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Darwin as a student of behavior

Darwin, un investigateur du comportement

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ABSTRACT

In *The Expression of the Emotions*, Charles Darwin documents evolutionary continuity between animals and humans, emphasizing the universality of expressions in man. Most of the book addresses human behavior, and its influence on the study of animal behavior has been weak. The issue of natural selection is remarkably absent from this book, which relies on the inheritance of acquired characters rather than on a genuine Darwinian logic. Yet Konrad Lorenz considered Darwin to be a forerunner of behavioral biology. The reason was to be found in *The Descent of Man* and chapter VIII of *The Origin of Species*, where Darwin provides an explanation of behavior through selection, stating that the same mechanisms explaining morphological changes also account for gradual improvements in instincts. He assessed the accuracy of his evolutionary theory by directly studying animal behavior, hence laying the foundations of behavioral research for the next century.

Mots clés :
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RÉSUMÉ

Dans *L'expression des émotions*, Charles Darwin apporte des arguments à la thèse de la continuité évolutionnaire entre animaux et êtres humains, soulignant l'universalité des expressions chez l'homme. La plus grande partie de l'ouvrage porte sur le comportement humain, et son influence sur l'étude du comportement animal est restée limitée. Il est remarquable que la question de la sélection naturelle soit absente de ce livre qui fait appel à l'hérédité des caractères acquis davantage qu'à la logique darwinienne. Konrad Lorenz considérait pourtant Darwin comme un précurseur de la biologie du comportement. La raison doit en être recherchée dans *L'ascendance de l'homme* et le chapitre VIII de *L'origine des espèces*, où Darwin explique le comportement en termes de sélection, affirmant que les mécanismes qui rendent compte des changements morphologiques sont également à l'œuvre dans le perfectionnement graduel des instincts. Il a évalué la pertinence de sa théorie de l'évolution en étudiant directement le comportement animal, jetant ainsi les bases de la recherche en comportement pour le siècle suivant.

1. Introduction

"He who understands baboon would do more toward metaphysics than Locke" (August 16, 1838) [1]. This famous quote from Charles Darwin testifies that he had firm beliefs in the potential benefits of a science of animal behavior. His works, however, covered much more than the need for the study of animal behavior. Although this has generally been overlooked, behavior played an important role in his thought. The variations observed in the animals and plants of the Galapagos Archipelago led

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Darwin to understand that species descended from each other. We also know how his idea of natural selection arose from studying artificial selection and reading the books of Malthus. In *The Variation of Animals and Plants Under Domestication*, Darwin reveals that knowledge about animal behavior was a supplementary and decisive factor in the development of his theory:

> "It long remained to me an inexplicable problem how the necessary degree of modification could have been effected, and it would have thus remained for ever, had I not studied domestic productions, and thus acquired a just idea of the power of Selection. As soon as I had fully realized this idea, I saw, on reading Malthus on Population, that Natural Selection was the inevitable result of the rapid increase of all organic beings; for I was prepared to appreciate the struggle for existence by having long studied the habits of animals" [2: 10].

We learn from Darwin's autobiography that as a youth, he used to collect minerals and insects [3]. He spent a lot of time angling, enjoyed bird-watching, and also shot birds. For his generation, such hobbies were hardly unexpected for someone developing a strong interest in nature. He soon became a naturalist who observed and recorded everything [3]. During the voyage of the Beagle from 1832 to 1836, he collected every aspect of geology, botany and zoology he could; his reports are full of observations on the habits of marine and terrestrial fauna, as well as human populations [4]. His interest in behavioral issues became more peculiar in his thirties: "My first child was born on December 27th, 1839, and I at once commenced to make notes on the first dawn of the various expressions which he exhibited" [3]. From 1839 to 1842, he lived in London a short walk away from the Zoological Gardens where he regularly followed mammals and birds [1]. Charles Darwin then settled with his family in the village of Downe, in Kent, where he spent the rest of his life, working in gardens and frequently walking and making observations in the countryside. His writings disclose that the study of behavior was of primary concern to him during his entire life.

2. The expression of the emotions

In *The Expression of the Emotions in Man and Animals* [5], Darwin explicitly aims to describe the expressive movements of animals and humans in different states of mind, and explains them. He provides detailed accounts of communicative behavior in birds and mammals, with special attention to monkeys, apes, and humans.

2.1. Description of behavior

First, let me tell how I myself first came across this book. In the 1980s, I was studying the social behavior of Tonkean macaques, one of the rare species of Sulawesi Island. I found that they differed from other macaques in the function of a particular facial expression, the silent-bared teeth display (Fig. 1a). In many monkeys, subordinates retract the lips and expose the teeth to express submission. In contrast, the same display is the equivalent of a smile in Sulawesi macaques and signals the performer's peaceful intentions [6–8]. Only quite elusive references were available about this issue at the time of my studies [9–11]. I found to my surprise that the most explicit reference to the affiliative significance of bared-teeth display in Sulawesi macaques was one century old. The *Expression* provided a beautiful illustration of the display (Fig. 1b), accompanied by an accurate comment about its occurrence context and form: monkeys displayed this facial expression "when they are pleased by being caressed", "the corners of the mouth are at the same time drawn backwards and upwards, so that the teeth are exposed. Hence this expression would never be recognized by a stranger as one of pleasure" [5: 135].

The book is full of accurate behavioral descriptions. Some of Darwin's novel insights went unnoticed for a long time. For example, he recognized what we now call the metacommunicative function of the signals advertising play intentions, that is, their ability to communicate about the significance of other communication signals [12]: "When my terrier bites my hand in play, often snarling at the same time, if he bites and I say gently, gently, he goes on biting, but answers by a few wags of the tails, which seem to say 'Never mind, it is all fun'" [5: 63]. Darwin was also aware of the intersubjective function of blushing, which involves the reading of others' minds: "It is not the simple act of reflecting on our own appearance, but the thinking what others think of us, which excites a blush" [5: 326–327].

2.2. Continuity and universality

A prime aim of the *Expression* is to give evidence for evolutionary continuity between animals and humans. In *On the Origin of Species by Means of Natural Selection*, Darwin first demonstrated the animal origins of humans, mainly based on the homology of anatomical structures [13]. He then broadened the issue to mind and behavior in *The Descent of Man, and Selection in Relation to Sex* [14]. He initially intended [3: 94–95] to devote one chapter of the *Descent* to the subject of *Expression* [3], which finally became a full book extending the argument of evolutionary continuity to emotions and their expression in animals and humans. In this respect, Darwin fully achieved his goal. He writes: "With mankind some expressions, such as the bristling of the hair under the influence of extreme terror, or the uncovering of the teeth under that of furious rage, can hardly be understood, except on the belief that man once existed in a much lower and animal-like condition. The community of certain expressions in distinct though allied species, as in the movements of the same facial muscles during laughter by man and by various monkeys, is rendered somewhat more intelligible if we believe in their descent from a common progenitor. He who admits on general ground that the structure and habits of all animals have been gradually evolved, will look at the whole subject of Expression in a new and interesting light" [5: 12]; "We may confidently believe that laughter, as a sign of pleasure or enjoyment, was practised by our progenitors long before they deserved to be called human;

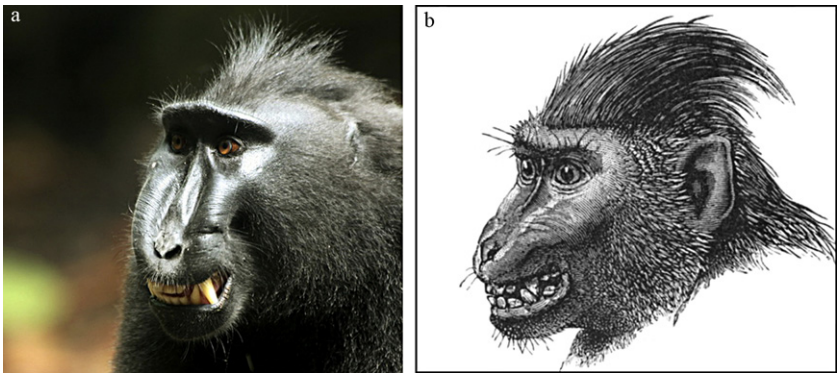

Fig. 1. The affiliative bared-teeth display of crested macaques: (a) Photograph of an adult male at the Tangkoko Batuangus Nature Reserve, North Sulawesi, Indonesia (credit: Jérôme Micheletta, *Macaca Nigra Project*), (b) Gravure taken from *The Expression of the Emotions*, p. 136 (reproduced with permission from John van Wyhe ed., *The Complete Work of Charles Darwin Online*).

for many kinds of monkeys, when pleased, utter a reiterated sound, clearly analogous to our laughter, often accompanied by vibratory movements of their jaws or lips, with the corners of the mouth drawn backwards and upwards, by the wrinkling of the cheeks, and even by the brightening of the eyes" [5: 361–362].

It is noteworthy that nobody surpassed Darwin on that subject for a long time. The comparative study of facial expressions reappeared with the development of primatology half a century ago. In the 1960s, van Hooff [9,15] published the first post-Darwin studies firmly establishing homology between the displays of non-human primates and the smile and laugh of humans.

A second objective of the *Expression* is to demonstrate that expressive movements are universal in form and meaning among humans. Darwin used innovative means to study them [16,17]. He was one of the first scientists to use photographs – those taken by the neurologist Guillaume Duchenne and the photograph Oscar Rejlander – in order to show the detail of behavior. He devised what we now name the judgment method, which consists of submitting pictures to different persons, and asking them what kind of emotion they recognize. He was interested in the facial expressions of young children, including some born blind – a method taken up by contemporary authors [18]. He also devoted a lot of time to questioning numerous correspondents about the expressive behavior of natives in different parts of the world. Darwin concluded that the same states of mind are expressed with remarkable uniformity in all people, pointing toward their common descent. In the first half of the 20th century, the ethologist Konrad Lorenz [19] followed the same logic by asserting that most communication signals are innate, whereas anthropologists [20,21] considered this behavior to be largely shaped by the cultural context. After decades of research on facial expressions, a consensus has now been reached that the connection between emotion and expression is universal in many respects, but that cultural learning can affect several aspects of it [22]. Yet today the research program of evolutionary psychology is built on the assumption of universality as the basis of human behavior [23].

2.3. Explanatory principles

In the first chapter of the *Expression*, Darwin formulates three chief principles aiming "to account for most of the expressions and gestures involuntarily used by man and the lower animals" [5: 27]:

(1) the principle of serviceable associated habits;
(2) the principle of antithesis;
(3) the principle of actions due to the constitution of the nervous system.

The first principle states that movements are acquired by individuals; while initially performed voluntarily, they become involuntary habits with repetition. They are then inherited through generations, and thus fixed in the species. Whereas this principle may remind us of the *ritualization* concept, later defined by ethologists as the evolutionary transformation of nondisplay behavior into display behavior [24], it strongly differs from it by exclusively resorting to the inheritance of acquired characters.

The second principle posits that opposite states of the mind should produce opposite movements. Though contrasts between a visual signal and the environment may favour its perception [25], to my knowledge nobody has ever attempted to test the relevance of the antithesis principle. Darwin himself had to admit that some expressions do not follow it. For example, Celebes macaques threaten by showing their teeth "so that the movements of the features from anger are nearly the same as those from pleasure; and the two expressions can be distinguished only by those familiar with the animal" [5: 138].

The third principle sets forth that some behavior represents involuntary responses of the nervous system. Nowadays, we would say that they are outputs from the autonomic nervous system. Quoting Richard Bell, Darwin notes that tears in screaming children are probably an outcome of the fact that "the muscles round the eyes are involuntarily contracted during violent expiratory efforts in order to protect these delicate organs from the pressure

of the blood" [5: 2]. Had he added that at first, tears had no expressive purpose, and that they were subsequently converted into an expression through natural selection, he would have made this a case for an evolutionary mechanism. But he did not.

Darwin's three principles are heterogeneous. He was not satisfied by them and neither are we. They likely represent post-hoc rationalization: "I arrived, however, at these three Principles only at the close of my observations" [3: 27]. As he admits, "It is however, often impossible to decide how much weight ought to be attributed, in each particular case, to one of our principles, and how much to another; and very many points in the theory of Expression remain inexplicable" [5: 82].

In the preface of a *fac simile* edition of the *Expression*, Lorenz wrote that "Ethology, which can be succinctly defined as the biology of behavior, has a special right to claim Charles Darwin as its patron saint. It is more immediately dependent on the selectionistic approach than any other biological science" [26: xi]. Yet, Richard Burkhardt remarked that the content of Lorenz's text bears little relation to Darwin's book. He even added: "One suspects that Lorenz wrote his preface without reading the pages by Darwin that were to follow" [27: 593]. It is true that three quarters of the *Expression* are devoted to human behavior. Secondly, with the exception of non-human primates, the animals considered in this work are primarily dogs, cats and other domestic species. Thirdly, the principles provided by Darwin fall short of explaining the function and evolution of behavior. When I myself first discovered this book, after having read the first chapters about explanatory principles and animal behavior, I leafed through it; I was disappointed for these three reasons, and I put the book back on the shelf without reading the remainder in detail. Many biologists would probably react in a similar way. The *Expression* had little influence on the biology of behavior. We find no reference to it in the founding works by Lorenz [19] and Tinbergen [28]. Only the principle of antithesis is briefly mentioned in textbooks published in the second half of the 20th century [29: 402; 30: 499, 501; 31: 179, 182].

A main Darwinian explanation is actually missing from the *Expression*, namely selection. I have compared the number of occurrences of the terms *natural selection* and *sexual selection* in three main works of Darwin: the *Expression*, the *Origin* and the *Descent*. It appears that the concept of selection occurs only four times in the first, compared with hundreds of occurrences in the latter two (Table 1). Despite having personally proposed the mechanism of sexual selection, Darwin did not envisage that conspecifics create selective pressures liable to shape communicative behavior. According to Radick [32], Darwin only looked for the immediate causes of expression. William Montgomery alternatively suggests that Darwin's explanatory principles antedated the main developments of his evolutionary theory, thus having been impervious to their implications [32]. Another reason could be that the *Expression* gives more emphasis to acquired behavior because it focuses on mental states in humans and other vertebrates, and pays little attention to "lower" animals (see below).

Darwin uses the emotions and the mind as a starting point, then examines how they are expressed, rather than to studying behavioral ouputs in order to make inferences about their function. He rarely uses a neutral word like *behavior* in his writings (Table 1), preferring the terms *instinct* and *habit* which both involve assumptions about the determinants of behavior. Envisioning behavior as an independent object of study had to wait until the rise of behaviorism [33] and ethology [19] in the 20th century. Following Lorenz's theory, instincts represent innate behavior whilst habits are representative of learned behavior, but this distinction was not available in the language tool kit of the nineteenth century. Like his contemporaries, Darwin believed that habits could gradually become innate, and he explicitly avoided any precise definition of instinct [12: 205]. In the *Expression*, the ratio of the occurrences of *habit* to those of *instinct* is three times higher than in his other two major works, pointing once again to the importance accorded to acquisition over selection processes (Table 1).

Darwin's emphasis on psychological reasons rather than on biological determinants explains why the *Expression* had little impact on following behavioral biology to come. Georges Romanes, his disciple, extended Darwin's ideas by comparing the intelligence of animals and humans. He claimed that we can understand the performances of animals by assuming that they are achieved

Table 1
Frequency of key concepts in three major books of Darwin.

	Origin of species (6th ed.)	Descent of man (2nd ed.)	Expression of emotions (1st ed.)
Occurrences of natural and sexual selection			
Natural selection	211	94	3
Sexual selection	14	163	1
Total	225	257	4
Ratio per page	0.53	0.41	0.01
Occurrences of behavior, habit and instinct			
Behavior	2	6	5
Habit (including habitual[a])	149	200	150
Instinct (including instinctive)	82	163	25
Ratio habit/instinct	1.8	2.0	6.0

Words were counted using the search engine of *The Complete Work of Charles Darwin Online*. Only occurrences within text were counted, excluding glossaries, indexes, titles, subtitles and corrections.

[a] As adjective of actions and movements.

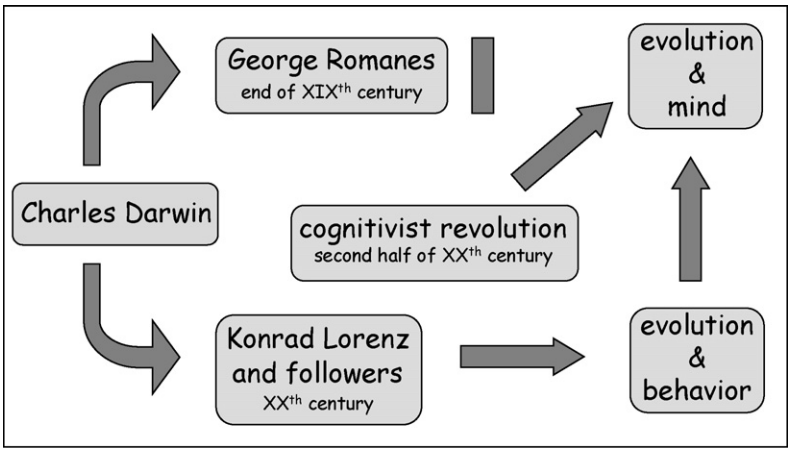

Fig. 2. The descent of current perspectives on animal behavior and mind.

using the same mental processes that we use: "there is no difference in kind between the act of reason performed by the crab and any act of reason performed by a man" [34: 337]. Note that Darwin himself wrote: "Even insects express anger, terror, jealousy, and love by their stridulation" [34: 350]. Such a stance led comparative psychology to a dead end for a while (Fig. 2). Romanes' introspective method had to be rejected – together with the inheritance of acquired characters – by Lloyd Morgan and others [35,36] before the study of behavior could be built on new bases. The cognitivist revolution finally revived the study of mind in the second part of the 20th century, without direct reference to Darwin (Fig. 2).

3. Other writings about of animal behavior

The *Expression* is regarded as the main Darwinian work about behavior. Yet this book is not Darwinian in the sense that it does not deal with the mechanism of natural selection. In addition, innumerable reports of animal behavior can be found in other works by Darwin, where they serve his theoretical purposes.

3.1. The Origin of Species

To explain why he looked on Darwin as the patron saint of ethology, Lorenz puts forward his contributions regarding variations in behavior, their inheritance, their homology in different species and their survival value, which gives rise to natural selection [26]. These classic Darwinian arguments are those found in Chapter VIII of the *Origin*, entitled "Instinct" [12]. In this chapter, Darwin states that instincts can originate either from habits or natural selection, and that he chooses to focus on the second alternative, arguing that instincts, just like morphological characters, may spring from the accumulation of profitable modifications. He then provides abundant evidence for gradation, heredity, homology and advantages brought by behavior.

Darwin made observations in order to counter arguments liable to undermine his theory of natural selection:

> "One of the strongest instances of an animal apparently performing an action for the sole good of another, with which I am acquainted, is that of aphides voluntarily yielding, as was first observed by Huber, their sweet excretion to ants: that they do so voluntarily, the following facts show. I removed all the ants from a group of about a dozen aphides on a dock-plant, and prevented their attendance during several hours. After this interval, I felt sure that the aphides would want to excrete. I watched them for some time through a lens, but not one excreted; I then tickled and stroked them with a hair in the same manner, as well as I could, as the ants do with their antennae; but not one excreted. Afterwards I allowed an ant to visit them, and it immediately seemed, by its eager way of running about, to be well aware what a rich flock it had discovered; it then began to play with its antennae on the abdomen first of one aphis and then of another; and each, as soon as it felt the antennae, immediately lifted up its abdomen and excreted a limpid drop of sweet juice, which was eagerly devoured by the ant (...) As the excretion is extremely viscid, it is no doubt a convenience to the aphides to have it removed; therefore probably they do not excrete solely for the good of the ants. Although there is no evidence that any animal performs an action for the exclusive good of another species, yet each tries to take advantage of the instincts of others" [12: 207–208].

Darwin gives a detailed account of how a slave-making ant (*Formica sanguinea*) exploits another species of ant (*F. fusca*) for its own sake:

> "I opened fourteen nests of *F. sanguinea*, and found a few slaves in all (...) During the months of June and July, on three successive years, I watched for many hours several nests in Surrey and Sussex (...) During the year 1860, however, I came across a community with an unusually large stock of slaves (...) [The slave-making ants] ruthlessly killed their small opponents, and carried their dead bodies as food to their nest, twenty-nine yards distant; but they were prevented from getting any pupae to rear as slaves. I then dug up a small parcel of the pupae

of *F. fusca* from another nest, and put them down on a bare spot near the place of combat; they were eagerly sized and carried off by the tyrants, who perhaps fancied that, after all, they had been victorious in their late combat (...) I laid on the same place a small parcel of the pupae of another species, *F. flava*, with a few of these little yellow ants still clinging to the fragments of their nest (...) I was curious to ascertain whether *F. sanguinea* could distinguish the pupae of *F. fusca*, which they habitually make into slaves, from those of the little and furious *F. flava*, which they rarely capture, and it was evident that they did at once distinguish them; for we have seen that they eagerly and instantly seized the pupae of *F. fusca*, whereas they were much terrified when they came across the pupae, or even the earth from the nest, of *F. flava*, and quickly ran away; but in about a quarter of an hour, shortly after all the little yellow ants had crawled away, they took heart and carried off the pupae" [12: 217-218].

Darwin's studies of honeybees deserve further quotations: "I believe that the hive-bee has acquired, through natural selection, her inimitable architectural powers. But this theory can be tested by experiment" [12: 222]; "I separated two combs, and put between them a long, thick, rectangular strip of wax: the bees instantly began to excavate minute circular pits in it" [12: 222]; "I then put into the hive, instead of a thick, rectangular piece of wax, a thin and narrow, knife-edged ridge, coloured with vermilion. The bees instantly began on both sides to excavate little basins near to each other" [12: 222–223]; "It suffices that the bees should be enabled to stand at their proper relative distances from each other and, then, by striking imaginary spheres, [they make] hexagonal cells" [12: 225]. From his results and additional geometrical considerations, Darwin concluded that bees succeed in building cells of due strength "with the greatest possible economy of labour and wax" [12: 227]. Predecessors like Réaumur [37] had already drawn similar conclusions in the 17th century, but Darwin was able to propose an explanation for such an outcome: natural selection tends to optimize the behavior of animals whenever possible. Future behavioral biology would not forget this lesson.

Lastly, it is worth recalling that in the chapter about instinct Darwin confronted a problem which could have been "fatal to the whole theory", namely the existence of sterile workers in insect societies, which by definition "cannot propagate their kind" [3: 228]. This problem was solved only 40 years ago with the theory of kin selection, which states that individuals favour relatives who possess the same genes by common descent [31]. It is noteworthy that Darwin had already suggested the right solution in these pages of the *Origin*: "This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears when it is remembered that selection may be applied to the family, as well as to the individual" [12: 230].

3.2. The Descent of Man

The *Descent* [13] is written in three parts. The first is a defence of the continuity in mind and behavior between man and animals, and of their homology. Its spirit is very much like those found in the *Expression*: "The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind. We have seen that the senses and intuitions, the various emotions and faculties, such as love, memory, attention, curiosity, imitation, reason, etc., of which man boasts, may be found in an incipient, or even sometimes in a well-developed condition, in the lower animals" [5: 126]. As previously mentioned, Romanes took up and amplified this view.

Darwin reports his own observations about the performances of mammals: intent and memory in dogs, anticipation in elephants, tool use in monkeys and apes. For instance, he describes at length how he verified that monkeys exhibit curiosity: "I took a stuffed and coiled-up snake into the monkey-house at the Zoological Gardens, and the excitement thus caused was one of the most curious spectacles which ever beheld. Three species of Cercopithecus were the most alarmed; they dashed about their cages, and uttered sharp signal cries of danger, which were understood by the other monkeys. (...) These monkeys behaved very differently when a dead fish, a mouse, a living turtle, and other new objects were placed in their cages; for though at first frightened, they soon approached, handled and examined them. I then placed a live snake in a paper bag, with the mouth loosely closed, in one of the larger compartments. One of the monkeys immediately approached, cautiously opened the bag a little, peeped in, and instantly dashed away. Then I witnessed what Brehm has described, for monkey after monkey, with head raised high and turned on one side, could not resist taking a momentary peep into the upright bag, at the dreadful object lying quietly at the bottom" [13: 72].

Darwin expresses contrasting views about the role of natural selection upon behavior in the *Expression* and Chapter VIII of the *Origin*. The issue appears mixed in the *Descent*; the term "natural selection" is relatively infrequent in its first part (0.20 occurrences per page), compared with the *Origin* (0.49). To account for the mental abilities of "higher" animals, Darwin mainly resorts to the inheritance of habits: "We may easily underrate the mental powers of the higher animals, and especially of man, when we compare their actions founded on the memory of past events, on foresight, reason, and imagination, with exactly similar actions instinctively performed by the lower animals: in this latter case the capacity of performing such actions has been gained, step by step, through the variability of the mental organs and natural selection, without any conscious intelligence on the part of the animal during each successive generation" (p. 68). Yet, in the third part of the *Descent*, Darwin uses the concept of sexual selection to explain higher intelligence in man. He recognizes that "It is, however, impossible to decide in many cases whether certain social instincts have been acquired through natural selection, or are the indirect result of other instincts and faculties, such as sympathy, reason, experience, and a tendency to imitation; or again, whether they are simply the result of long-continued habit" (p. 107).

The second part of the *Descent* is one long argument about the role of sexual selection in animal evolution. To substantiate his theory, Darwin reviews data from the literature on each category of animals in turn, emphasizing in the third part the relevance of selective processes for human evolution. It will suffice here to remark that sexual selection is a mechanism that depends above all on behavioral interactions. After Darwin's death, Alfred Wallace wrote a book entitled *Darwinism* [38], in which he dismissed the significance of sexual selection in evolutionary changes. After an eclipse of nearly one century following Wallace's criticisms, the study of sexual selection regained interest in the 1970s. Nowadays, the theory of sexual selection is regarded as one of Darwin's main achievements; textbooks about animal behavior are full of expositions about sexual ornaments, courtship, male competition, female choice, sex ratio, sexual dimorphism, mating patterns, etc. All of these issues were first delineated in the *Descent*.

3.3. Further works

It is worth adding a few words about books in which considerations about behavior would have not been expected. *On the Various Contrivances by Which British and Foreign Orchids are Fertilized by Insects* [39] and *Cross and Self-fertilization of Plants* [40] contain numerous first-hand accounts of the behavior of insects, spreading over thirty years of observation. Insects are at the heart of the pollinisation process. To show how natural selection shaped the sexuality of plants and the morphology of flowers, Darwin studied the interaction mechanics between insects and the different parts of flowers in the finest detail. He meticulously recorded their behavior and strategies. I will give just one example:

> "The extraordinary industry of bees and the number of flowers which they visit within a short time, so that each flower is visited repeatedly, must greatly increase the chance of each receiving pollen from a distinct plant. (...) I observed that in exactly one minute a humble-bee visited twenty-four of the closed flowers of the *Linaria cymbalaria*; another bee visited in the same time twenty-two flowers of the *Symphoricarpus racemosa*; and another seventeen flowers on two plants of a Delphinium. In the course of fifteen minutes a single flower on the summit of a plant of *Oenothera* was visited eight times by several humble-bees, and I followed the last of these bees, whilst it visited in the course of a few additional minutes every plant of the same species in a large flower-garden. In nineteen minutes every flower on a small plant of *Nemophila insignis* was visited twice. In one minute six flowers of a Campanula were entered by a pollen-collecting hive-bee; and bees when thus employed work slower than when sucking nectar. Lastly, seven flower-stalks on a plant of *Dictamnus fraxinella* were observed on the 15th of June 1841 during ten minutes; they were visited by thirteen humble-bees each of which entered many flowers" [40: 424–425].

Note that in the summers 1854 to 1861, Darwin repeatedly followed the flight paths of bumblebees with the help of his children: "The routes remain the same for a considerable time, and the buzzing places are fixed within an inch. I was able to prove this by stationing five or six of my children each close to a buzzing place, and telling the one farthest away to shout out 'here is a bee' as soon as one was buzzing around. The others followed this up, so that the same cry of 'here is a bee' was passed on from child to child without interruption until the bees reached the buzzing place where I myself was standing" [41]. Darwin drew a sketch of the paths of the bumblebees, but he did not publish his results. He regretted not to find out the function of this behavior: "I have also been unable to understand the purpose of this habit of always flying along the same routes and buzzing at the same places, thereby losing a great deal of time" [41].

As a matter of interest, I would like to recall that the first two chapters of *The Formation of Vegetable Mould, Through the Action of Worms* [42] address the habits of earthworms. In his last work, Darwin once again focused on the behavior of animals and demonstrated their role in the environment, developing an idea first published 40 years before [43]. He reported in particular various observations and experiments on the perceptual skills of earthworms, their excavating behaviors, and their ability to select the materials needed to plug burrows.

4. Conclusion

Darwin studied behavior in an astounding diversity of species, including humans: "It is so much more interesting to observe than to write" [44: 464]. This other Darwin doubtless instructed the better-known Darwin about the processes of evolution. Whereas it was common for naturalists in his time to investigate everything related to botany and zoology including behavior, it is one thing to opportunistically collect facts, it is quite another to systematically gather data to draw general laws.

It is acknowledged that two ways of thinking, old and new, were superimposed in Darwin's thought regarding the determinism of behavior, habits and instincts. His legacy in behavioral sciences appears consequently uneven. Ruse thinks that the *Expression* is "basically material left on the cutting floor after Darwin had finished *The Descent*" [45]. Ekman considers it as "an extraordinary book, radical for his time and for today" [17]. Together with the content of the first part of the *Descent*, its continuity argument paved the way for the rise of comparative psychology (Fig. 3), and its universality argument was at the root of the debate between nature and nurture in the following century. It is not mere chance that Mead [16] and Lorenz [19] each prefaced a different re-edition of the *Expression*.

Despite the wonderful "Instinct" chapter appearing in the *Origin*, the evolutionary approach to behavior was kept in the shadow for a while. It is as if the strong seeds sown by Darwin could grow only after behavior had become a definite object of study, when Lorenz [19], Tinbergen [28], and others started to study the adaptive function of behavior. In this sense, the influence of Darwin on

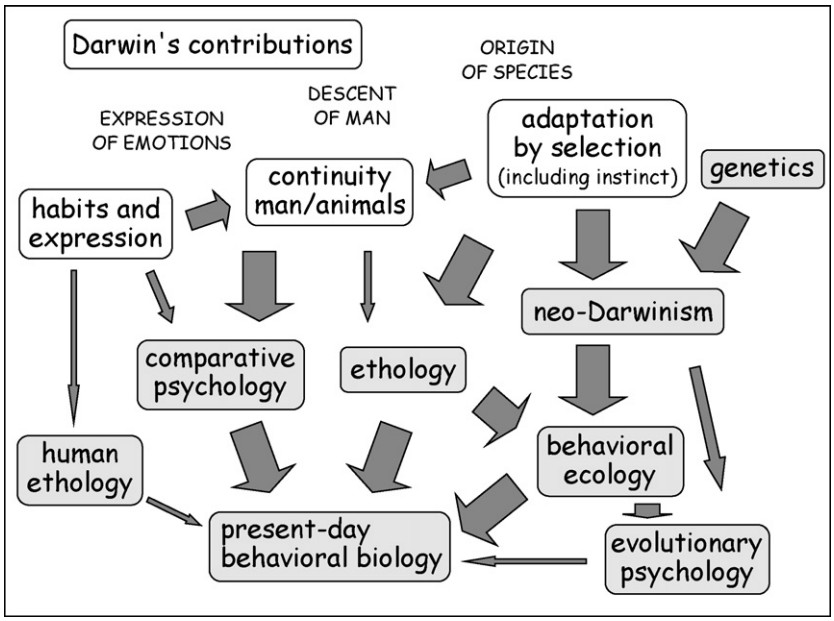

Fig. 3. Sketch of the influences of Darwinian thought upon the present biology of behavior.

behavioral biology was indirect rather than direct (Fig. 3). The same story was repeated with respect to sexual selection. The integration of Darwinism and genetics into the Modern Synthesis had first to occur in the 1930s, moving the emphasis from species to individual competition. The synthesis had still to be assimilated into the study of behavior several decades later – in the form of population biology – before sexual selection was finally recognized as a major evolutionary mechanism. Only then did it produce its full effect within the field of sociobiology [31] and behavioral ecology [25] (Fig. 3).

When *The Origin of Species* was published, palaeontology was a nascent discipline and the proofs that Darwin could draw from it were relatively limited. Conversely, the concepts provided by the theory of evolution were instrumental in the rise of palaeontological science. The same can be said for the biology of behavior. Each step of its development was sustained and enhanced by the strength of Darwinian thought. What Darwin had learned from animals' behavior thus fed back to the later study of behavior.

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