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Darwin and sexual selection: one hundred years of misunderstanding

Darwin et la sélection sexuelle : cent ans d'incompréhension

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ABSTRACT

Darwin's book on the *Descent of Man and Selection in Relation to Sex* (1871) is often viewed as the continuation of *The Origin of Species* published 12 years earlier (1859), both because of the implicit parallelism between natural selection and sexual selection, and because Darwin himself presents the book as developing a subject (man) which he intentionally omitted in the *Origin*. But the *Descent* can also be viewed as the continuation of his book on *Variation* published three years earlier (1868). Firstly because Darwin's hypothesis of pangenesis links the selection process to the origin of variation through use and disuse, an idea underlying his speculations on the origin of moral sense in humans. Second because like the action of the horticulturist on his domestic crops, sexual selection exerted by one sex on the other sex can develop fancy traits that are not easily accounted for by their utility to the selected organism itself, such as artistic taste, pride, courage, and the morphological differences between human populations. These traits are difficult to reconcile with pangenesis. They add up to other contradictions of the book possibly resulting from Darwin's erroneous inference about the mechanism of inheritance, like those on the determination of sex-ratio, or the confusion between individual adaptation and the advantage to the species. These inconsistencies inaugurate a weakening of the Darwinian message, which will last 50 years after his death. They contributed to the neglect of sexual selection for a century. Darwin however maintained a logical distinction between evolutionary mechanisms and hereditary mechanisms, and an epistemological distinction between evolutionary theory and Pangenesis hypothesis. In the modern context of Mendelian genetics, Darwin's sexual selection retrospectively appears as luminous an idea in its pure principle as natural selection, even though the mechanisms governing the evolution of sexual choice in animals remain largely unresolved.

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R É S U M É

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Le livre de Darwin sur *La filiation de l'homme et la sélection relative au sexe* (1871) est souvent vu comme la suite de *l'Origine des espèces* publié 12 ans auparavant (1859), du fait du parallélisme implicite entre sélection naturelle et sélection sexuelle, et parce que Darwin présente lui-même le livre comme développant un sujet (l'homme) qu'il avait préféré omettre dans *l'Origine*. Mais la *Filiation* peut être vue aussi comme la suite de son livre sur la *Variation* publié trois ans auparavant (1868). D'abord parce que l'hypothèse darwinienne de la pangénèse lie le processus sélectif à l'origine de la variation par la loi de l'usage et du non-usage, une idée sous-jacente à ses spéculations sur l'origine du sens moral chez l'homme. Ensuite parce qu'à l'image de l'action de l'horticulteur sur ses espèces cultivées, la sélection sexuelle exercée par un sexe sur l'autre a pu développer des traits de

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fantaisie en ce qu'ils ne s'expliquent pas par un critère d'utilité pour l'organisme sélectionné, comme le goût artistique, la fierté, le courage, et les différences morphologiques entre populations humaines. Ces traits sont difficiles à concilier avec la pangénèse, ajoutant à d'autres contradictions du livre résultant sans doute des inférences erronées de Darwin sur le mécanisme de l'hérédité, comme ceux sur le déterminisme du sex-ratio, ou la confusion entre adaptation individuelle et avantage de l'espèce. Ces incohérences inaugurent un affaiblissement du message darwinien qui durera 50 ans après sa mort. Ils contribueront à l'effacement de la sélection sexuelle pendant un siècle. Darwin maintient cependant la distinction logique entre mécanismes évolutifs et mécanismes de l'hérédité, et une distinction épistémologique entre théorie évolutive et hypothèse de la pangénèse. Dans le contexte moderne de la génétique mendélienne, la sélection sexuelle de Darwin apparaît rétrospectivement comme une idée lumineuse dans son pur principe, même si les mécanismes gouvernant l'évolution du choix sexuel chez les animaux restent largement non-résolus.

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1. On the origin of the Descent

In introducing his *Descent of Man and Selection in Relation to Sex* (1871) [1], Darwin apologizes for his late contribution to the subject, as many other naturalists had developed the matter since he published his *Origin of Species by Means of Natural Selection* [2] in 1859 (Table 1). He also apologizes for writing on a single species, as though evolutionary mechanisms were not universal. Finally, he also admits that he deliberately avoided referring to man in his *Origin*: “I thought that I should thus only add to the prejudices against my view”, pretending to ignore that most of his readers have read it as though the whole book were a demonstration of the descent of man from the apes. However, it would be erroneous to believe that nothing new was left to Darwin to write on man. His book is truly original. For instance, Huxley's book [3] was a presentation of pure facts showing that the chimpanzee and the gorilla are closer to humans than are any other species. It is famous for its illustrations presenting series of skulls, hands and feet, placed side by side to allow readers to determine for themselves which species is closer to which. It contains the oft-imitated figure presenting the complete skeletons a gibbon, an orang-outang, a chimpanzee, and a gorilla standing in queue with dangling arms following the skeleton of a man facing the same direction. Similarly, what has survived of Haeckel's *Natural History of Creation* is a genealogical tree stemming from the primeval “monere” to races of man, with lateral branchings leading to the other organisms: a tree loaded with meanings, quite the opposite of Huxley's devotion to pure facts.

The difference between Darwin's book and the former two is a matter of mechanisms. Already, the *Origin* was nowhere devoted to comparing species according to their homologous parts (as in Huxley) or in trying to visualize the tree of life (as in Haeckel). The *Origin* was actually not interested in the origin of life. Its sole illustration showed the simplest of all diagrams: a schematic tree so designed as to link intraspecific variation to interspecific divergence (the basis of natural selection), and which could represent any organic form. Like the *Origin*, Darwin's *Descent* is based on mechanisms. This is why it has survived. Huxley's and Haeckel's books are known nowadays mostly by historians, while Darwin's book is still inspiring for contemporary research, as some ideas in it can be experimentally tested. It involves two mechanisms. The first is Darwin's pangenesis hypothesis, now known to be wrong, but which was the conclusion of his book on the *Variation in Plants and Animals under Domestication* [4], published three years earlier (1868). The second is sexual selection, a mechanism which he already had in mind in his sketch of 1844, but which he had never developed extensively since. Mechanisms matter in evolutionary theory, since different mechanisms can lead to different outcomes (Fig. 1). But here we meet a controversial point: should we conclude that, for Darwin, humans deserve a special law of evolution? In his introduction, he comments:

“I have been led to put together my notes, so as to see how far the general conclusions arrived at in my former works were applicable to man. This seemed all the more

Table 1

Works cited by Darwin, as having preceded his *Descent of Man* in concluding that “man is the co-descendant with other species, of some ancient, lower and extinct form”.

J.B. Lamarck (1809)	<i>His main book on the subject is Zoological Philosophy</i>
C. Lyell (1863)	<i>The Geological Evidence of the Antiquity of Man</i>
T.H. Huxley (1863)	<i>Man's Place in Nature</i>
A.R. Wallace (1864)	<i>The Origin of Human Races deduced from the Theory of Natural Selection</i> (Anthropological review: published in: <i>Contributions to the Theory of Natural Selection</i> 1870)
K. Vogt (1864)	<i>Lectures on Man</i> (English translation)
J. Lubbock (1865)	<i>Prehistoric Times</i> (2d edition 1869)
F. Rolle (1865)	<i>Man in the Light of Darwinian Teaching</i>
E. Haeckel (1866)	<i>General Morphology</i>
L. Büchner (1868)	<i>Conferences on Darwinian theory</i>
E. Haeckel (1868)	<i>Natural History of Creation</i>

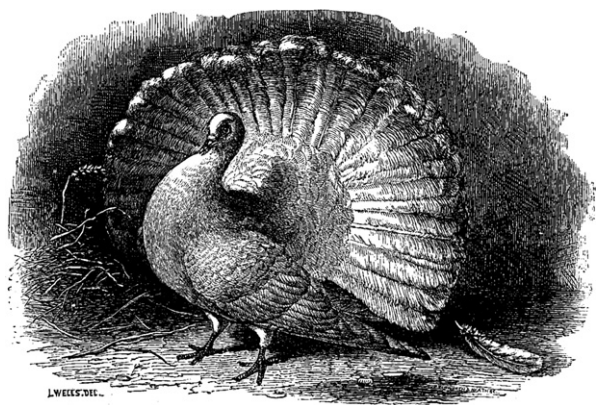


Fig. 1. The English Fantail pigeon, a typical product of artificial selection, in which “good birds walk in a singular manner, as if their small feet were stiff. Owing to their large tails, they fly badly on a windy day”. From Darwin’s *Variation of Animal and Plants under domestication*.

desirable, as I had never deliberately applied these views to a species taken singly.” [1,1st ed. Vol. 1: 2]

But further:

“During many years, it has seemed to me highly probable that sexual selection has played an important part in differentiating the races of man ; but in my *Origin of Species*, I contended myself by merely alluding to this belief. When I came to apply this view to man, I found it indispensable to treat the whole subject in full details. Consequently the second part of the present work, treating of sexual selection, has extended to an inordinate length, compared with the first part ; but this could not be avoided.” [1,1st ed. Vol. 1:4]

It is, however, doubtful that in 1871 he wrote the book he intended to write in 1859, since in the meantime he greatly increased the contribution of use and disuse to his theory. In definitively adopting the pangenesis hypothesis in his *Variation*, he also accepted the view that many new variations originate as useful adaptations of individuals. At first they emerge through use and disuse, then they become hereditary. In this, the *Descent* is not so much the continuation of the *Origin*, as it is of the *Variation*. Darwin’s inspiration for his *Descent* owes much to his *Variation*, both for the mechanism of inheritance, and for the similarity between artificial selection and mate choice. Thus, in the *Descent*, there is an intermingling of the fact that Darwin eventually extends the subject of the *Origin* to mankind, with the fact that he is defending a substantially different view of the contribution of hereditary mechanisms to evolutionary mechanisms.

Below, I will examine Darwin’s sexual selection for its inner consistency, for its meaning in his time, and for its long term influence on research until now. Many readings have been offered of the evolution of Darwin’s views. Some have stressed his need to respond to the objections of Jenkins or Wallace [5,6]. Others have emphasized his moral views on the unity of mankind, or his feelings towards religion. However, we also know that Darwin was a very rigorous thinker who was seeking consistency for its own

sake, not simply in order to counter other people. His books may appear as landmarks in the continuity of his meditation. Below, I will thus examine Darwin’s arguments for their consistency alone.

2. The book within the book

The introduction quoted above suggests that the first and the second halves of the *Descent* are very different. The first half actually includes an interesting review of whatever had been published in the few years before on the subject of the “Darwinian teaching” (according to Rolfe’s expression, Table 1) by other people. It examines the development of vertebrate embryos, the morphology, the physiology, and the five senses of man; the diverse adaptations and intellectual specificities of humans, including imagination, superstition, belief in God, moral sense and altruism. There is some tendency to categorize these advances into steps. Darwin seems to examine mankind as though he was “a zoologist from another planet” (as Wilson will attempt to do a century later [7]). This encyclopaedia mentions several doctrines on mankind, such as utilitarianism, eugenism and Spencerianism. It conveys a number of prejudices of the time about the rise and fall of nations: a nice example is the idea that the differential economic success of English and French Canadians demonstrates their different hereditary potential in the framework of the same environment; another one is the idea that the Inquisition counterselected the best endowed class of the Spanish people, allowing other peoples to rule America. Nowhere does this review turn into a synthesis. Its departure from Darwin’s personal style culminates in including in the second edition an appendix by Huxley himself, responding to one of his critics in comparative anatomy, a domain which was not Darwin’s firmest field. This first part terminates abruptly, as Darwin moves on to say that in order to tell how and why humanity evolved to its current state, he will now have to consider the whole animal kingdom and substantiate his theory of sexual selection. In the rest of the book, he will no longer elaborate on the views of others, except to cite here and there Bagehot, Spencer and Galton, and will exclusively present his own views.

Then another book begins, a pure marvel, as Darwin stops reviewing the writings of his contemporaries to review the sexual habits of the whole animal kingdom, from molluscs to primates. From an enormous collection and elaboration of scanty second-hand information on behaviour, and using magnificent figures of birds of Paradise or strange illustrations of sexually dimorphic heads of chameleons or beetle horns, Darwin writes one of the most influential books of the 19th century on sexuality. For instance, Freud’s *Totem and Taboo* imagined it to be a foundation of psycho-analysis. This masterpiece of natural history establishes his authority on the subject, but the really important two sections in it are the introduction, presenting the mechanisms, and the conclusion, presenting his conclusions on man, after a brief and final summary of mechanisms.

Of the conclusions, let us say that they present mankind as a mosaic of traits caused by a mosaic of evolutionary

forces. In short, they posit that moral sense developed in individuals through social interactions and have become hereditary through usage. Pride and courage developed through the habit of fighting between members of the same sex (in this case, human males) over access to the other sex; artistic sense, musical skills, the sense of beauty, and the morphological differences between human populations developed through mate choice. The mechanisms leading to these adaptations are presented in the opening of the second part of the book, where Darwin really uncovers his purpose. Interestingly, this means that to interpret the evolution of moral sense through the law of use and disuse, Darwin depicts this trait in the first part of the book, then presents his law of inheritance at the beginning of the second part, and eventually combines the two in the general conclusion. Likewise, the morphological differences among humans are presented in the first part, sexual selection at the beginning of the second part, and the two are combined by the end of the book. All of this contributes to make the beginning of the second part the cornerstone of the book.

3. The status of Darwinian mechanisms

The sixth and last edition of the *Origin* was published in 1872. Darwin probably had it in mind when writing the *Descent* in 1871. Historians have emphasized that the successive editions of the *Origin* show a trend towards an increased role for the law of use and disuse. This is why the different evolutionary mechanisms in the *Descent* are an important testimony of Darwin's ultimate state of mind. It contains two definitions of mechanisms. Firstly, Darwin summarizes his pangenesis hypothesis straightforwardly:

“According to this hypothesis, every unit or cell of the body throws off gemmules or undeveloped atoms, which are transmitted to the offspring of both sexes, and are multiplied by self-division.” [1, 1st ed. Vol. 1:280]

This mode of inheritance belongs to what tradition has called “Lamarckian inheritance”, even though it was never so precisely discussed and cautiously presented as by Darwin himself. This theory was criticized because although a lost organ would be unable to send off gemmules, mutilations are not hereditary. Skipping from mutilations to more ordinary variations, the positive aspect of pangenesis was to provide an explanation for the existence of quantitative variability in most species. Some variations are innovative, unlike mutilations. A popular view, which Darwin held, was that they originate through the law of use and disuse. While pangenesis does not in itself assume the mechanism of development by use and disuse, it constitutes a hereditary mechanism which can make it a significant factor in a theory of adaptation. This had interesting implications for natural selection, as summarized in the conclusion of the *Descent*:

“We may feel assured that the inherited effect of the long-continued use or disuse of parts will have done much in the same direction with natural selection.” [1, 1st ed. Vol. 2]

His hypotheses lead Darwin to assume there is a causal link between the adaptation of individuals to the environment (through physiological change) and heredity. This insures that advantageous variations are produced and submitted to selection. Natural selection becomes an auxiliary mechanism. Since chance variations play only a minor part, there is no real selection, but only some kind of reinforcement of developed traits. Pangenesis introduces an ambiguity in our reading of Darwin's theorising. He notices that heredity involves two elements, “the transmission and the development of characters”. Since the same environmental pressures act both on the development of a trait, and on the selection of individuals showing this trait, it becomes unclear what the expression “natural selection” refers to. Is it only the elimination of individuals having completed their development (as we nowadays understand it), or both this process and the upstream process of development through use and disuse? The ambiguity sometimes pervades whole chapters dealing with selection.

According to the *Descent*, use and disuse account for the origin of altruistic behaviour and moral sense. These adaptations are useful to the group, but not to individuals taken singly. In a social species, however, communication develops these functions through sympathy and common approval, so they become altogether beneficial to individuals and to the group, and thus are retained and propagated by natural selection acting at the scale of the whole group. This could be called “social-Lamarckianism”. In the first part of the book, Darwin writes:

“The habit of performing benevolent actions certainly strengthens the feeling of sympathy which gives the first impulse to benevolent actions. Habits, moreover, followed during many generations probably tend to be inherited”. [1, Vol. 1:164]

This opinion is reaffirmed in the general conclusion:

“It is not improbable that after long practice virtuous tendencies may be inherited”. [1, 1st ed. Vol. 2]

He seems to extend his mechanism to the inheritance of any kind of characters having been developed in the individual through social interactions. Commenting on language, he writes:

“A great stride in the development of the intellect will have followed, as soon as the half-art and half-instinct of language came into use; for the continued use of language will have reacted on the brain and produced an inherited effect”. [1, 1st ed. Vol. 2:2]

The second definition in the book concerns sexual selection, which is more concisely presented in the conclusion:

“Sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species; whilst natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. The sexual struggle is of two kinds; in the one it is between

individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners. This latter kind of selection is closely analogous to that which man unintentionally, yet effectually, brings to bear on his domesticated productions, when he preserves during a long period the most pleasing or useful individuals, without any wish to modify the breed." [1,1st ed. Vol. 2]

According to a modern analysis [8], any selective process must involve three components: (1) a community with an excess of members, to allow for a choice among them; (2) a selective agent; (3) and "heritable" variation in the selected trait.

In natural selection, the selected community (component 1) is the species as a whole, which is subject to demographic pressure, as suggested by Malthus's law. In sexual selection, the community is made up of the members of the same sex, generally males. The excess is not caused by demographic pressure, but by the fact that a subset of the males may be sufficient to fertilize all the females; for example, this is the case in species where males do not contribute to parental care, as their sole utility is to provide sperm.

The selective agent (component 2) differs between the two kinds of sexual selection. In one case, nowadays referred to as "intrasexual selection", it is the direct competition between members of the selected sex (generally males). This case is not very different from natural selection, but for the fact that there is no law of death. The contestants might or might not be hurt in the battle. The only constant criterion for this kind of selection is that the loser fails to mate, while the winner does mate. The other kind of sexual selection ("intersexual selection") involves a new selective agent. Its criterion is no longer in the adaptation of the organism to its environment, but in the interests of another animal. In his book on *Variation*, Darwin had also distinguished two kinds of selection, although only within the context of breeding. "Unconscious" selection referred to the survival of the best adapted individuals, whereas "methodical" selection was the conscious protection of individuals being bred by man "to create some improvement already pictured in his mind". Intersexual selection also refers to the welfare of the selecting agent, not of the selected population.

This point is very important for understanding the history of Darwin's theory. Ever since the new formulation of the theory of sexual selection by population genetics in the 1930s, historians of science have been discussing whether or not Darwin ever accepted the possibility that natural selection could have acted solely on purely random variation, as postulated nowadays in the framework of Mendelian genetics. The question seems endless, since Darwin never completely rejected the mechanism of use and disuse. He only changed the emphasis he placed on its importance. On the other side, historians have mostly discussed sexual selection to understand whether it was

distinct in nature from natural selection, or a mere component of it. But the real point is one of mechanism. Sexual selection strictly speaking differs of natural selection only in the fact that it is limited to part of the population (generally males) instead of to all of it, and has to do with only some of the adaptations of the organism, those pertaining to mating. The point that has attracted little attention from historians is that the architecture of the explanation is completely different between the two kinds of sexual selection. Intrasexual selection does not differ in its mechanism from natural selection, and is compatible with use and disuse. Intersexual selection, like artificial selection, is never reducible to use and disuse. It excludes it.

Variation in adaptive traits (element 3) requires there to be a source of variation. Modern biology shows that Mendelian heredity provides genetic variation for about everything. But this was not known in Darwin's time. Given pangenesis, intrasexual selection can be permanently fuelled with variation originating from use and disuse in battles between males. Whereas in intersexual selection, the aesthetic sense of females cannot logically support variation through use and disuse of male ornaments. Usage was never the only basis of heredity in Darwin's thought. He also admitted that adverse environmental conditions could increase variability. Likewise, he admitted that large-scale abnormalities, or "sports", could appear, and be selected by breeders. Thus, these traits could be exposed to swamping through blending inheritance. In the *Origin* [2: 89], Darwin confesses that he will not enter the subject of whether these traits are transmitted by males alone, or by the two sexes. In the *Descent*, he admits that they are transmitted bisexually, based on the evidence that ornaments in hybrid males are as a rule intermediate between those of males from the parental species.

This weakness of the theory is not discussed by Darwin, but would not go unnoticed by his contradictors. "If these variations appear in only a few individuals, their perpetuation is not possible, since they will soon disappear through crossing", concludes Morgan in 1903 in the first of his 20 rebuttals of Darwin's sexual selection theory [9: 213]. Like the initial concept of natural selection, which it mimics so well, mate choice would look as if it contradicted any realistic evidence of inheritance until the eventual introduction of genetics into evolutionary theory in 1930.

4. From Darwinian heredity to the good of the species

Gayon [5] has remarked that Darwinian selection may have been incompatible with Darwin's conception of hereditary variation. This appears as an insoluble contradiction in his discussion of the sex-ratio. At the end of his introductory chapter to the second part of the *Descent*, he opens a supplementary subchapter on the numerical proportions of the sexes. This may have seemed a vital point for his sexual selection theory, since the balance between individuals from each sex can increase or decrease the pressure of sexual competition. Darwin developed a correspondence with a large number of

people around the world to collect statistics on the sex-ratio in a number of species, as well as in human populations. His pangenesis hypothesis could apparently provide no explanation for the high frequency of observed sex-ratios of one male per female. In the framework of today's science, it may seem to us that the XY sex-determining mechanism in mammals is a straightforward reason why it should be so. This is misleading, however, since although sex is not genetically determined in all bisexual species, the sex-ratio often remains one male per female, whether it is determined by genes, or by the behaviour of the parents. For instance, in some reptiles the sex of the offspring is determined by the incubation conditions of the eggs. The rule of a 1/1 sex-ratio pre-exists any physiological or genetic determination. This suggests that it is an equilibrium determined by evolutionary laws, which are somewhat "above" the other laws, such as those of variation (Fig. 2).

In 1930, Fisher [10] provided the modern explanation for this apparent mystery by noting that reproduction necessitates an equal contribution from each sex. Each mating event involves one male and one female. Thus, if one sex is in numerical excess, its members will, on average, have fewer opportunities to mate than members of the other sex. If a parent is able to manipulate the sex-ratio of its progeny, it will pay for that parent to produce an excess of the rarer sex. This will not change the number of its offspring, but it will change their probability of mating. In other words, this parent will have more grand-children. Here is the evolutionary advantage of controlling the sex-ratio. It may be mathematically shown that the XY genetic determinism has evolved because, as soon as the sex-ratio of the population is not 1/1, whatever the direction of the disequilibrium, a parent producing an equal proportion of the two sexes always begets more grand-offspring than average, and hence is at a selective advantage. In modern evolution textbooks, Fisher's model is a famous example used to show that evolution is led by competition among individuals, not by the interest of the species as a whole. In species in which males provide no parental care, a few males would suffice to inseminate all females, and population growth would benefit from an unbalanced sex-ratio. A species with an excess of females would easily outcompete other species. However, Fisher's model shows that such excess cannot occur, since a population with a non-equilibrium sex-ratio will immediately be checked by natural selection.

Before examining Darwin's point of view, it is important to notice that Fisher's model is only loosely outlined, and thus can accommodate a variety of actual mechanisms (chromosome determination, behavioural determination) provided that, *in fine*, the transmission of the trait is hereditary in some way. Its only prominent property is frequency-dependence. It is thus understandable in terms of particulate inheritance (an assumption of genetics), but not in terms of blending inheritance (an assumption of Darwin's pangenesis).

The following fact is revealing. Between the first and the second edition of the *Descent*, Darwin's point of view evolved from a firm opinion which was relatively close to Fisher's one, to a doubtful opinion which seems further away from that of modern biology.



Fig. 2. The paradise bird *Paradisea papuana*, after Darwin's *Descent of Man and Selection in Relation to Sex*. Darwin assumes that male ornaments in dimorphic species were selected by females, in the same way as breeders select "fancy" varieties in domestic species. Fisher will later suggest that these ornaments were originally linked to some selectively advantageous trait, then became extravagant due to a "runaway process".

In the first edition, the supplementary subchapter on the proportional numbers of the two sexes includes a final part "on the power of natural selection to regulate the proportional numbers of the sexes, and general fertility". In it, Darwin posits very clearly that if a species produces an excess of one sex, those individuals producing fewer individuals of the "superfluous and useless" sex, "supposing the actual number of the offspring to remain constant", would necessarily produce more of the other sex, "and would therefore be more productive". He is worried by the question of polygamy in some species, a fact which he ascribes to the limits of the power of natural selection, but which does not look sufficient to him to rule out his explanation. He writes:

"Nevertheless, we may conclude that natural selection will always tend, though sometimes inefficiently, to equalise the relative numbers of the two sexes". [1, 1st ed, Vol. 1: 318]

Darwin's explanation seems at first glance acceptable to modern evolutionary biologists. But words do not have the same meaning for a naturalist of the 19th century as they do in the context of modern biology. The difficulty of translating Darwin's theory into current evolutionary thinking is illustrated by the strange fact that instead of considering the tendency to produce more females than males as a change in the trade-off between producing

either sex, Darwin explores two other lines of reasoning. First he examines the alternative of producing more females, then he examines the alternative of producing less males, as though the two followed independent modes of inheritance! This is evidence that Darwin's language is not reducible to ours. And this might be what will explain the failure of the second edition to resolve the point when he follows his rationale to its ultimate conclusions, as we will see below. At this point, let us simply note that if Darwin had retained the first part of his argument in the first edition, there would have been no "Fisher's theory of sex ratio", as it is universally known nowadays. Fisher would rather have put "Darwin's theory of sex ratio" in more rigorous words.

The title of this part of the text is less affirmative in the second edition of the *Descent*, having been changed to "the proportion of the sexes in relation to sexual selection". Nothing is left of the text of the first edition. It has been replaced by an examination of the subject in several human populations. Its most prominent element is a numerical example based on the case of the Todias, a people from India characterized by the infanticide of female infants, and an excess of males in the population. Darwin attempts to show that sex-biased infanticide tends to bias the sex-ratio at birth. Following the reasoning of Colonel Marshall, he considers the imaginary case where females would vary for the sex of their progeny. As shown in Table 2a, he reasons as though each female had six offspring, and these were comprised of either six males, or six females, or three males and three females. He also assumes that two thirds of the female offspring are killed by infanticide. He thus ends up with three females and nine males, who will reproduce. Since most of the surviving individuals originate from male-biased families, he concludes that the number of males will increase in the population.

"Thus the bias strengthens with each generation, until as we find, families grow to have habitually more sons than daughters. That this result would follow from the above form of infanticide seems almost certain: that is, if we assume that a sex-producing tendency is inherited". [1,2nd Edt, Vol. 2]

This reasoning is fallacious, since it does not take into account the fact that each child has a parent of each sex. Therefore, the number of matings effected by females, as a whole, is the same as it is for males, as a whole. This means that each of the three females, taken individually, is three times more fertile than each of the nine males, taken individually. In other words, in the ancestry of the next generation, the proportion of parents from female-biased

Table 2a
Offspring of three families from a tribe where it is customary to kill 2/3 of the daughters.

Type of mother	Born	Dead	Surviving
A (female biased)	6 ♀ - 0 ♂	4 ♀	2 ♀
B (male biased)	0 ♀ - 6 ♂	-	6 ♂
C (balanced)	3 ♀ - 3 ♂	2 ♀	1 ♀ - 3 ♂
Total	9 ♀ - 9 ♂	6 ♀	3 ♀ - 9 ♂

Table 2b
Composition of the breeding population at the second generation.

Females	Males
2/3 from a female biased family	2/3 from a male biased family
1/3 from a balanced family	1/3 from a balanced family

families is the same as the proportion of parents from male-biased families (Table 2b). The survival of females is lower than for males, but their fertility is higher, and exactly compensates for it. This blunder of Darwin is apparent in the context of 20th century mathematical models of population growth, which show clearly that "Darwinian fitness" involves both survival and fertility [9]. But this is not enough for an explanation, since we have seen that fertility was clearly accounted for in the first edition, and that Darwin had been able to produce the correct line of reasoning about its contribution to determining sex ratios. In the second edition, despite the large number of individuals being killed, Darwin never uses the expression "selection". Instead, he refers to "families with a tendency to produce sons" or "daughters". How do these opposite tendencies coexist within blending inheritance? Darwin certainly did not expect blending inheritance between males and females to produce intersexuals! Thus he must have assumed some unexpressed mechanism for how the confrontation of the gemmules transmitted by the two sexes to the egg determine either a male or a female. Yet of this we have no idea. The least we can say is that Darwin did not possess the theoretical cues for solving the issue. This seems to be a case where Darwin's conclusions on the mechanisms of inheritance led his theory into a dead end.

Ultimately, he will be unable to identify the forces acting on sex-ratios. In giving up, he seems to refer to the first edition of his book when he admits:

"I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future". [1,2nd ed. Vol. 2]

Here, Darwin is caught in the act of confusing the advantage to the species with the advantage to the individual. While his theory proves that the adaptation of organisms may follow from a material cause, natural selection, he seems to exclude that the best solution for the individual might be distinct from the best solution for the species.

We judge this from the comfortable viewpoint of modern thinking, influenced by Mayr's distinction between "ultimate" and "proximate" factors in Darwinian evolution. This is a modern construction. The two levels are necessarily entwined in the framework of pangenesis. However, the words used by Darwin indicate that he himself made a distinction between the "provisional hypothesis" of pangenesis and the "theory" of natural selection. The evolutionary mechanism and the hereditary mechanism did not have the same status even though their parts overlapped. The fact that Darwin insisted on keeping

selection as the prevailing mechanism in this process could confuse his readers.

The theory of sexual selection fell into neglect in its time for reasons which are different from the criticisms of modern evolutionary genetics. Like many authors of his time, Darwin could have restrained himself to describing facts. He had written wonderful pages on the achievements of sexual selection in animals. But being the demanding naturalist that he was, the evidence of intuition was not enough for him, and he was ready to weaken the consistency of his theory by examining the ultimate consequences of his hypotheses, as exemplified in the case of sex-ratio.

Morgan [9], who was to become a founder of genetics, incisively criticised Darwin's sexual selection theory. When some females of some monogamous species have chosen the most beautiful males, he said, what bars the other males and females from mating together? Sexual ornaments are sometimes such a handicap to their carriers; why does selection not counteract their evolution? What use are beards to men and glabrous cheeks to women? And so on. There are so many inconsistencies in Darwin's *Descent*, that one can wonder why it survived. Only when it is framed in Mendelian heredity, will it look to be a very illuminating hypothesis.

5. The modern synthesis: sex in the gene pool

The evolutionary synthesis offered a second birth to sexual selection, although for a time, it was very different from Darwin's original theory. In 1937, Dobzhansky [11] defines evolution as a mere change in allele frequencies. Mayr's *Animal species and evolution* [12] establishes the new field on "population thinking": while adaptation is a property of individuals, evolution is a property of "gene pools". The biological species concept insists on the reproductive delimitation of species. Muller [13] puts forward a genetic model of the evolution of interspecific incompatibility. Speciation is thought of as an adaptive process: through "character displacement" [14], natural selection determines sympatric nascent species to occupy different ecological niches by evolving preferences for different resources: there is competitive exclusion between them. Sexual selection is thought to allow males and females of sympatric species to evolve different recognition signals through the "reinforcement" of isolating mechanisms by "ad hoc contrivances" [11,2nd ed: 285; absent from the 1st edition]. Thus, natural selection and sexual selection conspire harmoniously to delimit new species within the biological species concept.

In the meantime, Tinbergen, Lorenz and von Frisch developed the study of communication within the framework of a new field, ethology. The study of instinct shows that sexually dimorphic characters are not simply due to competition for mating. Such competition only exaggerates the features of a pre-existing adaptive system. As early as hatching or fledging, animals need to be able to recognize members of their own species and of other species in the wilderness of the environment. Responding in the right way is vital. Three kinds of animals can be encountered: (1) ones that can eat them, and from which

they need to escape swiftly; (2) ones that are their potential food, and which they need to approach wisely; and (3) ones that are their potential sexual partners, and which they must approach in the appropriate season, by displaying conspicuously and convincingly the courting signals of their species. In designing his theory of sexual selection, Darwin overlooked the fact that the primary utility of secondary sexual characters is to recruit a mate from the right species.

Population geneticists tried to substantiate Darwin's belief in the "aesthetic taste" of females as a theory of the utility of choosing a mate. Fisher [10] developed the theory of the "runaway process" to account for the origin of extraordinary male ornaments. Females would choose males on the basis of a signal linked to a heritable selective advantage in the struggle for life. But once males exhibiting this character are preferred by females, it is advantageous for them to increase the signal again and again, and increase their attractiveness, whether or not the advantageous trait is still present. As the process goes on, the male ornament and the female preference reinforce each other only because ornamented males and the females who prefer them produce most of the offspring. An oft-mentioned rebuttal of this is that the ornament may eventually become so costly that it may be at a disadvantage. For instance, it may be so conspicuous that it is detected by predators. Then males would tend to lose it, and females to return to cryptic males.

Genetic polymorphism was at the heart of evolutionary explanations, but almost nothing was known of the structure of the genome. Sexual selection was conceived as one of the mechanisms that could explain the "maintenance of polymorphism". It inspired experiments in *Drosophila*. This included the theory of the rare male advantage by Petit [15] and Herman [16], and the theory of the athletic advantage of the most polymorphic males [17,18]. These hypotheses flopped in 1966 when Lewontin and Hubby [19] discovered that natural populations are so polymorphic that any male is genetically rare, and that polymorphism is universal. Kimura and Ohta's neutral theory [20,21] showed that chance alone can explain observed levels of polymorphism. This would free the field of sexual selection from simplistic explanations based on sexual preferences for variation at a single locus, and the matter would be left to the rising field of evolutionary ecology.

For the centenary of the *Origin* in 1959, the chapter devoted to sexual selection in the collective book edited by Barnett [22] was written by Maynard-Smith and relied almost exclusively on the *Drosophila* work on athletic males, and on the theory of signals in ethology. A great change would occur in the following years, and the picture will be completely changed in the book edited by Campbell in 1971 [23] for the centenary of the *Descent*: sociobiology had unearthed Darwin's theory and was using it to explore the field of male-female conflicts.

6. Sociobiology and the sexual conflict over reproduction

It might seem unexpected that a relationship exists between the study of social behaviour, which is based on

altruism within groups, and that of sexuality, which is a very selfish behaviour. In fact, both of them are based on communication [24]. That is, they are based on the transmission of information between conspecific individuals, including between “him” and “her”. When a female chooses a mate, she uses cues which can help her evaluate the quality of a potential partner. For instance, a female from a monogamous bird species can evaluate the quality of a male’s territory, or of his nest, or of his ability to care for the eggs, or of his parasitic load which could spoil her future reproductive success, etc. In theory, a signal should be “honest”, meaning that its information about its bearer’s quality cannot be imitated. For instance, the colours of some bird feathers have been hypothesized to constitute indicators of male quality, since these colorations involve carotenoids, molecules which are also precursors in the immune system [25]. Thus, a large load of carotenoids would be an “honest signal” of the ability of a male to resist diseases. Of course, in the world of evolution, no honest signals are eternal, as they can be mimicked on the long run. The question is rather one of the relative confidence which can be put in a signal. For instance, you can buy a diamond with your credit card, even though some credit cards are fake, and sometimes so are diamonds. Evolution tends to maintain treachery within workable limits. The rationale behind this approach is that when two individuals cooperate to achieve some goal, they guard themselves against misinformation about their partner. One reason why the advantage of some extravagant secondary sexual characters is impossible for us to infer is that the evolution of communication is a succession of measures and countermeasures. There may be no objective reason why human males have a beard and why females have glabrous cheeks. In 1972, Maynard-Smith and Haigh [26] developed the theory of evolutionary games, to explain the ritualization of animal behaviour. An interesting feature of this theory is that you cannot predict which behavioural strategy is the best. Instead you can find the “evolutionarily stable strategy” (or ESS) of a game, which is the strategy that can be overcome by no existing alternative strategy (note that the neologism “evolutionarily” was especially designed for this expression). Thus, a behaviour (or a sexual character) would not be defined by its origin, but, looking backwards, by its stability. This is reminiscent of the process of a game of chess. Players usually start with a more or less constant sequence of moves, which confound a neophyte because the reason for this ritual is not apparent. Yet it has been selected in the history of chess, since alternatives led to weaker outcomes. The difference between chess and the game of life, is that chess has a finite number of possibilities. We can expect that some day a computer will be able to find the unbeatable strategy, and that will be the end of chess. Whereas the game of life involves millions of species, each with thousands of genes, and the rules of the game in ecosystems change over million years. Thus, the game is endless. A single odds-matrix may have many solutions. For instance, an individual being too weak to survive could choose to dissipate his energy into reproduction instead of surviving. Thus, it could decide to use its carotenoids to attract as many mates as possible and resign itself to being

killed shortly by parasites. Since genes are a determinant of behaviour, they can induce the weak body in which they happen to be to reproduce as fast as possible, even though this will quickly exhaust its resources and kill it. With a short and prolific life, its genes will be able to start the game over in another organism, in better conditions. So they are doing the best of a bad job. In a social species the best choice in the same conditions may be the opposite: a gene happening to be in a weak body may determine it not to reproduce by itself, but to save its energetic resources to live long and help the reproduction of its more prolific kin, so as to propagate the same genes in the form of duplicates in its brothers and sisters.

7. Of maleness and femaleness

With the rise of genetics, theories were put forward to understand why sex had evolved, whereas asexual reproduction had remained limited to a few lineages, such as dandelions and rotifers. Why did sex lead to separate reproductive strategies: those of males and those of females? What is the essence of each sex, and what is common to all males or to all females across species? The only factor shared by all females is the production of oocytes, which are large reproductive cells containing the metabolic reserves (yolk in animals) that allow the future egg to develop elementary organs before hatching. Such a large cell is unable to move. In comparison, the male gamete (sperm or pollen) is a small motile cell specialized in moving towards the oocyte to fertilize it. It is admitted that when originally unicellular organisms turned into multi-celled organisms (metazoans or metaphyts), they needed to produce gametes with these two complementary functions.

In 1948, Bateman [27] suggested that the differentiation of reproductive cells resulted in an eventual differentiation of male and female behavior. He experimentally studied mating success in laboratory strains of *Drosophila*. The number of males and females was the same, and so was the average mating success in the two sexes. But the variance was different. All females mated about once, and so their variance in mating success was very low. On the other hand, some males mated many times, while others did not mate at all, and so their variance was about as large as the mean. He concluded that females are the limiting sex for reproduction since they can provide only a limited number of oocytes, whereas males are not limited in sperm. The competition between the latter to fertilize the oocytes would determine “male eagerness” (an expression from Darwin), while females were “coy” and “choosy”. The resulting conflicts between males would explain their larger variance. Actually, Bateman’s interpretations were wrong. Only 34 years after Bateman’s work, it was noticed that the variance in male mating success was the value expected under a “Poisson law”. This was the value expected if the variation in their mating success resulted from random encounters with unmated females [28,29].

Bateman’s theory inspired yet another hypothesis on the fundamental difference between males and females. For the centenary of Darwin’s *Descent*, Trivers [28]

presented the theory of “parental investment”, concluding that the initially larger investment of females in their eggs, as compared to males’ investment in sperm, determined them to invest even more, including in parental care. This was to be explained by the fact that if either sex abandoned the young instead of taking care of it, the loss would be greater to the female than to the male, because of her larger investment in their common progeny.

“Since the female already invests more than the male, breeding failure for lack of an additional investment selects more strongly against her than against the male. In that sense, her initial very great investment commits her to additional investment more than the male’s initial investment commits him”. [30:144]

No theory ever went further in exploring potential conflicts between the sexes. This model was deeply criticized as an example of the “Concordian fallacy” [31]. This refers to the wrong choice of politicians concerning the Concord aircraft. They kept investing in a ruinous enterprise for the reason that they had already lost much money in it, not considering that investing even more money would make the enterprise even more ruinous. If a player consistently loses, and if a larger investment does not modify the expectation of a new bet, then it is not worth playing again. Likewise, the value of a parent’s continued investment in parental care will depend on the trade-off of the new investment, regardless of what the parent has already invested. Thus, it may be useless for a female to invest more. It may also be worthwhile for a male to invest in parental care, since he is not in competition with the female, but with the other males. In his book on the evolution of sex, Maynard-Smith devoted a model to this question, and showed that males can provide parental care, as is the case for instance in sticklebacks [32].

8. What are males fighting for?

A point at stake is whether males and females choose their mates for their “quality”. An explanation is known as the “good genes” hypothesis [33], which assumes that preferred males transmit “good genes” to their progeny. The question of whether such genes exist at all is at first glance contradictory to the idea that heritable variance in fitness is exhausted by natural selection, a consequence of Fisher’s [10] “fundamental theorem of natural selection”. At any time, this variance would be very low. Many critics of “good-genism” have explained that there is no reason for sexual selection to select heritable variation in fitness, since natural selection is already the most effective way to do so. There are, however, conditions under which cyclic changes in selective pressures may induce noticeable phenotypic effects that are indicative of the “genetic quality” of a male. For instance, parasites may invade a population for some generations, disappear when the population has evolved resistance, and occur again after some time, when part of the host population has lost its resistance. This would lead to genetic variation among hosts in resistance to parasites [34].

Resistant individuals may look more vigorous, and be worthwhile as mates. The benefit can also be non-genetic, if there is a lower probability that mates with a lower parasitic load transmit diseases to their mates and their progeny.

The complementary model is the “bad genes” hypothesis, which is based on the fact that recurrent deleterious mutations are produced in the genome, and that all individuals harbor such mutations. These mutations often have cumulative effects. Therefore, the viability of the offspring depends on the mutation load of the parents. As our knowledge of the genome grows, there is increasing evidence for this factor [35,36].

The original hypothesis put forward by Darwin himself has received little attention: in the intrasexual selection game, males would not be competing for just any females, but chiefly for the most fertile ones. Thus, the “best males” would eventually mate with the “best females”. Many critics of Darwin have objected that when the best males and the best females have chosen each other, the others will do the same and every individual will be able to leave progeny. However, the choice mechanism will be reinforced over time since it will be positively correlated with offspring number, if the most fertile males mate with the most fertile females. Since all individuals leave a progeny, sexual selection is a “costless” mechanism of selection. It uses up no reproductive excess. Few studies have attempted to detect whether competing males choose the females they court. However, male discrimination has been found whenever it was looked for [37]. Females contribute to their progeny, not only genetically, but also by producing yolk and milk, and by providing parental care. Phenotypic differences in these traits can result from genetic variation as well as from environmental variation. In either case, such differences should determine a variance in reproductive success, in which the probability of mating contributes less than the probability of producing a viable offspring. Phenotypic variation in females could thus be the main factor influencing the reproductive output of a pair. It may thus be worthwhile for males to mate with the best females, as recognized by Darwin:

“Thus the more vigorous females, which are the first to breed, will have the choice of many males; and though they may not always select the strongest or best armed, they will select those which are more vigorous and well armed, and in other respects the most attractive. Both sexes, therefore, of such early pairs, would as above explained, have an advantage over others in rearing offspring”.

And more generally:

“The same principle would apply if each sex preferred and selected certain individuals of the opposite sex; supposing that they selected not only the more attractive, but likewise the more vigorous individuals”.

After having overrated sexual conflict as the key to understanding sexual selection, contemporary evolution-

ary biology has come to a stasis, and possibly to a dead end. I suspect that returning to Darwin's intuition that the sexes mutually select each other would provide for a more fruitful research agenda.

9. Conclusion

The mechanisms envisioned by Darwin in the *Descent* are costless under some circumstances, that is, they require no reproductive excess. Thus, evolution through use and disuse is costless as long as evolutionary novelty is created at the stage in which the organism adapts to its environment through development, provided that the new characters are simply passed on to the next generation through pangenesis. However, Darwin does not exclude that natural selection may be acting "in the same direction". Likewise, sexual selection is costless when it consists only in an assortment of mates depending on a pre-existing differential fertility. These mechanisms may have looked closer to the experience of everyday life than the "law of the battle" to readers of Darwin. Of these two mechanisms, the first seems to have been exclusively designed for mankind, as it was framed in terms of some sort of social Lamarckianism, which allowed that moral traits developed within the group by mutual approval, then became hereditary. It relied necessarily on Lamarckian inheritance, and therefore was later ruled out by genetics. The second mechanism, sexual selection, is thought of as universal under its two modalities. Intrasexual selection is nothing other than natural selection applied to the male sex only, with the peculiarity that the success is not in survival, but in reproduction. Thus, its theoretical basis shows the same strengths and weaknesses as natural selection theory. Sexual choice is different, since it does not lend itself to heredity through "use and disuse", and since the underlying female aesthetic sense remains obscure. However, sexual dimorphism, and the extravagant appearance of males in some species, are so striking that the idea of sexual selection could only reappear once Mendelian genetics had cleared away the inconsistencies in Darwin's reasoning.

Darwin never confused the evolutionary mechanisms based on selection with the hereditary mechanism, pangenesis, which he merely thought to be "provisionally" the most likely hypothesis to explain known facts of heredity. The overlap of the two mechanisms in explaining a single process may have looked confusing, but he maintained their distinctness throughout, and the selective explanation always prevailed in his writing. The reevaluation of Lamarckian inheritance in Darwin's late works precluded a weakening of his theory which lasted until the rediscovery of natural selection around 1930. These dark ages were presented by Julian Huxley as the "eclipse of Darwinism" [38], an expression that became a reference in history of science [39]. The eclipse was actually not so much that of "Darwinism" itself, as this evasive word was used by a variety of doctrines. It was the eclipse of natural selection theory. But the maintenance of the concept in Darwin's works allowed it to be rediscovered by contemporary science.

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