age, anchored in the past, and without any evolution (Clifford 1988). Unfortunately, such assertions implicitly contributed to promoting discriminatory and racist perceptions of contemporary Indigenous[1] populations by conveying to the world the image of static and dying cultures (Domingo 2021). An image that has not yet been completely eradicated in the Western world. For this reason, the discovery of the famous polychrome ceiling of Altamira was received with so much skepticism by the scientific community, provoking the immediate and continuous denial of the authenticity for more than two decades. Acceptance would have suggested that those prehistoric barbarians may not have been so barbaric and developed a creative capacity and a symbolic thought quite similar to ours. In the second case, we are talking about the prevailing idea throughout the last century, and still latent in this century, of our supposed intellectual superiority over other members of our human lineage, which would place us at the top of human evolution and which would explain why we are the only survivors of our species (for a historical discussion see for example Zilhão 2001). Although the abilities of Neanderthals and Modern Humans seem increasingly homologous (Zilhão 2007), the construction of a narrative portraying them as inferior for a century (see for example William King's definition of a Neanderthal fossil skull in 1864[2]), and the exclusive attribution of

---

[1] I intentionally use the term with capital letter following and supporting current Indigenous groups' claims to use the terms Indigenous, Aboriginal or First Nations in capital letters as a sign of respect for populations that have suffered the effects of colonialism, forced displacement, exploitation, and marginalization. Therefore, I want to leave the term capitalized to refer to this reality, referring to recent definitions of these terms linked to these new political and historical realities.

[2] In his article "The reputed fossil man of the Neanderthal," King (1864) says "considering that the Neanderthal skull is eminently simial, both in its general and particular characters, I feel myself constrained to believe that the thoughts and desires which once dwelt within it never soared beyond

creative and symbolic abilities to Modern Humans (e.g., Lewis-Williams 2002; Mellars 2004[3]), seems to be making it difficult to accept that perhaps human creativity and symbolism are not traits unique to us, but shared with other members of our human lineage.

From my point of view, these two approaches, in one way or another, find their origins in the theories of evolution put forward 150 years ago by the English naturalist Charles Darwin in his book *The descent of man, and selection in relation to sex* (1871, *Descent* from now on) and his contemporaries (such as Huxley in his book *Evidence as to man's place in Nature* of 1863, Royer in his book *Origine de l'Homme et des Sociétés* of 1870, or Mortillet in his work *Le préhistorique: antiquité de l'homme* of 1883, among others). These theories still form the foundations of our current conception of the evolution of life on our planet, but in some aspects they have become more nuanced.

In this chapter, we will reflect on these two questions, synthesizing where the main debates on the origins of art and symbolic behavior are today.

13.2 Darwin, Evolutionism, and the Origins of Prehistoric Art Research

150 years ago, Darwin published *Descent*, where he explained his revolutionary theory of human evolution by natural and sexual selection, which gave a radical twist to the conception held until then on existential doubts such as where do we come from and how do we have become who we are. In this work, Darwin analyzed in detail the role, possible origins, and evolution of various human intellectual capacities and contrasted them with the capacities of animals trying to deduce differences and similarities and determine where they have come from and how each of the current human traits have evolved. But curiously, prehistoric art, one of the

---

those of the brute. The Andamaner [Indigenous populations of the Andaman Island, India], it is indisputable, possessed but the dimmest conceptions of the existence of the Creator of the Universe: his ideas on this subject, and on his own moral obligations, place him very little above animals of marked sagacity; nevertheless, viewed in connection with the strictly human conformation of his cranium, they are such as to specifically identify him with *Homo sapiens*. Psychical endowments of a lower grade than those characterizing the Andamaner cannot be conceived to exist: they stand next to brute benightedness.Applying the above argument to the Neanderthal skull, and considering that it presents only an approximate resemblance to the cranium of man, that it more closely conforms to the brain-case of the Chimpanzee, and, moreover, assuming, as we must, that the simial faculties are unimprovable-incapable of moral and theositic conceptions, there seems no reason to believe otherwise than that this similar darkness characterized the being to which the fossil belonged" (King 1864, p. 96).

[3] Perhaps it was the emergence of more complex language and other forms of symbolic communication that gave the crucial adaptive advantage to the fully modern populations and led to their subsequent dispersal across Asia and Europe and the demise of the European Neanderthals (Mellars 2004, pp. 464–465).

Fig. 13.1 Piece of portable art depicting a mammoth (La Madeleine, France) (after Lartet and Christy 1875)

indisputable signs of the existence of symbolic behavior, linked to the development of creative thought and the capacity for abstraction, did not deserve his attention. Although throughout several chapters he refers to the term art, he only does so in its meaning of "capacity, ability to do something". Thus, for example, he mentions that prehistoric humans (or more specifically men, since he formulates a vision of sexual differentiation that attributes to women a very secondary role in prehistory, which we still drag today) practiced "various arts to survive in various environments" or had developed "the art of making fire," "the art of shooting with bows and arrows," "the art of making rude canoes," or "the art of speaking" (Darwin 1871).

On the contrary, the other meaning of the term art, as "manifestation of human activity through which the real is interpreted or the imagined is shaped with plastic, linguistic or sonorous resources", did not receive any attention. And this, in spite of being closely related to certain intellectual capacities (such as imagination, memory, the capacity for abstraction, consciousness, etc.) to which Darwin did dedicate a few words.

This absence is even more striking when, on reviewing the scientific literature we discover that the first evidence of Paleolithic portable art dates back to the first half of the nineteenth century. In this period there are several singular finds in several French sites (a perforated baton decorated with a goat and a plant, discovered in 1833; and a reindeer horn with an engraved horse discovered in 1840) and later in Austria (a rib fragment with two engraved hinds discovered in 1853) (Roussot 1990). It is true that these first discoveries did not entail the recognition of their age and significance in terms of the capacities of humans who lived in prehistoric times. But in the 1860s, a few years before Darwin's publication, researchers Lartet and Christy (1864) published an article with several finds of portable art already attributed to the Paleolithic. One of these finds was particularly interesting, a mammoth horn with an engraved mammoth (Fig. 13.1) (Lartet and Christy 1875). Although at that time the piece could not be dated with today's scientific accuracy, the presence of a mammoth, an extinct species, indicated that it had to be ancient. However, curiously, this evidence was used more as proof of the ancient age of humans than as evidence of the creative capacity of our Paleolithic ancestors. These finds already opened interesting debates among researchers of the time who were skeptical of the idea that prehistoric humans, considered in a state of uncultured barbarism, could have developed what Lartet and Christy (1864) describe as "a certain degree of culture of the arts." According to Moro and González (2004) the consideration of those first finds of small-sized portable art as mere creations of craftsmanship, that is, as a minor art well away from the great works of art, helped accepting their Paleolithic chronology at a time when art and primitive seemed incompatible. These "minor" works of art were then considered as reflecting an extreme ingenuity, absent of any foresight or reflection and conceived only as a pastime. Thus, in his book *Le préhistorique: antiquité de l'homme* of 1883, Mortillet describes "These men, few in number, did not have to fight among themselves; war was unknown. Without religious ideas, the mad terrors did not disturb or pervert their imagination. They esteemed and admired nature. It is quite simple that, having free time, they strove to reproduce this nature as faithfully as possible. This is what led them to represent various animals with extreme truthfulness." In that context and with those convictions the samples of Paleolithic portable art were linked more to the field of decoration and ornamentation, than to advanced artistic procedures, considered fruit of the genius, aesthetic feeling and creativity of the true artists of more advanced moments of civilization.

This lack of recognition of Paleolithic portable art among prehistorians themselves may be behind the fact that, 7 years after Lartet and Christy's 1864 synthesis of portable art, Darwin does not even mention it in *Descent*. However, reading between the lines, Darwin does mention the creation and use of ornaments and body art, with which those early evidences of art had been associated in the archaeological literature. Likewise, in his work he also mentions the development of another artistic endowment: the ability to sing. But Darwin does not use these references to acknowledge the artistic capacity or symbolic behavior of prehistoric humans. On the contrary, his references and his comparison with the capacities of various animals show his denial that prehistoric humans and present-day Indigenous populations, whom he unsubtly disdains, have any capacity to develop the complex thinking that he considers necessary to produce and value the arts:

> Judging from the hideous ornaments, and the equally hideous music admired by most savages, it might be urged that their aesthetic faculty was not so highly developed as in certain animals, for instance, as in birds. Obviously no animal would be capable of admiring such scenes as the heavens at night, a beautiful landscape, or refined music; but such high tastes are acquired through culture, and depend on complex associations; they are not enjoyed by barbarians or by uneducated persons (Darwin 1871, p. 93).

It is curious how Darwin considers the use of ornaments, singing or the use of defensive weapons as eminently masculine capacities, more linked to instinct than to intelligence, and developed from sexual selection basically to amaze and excite women (Darwin 1871, pp. 210–211). A behavior that he considers quite similar to that of some animals, such as the perching birds of Australia and New Guinea, which

Fig. 13.2 Tracing of two bison from Altamira (after Breuil and Obermaier 1935)

decorate their nests with shiny objects (Darwin 1871, p. 381), the dances or gestures of love of other birds such as the galliformes (Darwin 1871, p. 380) or the songs of many birds (Darwin 1871, p. 368), all of them linked to a great extent to reproductive behavior. While Darwin did not consider any of these elements as early evidence of the development of art and symbolism among prehistoric populations, today they are all included within the range of expressions of human creativity pointing towards the birth of a symbolic behavior unique to humans, as we shall see below.

With the turn of the century, three decades after Darwin's work, we finally witnessed a significant change in the perception of prehistoric art. This change is due to the important increase in evidence of portable art in several sites in Europe (France, Belgium, Switzerland, Germany, Austria, Italy, etc.), the gradual increase in the number of rock art finds (such as the caves of Pair-non-Pair in 1883, Le Mouthe in 1895; Combarelles and Font de Gaume in 1901) (Palacio-Pérez 2013) and to the similarity between the new evidence of rock art and the themes identified in the portable art found in archaeological deposits dated to the Paleolithic.

In this context, and after many years of refusal, the French prehistorian Emile Cartailhac wrote in 1902 his famous article "Les cavernes ornées de dessins. La grotte d'Altamira, Spain. Mea culpa d'un sceptique," in which he acknowledged the authenticity of the Altamira paintings and finally gave credit to the finding of the already deceased Marcelino Sanz de Sautuola (Fig. 13.2). According to Moro and González (2004), this change of vision was also quite influenced by a weakening of evolutionism in the last decades of the 19th and early 20th centuries and, especially, by a greater awareness of the complexity of current Indigenous societies and their artistic creations, thanks to the intensification of the work of anthropologists and ethnographers (a good example is Spencer and Gillen's 1899 work describing *The Native Tribes of Central Australia*). From Cartailhac's article onwards, the artistic abilities of Upper Paleolithic humans were recognized, giving rise to the scientific investigation of prehistoric art. Simultaneously, the idea maintained throughout the twentieth century and partially also in the twenty-first century, that art and symbolic behavior are exclusive to Modern Humans, began to take root. This perception is behind the second major controversy in prehistoric art studies, the possibility that Neanderthals had also developed a symbolic thinking and a capacity for abstraction similar to ours.

13.3 Current Debates

More than a century after the controversy over the authenticity of Altamira, the twenty-first century surprises us with a new debate that has once again divided the scientific community, but with new actors. Now we no longer question the artistic capacities of Modern Humans living in prehistoric times, but those of our distant relatives, the Neanderthals.

Unlike what we saw in Darwin's writings, today the questions of the origins of art and of symbolic behavior play a significant role in debates on the birth of modern behavior characterizing present-day humans (e.g., d'Errico et al. 2003; de Sousa and Cunha 2012). This prominence is shared with other aspects also considered indicators of this behavior, such as cultural innovations, creative thinking, language, religious beliefs, burial of the dead, or the development of complex technologies (d'Errico and Stringer 2011).

If we focus on art, all the signs are, as Darwin already pointed out in 1871, that the use of ornaments, dances, and songs is not exclusive to humans. Neither does the use of certain plastic arts to make singular creations. We only need to have a look at the extraordinary ephemeral circular constructions made by the male pufferfish on the sandy seabed to attract the female (Fig. 13.3) (Kawase et al. 2013).

So, what is so extraordinary about the emergence of art among humans? Current debates go beyond discussing its value in demonstrating the development of aesthetic abilities, as done in the late nineteenth and much of the twentieth century, to focus on another fundamental aspect that differentiates the use of the arts between humans and animals: their use as communication tool for sharing information about the natural, cultural, and symbolic worlds. The message sent by animals through body decorations, dances, songs, or singular architectural constructions is always the same for all specimens of the same species and it is related to reproductive or survival instinct, as Darwin (1871) described. But those sent by humans are more complex, are not learned by instinct but through culture, and generally vary among different human groups. This difference is why we can speak of the existence of symbolic behavior, which today seems exclusive to humans (de Sousa and Cunha 2012).

Visual communication or the transmission of information through images and symbols is today one of the main communication tools we humans use. Nowadays it even surpasses the reach of oral and written language, thanks to the creation of universally shared symbols. In the street, shapes and colors combine to send us an infinite number of messages: an orange light alerts us to danger and a red one to a prohibition, a red cross with symmetrical arms speaks to us of health, while the one with asymmetrical arms is linked to a place of worship. In our mobile phones a

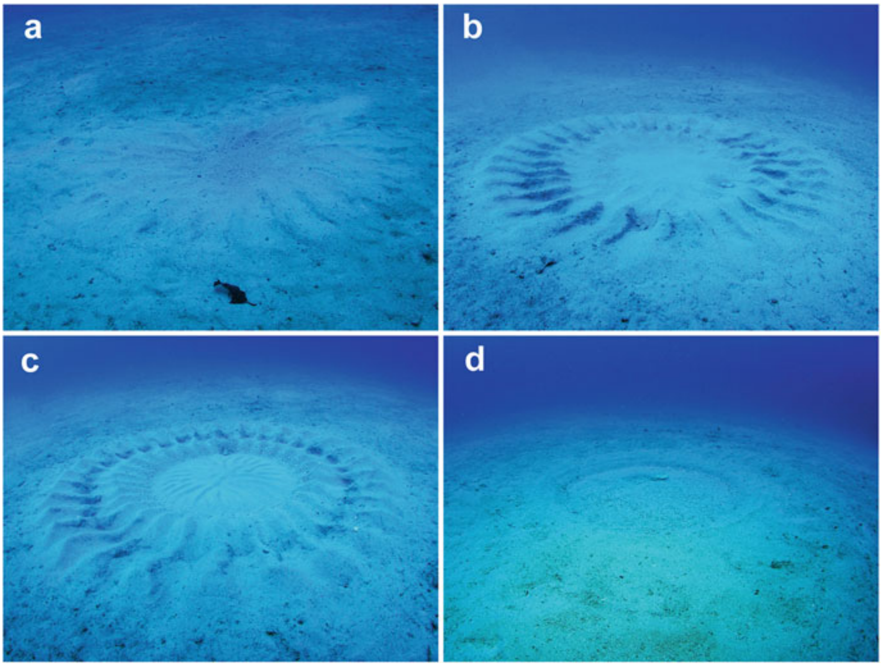

Fig. 13.3 Process of building a circular structure by male pufferfish (after Kawase et al. 2013; reproduced under CC BY NC ND 3.0 license)

whole series of emoticons replace words to express our feelings and emotions. The way we dress or the ornaments we use also convey information about who we are, our social status, or even our cultural background. In the midst of the COVID-19 pandemic, we have added a variety of symbols to our face masks that reveal our ideology or our links with certain groups. Even the most beautiful creations from an aesthetic point of view have behind them a socio-cultural background that shows a complex symbolic behavior. In my opinion, one of the definitions that best illustrates this role of art as a form of communication between human societies is the one I learned through ethnoarchaeology in Arnhem Land (Australia) (Domingo 2021). There, senior artist Thompson Yulidjirri, one of the last creators of rock art, told us that the visual arts are not an end, but a gateway to culture (May 2008). And the fact is that behind art there is always a story that is used to share information about beliefs, ancestral knowledge, traditions, social behavior, laws, or identities. Art is, therefore, a means of illustrating and sharing information in a more enduring way than oral communication. This visual art, which the Indigenous peoples of Arnhem Land have used for generations to educate, regulate, remember, celebrate, etc., in both every day and sacred contexts, is made meaningful through storytelling, music, song, dance, ceremony, and other art forms, from which they are inseparable.

Fig. 13.4 Sculpture of a horse from the German site of Vogelherd (after Floss 2015; reproduced under CC BY NC ND 4.0 license)

This definition of the visual arts as a vehicle of communication is applicable to all human societies and requires the development of a series of capacities to associate a thought, a feeling, or an idea to an image, a shape, a color, or a particular object, in order to create a visual language of more or less extensive scope. These capacities that derive from intellectual activity include reflection, creative thinking, and the capacity for abstraction, all of which are considered today as some of the traits that make us human and differentiate us from the rest of the animals.

It now seems to be accepted that the earliest archaeological evidence revealing the existence of symbolic behavior and visual language can be traced back to prehistoric times. However, tracing their origins is not an easy challenge, both because of the ephemeral nature of many aspects of human creativity and the materials that were used. Therefore, it is even difficult to determine what archaeological evidence reliably demonstrates this type of behavior. There is a certain consensus in accepting that the appearance of various forms of visual art (parietal or portable), and above all figurative art (reproducing elements of the real world), would be clear evidence of this symbolic behavior. Today, with the dates available, it appears that this type of figurative art is exclusive to Modern Humans and that the oldest evidence, dated between 32,000 and at least 45,500 years ago, is found in several places in Western Europe (Pike et al. 2012) and in Indonesia (Aubert et al. 2018; Brum et al. 2021) on parietal and portable media.

The oldest European finds are linked to what we know as the Aurignacian and include, among others, a unique set of animal sculptures (horses, mammoth, felines), the famous lion-man, and a headless Venus, carved on mammoth ivory (Floss 2015) (Fig. 13.4). These striking figurines come from several sites in the Swabian Jura Mountains in Germany. In France, a series of engravings and paintings with representations of sexual attributes (such as vulvas and phalluses) and some animal figures found in the sites of Castanet, Lausel, Blanchard, Ferrassie, Pataud, Le Cellier, among others, stand out. In Italy, and specifically in the archaeological deposits of Cova Fumane, some rock fragments detached from the wall were recovered, including schematic representations of humans and animals. Outside Europe, the oldest finds take us to Sulawesi, where the representation of a native pig has provided a minimum dating of 45,500 years (Brum et al. 2021) (Fig. 13.5).

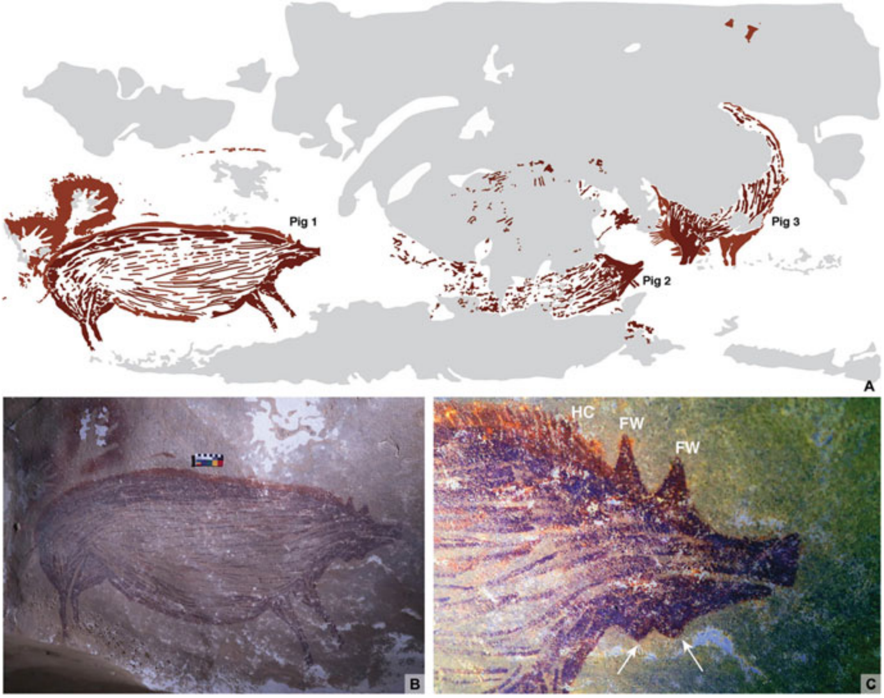

Fig. 13.5 Representation of a native pig that has provided the earliest known minimum dating for figurative art (Leang Tedongnge site, Sulawesi), (after Brum et al. 2021, reproduced under CC BY NC 4.0 license)

All this evidence already tells us of a creative turn in the evolution of symbolic thought, which far from starting from rudimentary forms, with the expected evolution from simplicity to complexity, is born on a certain variety of media and techniques, and with works of extraordinary quality and beauty. These creations provide us with clues about the symbolism of those first artists, although the messages behind these representations disappeared thousands of years ago with their authors and their closest descendants (Domingo 2020). Both the chronology and the geographical distribution of these first masterpieces of humanity seem to indicate that the birth of figurative art would be related, today, to the dispersal of Modern Humans throughout the world between 60 and 40,000 years ago. This evidence led to talk in the last century of the "Upper Paleolithic Revolution" and "the creative explosion" associated with the birth of the arts in Western Europe (Lewis-Williams 2002).

However, today the debates on the origins of art and symbolic behavior go beyond the first evidence of figurative art, and try to find out whether other early practices such as the use of coloring materials, of elements of personal adornment, or the first evidence of geometric or abstract symbology found on parietal and portable

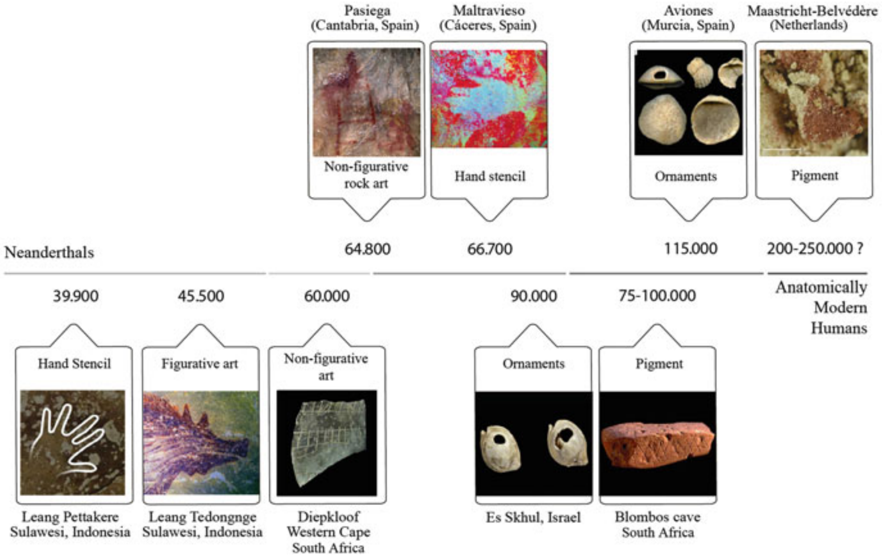

Fig. 13.6 Comparison showing the earliest evidence of art and symbolism between Anatomically Modern Humans and Neanderthals

media long before the appearance of figurative art, can already be considered as incipient forms of symbolic communication.

As far as coloring materials are concerned, their use by Neanderthals has been documented since ancient times. For example, in the archaeological deposits of Maastricht-Belvédère (The Netherlands), drops of a liquid, rich in hematite, have been identified, demonstrating a use of paint, with unknown purpose, from at least 200,000 to 250,000 years ago (Roebroeks et al. 2012) (Fig. 13.6). Some researchers have suggested that Neanderthals already made cosmetic use of dyes, as at the Cueva de los Aviones in Murcia (Zilhão et al. 2010) or that they used them to create body art, as at the French sites of Pech de l'Azé I and Pech de l'Azé IV (Soressi and D'Errico 2007). But determining whether these pigments were used for symbolic or practical purposes is not straightforward, as many of these raw materials also have preservative, antiseptic, abrasive, repellent, protective, or even medical properties (see, for example, Soressi and D'Errico 2007; Rifkin et al. 2015). It is very likely that many, if not all, of these properties were already known and used in prehistoric times. Therefore, the identification of pigment remains in archaeological sites cannot be directly related to the production of visual arts and a necessarily symbolic use. It is true, however, that ethnography reveals that the boundaries between the symbolic and practical realms are often blurred, and the two often coexist in the same object, tradition, or cultural practice. However, since symbolic uses do not usually have archaeological visibility, as they leave no material evidence, they are difficult to demonstrate.

More suggestive of the appearance of an early symbolism seem the first adornments, if in addition to using them for aesthetic purposes, they were also used as a sign of personal or group identity. Among Modern Humans we already find examples in chronologies of between 80,000 and 90,000 years ago in Africa and West Asia. Among the former, perforated shells with traces of coloring material from the South African sites of Blombos Cave, Sibudu, and Border Cave, dated to around 77,000 years ago, and the Moroccan shells from the Grotte des Pigeons, dated to 82,500 years ago, stand out. In Israel, several drilled Nassarius shells have been dated to chronologies between 100,000 and 135,000 years ago. What is most interesting in this regard is that, unlike figurative art, the use of shell and animal teeth ornaments is not exclusive to Modern Humans, but we also find them already linked to Neanderthals (Zilhão 2007; Zilhão et al. 2010). The appearance of this evidence initially in archaeological levels linked to the late Neanderthals of the Chatelperronian (about 45,000 years ago) was interpreted as the result of a mixture of sediments, as evidence that this industrial complex could not be associated with Neanderthals but with Modern Humans, or as proof that Neanderthals obtained them from their neighbors Modern Humans by imitation or exchange (d'Errico et al. 2003). All these theories illustrate the reluctance to accept that Neanderthals were able to produce ornaments autonomously. But the progressive increase in finds (d'Errico et al. 2003) and the recent dating of several perforated shells from the Murcia site of the Cueva de los Aviones to around 115,000 years ago has led to evidence that Neanderthals developed these symbolic practices autonomously (Hoffmann et al. 2018) (Fig. 13.6).

Somewhat weaker is the interpretation of the possible ornamental use that Neanderthals could have made of bird feathers (cova Fumane) (Peresani et al. 2011) and raptor claws (Cova Fumane, Rio Secco, Mandrin, grotte du Renne, Kaprina or Cueva Foradada, the latter in Catalonia) (e.g., Peresani et al. 2011; Finlayson et al. 2012, etc.). Interestingly, the proposals suggesting that this type of evidence located in sites with Neanderthal occupations points to an ornamental and symbolic use are not based on unquestionable empirical evidence of these uses, but on the impossibility of finding an alternative explanation to the existence of cut marks on phalanges and feathers of species that several researchers consider were not hunted to be consumed. In the case of the phalanges and claws, these do not have the perforations or attachment marks characteristic of other types of pendants. Furthermore, as Romandini et al. (2014) point out, it cannot be ruled out that the processing marks were linked to the extraction of the tendons, used in prehistoric times to bind the spearheads. Therefore, with the existing data, although these proposals are very suggestive, they do not provide irrefutable evidence of a symbolic use of the feathers and claws of raptors by Neanderthals.

As for the earliest evidence of geometric or abstract symbology, considered to be a precursor to the birth of art, until recently they all seemed to be linked to Modern Humans in several African sites dated between 100,000 and 60,000 years ago:

- A fragment of red ochre with geometric engravings discovered at Blombos Cave, South Africa, dated to about 80,000 years ago (Fig. 13.6).

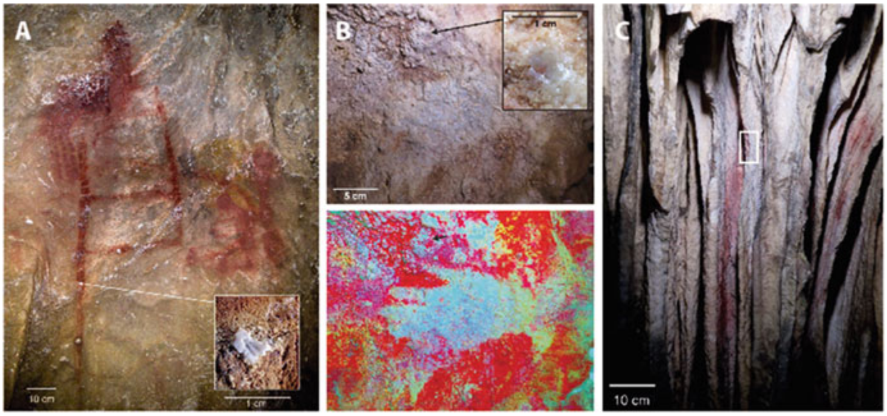

Fig. 13.7 Rock art samples, possibly Neanderthal, in the Iberian Peninsula. (**a**) scalariform from La Pasiega (Cantabria). (**b**) Hand stencil from Maltravieso (Cáceres). (**c**) Red pigment stains from Ardales (Málaga). (Images by Hoffmann et al. 2018. Reproduced with permission of AAAS)

– Geometric engravings made on ostrich egg fragments at the Diepkloof shelter, also in South Africa, dated to about 60,000 years ago (Fig. 13.6).
– A fragment of siliceous stone with red-painted geometric marks, also recovered at Blombos Cave and dated to around 73,000 years ago (Henshilwood et al. 2018).

The difficulty of finding a utilitarian purpose for these geometric designs has led researchers to propose a symbolic use by Modern African Humans, to communicate some kind of information that today is indecipherable. These evidences, therefore, seem to indicate that the seed of the birth of symbolic behavior is already found among these populations.

In the last decade, to these first evidences, new finds have been added suggesting a similar behavior among Neanderthals. I am referring to the Uranium-Thorium dating of calcite deposits covering several rock art samples (a scalariform, a hand stencil, and red stains) in three sites in the Iberian Peninsula (La Pasiega in Cantabria, Maltravieso in Cáceres, and Ardales in Málaga) (Fig. 13.7). The results obtained were revolutionary, providing minimum dates of between 64,000 and 66,000 years, i.e., when Modern Humans had not yet reached the Iberian Peninsula (Hoffmann et al. 2018). The debates surrounding these new dates, which suggest that Neanderthals may have been the first to mark the walls of several caves with geometric signs and hand stencils, have not been long in coming (Pike et al. 2012; Sauvet et al. 2015; Hoffmann et al. 2020; Villaverde 2020, among others). Some researchers question both the reliability of the dating method and the possible natural origin of the dated painting at the Ardales site. In response to this doubt, Hoffman et al. rule out the natural origin by clarifying that this mineral is not found anywhere else in the cave and that the application technique is clearly anthropic: blowing. Looking back, this new controversy recalls the skepticism generated by the discovery of Altamira, but with new actors: the Neanderthals. Today, some prehistorians continue to resist accepting that they had a symbolic communication capacity similar to that of Modern Humans, or at least that today we have irrefutable evidence that they did.[4] I am convinced that, as happened in the last century, the passage of time and new finds now unthinkable will allow us to close this debate and advance in the investigation of the origins of art and symbolic behavior.

References

Aubert M, Setiawan P, Oktaviana AA et al (2018) Paleolithic cave art in Borneo. Nature 564:254–257. https://doi.org/10.1038/s41586-018-0679-9

Breuil E, Obermaier H (1935) La cueva de Altamira en Santillana del Mar Nueva ventana. Tipografía de Archivos, Madrid

Brum A, Oktaviana AA, Burhan B et al (2021) Oldest cave art found in Sulawesi. Sci Adv 7: eabd4648. https://doi.org/10.1126/sciadv.abd4648

Cartailhac E (1902) Les cavernes ornées de dessins. La grotte d'Altamira, Spain. Mea culpa d'un sceptique. L'Anthropologie 13:348–354

Clifford J (1988) The predicament of culture: twentieth century ethnography, literature and art. Harvard University Press, Cambridge

d'Errico F, Henshilwood C, Lawson G et al (2003) Archaeological evidence for the emergence of language, symbolism, and music- an alternative multidisciplinary perspective. J World Prehist 17(1):1–70. https://doi.org/10.1023/A:1023980201043

Darwin C (1871) The descent of man and selection in relation to sex. John Murray, London

de Mortillet G (1883) Le préhistorique: antiquité de l'homme. C. Reinwald, Paris

de Sousa AA, Cunha E (2012) Hominins and the emergence of the modern human brain. Prog Brain Res 195:293–322. https://doi.org/10.1016/B978-0-444-53860-4.00014-3

d'Errico F, Stringer CB (2011) Evolution, revolution or saltation scenario for the emergence of modern cultures? Philos Trans R Soc Lond B Biol Sci 366(1567):1060–1069. https://doi.org/10.1098/rstb.2010.0340

Domingo I (2020) Art primer. Artistes de la Prehistòria. In: Domingo I, Palomo T (eds) Art primer. Artistes de la Prehistòria. Museu d'Arqueologia de Catalunya, Barcelona, pp 10–31

Domingo I (2021) Shifting ontologies and the use of ethnographic data in prehistoric rock art research. In: Moro O, Porr M (eds) Ontologies of rock art. Images, relational approaches and indigenous knowledge. Taylor and Francis, Routledge

Finlayson C, Brown K, Blasco R et al (2012) Birds of a feather: Neanderthal exploitation of raptors and corvids. PLoS One 7(9):e45927. https://doi.org/10.1371/annotation/5160ffc6-ec2d-49e6-a05b-25b41391c3d1

Floss H (2015) The Oldest Portable Art: the Aurignacian ivory figurines from the Swabian Jura (Southwest Germany). Palethnologie. http://journals.openedition.org/palethnologie/888. Accessed 5 February 2021

Henshilwood CS, d'Errico F, van Niekerk KL et al (2018) An abstract drawing from the 73,000-year-old levels at Blombos cave, South Africa. Nature 562:115–118. https://doi.org/10.1038/s41586-018-0514-3

Hoffmann DL, Standish CD, García-Diez M et al (2018) U-Th dating of carbonate crusts reveal Neanderthal origin of Iberian cave art. Science 359:912e915. https://doi.org/10.1126/science.aap7778

---

[4] We have no proof that Neanderthal society needed a long-lasting means of communication to consolidate its values and beliefs. A high degree of chronological certainty is required if that view is to be falsified. In short, there is still no convincing archaeological evidence that Neanderthals created Iberian cave art (White et al. 2019, p. 6).

Hoffmann DL, Standish CD, García-Diez M et al (2020) Response to White et al's reply: 'still no archaeological evidence that Neanderthals created Iberian cave art'. J Hum Evol 144:102810. https://doi.org/10.1016/j.jhevol.2020.102810

Huxley TH (1863) Evidence as to man's place in nature. D. Appleton and Company, New York

Kawase H, Okata Y, Ito K et al (2013) Role of huge geometric circular structures in the reproduction of a marine pufferfish. Sci Rep 3:2106. https://doi.org/10.1038/srep02106

King W (1864) The reputed fossil man of the Neanderthal. Quart J Sci 1:88–97

Lartet L, Christy H (1864) Sur des figures d'animaux gravées ou sculptées et autres produits dart et dindustrie rapportables aux temps primordiaux de la période humaine. Revue Archéol 5:233–267

Lartet L, Christy H (1875) Reliquiae Aquitanicae; being contributions to the archaeology and palaeontology of Perigord and the adjoining provinces of southern France. Thomas Rupert Jones, London, pp 1865–1875

Lewis-Williams D (2002) The mind in the cave. Thames and Hudson, London

May SK (2008) Learning art, learning culture: art, education, and the formation of new artistic identities in Arnhem Land, Australia. In: Domingo I, Fiore D, May SK (eds) Archaeologies of art: time, place and identity. Left Coast Press, California, pp 171–194

Mellars P (2004) Neanderthals and the modern human colonization of Europe. Nature 432:461. https://doi.org/10.1038/nature03103

Moro O, González MR (2004) 1864-1902. El reconocimiento del arte paleolítico. Zephyrus 57: 119–135. http://hdl.handle.net/10366/71600

Palacio-Pérez E (2013) Génesis, consolidación y crisis del concepto de 'arte paleolítico'. Krei 12: 83–117

Peresani M, Fiore I, Gala M et al (2011) Late Neanderthals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane cave 44 ky B.P., Italy. Proc Natl Acad Sci U S A 108(10):3888e3893. https://doi.org/10.1073/pnas.1016212108

Pike AWG, Hoffmann DL, García-Diez M et al (2012) U-series dating of Paleolithic art in 11 caves in Spain. Science 336:1409–1413. https://doi.org/10.1126/science.1219957

Rifkin RF, Dayet L, Queffelec A et al (2015) Evaluating the photoprotective effects of ochre on human skin by in vivo SPF assessment: implications for human evolution, adaptation and dispersal. PLoS One 10:e0136090. https://doi.org/10.1371/journal.pone.0136090

Roebroeks W, Sier MJ, Nielsen TK et al (2012) Use of red ochre by early Neandertals. Proc Natl Acad Sci U S A 109(6):1889–1894. https://doi.org/10.1073/pnas.1112261109

Romandini M, Peresani M, Laroulandie V et al (2014) Convergent evidence of eagle talons used by late Neanderthals in Europe: a further assessment on symbolism. PLoS One 9(7):e101278. https://doi.org/10.1371/journal.pone.0101278

Roussot A (1990) La découverte de l'art mobilier. Le rôle de Lartet et Christy. Paleo hors-serie. pp 32–33

Royer C (1870) Origine de l'Homme et des Sociétés. Guillaumin et Cie, Paris

Sauvet G, Bourrillon R, Conkey M et al (2015) Uranium–thorium dating method and Paleolithic rock art. Quat Int 432:86–92. https://doi.org/10.1016/j.quaint.2016.04.020

Soressi M, D'Errico F (2007) Pigments, gravures, parures: les comportements symboliques controversés des Néandertaliens. In: Les Néandertaliens: biologie et cultures, documents préhistoriques, 23. Éditions du CTHS, Paris, pp 297–309

Spencer B, Gillen FJ (1899) The native tribes of Central Australia. Macmillan, London

Villaverde V (2020) La mirada neandertal. Orígenes del arte visual. Publicacions de la Universitat de València, Valencia

White R, Bosinski G, Bourrillon R et al (2019) Still no archaeological evidence that Neanderthals created Iberian cave art. J Hum Evol 144:102640. https://doi.org/10.1016/j.jhevol.2019.102640

Zilhão J (2001) Anatomically archaic, behaviorally modern: the last Neanderthals and their destiny. Stichting Nederlands Museum voor Anthropologie en Praehist, Amsterdam

Zilhão J (2007) The emergence of ornaments and art: an archaeological perspective on the origins of behavioral modernity. J Archaeol Res 15:1–54. https://doi.org/10.1007/s10814-006-9008-1

Zilhão J, Angelucci D, Badal-García E (2010) Symbolic use of marine shells and mineral pigments by Iberian Neandertals. Proc Natl Acad Sci U S A 107(3):1023–1028. https://doi.org/10.1073/pnas.0914088107

Chapter 14
Sexual Selection: Following Darwin's Legacy

Roberto García-Roa and Pau Carazo

Abstract Much of the knowledge we treasure about evolution, and biology in general, rests on Darwin's ideas about sexual selection put forward 150 years ago. In his work *The Descent of Man, and Selection in Relation to Sex*, Darwin posited two fundamental mechanisms of competition for reproduction: intrasexual competition and mate choice. Since then, we have come to understand that, along with these two mechanisms, competition over reproduction also depends on sperm competition and cryptic mate choice. In this chapter, we review what we have learned about these four mechanisms and discuss general aspects about the sex roles, the evolutionary battle between the sexes, and the overall relevance of sexual selection for our understanding of the natural world. After 150 years of studying sexual selection, today we know that with this idea Darwin not only completed the general outline of his Theory of Natural Selection, but also laid the foundations of what has become one of the most complex and stimulating fields in the study of evolution. A vital process to understand not only the evolution of males and females, but also the processes of speciation, the ability of populations to adapt to changing environments, or the evolution of sexual reproduction itself.

Keywords Evolution · Sexual selection · Animal behavior · Sexes

14.1 Introduction

Parson's chameleon (*Calumma parsonii*) is one of the most spectacular reptiles on the planet. This chameleon is not only striking for its size (currently recognized as the heaviest chameleon species), but also for the imposing rostral protuberances of males (Fig. 14.1). Such protuberances have been described in other chameleons, where they range from subtle supranasal lobes to prominent antlers. In the case of beetles of the family Lucanidae, which includes the iconic stag beetle (*Lucanus*

R. García-Roa (✉) · P. Carazo
Laboratory of Ethology, Behaviour and Evolution group, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia, Spain
e-mail: Roberto.Garcia-Roa@uv.es

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_14

Fig. 14.1 Males of *Calumma parsonii* (left), *Calumma oshaughnessyi* (top) and *Furcifer willsii* (bottom). Photographs by Roberto García-Roa

cervus), males of some species possess such hypertrophied mandibles that they can be longer than an adult female. In birds of paradise (Paradisaeidae), males sport very distinct finery in the form of conspicuous plumage colourations accompanied by a variety of feathery structures, such as plumes, wires, or diadems. In addition, the males of these species usually exhibit sophisticated dances that, to the sound of their attractive melodies, combine colour and movement in one of the most amazing spectacles of nature. The males of some species take meticulous care even of the scenery for these dances, as is the case with the Western Parotia bird of paradise. In this species, males choose a clearing in the forest and spend hours cleaning it of branches and leaf litter to ensure the perfect staging for their dance.

These are just a few examples of the kind of traits that challenged the Theory of Natural Selection as Darwin (1859) formulated it in *The Origin of Species* (*Origin* from now on). In a world supposedly dominated by competition for survival, how to explain the evolution of such extravagant and apparently costly traits for the survival of organisms? This question was a real headache for Darwin, as he reflected in a letter to his friend the American botanist Asa Gray: “The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick!” (3 April 1860, letter DCP-LETT-2743).

In *Origin,* Darwin devoted a few paragraphs to speculate on the role of those phenotypic traits in males that could be used as weapons in the battle for reproduction (Darwin 1859). However, it was not until 1871 when, in his book *The Descent of Man* (*Descent* from now on), Darwin formalized sexual selection as a process that could explain the evolution of what he called secondary sexual characteristics [following Hunter 1837]: the “armaments” for combat that he had alluded to in *Origin* and the “ornaments” that had so obsessed him, such as the intriguing feathers of the peacock (Darwin 1871). In essence, Darwin described sexual selection as a process analogous to natural selection, but where competition between individuals of the same species occurs over reproducing more and/or with the best available mates.

One hundred and fifty years after the publication of his work (Darwin 1871), we know that Darwin was right: the display of colour, sound and movement of males in birds of paradise seeks to captivate females (Diamond 1986), the jaws in stag beetles are used as tools with which to dislodge potential mating competitors, and the rostral protuberances of chameleons seem to play an important role both in male-male combat and in seducing females (Karsten et al. 2009; Emlen 2014). Indeed, sexual selection has turned out to be a central evolutionary phenomenon for understanding evolution along the tree of life, and it is underpinned by the same principle that Darwin formulated 150 years ago: the variability of heritable traits involved in competition for reproduction (Darwin 1871). What Darwin could never have guessed is the extraordinary complexity and sophistication of the different mechanisms of sexual selection, a labyrinth of processes that all emanate from that apparently simple but devilishly intricate principle, competition for reproduction.

14.2 Pre-copulatory Mechanisms: Darwin's Jigsaw Puzzle

In *Descent,* Darwin explains sexual selection on the basis of two mechanisms that in turn reflect two types of competition for access to mating. First, competition between individuals of the same sex (usually males) through adaptations that increase their success in confrontations with other competitors (e.g. armaments), either by intimidating or reducing the opponent. An example of this is the aforementioned jaws of the stag beetle. Second, competition between individuals of the same sex (usually males) to be more attractive to the other sex, which chooses suitors through a phenomenon known as mate choice. For example, the choice by female birds of paradise for those males with more showy displays (e.g. ornaments).

14.2.1 Intrasexual Competition: Fighting for Mates

Intrasexual competition occurs when there is a direct confrontation between individuals of the same sex for access to mating. It should be noted that this type of competition occurs in both males and females. However, and for reasons that we will discuss later, in general terms it is much more intense among males, something that Darwin already recognized in *Descent*:

> [. . .] it is, with rare exceptions, the male which has been the more modified. [. . .] The cause of this seems to lie in the males of almost all animals having stronger passions than the females. Hence it is the males that fight together and sedulously display their charms before the females (Darwin 1877, p. 221).

Thus, intrasexual competition explains the development of adaptations such as the large antlers on the males of some ungulates (or the serrated femurs possessed by the males of some species of sucking bugs). These adaptations have evolved because

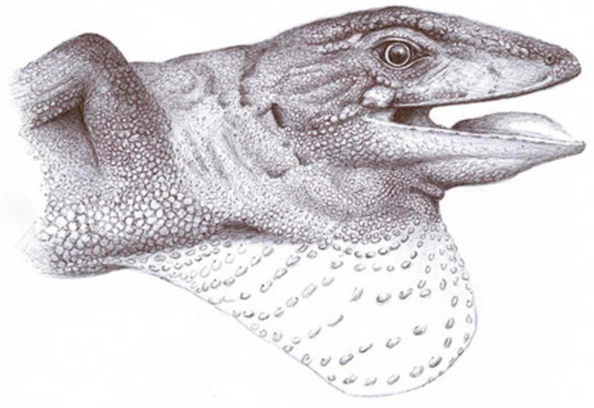

Fig. 14.2 *Anolis wermuthi* showing its gular crest. This behaviour is typical in this genus of lizards and seeks to intimidate possible competitors during social interactions. Drawing by Frutos García García

they increase reproductive success when in direct confrontation with individuals of the same sex (Andersson 1994).

Although the ultimate goal is clear, access to mating, the way to achieve it varies between species. For example, combat between males can occur with the aim of dominating one or more females (a harem), as in the case of lions. On the other hand, competition may be for dominance of a good territory, one with ample food sources, water, a wide range of hiding places or other resources important to the species. Better territories will attract more females to mate with (i.e. *resource-defence polygamy*).

Intrasexual competition sometimes involves physical contact that can become very violent. Fights are usually not deadly, but they can be harmful even for winners. Because of these costs, intrasexual competition does not usually involve combats. Evolution has endowed males and females with different mechanisms for assessing the quality of their competitors, and thus weighing the costs/benefits of escalating combat. As a result, confrontations are usually ritualized and only sometimes (when there is no clear winner in the ritualized phase) become fierce fights. Striking colourations, extravagant morphological structures and displays are some of the most common mechanisms that seek to intimidate and discourage the opponent before direct contact is made (Andersson 1994). In this process, evolution has favoured phenotypic traits that are good indicators of competitive quality. For example, males of the genus *Sitana* lizards display the extensible fan of skin they possess in the throat area (called the “gular fan”) in order to signal vigour in front of other males (Kamath 2016). The gular fan is involved in the social interactions of many species of lizards, such as American lizards of the genus Anolis (Fig. 14.2) or Asian lizards of the genus Draco. Thus, by means of this type of structure, males minimize the costs of their confrontations. In fact, in species with extreme armaments (e.g. venomous snakes), fights never fully escalate and are fundamentally ritualized.

14.2.2 Intersexual Competition: Mate Choice

In addition to directly, through ritualized and/or fierce combat, individuals of the same sex may compete with each other, indirectly, to see who is more attractive to potential mates. Darwin called this phenomenon "intersexual competition" because selection occurs via the opposite sex, through "mate choice". In mate choice, evolution will tend to favour those individuals who find attractive traits that are good indicators of benefits associated with their potential mate, which we classify as direct and indirect (Andersson 1994; see Edward and Chapman 2011).

We speak of direct benefits when choice is made on the basis of material resources (Andersson 1994). For example, males may collaborate in parental care (or even take care of it exclusively), serve as protection against other males or predators, offer nuptial gifts (e.g. nutrients transmitted before or during copulation), or a good territory (e.g. with ample food resources, hiding places and/or low parasite density). We call these benefits "direct" because they translate into a greater investment of resources for offspring. In the spinach fish (*Spinachia spinachia*), for example, males fan their nests to improve oxygen flow to the eggs. This increases hatching rate and, consequently, reproductive success for both parents. In this species, females prefer males that perform stronger flapping and body shaking during courtship, which serve as indicators of their parental quality (Östlund and Ahnesjö 1998).

In contrast, we speak of indirect benefits when choice has to do exclusively with effects that derive from the genes that the offspring will inherit from the couple. That is, the benefits here have to do exclusively with improving the quality of offspring. Indirect benefits result from inheriting genes that, on average, will be different from those inherited if females randomly mated (i.e. they are not the result of a greater investment in resources). Different models have been proposed to explain how mate choice may have evolved based on these types of benefits. According to the *good genes* model, females benefit from mating with males whose genes increase the viability of their offspring (Möller and Alatalo 1999). By viability here we mean genes that increase an individual's ability to survive, such as its ability to flee predators, metabolize nutrients, etc. According to this model, selection will favour the evolution of preferences for those traits that are good indicators of viability, so that the underlying genes are inherited by offspring.

Alternatively, Fisher proposed that secondary sexual characteristics may evolve because they are attractive to females per se, known as the "*sexy sons*" model (Fisher 1930). Let's say that a preference for a particular trait arises in a population. For example, a preference for long caudal feathers in males because these increase flight efficiency and, therefore, offspring viability. Since females carrying the genes "for" such preferences will mate with males carrying the genes "for" long tails, the two will tend to be transmitted together. If the preference in females is for "longer" tails, a process of directional selection (*runaway selection*) will be initiated, where traits are exaggerated generation after generation even beyond the point where they are no longer advantageous for flight, but costly. This process explains the evolution of traits that can compromise survival, simply because carriers with more exaggerated traits have greater reproductive success (Kirkpatrick 1982). In fact, this process of rampant selection will only cease when the costs in terms of survival are equal to or greater than the benefits of being “sexy”. Fisher’s model could explain the appearance of such extravagant traits as the peacock’s tail.

14.3 Post-copula Mechanisms: The Invisible Competition

From the second half of the twentieth century onwards, the definition of sexual selection expanded as we understood that this process transcends mating. On the one hand, because the development of molecular techniques shows that polyandry (i.e. a female mates with more than one male in the same reproductive cycle) is very common in the animal kingdom (Arnqvist and Nilsson 2000). On the other hand, because data accumulate from species in which females have specialized structures that allow sperm storage for prolonged periods of time (e.g. Holt and Lloyd 2010). The sum of these two factors sets the scene for the war over reproduction to continue after mating, in the reproductive tract of females, through sperm competition (Simmons 2001) and cryptic choice (Eberhard 1996).

14.3.1 Sperm Competition: Fighting for Fertilization

Since the number of eggs a female can produce is limited, evolution will favour any adaptation that allows males (i.e. their sperm) to fertilize more eggs than their competitors (Parker and Pizzari 2010). This postcopulatory competitive mechanism was described in insects by Geoff Parker, who called it “sperm competition” (Parker 1970). Fifty years later, thanks to the use of molecular techniques, we know that this phenomenon occurs in a multitude of vertebrates and invertebrates (Smith 2012). For example, in many species males modulate the amount of sperm with which to inseminate females according to the number of competitors. Since sperm production is not costless (Parker and Pizzari 2010), evolution favours those males able to optimize their sperm investment according to the number of opponents. Increasing the number of matings with the same female and predicting her peak fertility are mechanisms that also favour the success of males in fertilization (Smith 2012). In addition, sperm motility and viability, as well as other characteristics of the ejaculate, are crucial in sperm competition (Smith 2012).

In addition, males may adopt strategies that prevent or reduce the competition that their own sperm will face within the female reproductive tract. For example, males of some species escort females during and after mating to prevent them from being inseminated by competitors, a behaviour called “mate guarding”. A classic example is dragonflies (Fig. 14.3), where males may remain attached to females for extended periods of time to prevent females from re-mating (Alcock 1994). One need only

Fig. 14.3 Dragonfly mating (Belgium). Photograph by Roberto García-Roa

look closely at a pond in spring to see tandems of dragonflies flying, with the males clinging to the females by means of genital *claspers*, until females stroke the surface of the water to deposit their eggs there. The variety and elaboration of adaptations for sperm competition is extremely diverse, from structures that allow them to "sweep away" the ejaculate of their opponents, as in the case of the mealworm beetle *Tribolium castaneum*, to nuptial plugs that are anchored to the genital opening of the female after copulation to make it difficult for other males to insert their sperm (Andersson 1994).

14.3.2 Cryptic Female Choice

The role of females in postcopulatory competition is not limited to serving as a battleground for sperm competition. In many species, females play a decisive role in the competition for fertilization. Polyandry gives them the opportunity to favour the sperm of the males that confer the greatest benefit to them. This process was termed "cryptic mate choice" by Thornhill (1983) and involves a variety of morphological, physiological or behavioural mechanisms (Eberhard 1996). For example, females can avoid full intromission of the penis of lower quality males, thereby reducing the amount of ejaculate inseminated. They may also terminate copulation earlier or prevent mating males from displacing the sperm of previous males (Eberhard 1996). Even after successful copulation, females may bias the use of one male's sperm by discarding the sperm of others, by transferring unselected sperm to locations where another male could displace it, or simply by storing the sperm of the preferred male so that it is the one that preferentially fertilizes her eggs. Females may also vary offspring production depending on the male they mate with, ceasing ovulation and/or egg maturation, failing to prepare the uterus for development, or even aborting when mated with an unwanted male (see Eberhard 1996).

14.4 Sex Roles and the Evolutionary Battle of the Sexes

Darwin observed that, while males of most species were willing to copulate frequently, females were more cautious (Darwin 1871). As we have seen above, sexual selection tends to be more intense in males: either directly through intrasexual competition or indirectly through mate choice. In 1948, geneticist Angus John Bateman used the vinegar fly (*Drosophila melanogaster*) in an attempt to understand this widespread principle (Bateman 1948). In his work, Bateman concluded that, while females achieved their greatest reproductive success after only a few copulations, that of fervent males increased linearly with the number of matings. He suggested that, compared to males, females were more constrained in the number of offspring they could produce. This essentially has to do with anisogamy, whereby female gametes are much larger and more expensive than male gametes. This greater investment in a smaller number of gametes means that females tend to have a potentially much lower reproductive rate than males. This, in turn, has conditioned the evolution of parental care and, in general, of investment in offspring, favouring divergent reproductive strategies; the so-called “sex roles” in males and females (Trivers 1972; Lehtonen et al. 2016). Thus, while selection tends to favour the evolution of strategies that maximize the number of females males mate with, in females it tends to favour strategies that maximize the quality and survival of their offspring. As a consequence, males tend to vary much more than females in their reproductive success (i.e. there is a greater difference in reproductive success between the best and the worst male in a population than between the best and the worst female). This, in turn, implies that sexual selection acts much more intensely on males, as often only the few best males monopolize access to females. Although this paradigm has many exceptions (e.g. species with reversed sex roles), this general trend holds true throughout the tree of life (Janicke et al. 2016).

An unsuspected consequence of the existence of sex roles in nature is that the sexes often have different ways of maximizing reproduction. In fact, the evolutionary interests of males and females rarely coincide, so that their fitness cannot be optimized simultaneously (Parker 2006). This phenomenon, known as “sexual conflict”, is associated with intense competition between males and often triggers an arms race (i.e. antagonistic co-evolution) between the two sexes (Arnqvist and Rowe 2005) that Dawkins referred to as “the evolutionary battle of the sexes” (Dawkins 1976). Sexual conflict has received increasing attention in recent years, to the point of being recognized today as one of the main phenomena of sexual selection. First, because it is essential for understanding why males and females respond as they do to sexual selection. Second, because it can act as a driver of biodiversity, favouring processes of inter-population evolutionary divergence and even speciation (Gavrilets 2014). Third, because it can have very negative consequences for populations. For example, in response to intense sperm competition, males of some insect species have evolved genitalia with spines that cause considerable damage to females during mating. Such male harm increases female investment in reproduction in the short term (by diminishing their future survival) and reduces female re-mating, thus increasing the reproductive success of the male, but at the expense of the female (Parker 2006). Similarly, *D. melanogaster* males transfer a "sex peptide" in their ejaculate that manipulates females to lay more eggs in the short term and reduce their receptivity to other males, again at the expense of their longevity and their own fitness (Wigby and Chapman 2005). Spiked genitalia and toxic ejaculates are but examples of how high levels of competition between males (i.e. intense intrasexual competition) can result in adaptations that, while serving to compete effectively against other males, in doing so harm females, reducing their fitness (Parker 2006). Male harm to females is not only extraordinarily widespread in nature, but can lead to a "reproductive tragedy of the commons" where sexual conflict can drastically reduce a population's capacity for growth and viability, even to the point of extinction (Rankin et al. 2011).

14.5 The Importance of Sexual Selection in Evolution

Throughout its different eras, the Earth has witnessed an infinite number of adaptations, of sounds, colours, morphologies and behaviours (Darwin 1859). Many of these adaptations have been sculpted by sexual selection, one of the two pillars of Darwinian evolution. Based on competition for reproduction and fertilization (Andersson 1994), sexual selection has become a cornerstone for understanding the evolution of adaptations in males and females and, ultimately, for understanding the history of life on earth. Sexual selection is a fundamental driver of speciation processes (Panhuis et al. 2001). For example, the extraordinary adaptive radiation of birds of paradise, whose elaborate courtships and ornaments we have already discussed, is largely due to the runaway action of sexual selection (Ligon et al. 2018). Moreover, sexual selection is also a determinant process for the viability of species and their populations, for their ability to adapt to changes in the environment (Pomiankowski and Moller 1995). We now know that sexual selection is a powerful mechanism that purges the genome of deleterious mutations (Radwan 2004), which protects populations against inbreeding depression, a key phenomenon in extinction (Lumley et al. 2015). Indeed, sexual selection is such an effective evolutionary mechanism that it often dominates natural selection.

First, secondary sexual traits favoured by sexual selection tend to be closely linked to traits with direct impact on the condition of their carriers, including traits that directly influence the average fitness of the population, such as survival (e.g. anti-predator abilities, ageing), fecundity, or the quality of their offspring (e.g. parental care). Today we know that the expression of complex armaments and ornaments depends to a large extent not only on the inheritance of certain alleles "for" these traits, but also on the general condition of the organism, its overall "genetic quality". Thus, sexual selection tends to select genotypes with generally good combinations of traits, most of which need not be directly linked to reproduction, in a process called "genic capture" (Rowe and Houle 1996).[1] Second, because sexual selection is more intense in males than in females, it is an extraordinarily efficient evolutionary mechanism because most of the costs of selection are paid by males, the non-reproductive sex. In other words, at the population level, the best genes are filtered out (genic capture) at the cost that many males do not leave offspring, while most of the females in a population do reproduce. This selective filtering tends to increase average population fitness, and considerably increases the speed at which it evolves and, therefore, its ability to adapt to sudden changes in the environment. This is especially true in reference to directional and sustained environmental changes, such as climate change. These evolutionary advantages possibly explain why the overwhelming majority of animals, plants and fungi reproduce sexually even though, at first glance, it seems more costly than asexual[2] reproduction.

14.6 Conclusions

We still have a long way to go, a long list of challenges in the study of sexual selection that undoubtedly hide great discoveries to be made. For example, we still do not fully understand the evolution and characteristics of mate choice preferences. We still ignore basic aspects related to the distribution, variability and shape of preference functions, the costs associated with choice, or the role of the social environment and the cognitive mechanisms involved in mate choice (see the chapter by Santos and Varela in this volume). Likewise, we have paid too little attention to intrasexual competition in females or to the evolution of sex between individuals of the same sex, both phenomena that are much more widespread than we suspected. Nor do we understand well how sexual selection operates in complex environments, subject to the environmental variations that are characteristic of most habitats in which organisms reproduce in nature. Most of the advances we have made to date in

---

[1] Genic capture is one of the processes that could resolve the Lek paradox, since most of the phenotypic variability in the expression of secondary sexual characteristics would not be directly linked to genetic variability in the alleles directly responsible for the expression of secondary sexual characteristics, but to the general condition of the individual which, in turn, would condition the development of these characteristics (Rowe and Houle 1996).

[2] An asexually reproducing organism transfers all its genes to its offspring (not just half) and reproduces twice as fast as a sex-differentiated organism (where one of the sexes does not reproduce), known as the "*two-fold cost of sex*" (i.e. Smith 1971; Smith and Maynard-Smith 1978).

the field of sexual selection have focused on studying the mechanisms of sexual competition in stable environmental conditions, such as those of the laboratory, and therefore we are far from understanding how these discoveries translate to nature. Another major challenge is to understand what factors are determinant in the evolution of sexual conflict, why this phenomenon, so widespread in nature, results in damage to females in many species and not in others, and what consequences it has for population viability. It will also be crucial to fully explore the role of phenotypic plasticity in secondary sexual traits, and how such responses can give rise to feedbacks between ecological and evolutionary processes; fundamental both for understanding how sexual selection operates and its role in adapting to the increasing demands of change that challenge this planet's biodiversity.

In short, we have come a long way since the publication of Darwin's second and often forgotten masterpiece, his massive *Descent* in 1871. Probably because Darwin devoted the main title and much of this book to human evolution, it may give the impression that sexual selection is a secondary aspect of this work. On the contrary, Darwin's ideas on sexual selection are undoubtedly the main contribution of this book to the study of evolution, and to the study of biology in general. By presenting his ideas on sexual selection 150 years ago, Darwin not only completed the general outline of his theory of natural selection, but also laid the foundations of what has become one of the pillars of evolutionary biology. A field that, since the 1970s of the last century, has exploded to reveal itself as one of the most complex and exciting in the study of evolution. What better testimony to Darwin's second greatest idea?

References

Alcock J (1994) Postinsemination associations between males and females in insects: the mate-guarding hypothesis. Annu Rev Entomol 39:1–21

Andersson M (1994) Sexual selection. Princeton University Press, Princeton

Arnqvist G, Nilsson T (2000) The evolution of polyandry: multiple mating and female fitness in insects. Anim Behav 60:145–164

Arnqvist G, Rowe C (2005) Sexual conflict. Princeton University Press, Princeton

Bateman AJ (1948) Intra-sexual selection in Drosophila. Heredity 2:349–368

Darwin C (1859) On the origin of species: a facsimile of the, 1st edn. Harvard University Press, Cambridge [1964]

Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London

Darwin C (1877) The descent of man, and selection in relation to sex, 2nd edn. John Murray, London

Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

Diamond J (1986) Biology of birds of paradise and bowerbirds. Annu Rev Ecol Syst 17:7–37

Eberhard W (1996) Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton

Edward DA, Chapman T (2011) The evolution and significance of male mate choice. Trends Ecol Evol 26:647–654

Emlen DJ (2014) Animal weapons: the evolution of battle. Henry Holt and Co, New York

Fisher RA (1930) The genetical theory of natural selection. Oxford University Press, London

Gavrilets S (2014) Is sexual conflict an "engine of speciation"? Cold Spring Harb Perspect Biol 6: a017723

Holt W, Lloyd RE (2010) Sperm storage in the vertebrate female reproductive tract: how does it work so well? Theriogenology 73:713–722

Hunter J (1837) An account of Mr. Hunter's method of performing the operation for the cure of the popliteal aneurism. Lond Med J 3:594–612

Janicke T, Häderer IK, Lajeunesse MJ et al (2016) Darwinian sex roles confirmed across the animal kingdom. Sci Adv 2:e1500983

Kamath A (2016) Variation in display behavior ornament, morphology, sexual size dimorphism, and habitat structure in the fan-throated lizard (Sitana, Agamidae). J Herpetol 50:394–403

Karsten KB, Andriamandimbiarisoa LN, Fox SF (2009) Sexual selection on body size and secondary sexual characters in 2 closely related sympatric chameleons in Madagascar. Behav Ecol 20:1079–1088

Kirkpatrick M (1982) Sexual selection and the evolution of female choice. Evolution 36:1–12

Lehtonen J, Parker GA, Schärer L (2016) Why anisogamy drives ancestral sex roles. Evolution 70: 1129–1135

Ligon RA, Diaz CD, Morano JL et al (2018) Evolution of correlated complexity in the radically different courtship signals of birds-of-paradise. PLoS Biol 16:e2006962

Lumley AJ, Michalczyk Ł, Kitson JJ et al (2015) Sexual selection protects against extinction. Nature 522:470–473

Möller AP, Alatalo RV (1999) Good-genes effects in sexual selection. Proc R Soc Lond B 266:85–91

Östlund S, Ahnesjö I (1998) Female fifteen-spined sticklebacks prefer better fathers. Anim Behav 56:1177–1183

Panhuis TM, Butlin R, Zuk M et al (2001) Sexual selection and speciation. Trends Ecol Evol 16: 364–371

Parker GA (1970) Sperm competition and its evolutionary consequences in the insects. Biol Rev 45: 525–567

Parker GA (2006) Sexual conflict over mating and fertilization: an overview. Philos Trans R Soc Lond B Biol Sci 361:235–259

Parker GA, Pizzari T (2010) Sperm competition and ejaculate economics. Biol Rev 85(4):897–934

Pomiankowski A, Moller A (1995) A resolution of the lek paradox. Proc R Soc Lond B 260:1–29

Radwan J (2004) Effectiveness of sexual selection in removing mutations induced with ionizing radiation. Ecol Lett 7:1149–1154

Rankin DJ, Dieckmann U, Kokko H (2011) Sexual conflict and the tragedy of the commons. Am Nat 177:780–791

Rowe L, Houle D (1996) The lek paradox and the capture of genetic variance by condition dependent traits. Proc R Soc Lond B 263:1415–1421

Simmons LW (2001) The evolution of polyandry: an examination of the genetic incompatibility and good-sperm hypotheses. J Evol Biol 14(4):585–594

Smith JM (1971) What use is sex? J Theor Biol 30(2):319–335

Smith RL (ed) (2012) Sperm competition and the evolution of animal mating systems. Academic Press, London

Smith JM, Maynard-Smith J (1978) The evolution of sex, vol 4. Cambridge University Press, Cambridge

Thornhill R (1983) Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. Am Nat 122:765–788

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man, 1871–1971. Aldine Publishing Co, Chicago, pp 136–179

Wigby S, Chapman T (2005) Sex peptide causes mating costs in female *Drosophila melanogaster*. Curr Biol 15:316–321

Chapter 15
Genetic and Cultural Evolution of Mate Choice

Mauro Santos and Susana A. M. Varela

Abstract Darwin suggested that female mate choice explains the evolution of exaggerated male traits, such as an extravagant plumage in birds, which could reduce the survival chances of individuals bearing them. Around 60 years later, Fisher gave a formal verbal expression to the runaway genetic model of female mate choice, where female mating preferences can, by themselves, lead to the evolutionary exaggeration of favored male traits. However, the idea that female preferences are genetically fixed was demolished in the 1990s when it was shown that female mate choice is also affected by cultural transmission, which can even prevail over the fixed genetic preferences. This cultural transmission of behavior is now commonly known as mate-choice copying, or mate copying, and is a widespread mating strategy in animals, from invertebrates to humans. Although this behavior has been claimed to have a significant role in evolution, some initial theoretical models suggested that it could be maladaptive in the long term because it induces a frequency-dependent bias that helps to establish a male trait that decreases male fitness. This conclusion is, however, model dependent and, under some conditions, mate-choice copying can increase a population's average fitness relative to populations without this behavior. An exciting question is to what extent mate-choice copying is a by-product of a general associative learning process or, rather, it is a domain-specific adaptation.

Keywords Copying · Mate choice · Social learning · Speciation · Hybridization · Evolutionary psychology · Associative learning

---

M. Santos (✉)
Department of Genetics and Microbiology, Universitat Autònoma de Barcelona, Barcelona, Spain
e-mail: mauro.santos@uab.es

S. A. M. Varela
cE3c—Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisbon, Portugal

Instituto Gulbenkian de Ciência, Oeiras, Portugal

ISPA—Instituto Universitário, Lisbon, Portugal

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_15

15.1 Introduction

In Chap. IV of *On the Origin of Species*, Charles Darwin wrote:

> Thus it is, as I believe, that when the males and females of any animal have the same general habits of life, but differ in structure, color, or ornament, such differences have been mainly caused by sexual selection; that is, individual males have had, in successive generations, some slight advantage over other males, in their weapons, means of defence, or charms; and have transmitted these advantages to their male offspring. (Darwin 1859, pp 89–90)

Some years later, in *The Descent of Man,* Darwin (1871) described those differences between sexes as "secondary" sexual characters; that is, characters that are not directly connected with the act of reproduction. Darwin was, therefore, admitting that those secondary sexual characters which augment a male's ability to win in fights with other males for the access to females may be ascribed to sexual selection, although Wallace (1889) considered male rivalry as a form of natural selection. But Darwin also included a male's "charm" in his description, clearly suggesting that sexual selection not only operates through males competing with other males but also through females being attracted by more charming males. Wallace was also skeptical about this and raised the problem of whether females are capable of choosing among a series of males that show subtle differences from one another.

Why should females even bother to choose males on the basis of these differences, rather than simply mate at random? This question was tackled by Fisher (1930), who first described (in a cryptic way) an evolutionary process that could lead to the evolution of female preferences for exaggerated male traits: Fisher's runaway process, where the indirect benefit of sexually attractive offspring is not due to natural selection. However, few people gave much credence to the idea or even understood what Fisher was talking about. The situation changed when Lande (1981) published a comprehensible model with two sex-limited quantitative characters that explained Fisher's insight. The basic conclusion is that there is coevolution between courter traits and chooser preferences: a trait expressed in males can increase in frequency even if it is maladaptive (e.g., an exaggerated male ornamentation that hinders survival) because an increasing frequency of females over generations prefers to mate with these (ornamented) males. Perhaps the most convincing demonstration of runaway genetic selection was provided by Wilkinson's (1993) work with the stalk-eyed fly *Cyrtodiopsis dalmann*. Stalk-eyed flies are weird insects with the eyes located at the end of long structures (eyestalks) that are projected from both sides of the head. After artificially selecting for males with long or short eyestalks, he found a positive association between the length of male eyestalks and female preference for this trait; that is, female preferences changed as a correlated response for selection on male eyestalk length.

At this point, many feminists could complain, with good reason, that most authors use "female" and "male" as convenient shorthand for the individuals who choose and for the individuals who court, respectively. Part of the reason can be traced to an influential paper by Trivers (1972) on the investment of each parent on each offspring. In a nutshell, the argument is that in a sexually reproducing species the total offspring produced must be equal for both sexes, and competition for mates usually involves males because their variance in reproductive success is higher (i.e., most females tend to mate but sometimes a substantial proportion of males do not mate). However, this is not always the case and a growing body of work emphasizes the role of male mate choice, and that sexual selection can act strongly on females (Clutton-Brock 2009). Therefore, a suitable definition of mate choice is that it is "any aspect of an animal's phenotype that leads to its being more likely to engage in sexual activity with certain individuals than with others" (Rosenthal 2017, p 11).

A quite extreme case of variance in reproductive success between sexes occurs in lekking species; species where males aggregate and females survey potential partners for copulation. In a classical lek the males do not provide parental care and the only resource required by females are the males themselves. A common observation is that single males achieve a large proportion of matings, which strongly suggests that females are actively choosing the best males to mate with, although this is debated. For instance, in white-bearded manakins a single male in a lek of 10 males attained 73% of 438 copulations, and six males mated only 10 times (Lill 1974). This mating system has generated the "paradox of the lek." The idea is that if females are choosing males on the basis of their genetic quality then the genetic variation in those particular male traits targeted by females should eventually be eroded, and the benefits of having chosen these males would disappear. Yet, mate choice still continues. Some seminal papers (Bradbury and Gibson 1983; Wade and Pruett-Jones 1990) came, however, with the idea that a learning process instead of female innate preferences might explain such high variance in male mating success of lekking species. The behavior was termed "female copying" (now commonly known as mate-choice copying, or mate copying), and was defined as "a type of non-independent choice in which the probability that a female chooses a given male increases if other females have chosen that male and decreases if they have not" (Pruett-Jones 1992, p 1000). The sex-biased definition is because mate-choice copying has mostly been described in females, although there is now evidence that it can also occur in males (Davies et al. 2020).

The notion that there could be a cultural transmission of mate preferences through copying behavior spurred a substantial interest on the topic that still continues. By referring to mate-choice copying as a special case of "cultural transmission" we explicitly acknowledge that the concept of culture is not restricted to humans, and a valuable shorthand definition is that "culture is variation acquired and maintained by social learning." Here "social learning" refers to any gathering of information based on observing, interacting with, and/or imitating others in a social context. This learning can result from personal experiences with others, or by observing others' individual experiences or behaviors. Cultural transmission through social learning in the context of mate choice reveals that animals not only rely on fixed innate preferences but that they can also acquire preferences later in life by observing others mating and use them as cultural habits.

15.2 Mate-Choice Copying: Empirical Evidence

The standard view that females have genetically innate and fixed preferences for certain male traits was demolished in 1992 when Dugatkin (1992) and Dugatkin and Godin (1992) showed that in guppies (*Poecilia reticulata*) females display mate-choice copying. Since then, mate-choice copying has been documented in a wide range of species, from invertebrates to humans (see recent meta-analyses in Davies et al. 2020; Jones and DuVal 2019). Interestingly, Mery et al. (2009) were the first to show that mate-choice copying occurs in a simple invertebrate (*Drosophila melanogaster*), which has opened the possibility of using the vast set of molecular tools and mutants available in *D. melanogaster* to dissect the genetic pathways and the neural basis of this behavior, as we discuss below.

Mery et al. (2009) performed two types of experiments. In one experiment they used the setup illustrated in Fig. 15.1, which consists of two vials separated by a thin glass partition. A virgin female (prospector) is introduced in a vial and can observe a pair of flies in the other vial: a model female and a male. Two male phenotypes were artificially generated by dusting flies with green or pink powder. The prospector female was allowed to witness a green (pink) male copulating with the model female

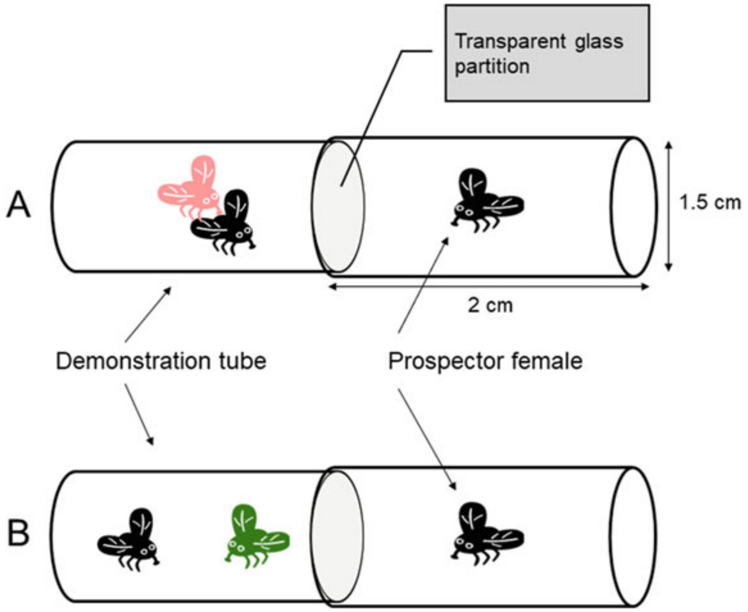

Fig. 15.1 Setup for the mate-choice copying experiment. (**a**) A prospector virgin female can observe a model female mating with an artificially generated pink male. (**b**) The prospector female witnesses an artificially generated green male that does not copulate with a model female. Later, when given the choice between two males dusted with pink or green powder, the prospector female preferably mates with the color (pink in this example) associated with active copulation. (After Mery et al. 2009)

and then a second pink (green) male that did not copulate because the model female was nonreceptive. As a result, the prospector females preferably mated with the male dusted with the color (either green or pink) associated with active copulation. In another experiment, Mery et al. (2009) showed that prospector females can change their preference for good condition males and rely instead on social information after observing model females mating with poor condition males. These results raise two important points. First, *Drosophila* females learn to prefer any male with a given trait (i.e., green or pink). This is called trait-based mate copying in contrast to individual-based mate copying, where females prefer one particular male over another. Because trait-based mate copying applies to various individuals in the population, it has greater chances to widespread cultural transmission of preferences. Second, mate-choice copying can induce a significant fitness cost for *Drosophila* females because they do not conform to Bayesian decision theory, which suggests that a female should perform mate-choice copying only when her own perception does not indicate much difference between two males (Uehara et al. 2005). Thus, it might be the case that there are nonadaptive reasons for the expression of mate-choice copying and the question arises: how and why is this behavior maintained, and why did it evolve?

15.3 Mate-Choice Copying: Theoretical Approaches

A common argument offered to explain the evolution of mate-choice copying is that it is a strategy used by females to assess the quality of potential partners for copulation. The argument goes as follows (Nordell and Valone 1998): a focal female tries to assess the quality of two males but her perception is error-prone, so the best she can do is to select one male at random and have a 50% probability of mating the higher quality male. However, the focal female can observe another (model) female assessing the two males and use this social information to perform mate-choice copying. If the model female also cannot discriminate against the males, she would mate at random and have a 50% probability of mating with the higher quality male. Thus, copying the model female or not copying and mating at random both result in the same 50% probability of mating with the higher quality male and, hence, the focal female is not worse off by copying than by mating at random using her own inadequate assessment ability.

This line of reasoning seems straightforward and agrees with the argument that females can only express (innate) mating preferences when there is sufficient phenotypic variation among males to detect differences, and that choosiness should increase when there is greater variation in male quality (Dugatkin 1996). The problem is, however, that this is not always the case. As explained above, *Drosophila* females rely on social information even when it contradicts their individual assessment of male's quality. Although it could be argued that in this situation the reproductive output of copying females would be about the same than that of model females, mate-choice copying is still maladaptive because it induces a significant fitness cost.

An important shortcoming of the “quality assessment” argument to explain the evolution of mate-choice copying is that it does not consider the coevolution of female mate choice and male trait, nor the interplay between innate and learned mating preferences. Kirkpatrick and Dugatkin (1994) studied the coevolution of learned female preferences and male traits, and showed that a process akin to Fisherian runaway selection can occur. They assumed that all females are born with an innate preference (which cannot evolve in the model) for the more common, unfit males, and that naïve females copy the choices of mature females and evolve (only through cultural evolution) a stronger preference for the male type they most frequently saw mating. Their results show that the male trait and the learned preference coevolve with a positive frequency-dependent advantage to the more common male trait; that is, there is a runaway cultural sexual selection where the most preferred individuals will receive the most benefits from copying. Analogous to the standard Fisherian case, in this model mate-choice copying can be maladaptive because it hampers the spreading of a novel, fitter trait in the population (but see Santos et al. 2017).

The last years have witnessed a growing interest on the role of gene-environment interaction (G × E) in sexual selection and mate choice. In spatially heterogeneous populations G × E contributes to the maintenance of genetic variation because migrants continually introduce alleles that are not locally adapted. Migration can be costly because females do not know with whom to mate in a new habitat, as they ignore which male phenotype is best locally adapted. By mating randomly with local males or mating with other migrant males will make them produce offspring that will be less fit to the new environment and, hence, less competitive than local females’ offspring. So, migration should be counter-selected. Mate-choice copying can provide a rather interesting and perhaps unexpected solution to this problem. As we have shown (Sapage et al. 2021), if migrant females have the ability to copy, compared to populations in which females do not copy, they will learn from local females who are the best locally adapted males and hence produce, by mating with them, better adapted offspring. The offspring will still carry their mother’s nonadapted alleles but will also carry the alleles of the best local males, reducing considerably the reproductive cost of migration. We found that this effect does not only promote the spread of the copying allele across generations but also increases migration between patches, meaning that migration has become highly adaptive due to mate-choice copying. Taken together, these results are the first evidence that, in spatially heterogeneous environments, mate-choice copying can influence the evolution of another (nonsexually related) trait, and that it can preserve genetic variation within patches. This can contribute to resolve the lek paradox (although such an effect was not explicitly tested) and revives the discussion about whether mate-choice copying can be adaptive or not.

An important point is that population genetic models assume that there is genetic variation for mate-choice copying, but empirical evidence so far is limited. To our knowledge, the only paper published to date studying the heritability of mate-choice copying (Dugatkin and Druen 2007) suggests that in guppies this behavior has little if any significant heritability. There remains a pressing need for empirical studies to identify the relative contributions of genetic, social influences and their interaction to the phenotypic variance in mate-choice copying. The model species *D. melanogaster* offers a wonderful possibility.

15.4 Mate-Choice Copying and Speciation

Several conditions need to be met for a learned mate preference by mate-choice copying to be considered a true cultural habit (Danchin et al. 2018): social learning; generalization of the learned preference for a particular male to all the males in the population sharing the same trait; high durability of the learned preference, at least until the copying female mates; transmission to other females (informational cascades); and conformity to the majority, that is, the tendency to copy the most common mate choices by demonstrator females in the population. As described above, the theoretical evidence on mate-choice copying, using all or most of these conditions, has been able to show that mate-choice copying can cause evolutionary changes within and between populations. Darwin, who did not think about evolution in genetic terms, also believed that habit could contribute to evolutionary changes:

> All animals present individual differences, and as man can modify his domesticated birds by selecting the individuals which appear to him the most beautiful, so the habitual or even occasional preference by the female of the more attractive males would almost certainly lead to their modification; and such modifications might in the course of time be augmented to almost any extent, compatible with the existence of the species. (Darwin 1871, vol. 2, p 124)

One possible implication of such cultural sexual selection mechanism is that of speciation, the evolutionary process by which populations evolve to become distinct species. Because mate-choice copying can accelerate the fixation of a preferred male trait allele, despite whether it is the best fit allele or not (Kirkpatrick and Dugatkin 1994; Santos et al. 2014), it has the potential to cause genetic divergence of male traits between populations with different copying traditions (e.g., Danchin et al. 2004; Mery et al. 2009). However, as we have discussed in a previous conceptual work (Varela et al. 2018), speciation exclusively by mate-choice copying is unlikely. Sexual imprinting (the process by which a young animal learns the characteristics of a desirable mate), for example, is another type of nongenetically inherited female preference trait that has been shown, both theoretically and empirically, to cause speciation. Sexual imprinting is different from mate-choice copying because it occurs very early in life, causes remarkably stable mating preferences (that cannot be easily reversed), and it is restricted to vertical transmission, thus preserving linkage disequilibrium between the female preference and the male trait (Verzijden et al. 2012). Mate-choice copying, on the other hand, occurs at sexual maturity, does not cause irreversible mate preferences, and occurs mostly between unrelated individuals. This makes the process of speciation by mate-choice copying to require more stringent conditions, such as spatially structured populations with some initial degree of genetic divergence due to habitat selection and absence of migration between patches (or rejection of migrants by local individuals, which would lead to the elimination of migration). With these conditions, mate-choice copying has the potential to facilitate, reinforce, or accelerate reproductive isolation between populations (Varela et al. 2018).

15.5 Mate-Choice Copying in Humans

In 1992 Barkow et al. edited the book *The Adapted Mind* with the aim of introducing to a wider audience the emerging field of evolutionary psychology, defined simply as "psychology that is informed by the additional knowledge that evolutionary biology has to offer, in the expectation that understanding the process that designed the human mind will advance the discovery of its architecture" (Cosmides et al. 1992, p 3). Evolutionary psychology started as a reaction against what Tooby and Cosmides (1992) coined as the "Standard Social Science Model" (SSSM), which they claim conceives the mind as a general-purpose cognitive mechanism shaped almost entirely by culture (a "blank slate"; Pinker 2002). Some scholars have criticized the way evolutionary psychology identified social scientists and conceptualized evolutionary biology (e.g., Rose and Rose 2000).

Critical voices notwithstanding, evolutionary psychology is now widely accepted as an academic discipline and has dominated research on human mate choice but remains contentious. A central goal of evolutionary psychology is to provide explanations of our natural psychological capacities in terms of natural selection, and assumes that our ancestors' ambient for evolutionary adaptation was the hunter-gatherer environment during the Pleistocene era (from 2.58 million years ago to 11.650 years before the present): today's behaviors that appear to be maladaptive is because we were not designed for modern life, which in human history spans an insignificant amount of time for natural selection to have reshaped our cognitive programs. This is a misguided view because if human-specific cognitive adaptations evolve because they enhance our ability to survive and reproduce, the implication is that the lag load, understood as the relative decrease in the average fitness of a population compared with the fitness it would have if the average allele frequencies had matched the current environmental conditions, will raise at accelerating speed in human populations given the exponential increase of technological progress. If we were not adapted to modern life it is a miracle that we still exist.

Embedded in their panselectionist paradigm, where virtually all traits are described as adaptations and little room is left for other evolutionary processes, evolutionary psychologists expect "evolution to produce supremely rational mechanisms of mate choice, rational in the sense that they lead to wise decisions rather than impetuous mistakes" (Buss 2000). Along the same vein, Miller and Todd (1998, p 191) claim that "individuals carrying genes for bad mate choice mechanisms pick bad mates, so that these genes usually end up in fewer or lower quality offspring, who take them with them to evolutionary oblivion." These claims are misleading. As Slovic (1995, p 365, our addition between brackets) put it: "it is now generally recognized among psychologists that utility maximization [i.e., to pick the optimal good in a set] provides only limited insight into the processes by which decisions are made." In addition, it is clear among evolutionary biologists that females cannot always make the "wise" choice when applying a preference function to assess males; that is, mate choice decisions can be nonadaptive or maladaptive (Rosenthal 2017). Fisherian benefit of sexually attractive offspring can occur notwithstanding natural selection against exaggerated traits. Similar nonadaptive or maladaptive mating decisions could happen with mate-choice copying.

Mate-choice copying has been reported in humans, mostly in women. This finding, by itself, questions Buss' claim because if evolution had produced "supremely rational mechanisms of mate choice" there would be no reason for a woman to rely on other women's decisions to choose a good mate. (True, modern contraceptives gave women control over their fertility but, according to evolutionary psychologists, women's underlying sexual psychology evolved during the Pleistocene.) A recent review by Gouda-Vossos et al. (2018) points that most studies of mate-choice copying in humans have focused on individual-based mate copying, where attractiveness is scored by presenting the target individual alongside the opposite sex or alone. Actually, Darwin (1871) attributed the physical differences among human "racial" groups to diversifying mate preferences. These diversifying preferences can have a genetic basis or can result, at least partially, from a within-group social convention about attractiveness. To what extent is there genetic variation for preference in humans?

Heritability quantifies the relative contribution of genetic influence on phenotypic differences. The classical approach in humans to estimate heritability is the use of identical (monozygotic; MZ) and nonidentical (dizygotic; DZ) twins. A rough estimate of heritability in a twin study can be made by doubling the difference between the identical and fraternal (dizygotic) twin correlations. This is because MZ twins are identical genetically and DZ twins are 50 percent similar genetically; the difference in their correlations reflects half of the genetic effect and is doubled to estimate heritability. Using a large twin dataset, Zietsch et al. (2012) estimated broad sense heritabilities for 13 trait preferences in women: physical attractiveness, exciting personality, kindness, earning capacity, and health had the highest heritabilities. After combining all trait preferences, the authors report a highly significant heritability of 20% in women (for men the value was marginally significant). Therefore, it seems that there is sufficient variation in preferences for a woman to have any reason to switch from her innate to an observed preference. Zietsch et al. (2012) caution, however, that realized mate choices display much lower heritability (around 5% for both sexes averaged over numerous traits), thus suggesting that across groups diverging preferences largely arise from social conventions. Mate-choice copying could reinforce the social transmission of preferences and increase the among-group variance without any clear connection with adaptation. Actually, empirical evidence suggests that socially acquired information can occasionally be incorrect and still spread within groups (Richerson and Boyd 2005).

15.6 Mate-Choice Copying: Asocial or Social Learning Mechanism?

Mate-choice copying is based on a social associative learning process. Social, because it occurs by observation of other females' mating interactions, and associative learning, because copying females learn to associate a male phenotypic trait (the conditioned stimulus) with the preference (or rejection) expressed by demonstrator females (the unconditioned stimulus). This associative process can be broken down into four information processing mechanisms: stimuli input (detection and attention to other females' mating interactions), encoding (the actual associative learning stage), storage (memory formation), and retrieval (memory recall, leading to the expression of the copying behavior).

We know, from theoretical studies, that when females copy, their behavior not only helps increase the spread of the preferred male trait allele over generations, but also the spread of the copying allele itself (Santos et al. 2017; Sapage et al. 2021). But what does the copying allele really represent? This has never been formally asked nor described in this literature. However, it must intrinsically represent some kind of cognitive ability. Is it a general-purpose ability that females can use for learning any kind of association in any functional domain, social or nonsocial? Or is it a special-purpose ability that females can use for learning any kind of association in the social domain? Or yet, is it a special-purpose ability that females can only use for learning mate preferences? Making these distinctions is relevant if we wish to know more about the evolutionary history and adaptive value of mate-choice copying. If mate-choice copying is correlated with a general-purpose cognitive system, the hypothesis that it is not adaptive per se could be correct. Mate-choice copying, in this case, could simply be expressed as a by-product of associative learning in general. But if mate-choice copying is correlated with a special-purpose cognitive system, such as social cognition, or even a more specialized and unique adaptation to learning in a sexual context, the hypothesis that this behavior is adaptive per se would be reinforced.

This type of reasoning enters directly in the old but vivid debate about whether associative learning is a general-purpose cognitive mechanism or if it can be specialized (Heyes 2012). Because associative learning is known to be widespread in nature, forming the basis of all animal cognition (Ginsburg and Jablonka 2010), a general ability to learn should be the default condition in all animals. But this system should be able to evolve: if selective pressures in the social and nonsocial domains are different from each other (e.g., mating and territorial interactions with conspecifics seem very different problems than searching for food or escaping from predators), they should favor the evolution of specialized social and nonsocial behavioral solutions, which in turn should favor the evolution of specialized cognitive mechanisms able to produce those adapted behaviors (Varela et al. 2020).

Specialized cognition is well known at the level of input mechanisms. Some of these specializations are in the social domain, and include, for example, specialized sensory structures for nest mate recognition in ants (Ozaki et al. 2005), sex pheromone orientation in moths (Namiki et al. 2014), and alarm-pheromone sensing in fruit flies, zebrafish, and mice (Enjin and Suh 2013). Modularity at the encoding, memory, and retrieval levels is more contentious (e.g., Heyes 2012), although in mice there is evidence of a specialized olfactory subsystem that processes socially transmitted food preferences and seems to include both the input and encoding information processing mechanisms (Munger et al. 2010).

When, in theoretical studies, researchers allocate the copying allele only to some females of the simulated populations, it is implicitly assumed that mate-choice copying does not rely on a general widespread cognitive mechanism, but that it requires specialization. We ignore if this is truly the case, but we know that by studying the underlying cognitive mechanisms of mate-choice copying we will be able to more deeply understand its adaptive value and evolutionary history. This is also relevant for social cognition in general: if we wish to understand the evolution of sociality, we need to be able to see how specialized the mechanisms that control these behaviors are.

15.7 Concluding Remarks

The accumulated empirical evidence since Dugatkin (1992) and Dugatkin and Godin (1992) first observed mate-choice copying in guppies indicates that this is a widespread behavior in animals, from invertebrates to humans. What would be important to know is whether or not the presence of mate-choice copying mirrors the mating system of a species because we have hypothesized that a high incidence of female remating will significantly weaken any selection for mate-choice copying (Santos et al. 2014). Besides, important avenues for future research are: discerning the role of mate-choice copying in promoting migration, hybridization and, eventually, speciation; and knowing whether or not mate-choice copying is a by-product of social learning or, rather, it is a domain-specific adaptation.

Acknowledgments Great thanks to Jaume Bertranpetit and Juli Peretó for inviting us to write this review. MS is supported by research grant CGL2017-89160-P from the Ministerio de Economía, Industria y Competitividad, and research grant 2017SGR 1379 from Generalitat de Catalunya. SAMV is supported by research grant PTDC/BIA-COM/31887/2017 from the Fundação para a Ciência e Tecnologia (FCT).

References

Barkow JH, Tooby J, Cosmides L (eds) (1992) The adapted mind. Oxford University Press, New York

Bradbury JW, Gibson RM (1983) Leks and mate choice. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 109–138

Buss DM (2000) The dangerous passion: why jealousy is as necessary as love and sex. The Free Press, New York

Clutton-Brock T (2009) Sexual selection in females. Anim Behav 77:3–11

Cosmides L, Tooby J, Barkow JH (1992) Introduction: evolutionary psychology and conceptual integration. In: Barkow JH et al (eds) The adapted mind. Oxford University Press, New York, pp 3–15

Danchin E, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. Science 305:487–491

Danchin E, Nöbel S, Pocheville A et al (2018) Cultural flies: conformist social learning in fruitflies predicts long-lasting mate-choice traditions. Science 362:1025–1030

Darwin C (1859) On the origin of species: a facsimile of the, 1st edn. Harvard University Press, Cambridge [1964]

Darwin C (1871) The descent of man, and selection in relation to sex. 2 vols. John Murray, London

Davies AD, Lewis Z, Dougherty LR (2020) A meta-analysis of factors influencing the strength of mate-choice copying in animals. Behav Ecol 31:1279–1290

Dugatkin LA (1992) Sexual selection and imitation: females copy the mate choice of others. Am Nat 139:1384–1389

Dugatkin LA (1996) Interface between culturally based preferences and genetic preferences: female mate choice in Poecilia reticulata. Proc Natl Acad Sci U S A 93:2770–2773

Dugatkin LA, Druen J (2007) Mother-offspring correlation and mate-choice copying behavior in guppies. Ethol Ecol Evol 19:137–144

Dugatkin LA, Godin JGJ (1992) Reversal of female mate choice by copying in the guppy (Poecilia reticulata). Proc Biol Sci 249:179–184

Enjin A, Suh GS-B (2013) Neural mechanisms of alarm pheromone signaling. Mol Cell 35:177–181

Fisher RA (1930) The genetical theory of natural selection. Clarendon Press, Oxford

Ginsburg S, Jablonka E (2010) The evolution of associative learning: a factor in the Cambrian explosion. J Theor Biol 266:11–20

Gouda-Vossos A, Nakagawa S, BJW D (2018) Mate choice copying in humans: a systematic review and meta-analysis. Adap Hum Behav Physiol 4:364–386

Heyes CM (2012) What's social about social learning? J Comp Psychol 126:93–202

Jones BC, DuVal EH (2019) Mechanisms of social influence: a meta-analysis of the effects of social information on female mate choice decisions. Front Ecol Evol 7:390

Kirkpatrick M, Dugatkin LA (1994) Sexual selection and the evolutionary effects of copying mate choice. Behav Ecol Sociobiol 34:443–449

Lande R (1981) Models of speciation by sexual selection on polygenic traits. Proc Natl Acad Sci U S A 78:3721–3725

Lill A (1974) Sexual behavior of the lek-forming white-bearded manakin (*Manacus manacus trinitatis* Hartert). Z Tierpsychol 36:1–36

Mery F, Varela SA, Danchin E et al (2009) Public versus personal information for mate copying in an invertebrate. Curr Biol 19:730–734

Miller GF, Todd PM (1998) Mate choice turns cognitive. Trends Cogn Sci 2:190–198

Munger SD, Leinders-Zufall T, McDougall LM et al (2010) An olfactory subsystem that detects carbon disulfide and mediates food-related social learning. Curr Biol 20:1438–1444

Namiki S, Iwabuchi S, Pansopha Kono P, Kanzaki R (2014) Information flow through neural circuits for pheromone orientation. Nat Commun 5:5919

Nordell SE, Valone TJ (1998) Mate choice copying as public information. Ecol Lett 1:74–76

Ozaki M, Wada-Katsumata A, Fujikawa K et al (2005) Ant nestmate and non-nestmate discrimination by a chemosensory sensillum. Science 309:311–314

Pinker S (2002) The blank slate: the modern denial of human nature. Viking, New York

Pruett-Jones S (1992) Independent versus nonindependent mate choice: do females copy each other? Am Nat 140:1000–1009

Richerson PJ, Boyd R (2005) Not by genes alone: how culture transformed human evolution. University of Chicago Press, Chicago

Rose H, Rose S (eds) (2000) Alas poor Darwin: arguments against evolutionary psychology. Jonathan Cape, London

Rosenthal GG (2017) Mate choice. The evolution of sexual decision making from microbes to humans. Princeton University Press, Princeton

Santos M, Matos M, Varela SA (2014) Negative public information in mate-choice copying helps the spread of a novel trait. Am Nat 184:658–672

Santos M, Sapage M, Matos M et al (2017) Mate-choice copying: a fitness-enhancing behavior that evolves by indirect selection. Evolution 71:1456–1464

Sapage M, Varela SAM, Kokko H (2021) Social learning by mate-choice copying increases dispersal and reduces local adaptation. Funct Ecol 35:705–716.

Slovic P (1995) The construction of preference. Am Psychol 50:364–371

Tooby J, Cosmides L (1992) The psychological foundations of culture. In: Barkow JH et al (eds) The adapted mind. Oxford University Press, New York, pp 19–136

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine Publishing Company, Chicago, pp 136–179

Uehara T, Yokomizo H, Iwasa Y (2005) Mate choice copying as a Bayesian decision making. Am Nat 165:403–410

Varela SAM, Matos M, Schlupp I (2018) The role of mate-choice copying in speciation and hybridization. Biol Rev 93:1304–1322

Varela SAM, Teles MC, Oliveira RF (2020) The correlated evolution of social competence and social cognition. Funct Ecol 34:332–343

Verzijden MN, Ten Cate C, Servedio MR (2012) The impact of learning on sexual selection and speciation. Trends Ecol Evol 27:511–519

Wade MJ, Pruett-Jones SG (1990) Female copying increases the variance in male mating success. Proc Natl Acad Sci U S A 87:5749–5753

Wallace AR (1889) Darwinism: an exposition of the theory of natural selection, with some of its applications. Macmillan and Co, London

Wilkinson GS (1993) Artificial sexual selection alters allometry in the stalk-eyed fly Cyrtodiopsis dalmanni (Diptera: Diopsidae). Genet Res 62:213–222

Zietsch BP, Verweij KJH, Burri AV (2012) Heritability of preferences for multiple cues of mate quality in humans. Evolution 66:1762–1772

Chapter 16
How Past Shapes Future: The Biological Future of Humankind

Jaume Bertranpetit and Juli Peretó

Abstract Ever since Darwin proposed natural selection as the engine of evolution, concern has arisen about the extent to which human culture might be changing the course of our own evolution by allowing individuals who would not otherwise pass on their genes to their offspring to survive and reproduce. What we humans essentially do is change the environment through culture and diminish (but not eliminate) purifying selection. This leads to a genetic equilibrium defined by a new environment in which previously disadvantageous genetic variants are accommodated. Other evolutionary forces have been greatly diminished (positive selection, drift, migration, and introgression) and, instead, hybridization of individuals from populations that had differentiated in ancient times increases. On the other hand, the possibility of modifying our genome opens up the possibility of trying to design our genetic future: it will be possible to make modifications, especially therapeutic ones, to specific individuals, but this will not have a significant impact on humanity as a whole. For better or worse, the genetic future of humanity will be made up of components very similar to those we have now and we will have to rely on technology if we want, as a species, to reach goals beyond our genomic potential.

Keywords Human evolution · Purifying selection · Hardy-Weinberg equilibrium · Genome edition · Transhumanism

---

J. Bertranpetit (✉)
Department of Medicine and Life Sciences (MELIS), Institut de Biologia Evolutiva IBE (Universitat Pompeu Fabra-CSIC), Universitat Pompeu Fabra, Barcelona, Spain
e-mail: jaume.bertranpetit@upf.edu

J. Peretó
Department of Biochemistry and Molecular Biology, Institut de Biologia Integrativa de Sistemes I2SysBio (Universitat de València-CSIC), Universitat de València, Valencia, Spain
e-mail: juli.pereto@uv.es

J. Bertranpetit, J. Peretó (eds.), *Illuminating Human Evolution: 150 Years after Darwin*, Evolutionary Studies, https://doi.org/10.1007/978-981-19-3246-5_16

16.1 Background: If There Has Been a Past, There Will Be a Future

When Charles Darwin published *The Descent of Man* in 1871 he proposed not only that our species is the result of evolution and that, therefore, we are just another species in the natural world, but, more importantly, he applied to us the mechanism of the evolutionary process: natural selection. Thus, the essential fact of the Darwinian proposal was to establish the causal mechanisms that lead to the evolution of species, including humans. This opened the way to two questions that we will deal with. The first is that all species (including humans) have a past that is different from the present and, therefore, that there is a temporal vector that indicates that there will be a future, which may be different from the present. And hence the question: what will humans be like in the future?

The second issue that Darwin's work opened up refers to the mechanism proposed as the basis of evolution: selection, especially natural selection. We will also deal with sexual selection as another evolutionary mechanism (for more details, see Chaps. 14 and 15 in this volume). The key is that we are dealing with a process, evolution, and with mechanisms that can be studied and measured. Knowing the mechanisms will allow us, when speculating about the future, to analyze how evolutionary forces have been modified by human action and, therefore, give the possibility of making predictions from the present based on the strength of the evolutionary forces. The essential point here is to identify and measure these forces and recognize whether humans can change them and, if so, how the evolutionary course that would have occurred if human action had not taken place would be modified.

In this chapter we will analyze the evolutionary mechanisms that have acted in the past, and how human action, in a new way in natural history and through human culture, has produced changes in multiple aspects of our lives and our environment. We will study how these changes have affected the way in which evolutionary mechanisms acted in humans before our cultural uniqueness. We will look at how the factors that influence our ability to evolve have changed both from within the processes themselves and through changing external factors. The acceptance of the cultural fact as defining a new environment will lead us to infer our future both through the changes in the environment and through the changes that we can induce directly on the genome in future generations. The final objective is to be able to speculate about the future with the maximum rigor that the knowledge of evolution and the perspectives of biotechnological changes can give us.

16.2 Knowing the Past to Predict the Future?

Historians and many other scholars insist on a quote, “To build the future, you have to know the past.” To what extent can this apply to the history of life? Can knowing the past help us predict the future? There are different ways to approach the possible answers. One that has got biologists thinking is the following: if we take a starting point from the past, with the organisms that were there, and *replay the tape of life*, what result would we get? The same as we observe now or something very different? Is the outcome of the evolutionary process predictable given an initial state? Gould (1989) proposed this question based on the enormous diversity of fossil life preserved in the *Burgess Shale*, a famous paleontological site in Canada, some 540 million years old, at the beginning of the Cambrian period. Gould proposes that chance and contingency (i.e., nondeterministic factors) would be at the basis of the production and diversification of life. Evolution would be a process of historical contingency, strongly sensitive to small unpredictable processes of initial change. That is to say, if we were to set the “tape of life” in motion repeatedly, we would obtain very different results each time and, above all, there would be a total unpredictability of the results of each of the trials.

This purely appreciative view is still under debate (Reiskind et al. 2021) and, fortunately, we can subject it to experimental contrast (Orgogozo 2015; Blount et al. 2018). Several studies of evolution in the laboratory, especially in bacteria, show that the responses in the various replicates of experiments are very often similar and that, if the initial divergence is larger, the similarities are smaller. There would therefore be, despite the unpredictability at the most basic level of evolutionary processes at the genomic scale, a certain degree of predictability at higher scales. It should be borne in mind that the same phenotypic solution can be based on different genotypic combinations. We can “push” a population of the bacterium *Escherichia coli* to use a certain carbon source, even CO_2, making it switch from its heterotrophic idiosyncrasy to an autotrophic lifestyle. In different experiments, with the right conditions, we always arrive at the same metabolic solution (the transition from heterotrophic to autotrophic), but the combination of mutations behind each of the evolutionary trajectories is different (Gleizer et al. 2019).

At present we cannot admit an evolutionary predictability, although we know that the diversification between species (or that which would occur in different experiments of re-running the tape of life) does not explore the whole space of possible forms, but only a small part of it (Fig. 16.1). For fundamental reasons of matter, and based on the biochemistry of terrestrial life, there are many possible biological constitutions that will never occur naturally due to the existence of intrinsic constrictions. This does not mean that we cannot explore, through synthetic biology, the space of the possible, artificially constructed (Peretó 2021). In cell and developmental biology there are also many sets of unexplored forms and others that, once explored, are highly efficient and there will be a great diversification from them.

We do not have laws of evolution that allow us to predict what the forms of living beings of the future will be like. There have been attempts to look for laws in the

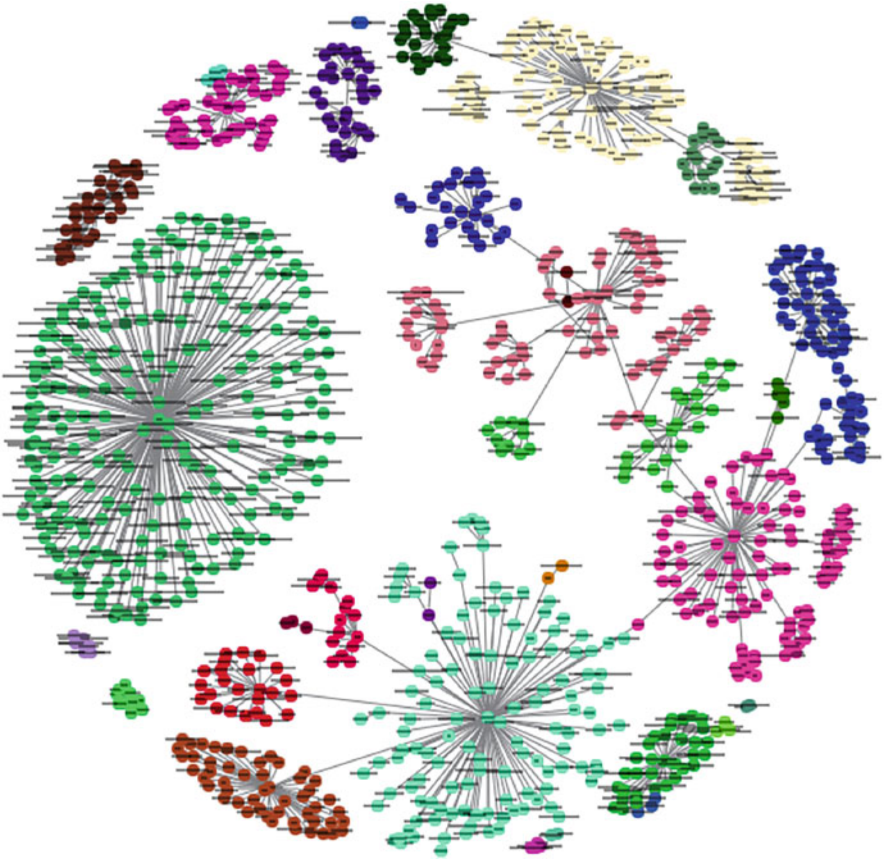

Fig. 16.1 In a multidimensional space of morphologies (here drawn only in two dimensions) not all space is or can be occupied. Evolution intensively explores small parts of space from variations on innovations that are at the basis of adaptive radiations

evolution of the genome (Koonin 2011), with little explanatory power, which do not take into account natural selection and cannot be related to specific phenotypes. It is true that, given that the space of possible morphologies is relatively restricted, the surprising phenomenon of morphological convergence occurs. All this leads us to admit that, at present, we have no tools or data to predict evolution (Reiskind et al. 2021). What we can do, however, is to try to understand the effects that human modifications—in frequency and intensity—of evolutionary mechanisms may have on future evolution. We are not, therefore, trying to predict evolution.

To understand the mechanisms of evolution we must observe living beings at their internal, molecular base, the DNA that constitutes the genome. We can model and understand the changes in genomes from their description, from the study of their diversity and the mechanisms of change: this is the field called population genetics. Note that describing evolution (through fossils, for example) does not imply knowing the underlying mechanisms. The study of the molecular mechanisms of evolution, however, leaves us an important point to close: how the genotype (or the whole genome) informs the phenotype, especially when we study the phenotype as morphology. Genetics and genomics have come a long way in recent years, but they are still far from explaining external phenotypes, such as the shape of living beings, which are fundamental in adaptation and evolution and which is what we know directly from looking at fossils in ancient species.

16.3 The Mechanisms of Evolution

Since the formalization of population genetics in the early twentieth century, the starting point has been a view of evolution based on the dynamics of allele (gene variants) frequencies over time. The formalization is simple and proposes the conditions under which genetic diversity (and, therefore, the frequencies of variants) will not vary over time. It is what is called Hardy-Weinberg law or equilibrium, which sets the conditions of non-change. Therefore, the genetic change between generations will be nothing but the alteration of this equilibrium. If a population is large, with random mating, and all individuals survive and reproduce the same (i.e., there is no natural selection), the frequencies of genetic variants do not change and it is a matter of analyzing the possible exceptions to this equilibrium as they will be the drivers of evolution (Fig. 16.2).

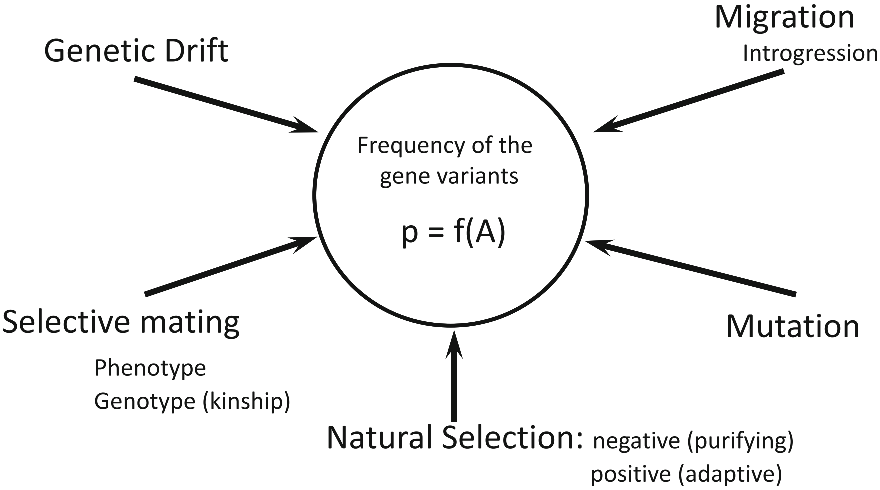

Fig. 16.2 Mechanisms that can produce changes in gene frequencies over generations. In fact, these mechanisms, which break the Hardy-Weinberg equilibrium, are the mechanisms of evolution

These factors are of very different importance from one another and include the production of new genetic variants (mutation), the mixing of individuals from distinct populations (migration and introgression), the effects of chance on reproduction in small populations, mating that is not random but gene-dependent, and, as a central point, natural selection. We will quickly discuss each of these to see if these factors may change in the future and thus help to understand the changes that may occur in the action of these mechanisms.

It has sometimes been questioned whether the analysis of gene frequencies was sufficient to understand evolution and there has been argued that this only explains small changes in the process, sometimes called microevolution. Beyond it, there would be an evolution of large organizational schemes or macroevolution that would work separately or differently. The separation between the two concepts does not exist and we know well that all evolutionary change begins within a simple system, which can have a very variable phenotypic effect: from not involving any change at all to being part of a new plan of organization of the species. Normally after extensive changes (which we see by the formation of large groups of organisms, for example) diversification is produced again by evolutionary radiations that have in common having enjoyed the adaptations of the new organizational plan.

16.3.1 The Mutation

When a cell divides it gives rise to two daughter cells and in the process of genome replication errors may have occurred that cause the genome of the two cells to be different. We must differentiate the somatic mutation, in the cells that constitute our organism, from the germ mutation, which will affect the reproductive cells (eggs and sperm) and, therefore, the changes will be passed on to the next generation. The first one matter for the individual and we can see their effects in aging and cancer. The latter occurs when the mutation deregulates the well-orchestrated processes of cell division and growth of the cells in an organism.

Mutations can affect a single nucleotide or have much more widespread effects. Recent studies have given us estimates of the simple changes that occur in our DNA: the mutation frequency is on the order of 10^{-8}, a very low value, but given the enormous size of the genome (3×10^9 nucleotides), it means that each of our two parents put on the order of 30 new mutations in their egg or sperm. What is important to consider is that all the diversity of life on Earth has initially been produced by a single mutation phenomenon. Later, evolutionary factors will decide its fate.

External factors, such as radiation or certain chemicals, increase the frequency of mutation and we can think what effects have had some well-known cases of high doses, for example the people who were near the Chernobyl nuclear power plant after the explosion. There have been many studies of the consequences on human health, agriculture, and its biological effects ranging from the DNA level to entire ecosystems (Orizaola 2020; Chernobyl Forum 2006). It is clear that radiation produced (and continues to produce) a significant amount of somatic mutations and the increase in cancer cases is a direct effect. However, the consequences on germline mutations have been much smaller than expected, especially because many germ cell mutations have not succeeded due to the lack of viability of gametes or early stage embryos (Yeager et al. 2021). On the other hand, it has also been suggested that radiation-induced increases in genetic diversity facilitate the selection of forms adapted to persistent radiation (Orizaola 2020).

Mutation always occurs randomly and anthropogenic action may cause a slight increase in rates, with no predictable outcome. Therefore, when thinking about the genetic future of humanity we must deduce that there will be little impact due to the increase of mutation rates. We should not expect new sources of genetic innovation from increased mutation.

16.3.2 Genetic Drift

When the number of individuals in a population or species is very small, there is a change in gene frequencies between successive generations simply due to the random choice of different variants of a gene. It is like flipping a coin a small number of times that can give proportions far from the expected 50%. The drift can result in the fixation of one of the variants and the loss of the others (like getting all heads or all tails when flipping a coin).

It is evident that this mechanism has a much lesser importance in the present and, foreseeably, in the future humanity. There are no longer very small and isolated populations, there is no more founder population effect (few individuals founding a population that grows a lot, as must have been the case in the "*Out of Africa*" model in our evolution) or population bottlenecks, with strong temporary reductions in the size of populations.

Drift, although it has been a very important factor in human evolution for long periods of our history, is not expected to have an impact in the future.

16.3.3 Migration

In a general process of diversification of a species, differences increase among populations when there is, between them, a barrier to interbreeding, often geographical, which makes the differences between the populations increase over time, mainly by drift in small populations. When individuals from another origin arrive in a population, if there are genetic differences between them, the gene frequencies of the receiving population will be altered. The history of mankind is full of cases of migrations with genetic consequences and the case of the formation of the current American population is paradigmatic, with Amerindians, Europeans, and Africans in significant numbers depending on the place.

In human evolution there have also been cases of migrations and mixing between groups already strongly differentiated and in this case we speak of introgression. Interesting cases are the introgressions of Neanderthals, Denisovans and, perhaps, of a third group in the populations of modern humans that, having left Africa, expands across Eurasia (Mondal et al. 2019). All of these cases may have had an impact on our evolution. It is impossible, however, that similar events could happen in the future.

However, we see a large increase in mobility, an increase in admixture between individuals coming from distinct populations, and thus a dilution of the differences between populations. The differences between current human populations are, in general, small and admixture between individuals from different places does not and will not give major genetic changes (as in the case of heterosis by admixture of differentiated breeds of cattle) and the only expected effect is a decrease, much slower than it might seem, in the differences between humans across the earth, ironing out the differences that the separate evolution of populations had produced until recent times.

16.3.4 Selective Mating

In reproductive mate choice, theoretical models assume that it occurs randomly. The reality, however, is that there is clearly a choice of mates and that this choice has genetic implications as it can be produced by the choice of phenotypes that have a genetic basis (as in selective mating by height or skin color) or by direct choice by the genes themselves, when the choice is made based directly on the degree of relatedness (preferences that can be positive or negative, depending on cultural traditions).

Selective mating can be very important in some cases and that is what led Darwin to devote a good part of his book on human evolution to sexual selection. This evolutionary mechanism may have been very important in the formation of characters that have been selected by the opposite sex and the example of peacock plumage remains paradigmatic. Unfortunately, little is still known on its importance in human evolution or whether it is acting nowadays. Its impact, in any case, is likely to be very small.

16.3.5 Natural Selection

Today it is fully accepted that natural selection is an evolutionary engine that operates through heritable differences in the chances of individuals to survive and leave offspring. Moreover, it is considered to be one of the explanatory factors for the magnificence of the adaptations that exist in nature, which make us ask, all too often when we observe any structure, organ or characteristic of living beings, what is it for? When we ask this question we presuppose that there has been an action of natural selection in the evolution towards a particular structure, form, or function. But this thought can become toxic: not every detail has to be explained by natural selection, nor every specific character has to have a role in the survival and fertility of individuals. From the action of a particular gene, which usually has implications for different traits, to the large number of genes that influence most complex traits, everything shows us that there is a complexity of interactions that makes partial and particular causalities inadequate to provide explanations for every detail of life.

But it is clear that there is a natural selection that we can see in different ways. First, negative or purifying selection that eliminates the genetic variants that cause a phenotype that is deleterious, that is to say, that it has a low probability of being passed on to offspring because it gives low fertility or, more often, low viability. This is the case of genetic variants that produce diseases. Secondly, we have positive or adaptive selection, in which a genetic variant gives a phenotype that is better adapted than the ancestral one and, therefore, the individuals that carry it will have increased fertility or viability. In both cases, and this is a fundamental concept, the effects of genetic variants pass through the sieve of a specific environment: we must remember that selection acts on phenotypes, but its effects must be inscribed in the genes and, very often, the phenotype-genotype relationships, as we have already mentioned, are complex and poorly understood.

In Darwin's time, some of his followers, starting with his cousin Francis Galton, already realized that human action could influence natural selection. Today, if we ask ourselves how humans have been able to change the selective factors that act on us, we must analyze the consequences of the exceptional modifications in our environment we have produced, continue to produce, or are planning to produce. We will encompass them under a generic term: human culture as an agent modifying the environment and, consequently, as a factor altering the probabilities of survival and reproduction.

16.4 The Biological Effects of Human Culture

We will not go into the exciting issue of what human culture is, what the degree of specificity is, whether other species have a culture, or whether so-called cumulative culture (Mesoudi and Thornton 2018) is a defining feature of strictly human culture. The view that interests us here focuses on the impact of culture on natural selection: by influencing the environment, human culture makes survival and reproduction—better adaptation—more attainable in a way that is more independent of what individuals, and thus their genes, are like. It is also worth asking about the possible negative impact of environmental changes produced by humans, such as pollution or global warming; in these cases, the far-reaching impact is on health or the economy, but not on the evolutionary forces acting on humans. We must promote technological and lifestyle changes that reverse these phenomena that have a strong impact on the quality of life of many humans, regardless of their limited evolutionary impact.

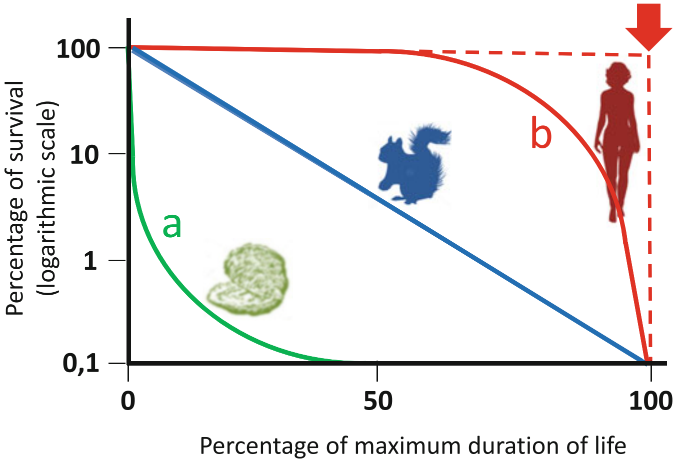

Fig. 16.3 Proportion of individuals remaining alive over time, showing different patterns of mortality, either very high at the beginning of life or at the end. Drawing by Juli Peretó

Modifying the environment to achieve better adaptation is not a human innovation: it is widespread in the animal world. In fact, how could we consider that the construction of dams by beavers is not a very genuine case of adaptation through behavior that leads them to build dams that allow them to obtain food? To go over these cases would take us a long, interesting way. But what concerns us here is the case of humans, in which the cultural fact has had a direct impact since ancient times on the possibilities of survival and reproduction. Imagine the impact that the domestication of fire, a source of heat and light, of protection from predators, with the possibility of making better weapons and cooking food, must have had. So many advantages for a cultural change! And, in fact, cultural development can be read as an increase in independence in relation to environmental factors that could exert their force as selective elements.

Culture has produced a "democratization" of genes: many variants that could have been deleterious are no longer deleterious and others that could have been the basis for new adaptations will not flourish. Many more genetic variants are "normal" and all this thanks to the change in environmental conditions, with the expansion of the environment into a space where many variants have ceased to have deleterious effects.

From a demographic (or ecological) point of view the action of cultural changes can be easily seen. There are species that have the *r* strategy (Fig. 16.3, III) in which they reproduce a lot and a good part of the offspring die in the early stages of life; others have the *K* strategy (Fig. 16.3, I), in which they have few offspring, in which a lot is invested in each of them and many survive to ages close to the maximum lifespan. Humans, like most mammals, follow the latter strategy. What we humans have done, however, has been to extraordinarily increase survival, getting close to maintaining a high proportion of individuals to ages close to the maximum lifespan. In this case what is implied is a meager action of purifying selection.

And with respect to fertility, there is also a strong cultural modification: present humans have very few children and above all the number is very similar between individuals. We would say that the average number of children has gone down, but the variance, a parameter that gives us the possibilities of the action of natural selection, has gone down even more.

These changes have made the genes we carry less important because we have made a change in the environment that has meant that phenotypes that would be maladapted in another environment (that would perhaps produce a disease) become neutral. It is not that we make individuals with negative alterations in their genes reproduce: we make the alterations in the genes to give a phenotype that we cannot consider negative, but "normal." And this kind of change is not simply a recent phenomenon, as in the last century, but we know that it has been with humans since ancient cultural changes, such as the one that must have occurred with food production (agriculture and livestock) about 10,000 years ago.

This vision wants to break with the simplistic idea that if we allow people with functional diversity (formerly called morons) to live and reproduce, their frequency will increase. If they can survive and reproduce there will be no purifying selection and the frequency of genetic variants will be constant in the population. Only in some rare case in which the mutation frequency is particularly high will there be a slight temporary increase, until a new equilibrium of production by mutation and loss by selection is reached. But, as we will see later, purifying selection continues and will continue to act in humans in cases where the defect that produces the genetic variant is really severe; this concept of "severe" is culturally changing and will continue to change over time.

In the nineteenth century, concern about the genetic future of humanity preoccupied a group of academics who gathered around Francis Galton and the new discipline he coined: eugenics. If culturally we had modified the action of natural selection and it had undesirable consequences, we had to highlight it and, above all, correct it. And if we had in our hands a way to improve, we had to apply it. This led, on the one hand, to positive eugenics, which aimed to encourage reproduction among genetically favored people and, on the other, to negative eugenics, preventing or hindering that of the "worst" through sterilization or segregation of those who were considered physically, mentally, or morally "undesirable." In fact, most Western countries enacted eugenic laws—the first in 1907 in Indiana, USA, in force until 1974—which, in many cases, led to the forced sterilization of thousands of people. The last eugenic law was repealed in Sweden in 1976 (Fig. 16.4).

One of the great problems of eugenics was to define objectively what were the positive and negative traits and, above all, to demonstrate that these had a relevant and simple genetic basis, as Galton had imagined. Eugenics enjoyed the support of many scientists and, until it was embraced by the Nazi regime in the 1930s, was considered a socially progressive science. The identification of eugenics and racism, and the political use of these genetic ideas to justify genocides, makes it difficult to discuss without prejudice an ideology that, dressed in an academic guise, has

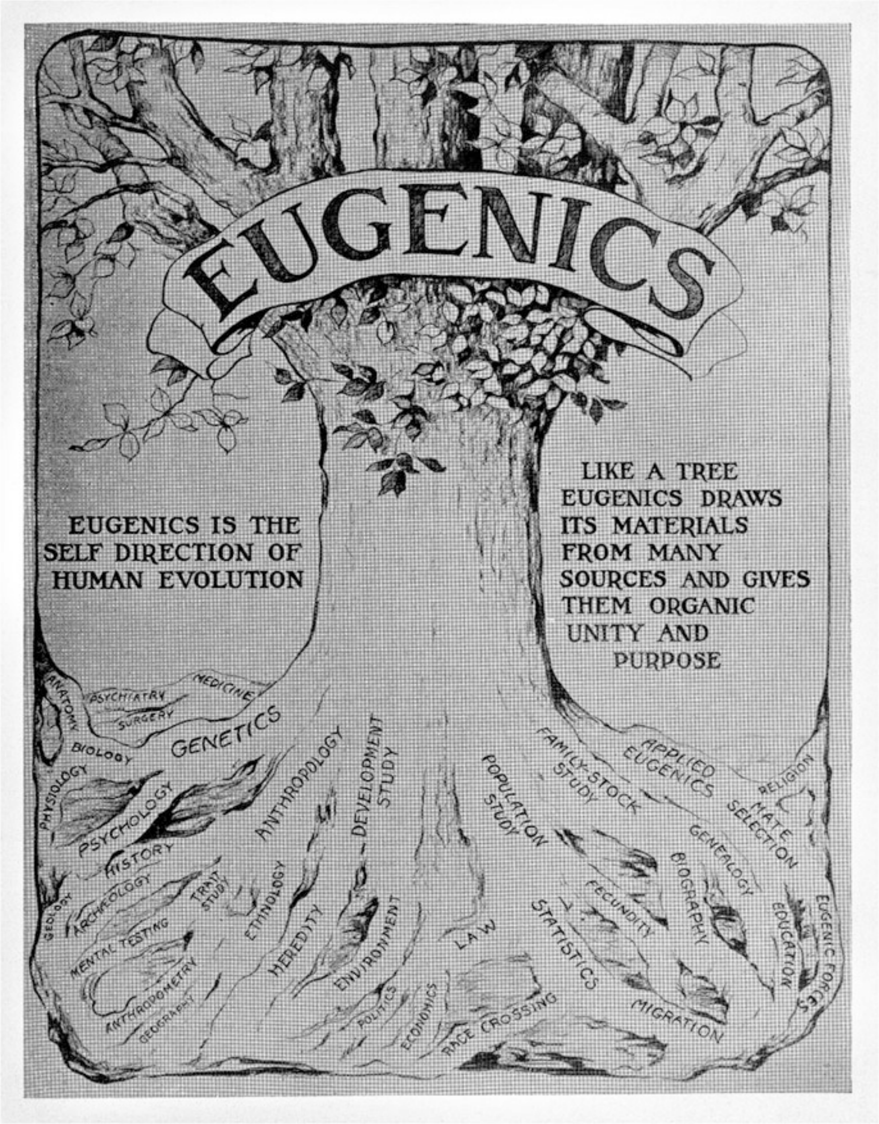

Fig. 16.4 "Eugenics is the self-direction of human evolution." Motto of the Third International Eugenics Congress, 1932, represented as a tree unifying a diversity of different fields. (Source: https://commons.wikimedia.org/wiki/File:A_decade_of_progress_in_Eugenics._Scientifi_Wellcome_L0032341.jpg)

reached our days and has damaged the progress of disciplines such as human population genetics (Saini 2019).

Concern about the genetic future of humanity is still valid today, in the age of genomics, and we must objectively ask what role natural selection really has today, whether there really is a genetic deterioration of humanity and what role genetic modification technologies may have in the future.

16.5 Natural Selection Today

Human culture has indeed had an effect on the action of natural selection. If we want to recognize whether it is still at work, we need to look for evidence. The action of natural selection can be detected, in a very precise way, in the genomes of individuals (in the case of mutations that prevent life, for example) or in populations (in the case of positive selection).

16.5.1 Purifying Selection

It is as clear and evident that purifying selection has ceased to act in some cases as it still acts in others. In the first case we find ourselves with Mendelian genetic diseases, most of them recessive (they need two copies of the altered gene to see it reflected in the phenotype) that before the current care or prevention were fatal for individuals, who can now survive and make a reasonable life. In these cases, what happens is that the variants that produced a reduced biological efficacy due to loss of viability now have normal viability. So there will be a slight increase until a new equilibrium given by the mutation frequency. One of the paradigmatic cases is that of phenylketonuria, with a frequency of about 1 in 10,000 births in Europe: those affected do not synthesize the amino acid tyrosine from phenylalanine, the accumulation of which has serious effects, with intellectual disability, seizures, behavioral problems, and mental disorders. Since newborns are tested for the defect, the solution for the positives is relatively simple and very effective: control the phenylalanine content of the diet. What matters to us here is to realize that we change the environment to make these individuals well adapted and the gene variant becomes neutral. It is no longer a “pathological” variant and this is the situation we must assume.

There are many genetic variants that produce very serious effects and in these cases purifying selection still exists. There is much evidence of the large number of miscarriages in the early stages of development, and this fact is now quite well known thanks to studies associated with assisted reproduction. For example, in a study of more than 20,000 oocytes (Kuliev et al. 2011) it was shown that the frequency of chromosomal abnormalities comprised more than half, preventing their viability. This phenomenon is very general in the very early stages of pregnancy and is a clear sign of the strict screening of purifying selection that acts, in a very efficient way, in the early stages of development.

16.5.2 Positive Selection

We now know how to detect very accurately the action of positive or adaptive selection in genomes (Bosch's chapter in this volume), especially in remote epochs, tens of thousands of years old. The question is whether we can detect the effects at recent dates. We can detect selection associated with the changes represented by the Neolithic and especially by animal husbandry (and zoonotic diseases) in the last 10,000 years. Some of these changes are very interesting, as they represent biological adaptations to changes introduced by culture. A notable case is the adaptation to the ingestion of milk in the adult, metabolizing lactose, a genetic change that in Europe occurred in the north and its frequency increased considerably about 6000 years ago (Ségurel and Bon 2017) due to the advantage that gave the nutritional utilization of milk to carriers of the genetic variant of persistence in the production of the lactase enzyme, responsible for metabolizing lactose and that normally stops being produced after lactation.

There have been many attempts to detect more recent selection (in the last 1000 to 2000 years) and several research groups are developing new tools to do so (Field et al. 2016; Speidel et al. 2019) or attempting to detect selection in ancient genomes. The results are not clear and it is very likely that the signal left in genomes by positive selection is not detectable. When signals from several genes informing the same complex trait have been put together, as in the case of stature, it seems clear that it has recently undergone selection. But there is a serious problem in its interpretation: what selective forces may underlie it? And only one viable explanation emerges, that of sexual selection as an explanation of the most recent changes that may have existed and which in their dynamics resemble that of positive selection. So, while some positive selection may exist today, its importance must be very small.

16.5.3 Sexual Selection in Humans

Darwin already postulated that characters that increase individual reproductive success can evolve, even if they entail a cost in terms of survival. He distinguished two forms of sexual selection: competition or struggle between males for access to females, or intrasexual selection, and male choice by females, or intersexual selection (Martín-Vivaldi and Cabrero 2002; Moreno 2013; Chaps. 14 and 15 of this volume).

It is perhaps one of the most controversial and open issues in the study of human evolution. On the one hand, there has been a great expansion in the field of evolutionary psychology, raising the many aspects that involve attempts to attract members of the other sex and how these preferences may have modulated, by sexual selection, our phenotypes (Puts 2010). Mate choice (especially by women) can be read as a selection (guided by unknown mechanisms) of the phenotypes, and thus of genes that are chosen to be integrated in the next generation. On the other hand, sexual selection by competition between males may explain why in our species males are more muscular and taller than females, and much speculation can be made on the associated psychological and social traits, which may have genetic bases, although they are often difficult to recognize.

Thus, although sexual selection probably also occurs in humans—and one can speculate on how our conception of beauty and attractiveness is related to a good genetic endowment and, therefore, has a biological basis—it is a field too open to speculation that, so far, has not achieved clear results.

16.6 Action of Genome Editing and Transhumanism

Throughout the twentieth century, biology has studied the molecular intimacies of life, opening the door to the modification of genomes to help understand them. Genome editing techniques have progressed and, in recent years, thanks to CRISPR technologies, can be applied in an efficient and multiple way (see review by Expòsit-Goy et al. 2020). These technologies are still in their infancy and successes are expected in animal and plant breeding and human therapy. It is very premature to consider germline modification in humans and, in fact, there is a worldwide ban, which does not prevent unethical and questionable edits from being made somewhere.

In any case, all this only translates into a few changes in the genome of some individuals. But we are far from thinking, as is often said, of modifying our species: the dream of directing our evolution does not take into account the large number of individuals of the species and, let us remember, we are still far from being able to influence complex traits, such as intelligence.

There is a lot of talk of transhumanism, a utopian evolution beyond the physical and mental limitations of current humans through technoscience (Diéguez 2017). The pretensions of transhumanism may be laudable, although, clearly, we should expect that many of "our" improvements will take place outside our body, not as "organic evolution" but as technologies that will help us in many of our abilities, both the current ones and the new ones that technoscience will invent. It is more fruitful to think on the limits of artificial intelligence than on whether evolved human brains will accommodate a hypothetical higher intelligence. This is independent of the improvement in prostheses and other technological developments, far, however, from transhumanist dreams. We are facing cultural changes (specifically technological) that pose interesting and urgent ethical challenges, but that do not envisage biological challenges in the short or medium term.

16.7 What, Then, Is the Genetic and Evolutionary Future of Humankind?

From what we have just presented we can conclude that most of the evolutionary factors operating in our past have now a lower intensity and that the genomes, with the current diversity, are in equilibrium or very close to it. It is to be expected that only a greater mobility of populations can have a certain evolutionary impact by increasing the mix of genomes that had diverged in the past. Culture, including science and technology, has produced remarkable changes in our environment that have softened the action of natural selection on human populations. The concept of adaptation must be broadened to encompass also an anthropogenic environment with health action and medicine, as well as the diversity of technologies that help us throughout our lives. We agree that modifications (edits) of genomes are very promising at the individual level but will not bring about any general evolutionary change in the species. The genetic and evolutionary future of humanity will be built on genomes that will diverge little from today's genomes: we cannot imagine that genome editing can be decoupled from our evolutionary history. However, the changes that humanity will undergo will not be reflected in its genomes but, at best, in the impact of technologies on the well-being of the species. We have to think that humans biologically like the current ones will have to direct the future development of humanity. A development that will end, like all species on the planet, with extinction. This is the only prediction of which we are absolutely sure.

References

Blount ZD, Lenski RE, Losos JB (2018) Contingency and determinism in evolution: replaying life's tape. Science 362(6415):eaam5979

Chernobyl Forum (2006) Chernobyl: the true scale of the accident. World Health Organization. https://www.who.int/news/item/05-09-2005-chernobyl-the-true-scale-of-the-accident

Darwin C (1871) The descent of man, and selection in relation to sex, 1st edn. John Murray, London

Diéguez A (2017) Transhumanismo: La búsqueda tecnológica del mejoramiento humano. Herder, Barcelona

Expòsit-Goy M, Bartrons R, Bertranpetit J (2020) Genome-editing technologies and their impact. A report by the biological sciences section of the Institute of Catalan Studies. https://publicacions.iec.cat/repository/pdf/00000301/00000024.pdf

Field Y, Boyle EA, Telis N et al (2016) Detection of human adaptation during the past 2000 years. Science 354(6313):760–764

Gleizer S, Ben-Nissan R, Bar-On YM et al (2019) Conversion of Escherichia coli to generate all biomass carbon from CO_2. Cell 179(6):1255–1263

Gould SJ (1989) Wonderful life. The Burgess shale and the nature of history. W W Norton & Co, New York

Koonin EV (2011) Are there laws of genome evolution? PLoS Comput Biol 7(8):e1002173

Kuliev A, Zlatopolsky Z, Kirillova I et al (2011) Meiosis errors in over 20,000 oocytes studied in the practice of preimplantation aneuploidy testing. Reprod Biomed Online 22(1):2–8

Martín-Vivaldi M, Cabrero J (2002) Selección sexual. In: Soler M (ed) Evolución. La base de la Biología. Proyecto Sur de Ediciones, Granada, pp 235–260. https://dialnet.unirioja.es/servlet/libro?codigo=5127

Mesoudi A, Thornton A (2018) What is cumulative cultural evolution? Proc Biol Sci 285(1880): 20180712

Mondal M, Bertranpetit J, Lao O (2019) Approximate Bayesian computation with deep learning supports a third archaic introgression in Asia and Oceania. Nat Commun 10(1):246

Moreno J (2013) Evolución por selección sexual según Darwin. La vigencia de una idea. Ed Síntesis, Madrid

Orgogozo V (2015) Replaying the tape of life in the twenty-first century. Interface Focus 5(6): 20150057

Orizaola G (2020) From nuclear desert to evolutionary lab: the response of living organisms to Chernobyl's ionising radiation. Metode Sci Stud J 10:193–199

Peretó J (2021) Transmetabolism: the non-conformist approach to biotechnology. Microb Biotechnol 14(1):41–44

Puts DA (2010) Beauty and the beast: mechanisms of sexual selection in humans. Evol Hum Behav 31:157–175

Reiskind MOB, Moody ML, Bolnick DI et al (2021) Nothing in evolution makes sense except in the light of biology. Bioscience 71(4):370–382. https://doi.org/10.1093/biosci/biaa17p

Saini A (2019) Superior. The return of race science. 4th Estate, London

Ségurel L, Bon C (2017) On the evolution of lactase persistence in humans. Annu Rev Genomics Hum Genet 18:297–319

Speidel L, Forest M, Shi S et al (2019) A method for genome-wide genealogy estimation for thousands of samples. Nat Genet 51(9):1321–1329

Yeager M, Machiela MJ, Kothiyal P et al (2021) Lack of transgenerational effects of ionizing radiation exposure from the Chernobyl accident. Science 372:725–729