



Evolution / Évolution

Darwin's puzzling *Expression*

L'expression des émotions : un ouvrage troublant

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ABSTRACT

Charles Darwin's *The Expression of the Emotions in Man and Animals* (1872) is a very different kind of work from *On the Origin of Species* (1859). This "otherness" is most extreme in the character of the explanations that Darwin offers in the *Expression*. Far from promoting his theory of natural selection, the *Expression* barely mentions that theory, instead drawing on explanatory principles which recall less Darwinian than Lamarckian and structuralist biological theorizing. Over the years, historians have offered a range of solutions to the puzzle of why the *Expression* is so "non-Darwinian". Close examination shows that none of these meets the case. However, recent research on Darwin's lifelong engagement with the controversies in his day over the unity of the human races makes possible a promising new solution. For Darwin, emotional expression served the cause of defending human unity precisely to the extent that natural selection theory did not apply.

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R É S U M É

L'expression des émotions chez l'homme et les animaux de Charles Darwin (1872) est un ouvrage d'un type très différent de *l'Origine des espèces* (1859). Cette « étrangeté » est des plus extrêmes dans le caractère des explications offertes par Darwin dans *l'Expression*. Loin de promouvoir sa théorie de la sélection naturelle, *l'Expression* mentionne à peine cette théorie, préférant tracer des principes explicatifs qui appellent moins l'approche théorique darwinienne que celles du lamarckisme et de la biologie structurale. Avec le temps, les historiens ont proposé toutes sortes de solutions à l'intrigante raison qui rend *l'Expression* à ce point « non-darwinienne ». Un examen approfondi montre qu'aucune ne répond au problème. Cependant, les recherches récentes sur l'engagement constant de Darwin dans les controverses de son temps sur l'unité des races humaines permettent d'envisager une nouvelle solution prometteuse. Pour Darwin, l'expression des émotions servait la défense de l'unité de l'homme précisément à partir du point où la théorie de la sélection naturelle ne s'appliquait pas.

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1. Introduction

Flip the pages of Charles Darwin's *The Expression of the Emotions in Man and Animals* (1872) and one difference from *On the Origin of Species* (1859) leaps to the eye. The

Expression is full of the most remarkable images. Numerous engravings and photographs show, among other things, human faces with exposed musculature, fight-primed cats and dogs, a chimpanzee "disappointed and sulky", crying babies, well-dressed men in hammy poses, a bedraggled one with facial muscles stimulated by (sometimes visible) galvanic instruments, and a woman with frizzy hair supposedly expressive of her insanity. The *Origin* by

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contrast is visually bare. It features just one illustration, and that a schematic diagram, of the branching pattern that Darwinian species form as they diverge over time [1].

Other differences between the books are less conspicuous but no less striking. Consider the well-known division of the 19th-century biological sciences into parallel traditions, one natural-historical (think Cuvier), the other laboratory-physiological (think Bernard). Whereas the *Origin* fits comfortably on the Cuvier side of this divide, the *Expression* straddles. Its evolutionary arguments draw on the work of some of the classiest experimental physiologists of the day, including Bernard, G.B. Duchenne de Boulogne (galvanical explorer of human facial expressions), Hermann von Helmholtz, and F. C. Donders, a Dutch expert in optic physiology. In the late 1860s, Darwin collaborated by correspondence with Donders on expression, getting him to take up experimental study of the effects of strong, sudden breathing out – “violent expiration” – on the passage of blood through vessels around the eye [2]. Darwin, in the *Expression*, appealed again and again to this phenomenon in accounting for a variety of human emotional expressions [3].

Here I wish to concentrate on still another difference, to do with the explanatory projects of the books, and in particular the position in those projects of Darwin’s theory of natural selection. Developing and defending natural selection theory was one of the main burdens of the *Origin*, right up to the final, sixth edition, published in the same year as the *Expression*. And in the book from which the *Expression* was an outgrowth, *The Descent of Man*, and *Selection in Relation to Sex*, published the year before (1871), natural selection theory featured prominently. Yet it is mostly absent from the *Expression*. Indeed, Darwin instead calls throughout upon explanatory principles which, to present-day Darwinians, look distinctly “non-Darwinian”. How to explain this explanatory oddity? Several attempts have been made, and these will be explored below. We shall see that none is adequate, although understanding why will help set the stage for a

new explanation, to be sketched toward the end. At the start, a brief review of Darwin’s “general principles of expression” is in order.

2. Darwin’s three general principles of expression

The *Expression* asks how the emotions came to be expressed by their characteristic movements: crying for sadness, smiling for happiness, and so on. It opens with three chapters that respectively introduce the three principles of expression. For each principle I shall give Darwin’s name, followed by a more humble alias that I have found helpful for keeping mental hold of the principle, and then a brief exposition with an example from the book.

2.1. Serviceable associated habits (“Old habits die hard”)

On this principle, when humans and non-human animals are in the grip of an emotion, and they act in a way that gratifies or relieves – and, in this sense, “serves” – the emotion, the action and the emotion become linked. Or to put it another way, the gratifying action becomes habitual under that emotion. One such link that Darwin identifies in humans is between a fight-primed posture and an indignant frame of mind. According to Darwin, if someone insults you, you tense up, ready to fight, like the men in the *Expression*’s “indignation” photographs: head erect, mouth closed, eyebrows down in frowning mode, shoulders squared, chest out, arms rigid at the sides, fists clenched (Fig. 1). For Darwin, this link exists because going through with the action – taking a swing at the insulter – has in the past brought relief from the mental discomfort of indignation [6].

Three further points deserve mention here. First, note that, although the posture is functional with respect to indignation (it makes relief from indignation possible), the function of the posture is not to *express* indignation. On Darwin’s view, we tense up when indignant not so that others will know, even without our saying so, that we have

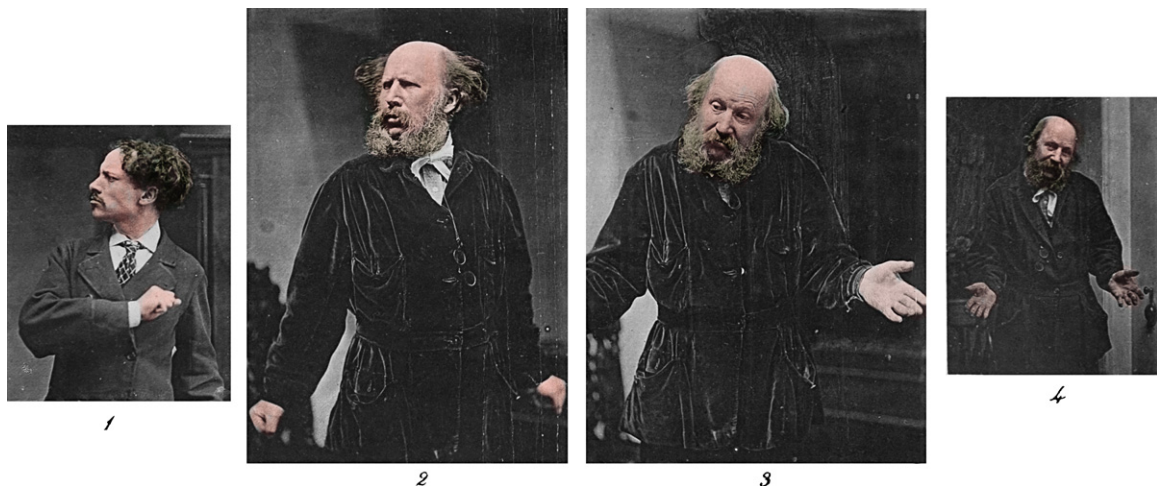


Fig. 1. Photographs from the *Expression* illustrating indignation (1 and 2) and helplessness (3 and 4) [4]. The man in the second, third and fourth photographs is the photographer Oscar Gustave Rejlander; the man in the first is probably Rejlander’s photographer friend Walter Bentley Woodbury [5]. Reproduced with the permission of the Brotherton Collection, Leeds University Library.

taken offence, but because tensing up prepares our bodies for fighting and thus gratification. Certainly the posture is communicative of the linked inner state, and certainly the posture's being communicative in this way can be functional (my insulter may immediately apologize, thus preserving the peace). But, for Darwin, communicative functioning played no role in fixing the posture – or any other emotion-linked habit – into the human expressive repertoire.

Second, once such links form, they stay formed – or, in my paraphrase, they die hard. Even when a linked action is not functional, the emotion brings the action. Look into a mirror, Darwin advises, and imagine that you have just been insulted. Your body will assume the fight-primed posture, even though there is no one to fight, and so no prospect of gratification [7]. So it is with expressions generally: by a kind of physiological inertia, actions remain tied to emotions even when the actions have long ceased to be serviceable.

The inertia acts within an individual, but also, by inheritance, within a lineage. This is the third point: action-emotion links are, for Darwin, inheritable. Hence even those of us who have never taken a punch at someone who insulted us, or have never done so often enough to have got into the habit, nevertheless tighten our fists and so on when feeling indignant. We do so, on Darwin's view, because we are the descendants of ancestors who did so, and who, in doing so, found their indignation relieved.

2.2. Antithesis (“Reverse habits come for free”)

When, thanks to the workings of the first principle, an action-emotion link comes into being, then so, at the same time, does a link between an opposite action and an opposite emotion. What is the opposite of indignation? According to Darwin, it is helplessness or impotence. Against the mental state summed up by the question “What do you mean by insulting me?”, Darwin counterposes the mental state that effectively answers “I really could not help it”. With additional photographs, Darwin shows how, point by point, the fight-primed posture expressive of indignation is reversed in the posture expressive of helplessness: head lolling, mouth open, eyebrows up, shoulders shrugged, chest sunk, elbows bent, palms and fingers open (Fig. 1). On Darwin's second principle, then, helplessness takes the bodily form it does because its opposite, indignation, takes the bodily form it does (due to the operation of Darwin's first principle) [8].

2.3. Actions due to the constitution of the nervous system (“Extreme emotion makes for excess motion”)

The idea here is that emotional extremes are accompanied by surges of nervous energy which need to go somewhere, and so discharge through whatever channels are most readily accessed. An example Darwin gives – interesting not least for illustrating the way he combined his principles in explaining the origins of expressions – is the tendency of tails to vibrate when animals become excited. He reasons that such may have been the beginnings of the rattle on rattlesnakes. Suppose, he

suggests, that there was once a snake species with a single, hard-to-cast-off scale covering the end of its tail, so that, over the lifetimes of individual snakes of this species, successive molts would result in the tail ends gradually enlarging – for such, Darwin reports, can be seen in some snake species today. As the occasionally overloaded nervous systems in these snakes dissipated excess nervous energy via tail vibration (the third principle), tail vibration would have become habitual whenever these snakes were excited (the first principle). And since rattling snakes would have had a better chance of frightening off would-be predators, any variations tending to improve the rattle's sound-producing power would have been preserved and amplified down the generations (natural selection) [9].

Nowhere else in the book does Darwin give such extensive, positive notice to natural selection. He mentions it only from time to time, and then, for the most part, as an explanation of last resort or as probably having little or nothing to do with the origin of what he is discussing. I shall draw attention to one invocation along the latter lines below. For now, it is enough to stress how fully Darwin relies in the *Expression* on the three general principles above, and how awkwardly they fit with common notions of what counts as “Darwinian”. Reckoned against the standard 19th-century evolutionist “isms”, these principles are far more Lamarckian and structuralist. Habits are acquired and then inherited not because habits adapt organisms to their environments but because bodies are habit-forming and habit-inheriting. Bodies being as they are, structured in certain ways, likewise explains why habits generate their opposites and why excess motion follows from extreme emotion.

The upshot is a picture of animals, and above all humans, as helplessly, pointlessly expressive of their emotions. On the whole, we express emotions as we do because we are descended from creatures whose bodies packaged those emotions with those actions – not, again, because those packages helped our ancestors, or help us, become ancestors, by somehow improving abilities to survive and reproduce, but simply because of the nature of bodily construction in our region of the tree of life. For Darwin, emotional expressions are, in this sense, supremely non-adaptive. The challenge is to understand why he thought so.

3. Explaining the *Expression*: a brief critical history

Why did Darwin exclude adaptive considerations, and thus natural selection theory, so comprehensively from his treatment of expression? Several historians of science have had a crack at the problem. One is Richard Burkhardt, Jr., who wrote on it in the mid-1980s [10], and whose answer continues to circulate thanks to various endorsements, especially the one in the anthropologist Paul Ekman's generously annotated 1998 edition of the *Expression* [11]. For Burkhardt, the key is Sir Charles Bell's creationist view of emotional expression. In his famous study of the “anatomy and philosophy” of expression, Bell had argued not only that emotional expression in humans was discontinuous with emotional expression in animals, but that the human face had muscles specially designed for the

purpose of expression [12]. Concerned to undermine Bell, Darwin “appears to have overreacted”, wrote Burkhardt. In the *Expression*, Darwin made impressive cases for continuity (by showing how the same principles applied equally to animals and humans) and for evolution (by supplying expressions with gradual, natural origins). But he threw the Darwinian baby out with the creationist bathwater in further denying that expressions have any communicative function, “thereby leaving himself ill-disposed to develop an idea that would later be advanced by the ethologists of the 20th century – the idea that certain expressive actions, whatever their primary origin, had been developed over time by natural selection” [13].

Undeniably Bell’s creationism was a major target in the *Expression*. Darwin wrote as much, there and elsewhere. Furthermore, Burkhardt makes a valuable supplementary point in stressing that, by the time of the *Expression*, Darwin had become unprecedentedly and publicly self-critical about what he saw as a tendency in his earlier work to assume adaptedness, and so to exaggerate the explanatory scope of natural selection. If ever, then, Darwin watchers might have expected a book emphasizing non-adaptive phenomena, explained non-selectionally, it was around the time of the *Expression*. Even so, and as Thomas Dixon pointed out in his study of the emergence of “emotion” as a psychological category, Burkhardt’s over-reaction explanation takes us only so far [14]. For one thing, the *Descent of Man* – in which the self-criticism appears, and from which, recall, the *Expression* grew – is a thoroughly adaptationist and selectionist book, though no less anti-creationist than the *Expression*. Granted that Darwin was more prepared than ever to discuss non-adaptive evolution, we still need to know why he judged emotional expression in particular to fall among the non-adaptive phenomena – and this despite expression being, from the perspective of later Darwinians (Ekman’s frustrated commentaries in his edition are instructive here), eminently suited to adaptive, selectional analysis. To put the point another way: given that creationist opponents could be found all over the scientific shop, we need to know what it was about emotional expression, as distinct from the many other human topics that Darwin handled at this time, which prompted Darwin to “overreact”.

A second explanation, of the same vintage as Burkhardt’s, is due to William Montgomery [15]. He stresses the evidence of Darwin’s post-*Beagle* notebooks of the late 1830s, in particular the M and N notebooks, dedicated to expression and other “metaphysical” topics (that is, to do with the theory of mind). In the M notebook, filled between July and early October 1838, Darwin stated what can now be identified as the first two of his three general principles of expression [16]. Indeed, it is clear from the notebooks, as it is not from the *Expression*, that Darwin’s associationist-evolutionary approach to expression was taken over from the *Zoonomia* (1794–6) of his grandfather, Erasmus [17]. For Montgomery, just as significant as the intellectual character of these notebook entries is their timing. In his view, they show that Darwin’s basic approach to expression was hammered out *before* he developed, from late 1838, his theory of natural selection. According to

Montgomery, the non-Darwinian character of the *Expression* is thus explained by the fact that its explanatory principles predate natural selection theory and, apparently, never struck Darwin as in need of replacement in the years that followed. “These principles survived intact”, wrote Montgomery, “because they served a useful purpose in his case against Bell and because he (Darwin) faced no serious counterarguments” [18].

Again, we have here an insightful account which nevertheless falls short of solving the puzzle. Having *Zoonomia* in view as a major private source for Darwin on expression helps hugely in making sense of the later, public theorizing as a product of the same mind, indeed the same creative period, that produced natural selection theory. With the Erasmian roots of the *Expression* thus exposed, we can even, in a kind of reflexive homage, go beyond Montgomery and see the book as the result of associations formed during Darwin’s medical student days at Edinburgh, when he became an admirer of *Zoonomia* (under the influence of his Lamarckian mentor Robert Grant [19]), and when, at the 17-year-old’s first meeting as a member of the student natural history society in late 1826, he watched his sponsor deliver a paper aiming to refute Bell on expression [20]. What needs supplementing, however, is Montgomery’s claim that Darwin’s expression principles survived from the 1830s to the 1870s “because he faced no serious counterarguments”. In support, Montgomery notes that Darwin in the late 1850s abandoned a Lamarckian explanation of instinct in social insects for a natural-selectional explanation when he realized that the latter dealt satisfactorily with an outstanding difficulty (the origin of sterile workers). So, since Darwin never abandoned his Lamarckian explanation of expression, he must, Montgomery argues, never have encountered any similar, selection-resolvable difficulty [18].

But the comparison with the insect case is inapt. There Darwin concurred with the opinion of natural-theological writers on the adaptive value of the phenomenon, and merely switched allegiance from one design-undermining explanation (based on habit inheritance) to a different one (based on chance variation and natural selection among groups) [21]. With expression, however, Darwin dissented not just from the design explanation, but from the description of the phenomenon as adaptive. What needs explaining is his dissent on the description. One might, drawing on Montgomery, reply on his behalf that Darwin simply took over his sense of the nonadaptive origins of expression from his grandfather’s work, alongside the associationist explanatory style. Up to a point, that seems right; but again, it only puts back a crucial and unanswered question, namely, why Erasmus should have been treated as authoritative on this topic but not on so many others. And in any case, it was not generally true of Darwin that he gave up on theories only when they had run into difficulties. It seems, for instance, that in 1838 he dropped his earlier theorizing on species origins for natural selection theory without there having been some outstanding problem for which natural selection provided an answer [22].

A more subtle problem with Montgomery’s account, and Burkhardt’s too, is that they do not really capture

Darwin's positive attitude in the *Expression* to his own explanations. The book does not read as if Darwin is using non-selectional resources inadvertently or *faute de mieux*, as if he had never gotten around to seeing that natural selection theory might, in fact, be the better option. Something about Darwin's expression principles made them, in Darwin's circa 1870 perspective, the right tools for the job, in preference to natural selection theory. But what? In a 2002 article, I suggested that Darwin's deep loyalty to the *vera causa* methodological ideal had a bearing here [23]. To conform one's theorizing to this ideal was to show, well before giving a causal explanation, that the specified cause was real (not merely hypothetical) and adequate to producing effects of the right magnitude. Hence the premium, for the *vera causa* theorist, on explanations that drew upon causes whose action had been observed or, if not observed, inferred by analogy from the observed. Simply in the way Darwin structured the *Expression*, with his explanatory principles laid out first and argued for in a general, expression-independent way, the book is a *vera causa* book. But it is also so, I urged, in placing habit formation at the explanatory center. Circa 1870, it was a matter of common observation that habits form and die hard; it was equally a matter of common observation (or so the likes of Darwin believed) that these habits could be inherited. By contrast, the observational credentials for what natural selection theory required – spontaneous changes in brains, such that certain emotions became linked to certain movements – were feeble.

By way of backing this view, I cited a passage from the book's conclusion. "Some expressive movements", wrote Darwin, "may have arisen spontaneously, in association with certain states of the mind ... and afterwards been inherited. But I know of no evidence rendering this view probable" [24]. Here Darwin explicitly considered and rejected, as evidentially wanting, the possibility that inborn, inheritable variation – the *sine qua non* of natural selection – had played a role in bringing into being at least some of the expressions for which he had supplied habitual origins. So taking seriously Darwin's career-long respect for well-evidenced argumentation can help us take seriously his own regard for his expression principles and their non-selectional character. But it cannot, in the end, do any better in explaining the *Expression's* explanatory project than Burkhardt's or Montgomery's analyses did. After all, Darwin did not in general think that selectional explanations of animal behavior failed to meet the *vera causa* standard (consider the insect-instinct case). His judging that selection theory nevertheless fell short for expressive behavior thus requires further explanation on the historian's part. What lay behind Darwin's judgment? Why not switch to adaptive descriptions and selectional explanations once natural selection theory – Darwin's explanatory pride and joy – was around?

4. Toward a new explanation: expression, natural selection, and human unity

New light on these questions has come in this Darwin anniversary year with the publication of Adrian Desmond and James Moore's *Darwin's Sacred Cause: Race, Slavery*

and the Quest for Human Origins [25]. Opposition to black slavery was a tradition in Darwin's family, going back to Erasmus's day. (Darwin's other grandfather, the pottery magnate Josiah Wedgwood, manufactured the famous "Am I not a Man and a Brother?" antislavery cameo.) So much is long familiar. But no one previously has brought out the depth of Darwin's immersion in the crusading world of British antislavery or – the truly far-reaching point – the intellectual consequences of that immersion. Confronting slavery in the first half of the 19th century meant confronting the scientific arguments developed to defend it, including the view that blacks could be enslaved because they belong to a different, inferior species, derived from an aboriginally distinct stock. Against such pluralism about the human races/species, antislavery campaigners upheld the "unity of man", arguing for the shared ancestry of the races, and their status as races within a single species. For Darwin, as Desmond and Moore show, there was never any serious doubt about which side of this debate he was on. Darwin was a unity-of-man man from the beginning. Nor did his commitment ebb after slavery was finally outlawed in the British Empire in the 1830s. Slavery in the United States became the focus, and kept antislavery passions inflamed well into the 1860s.

Desmond and Moore reconstruct the manifold impact of Darwin's antislavery attitude on his species theorizing, from his days on the *Beagle* voyage through to his writing of the *Descent* [26]. Given this time frame, the *Expression* falls outside their purview. Yet it looks an obvious fit for their theme, since the documenting of the unity of the human races is, for Darwin, one of the major results of the book. Mindful as ever of *vera causa* etiquette, he is careful to represent such documentation as a result – an incidental but welcome spin-off of an inquiry otherwise directed. He explains in his introduction that his interest in human races and emotional expression is in the first instance an interest in sorting "innate or instinctive" expressions from those which, like languages, are acquired conventionally, on the view that if lots of different races express the same emotion in the same way, the expression is probably innate. To this end, he had sent a questionnaire on expression to correspondents around the world, 36 of whom had replied. "It follows, from the information thus acquired", wrote Darwin, "that the same state of mind is expressed throughout the world with remarkable uniformity; and this fact is in itself interesting, as evidence of the close similarity in bodily structure and mental disposition of all the races of mankind" [27].

Darwin's efforts in the *Expression* on behalf of the universality of human emotional expression are well remembered, not least thanks to Paul Ekman's experimental updating of Darwin's investigation. Less well remembered is that, in Darwin's view, universality was not enough to establish human racial unity. The trouble was that an emotion-expression package could come to be universal in one of two ways, with different consequences for human unity. Either the package was a common inheritance from a shared ancestor. Or it was independently derived in different human groups via natural selection, acting to preserve beneficial chance variation as

it arose independently in these groups. Under the common-inheritance interpretation, humans are unified. Under the natural selection interpretation, humans are not unified. So how to choose?

For Darwin, the choice turns on the closeness of the similarity in emotional expression in the different races. And on the evidence collected, as he interprets it, the similarity is indeed close, to the point of constituting identity, sameness. Darwin put the point as follows in his conclusion:

“I have endeavoured to show in considerable detail that all the chief expressions exhibited by man are the same throughout the world. This fact is interesting, as it affords a new argument in favour of the several races being descended from a single parent-stock, which must have been almost completely human in structure, and to a large extent in mind, before the period at which the races diverged from each other. No doubt similar structures, adapted for the same purpose, have often been independently acquired through variation and Natural Selection by distinct species; but this view will not explain close similarity between distinct species in a multitude of unimportant details. Now if we bear in mind the numerous points of structure having no relation to expression, in which all the races of man closely agree, and then add to them the numerous points, some of the highest importance and many of the most trifling value, on which the movements of expression directly or indirectly depend, it seems to me improbable in the highest degree that so much similarity, or rather identity of structure, could have been acquired by independent means. Yet this must have been the case if the races of man are descended from several aboriginally distinct species. It is far more probable that the many points of close similarity in the various races are due to inheritance from a single parent-form, which had already assumed a human character.” [28].

Darwin here flags the novelty of this argument for human racial unity as well as the importance for the argument of emotional expression turning out to be beyond the reach of natural selection. Yet this passage, along with the racial element in the *Expression* generally, have been overlooked by commentators curious about the non-selectional character of the book. The temptation has been to treat Darwin's unity argument more or less as Darwin presented it – as a nice surprise, noticed at the end of the inquiry, and of no more interest than lots of other points Darwin raises in his conclusion. Desmond and Moore's historical *tour de force* makes plain that whether humans are one species or many was not, for Darwin, just another question. To have developed a new argument for human racial unity would have mattered a great deal to him. It was not something that would have caught him unawares. And although we do not know when he first understood that emotional expression could serve such an argument, or that natural selection could undermine it, a good bet is that he understood these things long before he wrote the *Expression*, and that his resolve to stick with non-functional descriptions and non-selectional explanations firmed up accordingly.

Above I mentioned Thomas Dixon, who wrote a pioneering analysis of the *Expression* historiography. There he formulated two desiderata for a good explanation of the *Expression*. First of all, it needs to make intelligible the division of labor between the *Descent* and the *Expression*. Second, it needs to explain why, for all Darwin's indifference and even hostility to natural selection theory in the *Expression*, he nevertheless grants it a role in the explanation of some emotional expressions [29]. On both counts, the human-unity explanation does rather well. To take first the question of why Darwin invokes natural selection theory when he does, consider Darwin's calling upon it to explain the evolution of the rattlesnake rattle but not the evolution of the human indignation posture. As noted previously, that posture has an obvious functionality, and would thus seem susceptible of elaboration via natural selection. Yet Darwin does not go there. Generalizing, one can say, on the new explanation, that Darwin was prepared to acknowledge a contribution from natural selection only for emotional expressions where human unity was not at stake – as it was not at stake with the rattlesnake rattle, or the various anatomical means by which frightened animals make themselves appear larger [30]. A good test of the correctness of this view is whether Darwin in the *Expression* deploys natural selection theory occasionally in explaining animal expressions but never in explaining human ones. And such is indeed the pattern, as William Montgomery pointed out – though he offered little insight into why the pattern holds [31].

On the *Expression's* relationship to the *Descent*, the human-unity explanation promises to revise substantially our understanding of how these books hang together. For of course, and as Desmond and Moore emphasize, Darwin in the *Descent* was very much concerned to defend the unity of the human races. Moreover, Darwin's *Descent* case for unity was just as dependent as in the *Expression* on some traits – external differences between the human races (skin color and so on) – being characterized as non-functional in the struggle for survival and therefore outside the domain of natural selection [32]. And again as with the *Expression*, Darwin in accounting for these non-functional traits introduced a distinctive set of explanatory principles, the “principles of sexual selection” (to quote Darwin's chapter title [33]), which he propounded in a general way before making the case for their real action, first among non-human animals, then finally among humans. With such commonalities in view, we can now see Darwin's human evolution project as extending over three separate books, each centered on a different set of questions and a different set of explanatory principles: one on how ancestral humans originated from non-human animals via natural selection (*The Descent of Man*); one on how those ancestral humans diverged into the separate but still human races via sexual selection (*Selection in Relation to Sex*); and a third on how, throughout all that divergence, a common legacy of emotional expressions remained constant, after initial fixing via habit-formation and -inheritance (*The Expression of the Emotions in Man and Animals*).

It would have made sense, as Darwin intended, for these three inquiries to be published as parts of a single book

[34]. Contingencies of production (what he wrote first) and publication (what he reckoned his publisher was willing to publish in one go) no doubt contributed to the appearance of these inquiries as we have them, in a form that invites readers to see an illusory homogeneity between the first two, and an illusory heterogeneity between those two and the third. By restoring Darwin's abiding concern with human unity to our picture of him, we thus recapture Darwin's own sense of the intellectual unity across the apparently disparate parts of his argument on human evolution.

5. Conclusion

The solution proposed here to the puzzle of Darwin's *Expression* – that behind the steadiness of his belief in the non-functional character of emotional expression lies his commitment to human racial unity – does not, if correct, render previous solutions defunct. As we have seen, each illuminates different aspects of Darwin's text and its context. But in the *Origin's* 150th year, it is especially appropriate to contemplate a solution that binds that book's one, spare illustration of the tree of life with the *Expression's* many, extravagant ones on behalf of the same. Indeed, if in the *Expression* Darwin felt that he could bolster the case for common ancestry only by limiting the scope of natural selection theory, then we have a new reason to take up the recent attempt to unpick what Darwin represented in the *Origin* as “one long argument” [35]. An anniversary that inspires rereadings along such critical lines will have been well spent.

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