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ORIGINAL PAPER

Of germ-plasm and zymoplasm: August Weismann, Carlo Emery and the debate about the transmission of acquired characteristics

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Abstract In this essay I discuss the contents and the context of Italian zoologist and entomologist Carlo Emery's discussion of the germ-plasm theory. August Weismann considered him one of his very few creditable supporters, and encouraged him to publish his theoretical reflections. In his *Gedanken zur Descendenz- und Vererbungstheorie,* which appeared between 1893 and 1903 as a series of five essays in the journal *Biologisches Zentralblatt*, Emery developed a very personal account, applying the concept of determinants to problems like atavism, sexual dimorphism, speciation, geographical isolation, transmission of characters, and putting forward, as early as 1903, the idea of a genetic program.

Keywords August Weismann · Carlo Emery · Neo-Darwinism · Lamarckism · Inheritance · Caste differentiation

For Christiane,
the heart and the spirit
of the Archivio Storico

In the preface of his last book but one, *Vorträge über Descendenztheorie* (1902–1903), August Weismann (1834–1914) complained that his germ-plasm theory had not found the positive response it deserved, noting only two prominent adherents:

> Notwithstanding much controversy, I still regard its fundamental features as correct, especially the assumption of "controlling" vital units, the determinants, and their aggregation into "ids;" but the determinant theory also implies

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germinal selection, which rejects the unfit and favours the more fit, [and] is, to my mind, a mere torso, or a tree without roots. I only know of two prominent workers of our days who have given thorough-going adherence to my views: Emery in Bologna and J. Arthur Thompson in Aberdeen. But I still hope to be able to convince many others when the consistency and the far-reachingness of these ideas are better understood. (Weismann 1904, I, viii; Weismann 1902, I, vi)

The second of the two adherents mentioned by Weismann was John Arthur Thompson (1861–1933), a Scottish veterinary and science populariser, who had translated the *Vorträge* into English and was later suspected of vitalism. The former was Carlo Emery (1848–1925), a recognised authority of entomology, in particular the study of ants (Sleigh 2007).[1] Weismann encouraged him to develop and publish his reflections on heredity and development. Yet, Emery's support was not as helpful as Weismann had hoped. Firstly, because Emery—though pleased with Weismann's words and inspired by his germ-plasm theory—was likewise eager to distance himself from some of its positions. Secondly, because Emery's own ideas did not meet with a broad consensus either. Even present-day accounts of the Darwinian debate in Italy in the late nineteenth century either do not mention him (see e.g. Pancaldi 1983; Corsi and Weindling 1985; Brömer 2008), or else just list his name among others (Landucci 1996). The only exception is Silvia Caianiello and Christiane Groeben's volume on *Darwinism in Naples* (2009). Still, Emery was one of the best-known Italian zoologists of his time, and open to polemics and speculation, a rather unusual characteristic for an Italian scientist of this period.

Emery was fourteen years younger than Weismann and his only true Italian correspondent. They had many things in common: both were frequent guests at the Stazione Zoologica, championed a broad naturalistic approach towards biological questions, studied fish and insects, opposed Lamarckism, and believed in a distinct material substratum of inheritance. Weismann's *Kopierbücher*, a chronologically ordered collection of copies of all the letters he had written, contain very few sent to Italian colleagues. Besides the expression of thanks for the nomination to academies and for publications sent to him, he corresponded only with the philosopher Eugenio Rignano (1870–1930)—who tried to convince Weismann several times to write for his *Rivista di Scienza*, an invitation politely but firmly declined—and with Emery.[2]

Emery was born in 1848 in Naples to Swiss parents who had become Italian citizens. In the Swiss woods near his grandfather's house the young Emery had

[1] Emery's collections and papers were dispersed after his death. His Coleoptera collection, containing about 9,000 species, was donated to the *Museo civico di zoologia* in Rome, the Hymenoptera collection to the *Museo di storia naturale Giacomo Doria* in Genoa. His manuscripts and drawings are conserved in the library of the *Dipartimento di scienze biologiche, geologiche e ambientali* in Bologna, and his correspondence in the library 'Gabriele Goidanich' of the Faculty of Agriculture in Bologna.

[2] He accepted the membership of the Accademia di Scienze naturali di Napoli (14 June 1893), the Società Veneto-Trentina di scienze naturali (19 May 1897), the Istituto Veneto di scienze naturali (February 1901), the Accademia di Scienze naturali di Torino (14 March 1905), and the Accademia delle Scienze di Bologna (18 February 1907); besides those of Emery and Rignano, he received essays and books from Giacomo Cattaneo (17 February 1887), from the Società editrice Dante Alighieri (9 May 1895) and from the Accademia di Scienze naturali di Napoli (30 October 1910); see Weismann's letters to Rignani (27 September 1906; 3 March 1907; 26 October 1909).

become a passionate collector of insects, especially beetles and ants. He studied in Naples, first medicine, specialising in ophthalmology and becoming a practising physician for 3 years, but then switching to natural sciences and research. His teacher and mentor Paolo Panceri (1833–1877) had been Anton Dohrn's first ally in the Neapolitan academic world. Between 1875 and 1889, Emery was a regular guest of the Stazione Zoologica—for him "une veritable famille" (Emery 1883, pp. 1–2)—and he authored the second volume of the *Fauna und Flora* series published by the Stazione (Emery 1880).

The impact of the Stazione on Italian zoology may be highlighted by recalling some numbers: up to 1904, 128 Italian researchers from many different biomedical branches worked at the Stazione; as early as 1889, thirteen laboratory tables were sponsored by various Italian institutions; and up to 1910, twenty-one out of thirty Italian zoologists and comparative anatomists called to a university chair had been guests of Dohrn (Dröscher 1996, pp. 94–96; 2001, p. 316; Groeben and Ghiselin 2001). Working there deeply influenced Emery's biological thinking and showed him how to combine his juvenile passion for naturalistic studies with scientific rigour. Contrary to Panceri's scepticism, Darwinism became the fundamental framework of his future studies (Caianiello and Groeben 2009, pp. 14–15) and of his project to modernize Italian zoology. Referring to American myrmecologist William Morton Wheeler's (1865–1937) definition, he called his approach "ethological": any life form had to be understood as part of a complex of interactions at the level of cytology, histology, morphology, physiology, embryology, zoogeography, ecology, ethology, palaeontology, and, above all, systematics and phylogenesis (Emery 1905, pp. 160–161; Ghigi 1923). In his polemics on evolutionism, atavism and heredity, he never missed an opportunity to reproach his colleagues for their lack of naturalistic knowledge, especially when they were physicians like Cesare Lombroso (1835–1909) and Enrico Morselli (1852–1929) (Emery 1899, 1900).

Emery was a proud naturalist, acclaimed for his precise descriptions and drawings (Forel 1925; Wheeler 1925). He investigated vipers, fish, annelids, and beetles. His main area of interest however was myrmecology. Together with Swiss Auguste Forel (1848–1931) and American William Morton Wheeler, Emery formed the "triumvirate in ant classification in the early twentieth century" (Sleigh 2007, p. 39). Besides his contributions to the systematics, taxonomy and geographical distribution of ants, he considered the study of social insects as pivotal for the understanding of the evolution of instincts, and for the fundamental mechanisms of inheritance.

He spoke and wrote fluently in Italian, German, French, English and Spanish, and also read Russian. Involved in international debate, half of his approximately 400 publications appeared in foreign journals or volumes where they received far more attention than they received in Italy. In 1881 he founded, together with physiologist Angelo Mosso (1846–1910), the *Archives italiennes de biologie*, a journal that republished outstanding Italian papers in French, to assure them a broader international audience. In 1900, he was a founding member of the *Unione zoologica italiana.*

After short periods in Palermo e Cagliari, he became professor of zoology at Bologna University in 1881, and stayed there for the remainder of his life. In this same year he translated Karl Gegenbaur's *Grundzüge der vergleichenden Anatomie*, but soon decided to publish his own textbooks. His *Compendio di Zoologia* (1891) was the most used in Italian universities until the first decades of the twentieth century (Alippi Cappeletti 1993). It went through two new, authorized editions in 1904 and 1911, and two further editions in 1920 and 1926–1927, which were edited by his student and successor Alessandro Ghigi (1875–1970). It was the first Italian zoological textbook containing a clear and appropriate exposition of recent cytological knowledge (Dröscher 1996, pp. 97–98; GHP 1899). It is therefore not surprising that he was Weismann's outstanding supporter in Italy.

Today August Weismann is mainly remembered for his contributions to evolutionary theory and for having sketched the first comprehensive concept of heredity (e.g. Churchill 1968, 1999; Winther 2001). Although his theory was highly speculative and many aspects were not confirmed by future researches, it is considered a conceptual precursor of genetics and of the modern synthesis (e.g. Mayr 1985, pp. 559–565). Omitting the modifications it went through, the principal points may be briefly summarised as follows: 1. a distinction between germ cells and somatic cells; 2. the identification of the germ-plasm as the material basis of inheritance; 3. the continuity of the germ-plasm from one generation to the next; 4. (from 1883 onwards) the localisation of the germ-plasm within the nucleus; 5. amphimixis, i.e. the exchange of maternal and paternal determinants during fertilisation, as source of new combinations of variations; 6. (from 1892 onwards) the precise hierarchical structure of the germ-plasm, made up of what Weismann called "idants" (chromosomes), "ids", "determinants", and "biophors"; 7. the progressive, qualitatively different distribution of the determinants during the cell divisions of ontogenesis as the cause of differentiation; and 8. the predominance of natural selection and (from 1894 on) germinal selection, i.e. the competition between the determinants, over other evolutionary factors.

The germ-plasm theory was not well received in Italy, for several reasons. Firstly, although there were some promising embryologists making remarkable contributions, like Giuseppe Belloncі (1855–1888), Davide Carazzi (1858–1923), Raffaello Zoia (1869–1896), and Andrea Giardina (1875–1948; see Fantini 2000), the field itself remained institutionally weak, resulting in a lack of experience with, and deeper understanding of, developmental processes (Dröscher 1996, pp. 83–88 and 130–140). Secondly, it was not before the 1860s and 1870s that cell theory saw a broader diffusion and application in Italy. These years were the heyday of protoplasm-theory, which became the basic framework of Italian cell concepts, and caused a general disinterest in the cell nucleus and its phenomena. Thirdly, Italian biology was characterised by a longstanding morphological tradition, and by a general unease over speculation. Finally, Lamarckism was widely prevalent in Italy (Pancaldi 1983; Corsi and Weindling 1985; Landucci 1996), where Ernst Haeckel's ideas in fact found a much wider audience than those of Darwin (Brömer 1993).

The explicit critiques against Weismann's theory put forward by Italian biologists like Giacomo Cattaneo (1857–1925), Daniele Rosa (1857–1944) and Ermanno Giglio-Tos (1865–1926) were based on two main objections: they insisted on the transmission of acquired characteristics and/or denied that the hereditary substratum could be localised in specific structures inside the nucleus (Cattaneo 1885; Rosa 1899; Giglio-Tos 1908). Giardina too remained sceptical, although he did admit that his studies on unequal cell divisions in the water beetle *Dytiscus* could be interpreted as representing evidence in Weismann's favour (Giardina 1901).[3]

In contrast to his Italian colleagues, Emery celebrated the theory of the continuity of the germ-plasm as "one of the most seminal hypotheses made in the field of evolutionary theory" (Emery 1893, p. 404). Likewise, he fully accepted the idea of the germ-plasm as composed of heterogeneous particles (Emery 1896, p. 344) and was even more enthusiastic about the idea of germinal selection (Emery 1897, p. 142). Between 1893 and 1903 he published his *Gedanken zur Descendenz- und Vererbungstheorie* as a series of five essays in *Biologisches Zentralblatt* (Emery 1893, 1894a, 1896, 1897, 1903), a widely read journal devoted to review articles and discussion pieces of general biological interest. From its very first volume in 1881 onwards, Emery was a regular contributor to this journal. It had been Weismann himself who had encouraged Emery in 1886 to publish his reflections: "If it is not all too immodest, I would like to say that I would be pleased if you consider it worthwhile to publish a paper on my last work. There are not many who really penetrate into such thoughts!" (Weismann to Emery, 20 February 1886; see also Churchill and Risler 1999, p. 78).[4]

In *Gedanken*, Emery in fact intended to illustrate the validity of Weismann's theory applying it to the problems of atavism, sexual dimorphism, speciation, instincts, to a new interpretation of the biogenetic law, and other features typical for the evolutionary debate of his time. His adherence, however, was not uncritical. Rather, from his very first letter to Weismann as well as in his papers, Emery took the opportunity on several occasions to emphasise points of disagreement. He was not a neo-Darwinist, but defined himself as a "Darwinian Darwinist", a distinction frequently made among Italian scientists (Landucci 1996, pp. 1004–1005; Volpone 2008, pp. 172–173). Paraphrasing Darwin's statement in the sixth edition of his *On the Origin of Species* (Darwin 1872, p. 421), Emery asserted that "natural selection is a highly important factor of evolution, which played the highest role in the determination of variability [*Variationsrichtungen*]; however, it is by far not the exclusive and probably not even the most effective one" (Emery 1897, pp. 397–398). He likewise defended a "soft" species concept.

According to Emery, neither natural selection alone nor Weismann's amphimixis could explain the origin of new species, because the former had only a negative effect and the latter produced merely a recombination of paternal and maternal traits and thus variation within the limits of the species, a phenomenon already known to Carl Linnaeus in the eighteenth century (Emery 1893, p. 408, 417). Emery agreed with John Thomas Gulick's (1832–1923) explanation, which proposed geographical isolation as a cause of speciation (Emery 1893, p. 406; Gulick 1872, 1890; see also

[3] Following Emery's advice, Weismann added Giardina's paper to the English translation of his *Vorträge* (Weismann 1904, p. 378).

[4] This letter is missing in the archive of the Biblioteca Goidanich. On 16 October 1898 Weismann wrote to Emery again, saying how much he would be delighted to exchange opinion about the germ-plasm theory. However, he never mailed this letter (Churchill and Risler 1999, p. 301).

Hall 2006; Weissman 2010; Rundell 2011). Emery conceived of speciation as a phenomenon based on intraspecific variation and on the accumulation of character varieties that were initially without selective value, and hence saw a certain distribution among the individuals of a species (Emery 1897, p. 143). As a consequence of such processes, "natural selection will have chosen not only a variety, but rather a variational tendency" (*die Naturauslese wird nicht nur eine Varietät, sondern eine Variationsrichtung ausgewählt haben;* Emery 1893, p. 418). Yet, contrary to Gulick, Emery tried to combine these concepts with Weismann's theory of determinants.

Along with amphimixis and spontaneous "intimate changes in the germ-plasm" (Emery later identified this with De Vries' mutations), he proposed a third source of variation: environmental influences leading to a progressive transformation of Weismann's ids (Emery 1893, p. 408; 1903, p. 359). Emery declared that some acquired traits were actually inherited, for instance, the immunity against certain pathogens, or the pebrine-disease of silkworms which is caused by spores injected into the germ-cells (Emery 1893, p. 410, 412). Yet he did not understand this as a relapse into neo-Lamarckism, to which he strongly objected on several occasions (Emery 1899, 1900). Although he was thus opposed to the idea of inheritance of somatic variations, he conceded that

> [o]ne may suppose that the modified activity of certain organs raises ferment-like products, which are assimilated into the germ-cell and transmitted, along with the germ-plasm (idioplasm), but without forming an integral part of it, to the organism generating out of this cell, and unfold their purely chemical effects during its development and further life. Such corpuscles exist also in the normal organism and each germ-cell contains various sorts of it; these constitute, besides the highly organised germ-plasm, whose components are distributed during cleavage to the single organ-forming cell groups, a more simple but in the whole body equally distributed component of the living being. I call this component of the germ-cell 'zymoplasm' (Emery 1893, pp. 411–412).

Weismann accepted Emery's arguments. He even made concessions about the crucial point of external influences on the germ-plasm:

> That is my opinion, too, yet I'm afraid I have been slightly misunderstood on this point, probably because I expressed my opinion all too shortly. […] Yet I think, that a direct modification of the structure of the germ-plasm by external influences has indeed to be assumed; but only in those cases when these external influences remain the same for a long time. Just as the most inferior unicellular organisms are directly modifiable, for me, also the germ-cells of the poliplastids are so. There are however good reasons to assume that these modifications do not appear easily and not as a result of every minor influence (Weismann to Emery 20 February 1886; see also Churchill and Risler 1999, p. 77).

Weismann expressed this conviction more clearly in his (1892) book, *Das Keimplasma. Eine Theorie der Vererbung*: "The primary cause of *variation* is always the effect of external influences" (Weismann 1893a, p. 463). These influences were mainly nutritional differences (ibid., 418). On this point, recent studies have emphasised that Weismann was much less Weismannian than he is generally said to have been (Griesemer and Wimsatt 1989). Winther (2001, pp. 526–528; see also Müller-Wille and Rheinberger 2012, pp. 86–89) limits Weismann's conviction of an uninfluenceable germ-plasm to the period 1885–1892, but the discussion with Emery shows that even in that period he was not very strict.

Yet Weismann's concessions towards the possibility of modifications of the hereditary substratum were limited to very exceptional cases. In his reply to Herbert Spencer's criticisms, he discussed Emery's arguments rejecting the opinion that his Italian colleague was a Lamarckian (Weismann 1893b, pp. 92–96).[5] For Weismann, the dispute evolved around the question of what exactly is inherited. From this point of view he considered Emery's zymoplasm to be only a kind of "infection" or "intoxication" of the germ-plasm.

In order to clarify his point of view, Emery resumed Weismann's discussion of the question how the sterile female worker castes in ant colonies transmit their often very different characteristics to the next generation. He relied on his own expertise in myrmecology to propose the hypothesis that qualitatively and quantitatively different feeding of the ant larvae was responsible for the polymorphism observed in the adults (Emery 1894b). Thus, their special structure and behaviour were not innate but acquired. Yet these "worker traits" were only apparently inherited, because the germ-plasm of all female eggs was actually identical. What was externally influenced by the feeding was the "reactivity" of the germ-plasm, which enabled the egg-cell to take different developmental paths (ibid., 57, 59).

Discussing and developing ideas about heredity stimulated Emery. In the last instalment of his *Gedanken* essays, he compared the germ-plasm to a Jacquard loom (Emery 1903, p. 360), a weaving mechanism invented around 1800 and based on a chain of perforated cards. Each row of punched holes stores the instructions for one row of design. This enables the automatic production of a great variety of different weaving patterns. The use of changing series of perforated cards is today considered a conceptual precursor of computer programming (Essinger 2004). Emery in fact saw in the loom-germplasm analogy a way of explaining how the determinants, like the rows of punched holes, regulate ontogenesis. This pioneering concept of a genetic program furthermore helped him to illustrate his idea of possible external influences on the germ-plasm as disorders or malfunctions of one or more cards, causing an error in one or more replications of the pattern. These errors, creating new patterns, are inherited by the next generations. He thought, however, that contrary to the single weaving loom, every single of the many ids possessed a complete collection of determinants. In the germ-plasm thus:

> the single ids, and the homologous determinants they contain, […] fight for the direction of the development of the entire organism as well as its parts. In this way the complicated conditions of latent mutations and inheritance are created, the phenomena of regression and atavism (Emery 1903, p. 360).

[5] These pages are missing in the English translation of Weismann's pamphlet (1893c).

In the summer of 1906, Emery suffered a severe apoplectic stroke. Paralysed down his right side, he nevertheless learned to use his left hand and continued writing, experimenting on ants, and even drawing. He also continued his theoretical reflections, but without recapturing the heuristic value of his *Gedanken*-essays. He did not succeed in establishing a scientific school which transformed his ideas into concrete research projects, nor did he convince his compatriots to direct more attention towards the hypothetical units of inheritance. Throughout the first half of the twentieth century, genetic studies remained "epistemic fragments" in Italy (Volpone 2008, p. 1). Nevertheless, Emery's basic ideas saw a widespread diffusion through his textbook, whose third edition was the first one to include a chapter on Mendelism (Emery 1911). Among his students were Alessandro Coggi (1864–1917), and, above all, Alessandro Ghigi and Paolo Enriques (1871–1946), who became central figures in the study of genetics in Italy (Volpone 2008, pp. 114–122, 221–225, 288–290).

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