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Editorial: Charles Darwin, Jean-Baptiste Lamarck, and 21st century arguments on the fundamentals of biology

1. Introduction

This volume of *Progress in Biophysics and Molecular Biology* publishes an article by Peter Corning on "Beyond the Modern Synthesis: a framework for a more inclusive biological synthesis" (Corning, 2020). Corning challenges some of the key assumptions of 20th century biology, by implication asking whether they are any longer relevant to the discoveries of the 21st century. He also proposes an alternative paradigm.

Corning's article reinforces and expands on the recent editorial article in this journal by Keith Baverstock (2019). Baverstock's analysis of the failure of genomics to live up to its 20th century promise of a "cure for all diseases" complements Corning's thesis of the parallel failure of gene-centric evolutionary biology to deal with many evolutionary mechanisms that have been discovered but which did not feature in the Modern Synthesis. Both amount to a call away from the gene-centric approach towards the multi-scale approach that has often featured in this journal, which is one reason why we welcome the debate on these issues. The multi-scale approach is precisely how the links between cell/systems biophysics and molecular biology need to be explored (Noble and Hunter, 2020). They are the two main foci of this journal, evident in its title.

Indeed, many previous articles in this journal and elsewhere have highlighted the advantages of multi-scale approaches. What is new in the Corning and Baverstock articles is a sense of urgency. Baverstock makes that clear in his warning of a "public health hazard" in the title. In the case of the Corning article it is clear in his forthright statement that "the Modern Synthesis obscures and sometimes seriously misrepresents the underlying causal dynamics in living systems, and in evolution. It has become an obstacle to our continued progress in understanding the evolutionary process … it is time to change the basic paradigm."

How can that urgency be addressed? *Progress in Biophysics and Molecular Biology* is open to one of the ways: by welcoming responses to such articles. The journal has recently established itself as such a medium in other controversial fields of biophysics and molecular biology and is ready to do so again. Offers to contribute to these discussions with further articles or commentaries, whether for or against the published articles may be addressed to the editors. To help in ensuring fairness of refereeing, we always use one or more of the referees proposed by authors, particularly if they are from different countries than the author.

In this Editorial I aim to stimulate that debate by presenting some historical ground-clearing on evolutionary biology in relation to the article by Peter Corning in this issue.

2. First a caricature of what we all learnt

Here is what I, and millions of others, learnt in school biology in the mid-20th century from textbooks and teachers steeped in the Modern Synthesis. We were taught that first came Lamarck in 1809 (Lamarck, 1994) who championed the idea of evolution of species one from another, but who made three grave errors:

- first that organisms tend to evolve towards greater complexity, on which he adopted the idea of a ladder of life[1]
- second that this is attributable to a life force (*le pouvoir de la vie*);
- third that organisms evolve by passing their acquired characteristics to their offspring.[2]

Along came Darwin in 1859 (Darwin, 1859) who sorted out all of these errors by replacing Lamarck's adherence to the ladder-of-life concept with the tree of life, and removing the need for a life force. What else does *natural* selection mean? Finally, he was represented as rejecting Lamarck's inheritance of acquired characteristics. This story was drilled into us by teachers who enjoyed amusing us by mocking Lamarck's 'idiocy' (Grove and Newell, 1944 chapter XIX). How could he have been so stupid? And we did indeed all laugh as teenagers.

One way of explaining the urgency is to show why that laughter rings hollow today. For a careful examination of the history tells a very different story. That history also vindicates Corning's statement above that the Modern Synthesis and the ways in which it is presented even today in the standard textbooks have "become an obstacle to our continued progress in understanding the evolutionary process."

3. Darwin's cautious humility

Charles Darwin was notoriously cautious – a very careful slow scientist. He took over two decades following his voyage in *The Beagle* (1831–36) to arrive at his conclusions and the formulation of his theory of evolution by natural selection.

After finishing *The Origin of Species* he wrote to the geologist Charles Lyell:

[1] An idea, incidentally, that dates way back to antiquity (Voss, 1952). "The history of keys and phylogenetic trees in systematic biology." J. Sci. Labs. Denison University **43**: 1–25, Kull. (2003). "Ladder, tree, web: The ages of biological understanding." Sign Systems Studies **31**: 589–603.

[2] The inheritance of acquired characteristics – this idea also was not invented by Lamarck. It was assumed by many biologists, including Darwin.

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> "I suppose that I am a very slow thinker, for you would be surprised at the number of years it took me to see clearly what some of the problems were, which had to be solved — such as the necessity of the principle of divergence of character—the extinction of intermediate varieties on a continuous area with graduated conditions — the double problem of sterile first crosses & sterile hybrids, &c &c —".

The Origin of Species was published in a hurry in 1859 only because Wallace was hot on his heels with a very similar theory. A further example of Darwin's caution is found in a letter that he sent to the explorer and natural historian Moritz Wagner much later in 1876:

> "In my opinion, the greatest error which I have committed, has not been allowing sufficient weight to the direct action of the environment, i.e. food, climate, etc., independently of natural selection."

His doubts seem to have increased with time, not the reverse. Note also that he refers to the *direct* action of the environment, *independently* of natural selection. This is extraordinary, given the strong bias in favour of attributing everything to natural selection in the early versions of the Modern Synthesis (for a brief summary of the ways in which The Modern Synthesis has since been extended and why it needs replacing see (Noble, 2016 chapter 5).

This is one, but by no means the only, reason that it would be wrong to view the full range of Darwin's work as well-represented in the Modern Synthesis. Nor is his work well-represented in the dogmatic certainties of many of its popularizations. That is why I have emphasized Darwin's caution and humility. He was not afraid of publishing because of the expected outcry. He was afraid because of his own doubts. The caution and humility came from within himself.

4. What did Lamarck actually show?

Lamarck was a very different character, as he had to be in the ferociously critical intellectual climate of 19th century Paris. But he, like Darwin, was also deeply concerned about whether his theories were correct. So much so that, when I first read his 1809 *Zoologie Philosophique* in his own language, I could hardly believe what I was seeing. Lamarck was the first to propose a branching Tree of Life! It is there in a diagram on page 649 of the Flammarion Press 1994 reprint of Lamarck's book (Lamarck, 1994). This is so important that I reproduce an image of that page as Fig. 1.

This diagram not only predates Darwin's famous "B" notebook diagram by 28 years, it is specific about which large animal groups developed from which, and how they branched. The difference in the two tree diagrams lies in the range of species to which they are applied: to the Galapagos finches in Darwin's notebook tree; to a different range of life forms in Lamarck's tree. Darwin's tree is also significant because the Galapagos studies led to his idea of geographical separation being a mechanism for speciation. But in both cases the idea is descent from a common ancestor.

Yet modern textbooks on evolution still claim that "Darwin's conception of the course of evolution is profoundly different from Lamarck's in which the concept of common ancestry plays no part." (Futuyma and Kirkpatrick, 2017 page 13). If by "common ancestry" we mean common to the specific tree diagrams then this statement is simply not true. It is true that Lamarck envisaged multiple origins of life, whereas modern evolutionary biology supposes a universal common ancestor. Although Darwin introduced this idea, he also hedges his bets. At the end of *The Origin of Species*

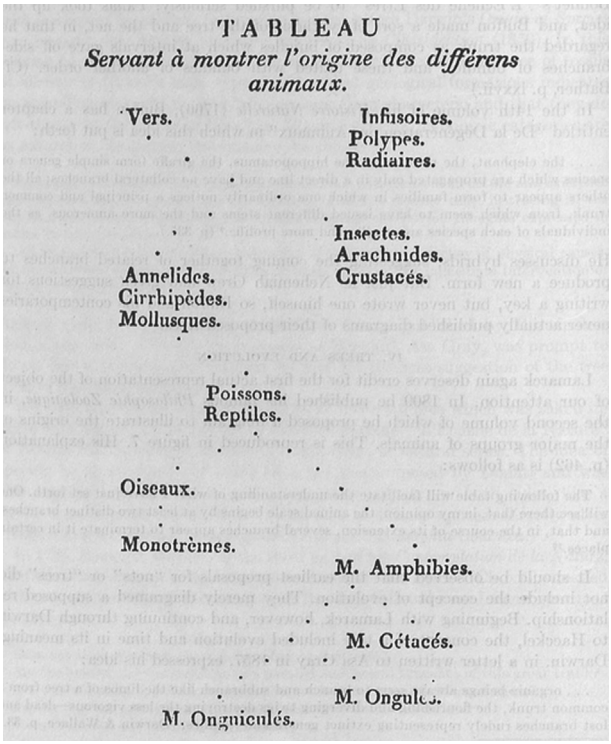

Fig. 1. Lamarck's Tree of Life, from *Philosophie Zoologique*, 1809. The root of the tree is at the top (vers = worms). There are then several branchings leading to many different kinds of animals. The edition in which I first saw this tree diagram was the Flammarion reprint of 1994 in which the dotted lines have been replaced with full lines. This version is taken from Voss (1952) and originally copied from the 1830 reprint. I use this version as a tribute to Voss' careful historical study of keys and trees in evolutionary biology.

he refers to life having been "breathed *into a few forms or into one*" (my emphasis). As I have noted in a previous editorial in this journal we still do not know which of these is correct (Noble, 2019). This is a very important open question that might be answered during exploration of our solar system for whatever forms of life we may find on other planetary bodies.

Why is Lamarck's tree not acknowledged in *The Origin of Species*? I rather suspect that Darwin never read the end of Lamarck's book. Had he done so who could doubt that he would have nodded in agreement? When I first made this discovery, I also wondered why it is not more widely known (actually it is acknowledged in several publications – (Bowler, 1984; Archibald, 2009; Hellström, 2012) (Voss, 1952; Misra, 2011; Oxenham, 2015). But then I recalled that Steven J Gould praised Lamarck in one of his books. I was right. It is in one of his last books (Gould, 2000). Not only does Gould refer to Lamarck's tree of life (though he does not reproduce the diagram), he comments:

> How can we view his [Lamarck's] slow acknowledgement of logical error, and his willingness to construct an entirely new and contrary explanation, as anything other than a heroic act, worthy of our greatest admiration and identifying Lamarck as one of the finest intellects in the history of biology?

Nor was the idea simply a passing whim in Lamarck's work. The 1809 diagram is just an addendum to his *Philosophie Zoologique*. But he developed the tree idea further in two subsequent books: *Histoire naturelle des animaux sans vertèbres* (Lamarck, 1815–1822) and in *Système analytique des connaissances positives de l'homme* (Lamarck, 1820), particularly pages 134–148 where he writes:

> The polyps … seem to divide into three branches'; ' … the crustaceans come from another branch separate from the arachnids'; ' … the reptiles … another branch seems to lead to the lizards, towards the mammals' (my translations)

Lamarck freely refers in French to *branche or branchement,* which is a further reason why I feel sure that his Tree concept does indeed involve successive branchings from common ancestors. The difference from Darwin is that he did not formulate geographical separation as a speciation process.

5. Did Darwin disagree on the inheritance of acquired characteristics?

Once again, I have had to delve deep into the history to find the answer. The answer is an unequivocal no. First, even a casual reading of *The Origin of Species* shows that it freely assumes the inheritance of acquired characteristics. Mayr, in his magisterial book (Mayr, 1982), identifies 12 places where this is the case. As the letter (above) to Moritz Wagner shows, this issue was one that fed Darwin's doubts and caution for many years. In his 1868 book (Darwin, 1868), he formulates his theory of gemmules, in which he solves his problem in almost exactly the same way as Lamarck did. Puzzled by the same question, which is how information from the soma could be transmitted to the germ-line, he postulated the existence of invisible "subtle fluids". Darwin's gemmules perform the same function as Lamarck's fluids.

But do they exist? This is a question as big as the one that followed the discovery of the circulation by William Harvey. That question was solved by the development of the light microscope and the discovery of microscopic capillaries. We have had to wait a long time for light microscopy to achieve the much higher resolution needed to view what are almost certainly Darwin's postulated gemmules. They have now been seen, they are numerous, and they are called exosomes. These are tiny extracellular lipid vesicles (EVs) packed with RNAs, DNAs and other molecules that contain information on the regulatory state of the genome from the cells that extruded them. It has taken a remarkable 10 fold increase in the resolution of light microscopy to visualise them (Edelstein et al., 2019).

Just as Darwin postulated, exosomes can transmit their RNAs, DNAs and other molecules to the germ-line, so crossing the Weismann Barrier, which was supposed by him and the founders of the Modern Synthesis to prevent precisely this transmission from happening. This is a profound break from the fundamentals of the Modern Synthesis. It is therefore important now to discover experimentally what transgenerational effects can be attributed to exosome uptake by the germline. There is a whole new field of research rapidly opening up here. The implications for the inheritance of disease states are important (see e.g (Rehan et al., 2013).

Darwin and Lamarck did therefore agree on at least some aspects of both the Tree of Life and the inheritance of acquired characteristics. Yet, we find no sign of this agreement in modern textbooks. Instead we find the categorical statement that "Lamarck's ideas of how evolution works were wrong." (Futuyma and Kirkpatrick, 2017 page 10). Darwin's gemmule theory is not even mentioned. If Lamarck was wrong on this issue then Darwin was also. Textbook writers cannot have it both ways. I think both were right. Research to test that belief is now required.

6. Is evolution by "natural" or "artificial" selection?

What about Lamarck's active force giving a direction to evolution? This is more controversial. Again, we need to note yet another of Darwin's puzzles. He realised that sexual selection (Darwin, 1871) was not "natural" selection, since the whole point of the theory of natural selection was that it was in contrast to "artificial" selection by human breeders of dogs and other species. The problem is that artificial selection is clearly directed by the organisms, humans, doing it. If that is so, then all selection of mates and other forms of discrimination between organisms by other organisms, e.g. (Leimgruber et al., 2016; Essler et al., 2017), also gives a directionality to the evolutionary consequences they entail. There is no clear biological reason for attributing what we might call 'directed' selection only to the human species.

Peter Corning also addresses this question in his article when he writes "humankind has become an increasingly important cause of natural selection over time, in many different ways." What then is natural about 'natural' selection? I suspect this is one of the reasons Darwin himself was so puzzled when he addressed issues raised by sexual selection. These puzzles largely dissolve when we realise that the term "natural selection" is itself a metaphor. There can be no hard and fast distinction between "artificial" and "natural". The rough and ready distinction we can draw is between what is done by an agent, whether human or not, and what is just a passive reaction to the environment. Moreover, now that humans have become so dominant in the environment, most selection becomes seen as agent-driven. Our species is itself now one of the great drivers of evolutionary change. As Corning says, this also was not anticipated by the founders of the Modern Synthesis. Agency has now become one of the biggest causes of evolutionary change. That also is a major conceptual break from the standard theory.

Moreover, the directionality in agent-driven selection does not come from ideas of Intelligent Design or Creationism. It comes from within organisms themselves just as Darwin's sexual selection idea says. Lamarck would have agreed. It is not widely-enough known that he was a materialist, strongly opposed to vitalism and similar theories (Pichot, 1994). His form of directionality was also viewed as a *natural* characteristic of organisms, and was far from any metaphysical speculations.

I am therefore left wondering what is left that seriously distinguishes Darwin and Lamarck. Of course, there is much else that Darwin contributed. That is not in question. But on the three central questions that concern us here, they were in essential agreement. It is not surprising therefore that in the preface to the 4th Edition of *The Origin of Species*, Darwin acknowledges Lamarck as a "justly celebrated naturalist …. who upholds the doctrine that all species, including man, are descended from other species." Yet our textbooks still claim that only Darwin had the concept of "common ancestry" – descent from other species.

7. Who did disagree?

That question is easy to answer. Darwin's acceptance of the inheritance of acquired characteristics was expunged from evolutionary biology by the 19th century geneticist, August Weismann. He specifically says so in his 1883 lecture:

> "In my opinion this [the hereditary substance] can only be the substance of the germ cells; and this substance transfers its hereditary tendencies from generation to generation, at first unchanged, and always uninfluenced in any corresponding manner, by that which happens during the life of the individual which bears it. If these views … be correct, all our ideas upon the transformation of species by means of exercise (use and disuse), as proposed by Lamarck, and accepted in some cases by Darwin, entirely collapses." (Weismann, 1889)

This lecture, and his formulation of the Weismann Barrier

became a cornerstone of the Modern Synthesis, which was formed by a fusion of the Barrier idea with Mendelian genetics (Noble, 2016 pp 126–133). The synthesis was published in 1942 in a famous book by Julian Huxley (1942). That book is often presented as a landmark since it "ended the eclipse of Darwinism and supplanted a variety of non-Darwinian theories of evolution."[3]

I hope I have shown that this is not true. The history shows that Charles Darwin's views of evolution included what are incorrectly referred to as "non-Darwinian theories of evolution." If this phrase refers to the inheritance of acquired characteristics, as I feel sure it does, then Darwin and Lamarck largely agreed. They would both be celebrating the discovery of their "invisible" fluids or gemmules in the modern visualisation of exosomes and their transmission of regulatory information to the germline.

Peter Corning has carefully laid out the challenge in his article, which I believe should be widely-read. The ball is now in the court of those who wish to defend the Modern Synthesis. The journal is open to articles for or against Peter Corning's article.

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[3] See https://en.wikipedia.org/wiki/Evolution:_The_Modern_Synthesis.