

On Darwinism, Weismannism and hologenism

F. M. SCUDO *

According to Darwinian and Lamarckian theories, the 'first origin' of morphogenetic reactions is mostly a behavioral or exogenous one — as by change in nourishment or direct effect of external conditions. The 'nature' or main properties of such reactions, however, is largely dictated by developmental laws, as in the form of negative and positive correlations. While similar views were also held by August Weismann, Weismannism and its derivatives maintain that the direct selection of hereditary variation is the prime or sole determinant of morpho-functional changes. Starting from the late 1920's, *a priori* reasoning in terms of mathematical models and various indirect evidences made clear that mass selection *within populations* of sexually reproducing organisms could only work very slowly — and often with very limited results — on Mendelian variants with modest or small phenotypic effects. As a result, Weismannists felt forced to embrace either some extreme macromutationism or some equally extreme gradualism — i.e. morpho-functional transformations would derive from a painfully slow accumulation of minute changes, due to a selection continuously operating on most individuals.

Darwinian theorists — Chetverikov, Elton, Wright, Haldane and Schmalhausen among others — opted to justify the 'internalization' or the 'stabilization' of novel morphogenetic reactions to changed circumstances almost solely through selection of genotypic variants with smallish up to very small effects (if variants with large phenotypic expression are, rarely, initial responses to changes in conditions, the very process of their selection would soon reduce their expression to a modest one). The same theorists opted for selection mainly *among* (rather than *within*) smallish,

* Istituto di Genetica Biochimica ed Evoluzionistica, CNR, Pavia, Italy.

semi-isolated populations as the main mechanism of adaptive 'internalization' of morphogenetic reactions and of modifications of previously established ones, much as in Wright's 'shifting balance theory'. According to Schmalhausen and others, standards or norms that are at first disrupted by a change in conditions would be reestablished, perhaps in changed forms, by *stabilizing selection* acting mostly on individuals. This would result in smallish changes in genotypic composition such that heterozygosity *at very many loci counteracts the effects of most disturbances tending to divert development from norms*, that are favoured as such in the new conditions. In this way the directional genotypic changes responsible for internalization — mostly through spurs of inter-population selection — do not need to have much, or anything in common with the stabilization of norms relative to specific conditions of life.

My aim here is to contrast the logically and historically very different ways through which 'Italian' and 'Russian' Darwinism arrived at analogous or complementary justifications of the evolution of norms. It would be hard, otherwise to account for the outstanding practical success of systematics in the Linnean tradition. At variance from Russian Darwinism, the Italian version had heavily drawn also from Lamarck's and Geoffroy's theories. At variance from any other, Italian Darwinism largely accepted Schiaparelli's theory that relied on morpho-functional transformations taking place mostly through discontinuous, 'fixed' steps. In this feature Schiaparelli's theory departs in different degrees from subsequent ones with analogous intents, such as by D'Arcy Thompson, Bohm or Thom. Mainly due to this peculiarity, Schiaparelli's theory was the first to succeed in accounting for features such as atavism and homology or parallelism in variations (much as in Vavilov's sense), for the patterns of mass extinction and for geographic distributions hardly compatible with migration from a single « center of creation ». Vito Volterra immediately welcomed Schiaparelli's theory as the first step towards rationalizing the theories of Lamarck, Geoffroy and Darwin, particularly if it is interpreted in terms of Pearson's biometry and Mendelism. Starting from the mid 1920's Volterra also provided strong, though indirect support to Schiaparelli's theory through his mathematical analysis of the struggle for existence. Thus complemented, the theories by Schiaparelli are much akin to those by Schmalhausen in terms of modes of evolutionary changes and their causes, while complementary to Schmalhausen's theories in their more explicit reliance on the effects of the struggle for existence at the levels of species and biocoenoses.

Unaware of Schiaparelli's theory till mid-way in his career, Rosa had interpreted the patterns of mass extinctions and the parallel origin of taxa in terms of genomic drives, as directly resulting in the *fission* of species almost regardless of external conditions. While largely accepting Schiaparelli's theory in his Hologensis of 1918, Rosa then drifted into still more extreme forms of internalism that ran contrary to his own starting points in Naegeli's theory, as well as to most of the evidence and the theories being developed in the 1920's and 30's. Much the same modes of divergence as Rosa's are predicted by Imanishi's theory, and are subsumed by cladists with hardly any justification. Schiaparelli did not provide any specific causal justifications for his 'centripetal force' that successfully contrasts most tendencies to deviate from 'fixed types' other than minor, individual ones. He did assume, however, that this force had the same causes as in Darwin's general analyses — i.e. developmental laws, use and disuse, changes in nourishment and diverse effects of the struggle for existence. My main contention is that, to the extent Schiaparelli's position does require specific selectionist justifications, only Schmalhausen's theory of stabilizing selection appears to provide such justifications at the present state of knowledge.