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THE ROOTS OF THEORETICAL ECOLOGY; II: EVOLUTION, BIOCENOLOGY AND POPULATION THEORY FROM THE 1880'S TO THE 1920's

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THE ROOTS OF THEORETICAL ECOLOGY; II. EVOLUTION, BIOCENOLOGY AND POPULATION THEORY FROM THE 1880'S TO THE 1920'S.

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Part I has briefly described a variety of developments in ecology and evolution up to Darwin's death. Particular attention was paid to Lamarck's phenomenological approaches, as compatible with the overall picture, which emerg~~ing~~es from Darwin's analysis of different levels of causation. Little attention was paid to some of Darwin's "late" ideas such as on speciation, which were substantially affected by interactions with other theorists. ~~While~~ Darwin had maintained a substantial consensus while alive, and his death unleashed a flurry of attempts to extend his theories or to reform them, at times drastically, in very different directions. This particularly applies to issues Darwin had [illegible] left partially unresolved, such as the relationships between machroscopic change and particulate inheritance and those between divergence of characters and reproductive isolation. Considering such general issues in § 1, references to some developments also after the 1920's comes natural, since hardly any progress towards a consensus took place in the century since Darwin's death. The slow process of maturation of modern ecology out of ~~the germs provided by~~ Darwin's and Wallace's germinal theories will be considered in § 2. Although many such progresses had obvious implications for evolution, or were directly answering limited evolutionary questions, theorizing on evolution prior to "Golden Age" hardly took notice of them. Finally § 3 will present a scatter of attempts to ~~quantitatively~~ formalize population thinking in quantitative ways, mostly also of limited impact.

1 THE MAIN "REFORMS" OF DARWINIAN THEORIES ON VARIATION, HEREDITY AND SPECIATION.

As pointed out in Part I, Darwin kept ~~changing~~ retining his views on how particulate carriers of inheritance control morphological and functional

features of organisms. Also, in "Variation of Animals..." he had hypothesized effects by non hereditary peculiarities of any part of the soma on the particulate carriers (the gemmulae), in their long jurneys back and forth the germinal line (see exp. Ghiselin, 1975). However Darwin did not spell out precisely and consistently the extent and directions in which the soma could alter the structure of gemmulae, and hardly ever did he explicitly use such possible influences in dealing with specific problems in evolution. Then Darwin's "provisional hypothesis of pangenesis" might be viewed as a logical excercise, on ~~[illegible]~~ his hypotheses of variation and selection being consistent with plausible properties of the unknown mechanisms of inheritance.

In particular there are different plausible ways in which Darwin's pangenesis could be compatible with his two main points on variation, i.e. on the tendency of hereditary variation to ~~change~~ increase in proportion to the magnitude of changes in conditions of life (I, § 3 b) and on many novel characters being at first acquired, and only after tending to slowly become "innate" or "hereditary". Again Darwin did not consistently spell out the extent in which the acquisition of characters should precede their selection. While maintaining throughout that both an indirect process of selection and a direct one are necessary, Darwin tended to emphasize the former in his later writings, ~~particularly~~ on the evolution of behaviour (e.g. 1873). In this paper the only instance for which he could confidently claim direct selection is the evolution of neutral castes in insect societies. Darwin's vague position became all the more unsatisfactory as his "pangenesis" was rendered less and less plausible by the advancing knowledge on cell structure and division behaviour of cells.

a) Naegeli's and Weissmann's "internalism", and the Mendelization of evolution.

Factual knowledge on cellular structure and function, and on their relationships with reproduction and heredity, was rapidly increasing in the second half of the 19th century. As jurneys of gemmulae back and forth the germinal line and the whole soma were appearing less and less plausible, models alternative to Darwin's became popular. ~~but~~ However no sizable consensus on them was achieved in the 19th century and in the early part of the 20th (see, e.g. Coleman, 1965). Among the unsettled historical problems connected with this lack of consensus, is the extent to which Mendel's investigations ought to be considered as an advance in transmission genetics "too far ahead of their times", rather than a clever presentation of "failed" hybridization experiments addressing quite different questions (for the latter views see Timiriazev, 1908, Olby 1979). Rather than with such issues, or with factual knowledge on cytology per se, here we shall deal with theories on variations which ended up reversing Darwin's main theoretical stand, i.e. rendered the law of Conditions of Existence grossly subordinate, or practically irrelevant, relative to the Law of Unity of Type (cf. I, § 3 b).

Of the two major "internalistic" theories of the 19th century, the one proposed by Naegely, starting from the 1860's, is markedly anti-Darwinian, and ideally suited to justify extreme forms of neo-Lamarckism. Very simply stated (see exp. Mondella, 1980), Naegeli claimed that, rather than occurring by chance, particulate variations would take place mostly in directions tending to increase the complexity of organization of living ~~orga-nisms~~ beings. Naegeli's theory accounts very well for most observed features of evolution, including those Darwin had serious problems justifying -- e.g. the apparent uselesness of many species-specific features in plants (cf. c). Natural selection at the level of individual variations would have a marginal role to occasionally eliminate less fit organisms of "intermediate" forms. Most natural selection would take place at the level of differentiated varieties among which cross-breeding, if at all occurring, would be irrelevant (Naegeli, 1874). This work is of interest to us since it tackled a major unresolved theoretical problem -- that of the stable coexistence of closely related forms -- through rather sophisticated mathematical models (see § 3 a). In this framework the crucial problem of the relationships between divergence of characters and reproductive isolation is automatically resolved or, rather, it hardly at all arises. This side of Naegeli's theoretizing might help justifying why he might have paid ~~little~~ insufficient attention to Mendel's results, a poorly documented fact perenially lamented by historians of Mendelism, ~~keep lamenting~~.

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Far more popular in the 19th century was a brand of internalism very different from Naegeli's, which became "dominant" in several cultures in its Mendelian "translation". It consists in reducing evolution to the direct selective accumulation of hereditary variations each with a small phenotypic effect, whose occurrence would have few relationships both with external circumstancies and with acquired somatic changes. This view most likely derived from oversimplifying Darwin's views in early editions of "Origin", and it had already became popular by the late 1860's under the label of "Darwinism". Best gauge of the popularity of this view are the criticism it was drawing (cf. Hull, 1973), most of them directed at Darwin himself quite out of context with the positions he was developping (for an exception see von Baer, 1871, alias Ber, cf. b).

An already popular Darwinism was made more precise and around the mid 1880's by Weissmann, mainly on the basis of his observations on the early separation of the germinal line in the development of some vertebrates. He postulated that this purportedly general developmental feature of metazoans resulted in protecting the germinal line from all sorts of somatic influencies. "Evidencies" such as this one or on the non inheritance of mutilations led Weissmann to formulate a rather genreal principle of "Non Inheritance of Acquired Characters". This principle is in fact made up of two components, an overt one which is quite well understood also historically, and a less well understood "criptic" ~~component~~ one. Let as look at both, at the latter in particular, as far as ~~allowed by~~ the present state of historical knowledge allows.

Mounting evidence that inheritance resides in special chemicals ("ideoplasm") in the nuclei of cells ~~were clearly making the~~ rendered much "travelling" by gemmulae hardly tenable (cf. again Coleman, Ibid.). ~~While~~ This alone would not rule out exchanges of hereditary material among cells, perhaps as en exceptional process. However "developmental sheltering" of germinal lines suggested that somatic influencies on ideoplasm would hardly be possible on ~~metazoans~~ lives so "sheltered" (Weismann, 1882). In plant and lower animals there was no strong reason, yet, to rule out exchanges by which hereditary variations induced in part of the soma could be transmitted to the progeny. On the other hand external physical factors affecting the whole body could easily induce hereditary variations, at times also in specific directions and regardless of "developmental sheltering" (cf. Weissmann, e.g. 1885). The impact of Weissmann's formulation at this stage is vividly discribed by Wallace in the 2nd edition of "Darwinism" (1889, Chapter XIV, cf. also c).

On the other hand it is not at all clear why the above shoud imply that all evolutionary changes in form and function consist only in the selective accumulation of specific variations in the structure of ideoplasm (or DNA for that matter). What might hold at the michroscopic level regarding the structure of ideoplasm was directly translated by Weissmann to all macroscopic levels, with hardly any justifications why the "plastic" changes of which he was aware ought to be disregarded. As far as I know, the best justification in this direction he did provide were such as those from experiments on the non-inheritance of mutilations. These were so obiectionable in design as to easily lend themselves to hilarious jokes such as those by Timiriazev (cf. c), or more massive and "serious" criticisms such as those by Romanes (1896). Within a few years the obvious alternative -- that selection should often proceed much in the same direction of acquired, established variations -- came to be pressed by many as alternative to "Weissmannism" (cf. c below). Yet, as far as I know, neither Weissmann nor no other 19th century neo-Darwinist ever bothered to produce any solid evidence, or argument, against this alternative. Rather, to defend the general validity of his principle, Weissmann had to admit more and more substantial directional effects on hereditary variation by external factors (e.g. 1891,1902), a view already in collision with the emerging Mendelism.

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As anticipated, the "rediscovery" of Mendel's laws at the beginning of this century was soon translated into a bold generalization of Weissmann's principle. As in Weissmann's late formulations, this would apply to all organisms regardless of "developmental sheltering" of germ lines, but it would also exclude mutagenic effects in preferential directions both by somatic and by external influencies. This further reduction of evolution

was bitterly resisted by many evolutionists, including Wallace (exp. 1908, cf. also b) and Cuènot, the pioneer of Mendelian genetics in mammals (e.g. 1910). Yet this same radicalization of Weissmann's principle became the a corner-stone of the "synthetic theory", as codified in the 1930's (see, e.g. Mayr and Provine eds. 1979). Besides selection on "random" mutations this theory considered only geographic isolation to justify the origin of new species when not due to major chromosomal changes (cf. c). By the time this theory was being codified, most 19th century developments in the theory of heredity were already forgotten. Then one can have extremes such as Fisher (1929, Chapter I) claiming that Darwin never had a particulate theory of inheritance, and that Mendelism was the first theory to save him from the "bancrupcy" of "blending". On grounds of this sort the synthetic theory of evolution managed to successfully defend the claim to be the only interpretation, of the original theories of both Darwin and Wallace. compatible with genetics.

b) From theories on "plastic" or "organic" selection to the modern theory of "phenocopy".

By looking at it from within, the ~~[illegible]~~ march to prominence of the "synthetic" theory appears as virtually uncontested till recently or, more precisely, as only having to contend with the "no-win" case of "neo-Lamarckians" (for the latter, see, e.g. Collective, 1979). In other words, till the 1960's Western "neo-darwinists" or "syntheticists" had largely failed to take notice of the substantial challenges to their views presented below.

Historically, the only consistent tradition opposing pan-selectionism was due embryologists who were affirming the primacy of internal modalities of change in development over most, or all selective ones. To them any change taking place prior to the very final stages in development, or epigenetic change, was viewed as a choice among relatively few and rather different potential alternatives in development. Both hereditary and non hereditary deviations from an established norm would affect the direction of development towards one such alternatives, but not the nature of these alternatives. This is expressed by ~~In other words~~ Galton's famous metaphor of development as a multi-faced spheroid, which could be made to thumble on one facet or on another while these facets could not be changed. According to many, this would apply to all evolutionary changes except "trivial" ones of "terminal" phenotypes. Till recently the extent to which such views could be regarded as sound ~~once~~ largely depended on inferred philogenies, whose reliability c~~an~~ould be questioned then, as of now (as witnessed by controversies between "adaptationists" and "cladists", e.g. Patterson, 1980).

In a way these points of view from ~~which~~ embryologists ~~opposed~~ ~~pan-selectionism~~ were already put forward before in a quite different context, i.e. by people such as Geoffroy the elder and Chambers to mitigate, or contrast, Lamarck's "pan-behaviourism" (see I, § 2 c). It is instructive in this respect that Ber, alias von Baer, at first rejected the "Origin" as nonsensical in whichever aspect it was not an encroachement of his own, earlier analyses of evolution. As Darwin's positions substantially changed, also formally incorporating his approach (cf. I, § 3 b), Ber switched to ~~an~~ accept Darwin's theory with some technical reservations (cf. von Baer, 1871, Zuvadskii, 1973, Scudo and Acanfora, 1983). As anticipated in b), Ber's near acceptance of Darwin went hand in hand with a bitter, clear cut rejection of "Darwinism". Haeckel's reaction to the "Origin" was only formally more positive than Ber's. While professing to be an enthusiast Darwinist also for "ideological" reasons (see e.g. Mondella, 1969) he felt compelled to "reform" Darwinism by assuming that hereditary variations were not only caused, but also <u>directed</u> by environmental necessities. Later on Haeckel emphatically opted for the opposite side of Weissmann's principle, and in so doing he much helped the growing tide of "neo-lamarckism" (see Dogherthy, in Collective, 1979). Till recently, the popularity of Haeckel's "biogenetic law" (according to which embryos would often rensemble the <u>adult</u> ancestors) had managed to eclypse in many Western circles "von Baerian recapitulation" (see Lovtrup, 1978). Ber and Haeckel typify extreme forms of a tradition of evolutionary embryology whose basic tenets were relatively uniform at least for a century and a half, possibly over two centuries (as far Wolff, e.g. 1759, did anticipated it). Major representatives of this tradition ~~are~~ were Mivart in the second half of the 19th century (e.g. 1871, as reprinted in Hull, 1973), Severtsoff in the first half of the 20th (see, e.g. Adams in Mayr and Provine, eds., 1980), and the already mentioned Lovtrup, is at the present time.

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The typical evolutionary embryologists mentioned above did not go further than claiming the primacy of "internal" modalities in any epigenetic (i.e. "non-terminal" change) ~~as affected by~~ relative to any "disturbance" of the established mode of growth, whether hereditary, external, somatic, behavioral or mixture thereof. Golschmidt (e.g. 1940, 1956), to whom we owe the now quite popular term of phenocopy, might be considered as the last great representative of this early~~er~~ tradition. ~~which~~ This tradition had little to say on temporal or causal relationships between the "acquired" and the "innate". A school of thought addressing itself mainly to this last problem, ~~and~~ claiming that selection woud mainly proceed in the direction of already established "plastic" changes, was initiated independently by Baldwin and Lloyd Morgan (see Baldwin, 1896 a and b, Lloyd Morgan, 1896 a and b).

To introduce the thinking of this school, let me report the central points among the 20 ones ~~by~~ in which Lloyd Morgan (1896, as in Klopfer, 1974, pp.) had summarized his position. Keep in mind that Lloyd Morgan ~~confines~~ uses the term variation ~~to those~~ for changes of "germinal" origin, and modification ~~to~~ for "plastic" ones:

"7. Under constant conditions of life, though variations in many directions are occurring in the organisms which have reached armonious adjustment to the environment, yet natural selection eliminates all those which are disadvantageous, and thus represses all variations within narrow limits.

8. Suppose, however, that a group of plastic organisms is placed under new conditions.

9. Those whose innate plasticity is equal to the occasion are modified, and survive. Those whose plasticity is not equal to the occasion are eliminated.

10. Such modification takes place generation after generation but, as such, is not inherited. There is no transmission of the effects of

modification to the germinal substance.

11. But variations in the same direction as the modifications are now no longer repressed and are allowed full scope.
12. Any congenital variations antagonistic in the direction to these modifications will tend to thwart them and to render the organism in which they occur liable to elimination.
13. Any congenital variation similar in direction to these modifications will tend to support them and to favour the organism in which they occur.
14. Thus will arise a congenital predisposition to the modification in question.
15. The longer this process continues, the more marked will be the predisposition, and the greater the tendency of the congenital variations to conform in all respects to the persistent plastic modifications; while
16. The plasticity still continuing, the modifications become yet further adaptive..
17. Thus plastic modifications leads, and germinal variations follows; the one paves the way for the other."

Possibly the most radical novelty to be noticed in Morgan's position is to no longer require the "directionality" in hereditary variations which appeared as necessary in various degrees to all "internalists", Weissmann and Haeckel included. Incidentally the whole argument starts from almost as clear a notion of "stabilizing selection" or "canalization" as Waddington (cf. 1975) ~~and~~ or Schmallhausen (e.g. 1946) were going to introduce, ~~independently (in Waddington's case, also idependently of Lloyd Morgan)~~. Also, in their assesment, Baldwin and Lloyd Morgan found their positions to be virtually identical, and soon formed a "common front" in which prior contributors in the same direction were warmly welcomed (see, e.g. Baldwin, 1867).

Rather similar views were also put forward at about the same time by Timiriazeff, with more explicit and more bitter anti-Weissmannist overtones. While it is not yet fully clear to me precisely when and how views of this sort originated in Russia, it is very evident that, at variance

form the West, they attained there a very high standing (cf. Zuvadskii, 1973, also Scudo and Acanfora, 1983). Much later these views were summarized by Timiriazev as (1909, p. 13): "... the historical process of the production of novel organic forms, discovered in nature by Darwin, is the inescapable result of the interaction of three factors, which undoubtedly act all the time on all features of organisms. The first of them, variability, provides the necessary raw material for this historical process. The second of them, heredity, fixes, integrates and elaborated this material. Finally the third one, overpopulation, gets rid of (or, to use Comte's expression, destroys) all forms that are partly or wholly unsatisfactory. Organic structures are perfected by the joint action of these three factors, a process one metaphorically calls "natural selection". A part from semantics -- variation being used in the opposite sense as Lloyd Morgan -- Timiriazev's general attitude is clearly much the same i.e. hardly any room is left for selection unless it operates much in the same direction as already acquired changes.

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Further progress in the direction of Baldwin & Co. were extremely slow and discontinuous. In the West they were often ignored or bitterly resisted till very recently, not rarely through open allegations of fraud (as in the notorius Kammerer case). Once more the harsh treatment Waddington's early presentations met from western neo-Darwinists (as "Lyssenkoist") closely parallels that of Schmallhausen by Lyssenkoists (as "Weissmann-Morganist", obviously referring to T.H. Morgan). ~~Other~~ Later attempts to re-propose the views of Baldwin & Co., such as those by Bateson (1962) or Hardy (1965) continued to fail as miserably as those by Piaget in the 1930's, ~~and~~ or those by Waddington in the 1950's (cf. below, also § 2 a). Ethologists would continue to realy on such notions, e.g. Lorenz on the Khunian ~~one~~ notion of "genocopy" (e.g.   ), Haldane and Spurway on Waddington's "genetic assimilation of acquired characters" (e.g. 1956) ~~However none of them~~ but they did not fared any better ~~and~~ (not even Haldane's leading status as theories of population genetics helped him in this respect). Occasionally Baldwin or Lloyd Morgan Would be "seriusly" considered by "syntheticists" just to be dismissed, ~~perhaps~~ more politely than Waddington, through some plausible argument. Such is (Mayr, 1970, pp. 364-5): "If the phenotype is highly plastic, the selection pressure may actually be reduced because there is no selective advantage in changing the genotype when an individual can adjust itself phenotypically to a current condition. Invoking a "Baldwin effect" in no way helps to clarify the evolutionary process".

~~This~~ Till recently the situation of stall just described kept dragging virtually unchanged in most Western cultures since 1896. Then in the mid-1970's there was a sudden switch to accept at least some role in evolution for "organic selection" or "genocopy" or "phenocopy" etc.. Lets us look, first, at how this situation had changed "from within". In 1974 Piaget re-presented his critical experiments and observations both in nature and in the laboratory (see § 2 a), which had been nearly forgotten. He did so in a far more general, and admittedly more satisfactory theoretical context (Piaget, 1974, p. 3). In the same year Slobodkin and Rapoport endorsed Bateson's views through powerful arguments of ecology, and a novel form of "game theory" suited to deal with evolution. The same Dobzhansky no was endorsing Schmallhausen years earlier, also endorsed this presentation. ~~Finally in~~ The next year Waddington (1975) presented an exhaustive and historically well grounded summa of his views, in the form of an annotated selection of his work. Piaget and Waddington were forming for the first time a "common front" which unified in the same theoretical set-up all problems of development, behavior and learning. And yet, while having also had some active role in this change (Scudo, 1975,1976), I have no clear idea why it took place. No new critical evidence was being provided in the mid 1970's, and none of the "syntheticists" who "switched" appears to have been aware of whichever bona fide theoretical progresses were takeing place in these years. If one were to interview the "switching" syntheticists, quite likely motivations connected with the growing popularity of ethology or a vague feeling of crisis of ~~the classic synthetic~~ conventional ~~views~~ mendelism would loom more prominent than any of the "technical" reasons presented above.

Then this tentative, and not particularly "Kuhnian" story (in the sense of the T.S.Kuhn), seems to end "well". However it is not clear to which extent the sudden switch by "neo-darwinists" was a real endorsment, rather than a new form of "exorcism", one more subtle and efficient that the

"excommunications" through derogatory lables of just a few years earlier. In fact far too often the switch only consists in warmly endorsing the general ideas of "phenocopy" etc. as a methodological premise. Of ~~which~~ it no concrete application is being made, so to get to the same general conclusions as ~~before~~ withouth. One among the first and most prominent examples of tis "change, no change attitude" is provided by Wilson, as one might gather by carefully comparing Wilson (1975), pp. 72-73 with the rest of this voluminous work and with Wilson (1971).

c) Early theorizing on the species problem.

I have placed this topic after heredity since, from a purely logical standpoint made more clear in § 2 b, theories on heredity should be critical as to theories on species and race formation. However, ~~the~~ basic, historically relevant positions on species and race formation were already formulated before the developments in a) and b) could have a meaningful impact. I choose this order of presentation since it might help getting a better insight, in retrospect, of how "holpless" was the task faced by early theoreticians, ~~were facing with~~ due to the scarce factual information then available.

From the outset Darwin's pronounced gradualism in the early editions of the "Origin" met the strongest criticisms precisely on the speciation issue. As already alluded in a), Naegeli had substantial evidence on specific differencies in plants having hardly any adaptive value. Whence the marginal role he had placed on natural selection at the level of individual variations, or utility principle as often called. In late editions of "Origin" Darwin partially concurred with Naegeli's observations, while justifying them in quite different ways (Chapter VIII). At about the same time Wagner made a strong case for geographic isolation ~~being~~ as a necessary precondition to divergence, interpreted mostly as a mass variation of individuals in which selection would have hardly any role. While Darwin at first held rather similar views (cf. Kohn, 1975), by then he had accumulated ample evidence suggesting that no isolation whatsoever was involved in many cases of plant speciation. Also on this basis, much later vindicated by cytology (cf. again § 2 b), at first Darwin flatly rejected Wagner's suggestion (cf. "Origin", Chapter V). Subsequent, even stronger rebuttals by Weismann prevented Wagner's views from having much effect during his lifetime. As already noticed, however, a suitably modified version of Wagner's views became one of the main explanatory mechanism of "syntheticists" (see Lesch, 1975).

As already anticipated, sometimes later Darwin partially reverted to his earlier positions, and Wagner's, on isolation. This novel and often ignored position runs as (Darwin, 1876, as in Barrett, pp.): "In two absolutely distinct countries inhabited by the same species, the individuals of which can never during long ages have migrated and intercrossed, and where, moreover, the variations will probably not have been identically the same, sexual selection might cause the males to differ. Nor does the belief appear to me altogether fanciful that, two sets of females, surrounded by a very different environment, would be apt to acquire somewhat different tastes with respect to form, sound, or colour". From the scarce historical analyses of which I am aware, it is not yet clear to which extent Darwin's "tentennations" on the species problem were influenced by the extensive discussions and correspondence he had with Wallace, ~~who refrained from pubblicizing his differencies on this and other matters till shortly before Darwin's death~~. Be as it might, sexual selection and geographic isolation provided to Darwin a sound model of speciation.

At this stage I am entering a chapter on which I was never able to make much sense of my own, while not being much helped by the few historical studies I came across, ~~such as Loesch (1975)~~. It is also a rather sad chapter, pitting Darwin's son and faithful assistant, Francis, against Romanes, Darwin's closest intellectual companion in his late years, this against Wallace and so forth. Failing to understand several of the scientific issues involved, at the moment I tend to partially interpret the differencies above as a "family squabble" over the grand man's heritage. Let me first present such squabbles as they tended to be perceived by outsiders. Then I shall hint why this perception should ~~have~~ be wrong ~~by perceived~~ to some extent ~~and~~ or, to the extent ~~they~~ it were not, they "squabbles" might have scientifically nonsensical or mainly "ethological" components.

While the species problem was a real gap in Darwin's theory, I fail to understand why the solution Wallace presented in Darwinism (1891, cf. below) failed to draw serius consideration, then as of now. This being the

case, the species problem continued to be perceived as a blatant theoretical gap also after 1881, and two further attempts to fill it were soon presented by Romanes ~~starting from~~ (1886) and, shortly after and independently from him, by Gulick.

According to Romanes spontaneous mass variations in local populations for some features of the reproductive system could easily guarantee reproductive isolation from the parent stock ~~population~~. This largely or wholly "non-selective" factor, called "phisiological selection", would also account for the apparent lack of adptive value in many species-specific characters. Gulick had come to much the same conclusions as Romanes through his detailed studies of the very many "races" or "species" of the land snail "Achatinellidae in Hawaiy, which are often bordering or cohexisting even under apparently identical external conditions. Romane's suggestion drew only harsh criticism form the leading English and German evolutionists, including Wallace and Francis Darwin. ~~and~~ Also Gulick's support did not help much his case (see,again, Lesch, 1975). By now it should no longer be surprising that just about the opposite ~~reverse have~~ happened in Russia. Here Romane's and Gulick's position, as well as Wagner's, would have been quite influential in further, autoctnous developments (see Zuvatskii, 1973).

Wallace's harsh dismissal of Romanes and his criticisms of Gulick's interpretations, but not of his data, appear to me as amply justified. ~~By~~ In his own account Wallace had already worked out the far more general theory of speciation to be considered below ~~already~~ by the late 1860's. As anticipated this was categorically rejected by Darwin altough, perhaps, the controversy helped stimulating Darwin's last foray into the theory of speciation. The very starting point of Wallace's theory was analogous to Gulick's or Romanes' but, if nothing else, more general, or more vague. Wallace's position was based on an extensive analysis of animal colorations, which stressed utility somewhat more than Darwin did. Substantial component of this position was a virtual rejection of Darwin's theory of sexual selection mainly because the "subordinate" sex would lack sufficient discriminative and selective powers (Darwinism, Chapter X). Wallace's rejection became intrenched in most biological cultures with the notable exception Russia, where "mainstream" theorists tended to dismiss in block all Wallace's criticisms to Darwin (Zuvaskii, 1973, cf. also Scudo and Acanfora, 1983).

Wallace's thesis on speciation is exposed in Chapter VII of "Darwinism", and beautifully summarized in a 11 points "theorem", the same he would have discussed in vain with Darwin in the late 1860's. As anticipated, for Wallace a Romanes or Gulick-like point is only a starter. It deals with the "trivial" cases in which, from the outset, different conditions of life have enough physiological consequencies to prevent a new colonists from intercrossing with the "mother populations", <u>which they usually border or overlap</u>. In this case selection can proceed to improve the general adaptation of the new colonists, without being swamped by intercrossing with the "parent" form. If a similar change only partially prevents intercrossing, selective divergence would be retarded at first and quite soon stopped. In this case, however, any variation reducing hybrid fertility or the tendency to "hybridize" would have a selective premium precisely where the new colonists tend to hybridize with the "mother" form. Once hereditary differences between the two population to reduce intercrossing are established in any one such area, the spread to other areas of inter~~breeding~~crossing more by a process of population replacement than by direct selection of the variant individuals. In this way selection to reduce inter~~breeding~~crossing would first arise as a local border phenomenon, allowing a larger adaptive divergence to general conditions. ~~between the two forms.~~ This, in turn, would place a greater premium on divergence to prevent intercrossing. Full speciation through divergence of signals, possibly accompanied by hybrid sterility, would be the final outcome of thse two distinct, self-reinforcing processes.

As anticipated Wallace's theory and a somewhat analogous one by Galton met with very scant sucess in the West (see again Lesch, op. cit.). Albeit for different reasons these proposals were also neglected in Russia, where Wagner's, Romanes and Gulick's ideas were far more successful than in the West (see again Zuvatskii, 1973 and Scudo and Acanfora, 1983). The possible scientific causes of the uniform insuccess of Wallaces and Galton's ideas on speciation are better discussed in connection with the largely empirical advances on the speciation problem in the early decades of this century (§ 2 c).

2 BIOCENOLOGY, ETHOLOGY AND "ECOLOGICAL GENETICS".

Ecology and transformism were born as vulgate sciences, and in general their progresses remained somewhat bound within sub-cultures or major scientific languages. The pubblication of the "Origin" was an exceptional event also in this respect. With it, and to a lesser degree also with Darwin's subsequent works, ecology, ethology and transformism were re-founded not only as much deeper sciences but also as truly cosmopolitan ones (much as physics continued being even after abandoning latin).

Further, in the last two decades of his life Darwin became somewhat more than a repositor and great unifier of knowledge in all fields of natural history. By keeping correspondence with most serius students of natural history of the whole world and opening his home to them, Darwin also became a person to relay of this knowledge, to a level which had no parallel before nor after him. Also Darwin's death was followed by more than the major theoretical split on inheritance just examined. Ecology, ethology and evolution borke up again into sub-cultures, and once more exchanges across language barriers became scarce again. Later Mendelism blossomed into a truly cosmopolitan culture, but mainly regarding its technical aspects. As pointed out in § 1), its main effect on evolution was to further aggravate the preexisting split over selection and inheritance. I left to this section ~~we shall deal with~~ progresses which, for the reasons just hinted, are mainly bound both to language and sub-cultures. In fact some such progresses hardly go beyond the individual level. One then wonders, at times, as to the extent there is any real history to talk about, rather than just lack of reliable historical reconstructions.

a) The rise of biocenology or "community ecology".

Not being aware of any detailed history of the "lists" of plant species, I can only give you some glimpse on this habit (generally regarded as an unwhorthy precursor of community ecology). At the outset the habit appears to consist in precious little beyond attaching latin names to qualitatively distinct floras, as so recognized by a pre-scientific perception already rooted in language. Attempting to do so was in itself interesting since, as we shall see in c), it soon led to recognize that the very same plant could have very different forms in different habitats.

Here I wish to take issue against the widespread notion that making species lists continued to have purely discriptive intents till way into this century. This is still true of any preliminary floral study, and it might as well be true that most floral studies did not go beyond the preliminary step of setting up lists. However in this I would not see anything more than a larger thuth: Most scientific studies are uninteresting whether concerning floras ar anything else. However even casual inspection reveals that at least two features going beyond mere description were already present by mid 19th century both in floral and in faunal studies. One was to sort out occasional stragglers form natural members of floras and faunas, and "why" such individuals were found "out of place". Still more important, causal explanations of observed floral and faunal distribution were already going far beyond still essentially pre-scientific connotations on weather, exposition, soil etc.. For instance Thurmann's "<u>phytostatique</u>" (1849) payed much attention to patchiness and its causes ("<u>phytostatique parcellaire</u>"), and the dynamic of floral change ("<u>dispersion</u>") is already related primarily to the nature of sub-soils. Then as of now, attempts to characterize the generally looser modes of association among free living animals were lagging far behind the "easier" sucesses of botanists. Yet studies on sessile animals and poorly motile ones (e.g. Forbes, 1844) had already began to recognize that abiotic factors interact in meaningful ways with biotic ones in yelding observed characteristic distributions. Haeckel's classic description of the association of three calcareus sponges in norvegian coasts -- later found to apply also elsewhere -- was among the first to extend naive notions of "community" to animals. Haeckel's contributions went little beyond this and proposing the term ecology, almost simultaneously with, and independently form Thoreau.

Credit for having introduced community ecology in a modern sense usually goes to Moebius. He also introduced the term <u>biocenosis</u> to denote

the resultant of the interactions among characteristic assemblages of species, which continue to occupy a given territory through reproduction. Moebius's classic study was largely motivated by the perturbations on oyster beds. These were destroyed along large factors of the French Atlantic coasts, and the mussel beds which took over were effectively preventing recolonization by oysters. Also, the artificial refuges offered for oyster implantation were not faring any better, since the young were not being sufficiently "thinned out".

Moebius overall theoretical framework is wholly analogous to Darwin's. His main merit is to display the precise nature of interactions in a case of "ideally" intermediate complexity, and one particularly suited to reveal spatial features. In spite of Moebius" major role, precious little historical information is available on him. Whichever I am ware of comes mostly form a study by Jahn which, as far as I know, has not yet appeared. According to it, ~~the several~~ Moebius' short studies on evolution ~~Moebius~~ pubblished at the ende of the century would express only a fraction of his theoretical ideas, as gathered form his personal notes preserved at the Museum fur Naturkunde in Berlin. Again I cannot do much more than point to still another golden mine of largely untapped historical material, on the first theorist of evolution explicitly in terms of community ecology.

With few exceptions among which Moebius is a major one, most of the intellectual progress in community ecology before Elton was strictly in botany (see expecially McIntosh, 1979). Here I just wish to point out some key features of phytosociology, as developed in the early decades of the century. By the turn of the century the notions of dominance and zonation, introduced by Wallace, were being applied routinely. Thus it had became clear that dominant plants were ubiquitous, i.e. their presence usually conveys little ecological information. It had also become clear (e.g. Braun-Blanquet and Furrer, 1913 as in Kormondy, ed. 1965, p.) that the search for "<u>a unit comparable to the species, capable of serving as a basis for research in comparative geographical botany</u>" had to go much beyond the starting point of species lists. In particular such lists also comprise temporary groupings which do not possess characteristic associatinal traits and mixed associations (the equivalent of newly formed hybrids in systematics). Much as also happening in the systematics of species, it soon became clear that at times the new systematics of plant associations could only be performed through appropriate stastical analyses. In true associations the number of different species per quadrat of any given size would be normally distributed, and the average number of species per quadrat would rapidly tend to a characteristic finite limit as quadrat area increases (see works by Du Rietz, Wicksell, Nordhagen, Palmgren, Klyn, Gelason etc. as, for instance, in Chouard, 1932). Most assemblages being studied either displayed such properties quite clearly or grossly failed to do so. Among the latter cases, mixed associations could be easily told apart form temporary groupings. Precisely on ~~this~~ such points, and on the extent in which successions are indicative of global ecology, controversy went on virtually unchanged since the 1920's. Those who do not attempt to sort out bona fide associations can easily claim that they are figments of the immagination. Those who do not attempt to sort out successions also from the point of view of the soil and sub-soil, previus disturbancies etc. can equally easily claim that this notion ~~of succession~~ is tautological, ecologically irrelevant a.s.o. (cf. e.g. Prenant, 1934, McIntosh, 1979, 1981).

Discussion on such points are often muddled by considering formulations such as Clements' rather than by Braun-Blanquet & Co.. Then I must fully agree with Ghiselin (1975, pp. 22-35) that the Clementsian notion of associations as "super-organisms" leaves much to be desired from an epistemological point of view, and so do the "Harvard crypto-vitalists" and the "Chicago School". With this, however, Ghiselin might appear to throw out also a legitimate object of investigation, i.e. the extent in which the formation of new assemblages could be the main causa of their co-evolution in characteristic directions, towards bona fide associations. Of course Ghiselin does not really imply anything of this sort, but the impressions is there. Clearly the extent to which it is legitimate, or necessary, to consider associations much in the same ways as species depends on a number of crucial, still poorly known features. Such are the extent to which characteristic associative traits might be present from the outset as "plastic" responses to ~~the~~ a novel mode of assembly, the extent in which genetic material is exchanged among closely interacting species,

such as a predator and its prey etc.. On these problems we shall return when dealing with Elton's and Lotka's in III.

b) The rise of moder ethology.

Theories on behaviour and evolution have already been considered ~~when~~ a propos of ~~dealing with~~ Lamarck and his followers, then ~~with~~ of Darwin. However a continuous tradition of ecological investigations only became established around the 1920's, ~~with~~ and its results on territorial, socio-sexual and predatory behaviours ~~which~~ are essential prerequisites to the rest of our story. Introducing this tradition also offers the opportunity to clarify ~~the~~ some historical features so far neglected, or to justify why this cannot be done at present.

There is a main reason why an exhaustive history of ethology is not yet possible. Most reasonable attempts to systematize detailed observations of behaviour might in some sense qualify as bona-fide ethology. Thus one might get along with Thorpe (1979) in recognizing St. Francis of Assisi (1181-1226) as one among the earliest ethologists, perhaps a relatively "modern" one at a phenomelogical level. In fact some description of his habit to "converse" with birds might ~~not~~ look as not much different form how a contemporary "social ethologist" works. Be as it might, St. Francis must be credited of a highly influencial change of attitude towards nature, which parved the way to the development of moder biology and, to some extent, also helped initiating it (cf. again Thorpe, 1979).

"Forerunners" of ethology cannot any longer be left out when one gets to a Leroy (1723-89) or a Spalding (1840-); their feats equal or surpass those of contemporary and slightly posterior "professionals". Without taking account of Leroy our reading of Lamarck might suffer somewhat. Our reading of Lloyd Morgan does suffer a lot without taking account Spalding's influence more precisely that he himself did. Yet, in spite of Haldane's and Thorpe's valiant efforts (Haldane, 1954, Thorpe, 1979) one can do little, as yet, than point to what could be gained by detailed ~~such~~ histories.

The very term ethology also adds to the difficulty of dealing with this science. While the term had various usages in the English, Geoffroy the younger had introduced it in 1864 (see Jaynes, 1969) to denote what we would call behavioural ecology, as viewed from an evolutionary angle. This usage persisted in France till the dawn of the "Golden Age" (Scudo, 1983), and it also had some popularity in Englands in the early decades of this century (see again Thorpe, loc. cit. and cf. below). This usage quite correctly subsumes that no deep understanding of animal ecology can be achieved unless the relevant features of behaviour are properly taken into account. For instance no sense can be made of the remarkable oscillatory behaviour of the mussels-barnacles biocenoses unless taking account, as Fisher Piette did (cf. a), that only starvation induces whelks to switch from their preferred barnacle diet to energetically more convenient mussles. The present usage of ~~the term~~ "ethology", as usually remote both from evolution and community ecology, might help justifying why major figures ~~such as~~ (e.g. Piaget) failed to use it. If this were not enough, one could well write separate histories for the study of behaviour in major taxa, i.e. two major ones for insects and birds and a number of lesser ones for taxa such as shellfish or primates.

In these optics above, precise notions on territorial behaviours had already been worked out on insects by the turn of the century. An example is the work the Peckam's on wasps (1905), which much improve over more andoctical evidence such as by Fabre. However territorial behaviours ~~in insects~~ are not as easy to study in insects than the best vertebrate cases, since it is often harder to disintricate territorial form social behaviours proper. As an example let me just mention the trivial case of "sleeping aggregates", which is also perhaps the simplest ~~case~~ form of animal society proper (for a review see Le Manse, 1952). In many insect species tens to hundreads or more individuals aggregate "just to sleep" in characteristic locations. ~~One of the~~ A main characteristics common to these diverse kinds of groupings is to never involve any sexual activity when comprising individuals of both sexes, which is relatively rare. More commonly only one sex of a species, generally the male, forms such aggregates, ~~or~~ Also, when both sexes do, the aggregates are usually separate. The case is interesting since animals aggregate "for the sake" of it, while doing precious little together besides sharing a convenient location. Sleeping aggregates are also of interest since they can involve a number of related species, they can alternate with other forms of socialization, they can be a starting point for hybernation

aggregates etc..

The term territoriality only came in wide use with Howard's classic study in birds (1920) where it takes its simplest, most easily recognizable forms: One or more individuals, often a pair, defend a fixed area of habitat from conspecific trespassers. The size of the territory being defended varies a lot depending on the species, and within a species depending on the individual. The purposes of this defense can also be the most different -- feeding, breeding, mating or just a refuge. The only feature common to all such behaviours is that an extreme intolerance to conspecifics switches to any degree of tolerance at a precise border. Also, while the initial establishment of a territory generally involves substantial amounts of aggressive behaviours, its maintenance hardly involves any -- song displays as in many birds or marking such as by urinating in several mammals are generally enough.

In mammals, however, territoriality can take more subtle and flexible forms and, as for insects, it is hard to disintricate them from social behaviours proper. Thus in domestic cats territoriality is manifested by temporary utilization of space in the vicinity, such as a path an animal is going through. Also each [illegible] individual tends to use any one space at different hours of the day (Leyhausen, 1965, 1980). In other words ~~the~~ a main manifestation of ~~cats~~ social rank in cats consists in a delicate arrangement on who uses which spaces at which hour. While this involves a lot of learning which is "understandable" to humans, many other behaviours connected with use of territory appear more remarkable, up to defying rational explanations as in cases of homing ~~from far away (e.g.~~ such as by bees or pidgeons.

Moving to better understood forms of learning, those affecting prey or host choices are of special interest here. Besides instinct these often involve trial and error, teaching or "imitation" (in most cases of this sort denoted by unfortunate technical terms such as "social facilitation"). As an example, let us consider once more Fisher Piette's analysis of whelks, in particular their reluctance to switch to mussels. This is well justified by the fact that a starving whelk very well knows how to bore but, at first, it has no idea on what to bore, i.e. unexperienced whelks start by boring empty mussle shells, perhaps from within towards the outside etc.

After the first success, however, an individual will no longer repeat such mistakes, nor will their progeny. While switching whelks have to learn by trial and error, their progeny appears to learn what to bore "by watching". Then, while not being well equipped instinctually to feed on mussels, whelks can easily maintain this habit as a "cultural tradition" as long as barnacles remain scarce.

More in general, the ability of animals to switch diet, and to somehow transmit preference for the new diet to their descendants, was already well known at the turn of the century. A classic example are Leisiocampus quercus caterpillers, which normally feed on the margin of oak leaves. The same can also feed on pine needles, despite that their jaw structure is not ideally suited to them, ~~also~~ and their descendants will no longer seek oak lives (Pictet, e.g. 1911, cf. Wardle, 1929). ~~Also~~ Further, "learned" switches of host can easily entail sexual recognition, and thus play a role somewhat analogous to a direct learn~~ing~~ed recognition of conspecifies.

Then host, prey and sexual preferencies can be in any degree affected by "one shot" forms of learning, which usually take place early in development and can be manifested much later. This bring us to latent learning or imprinting as a topic on its own right, and again ~~its~~ to a history which is far from being a "smooth" one. Although earlier ethologists such as Spalding were very familiar with such forms of learning, these started being studied systematically only around the 1930's (once more, independently for insects and for birds). Classic studies by Thorpe and co-workers on a parasitic Hymenopteroid (Nemeritis i.e. Idechtis canscens) showed that these would prefer an alternative host, even just by being exposed to ~~the~~ its scent ~~of this host~~ when newly emerged. At about the same time Lorenz's classic studies on the following responses of young birds and on the effects of early experience on sexual preferences led to the notion of "imprinting". In its "canonical" form it consists in learning to recognize some specific "releaser" within a well defined "critical" period in growth, and in the effects being irreversible. Later on, the key role of this and other forms of learning for predatory habits has been studied in great detail (e.g. Leyhausen, 1959, 1980, Curio, 1979), thus much improving our present understanding of how predation works in nature.

Even relatively primitive studies of rather "lowly" animals, such as those by the Peckhams and by Fisher Piette, pose the central problem of how animals supplement their insticts by learned behaviours of an "intelligent" sort. Connected with "intelligence" is also a flexible use of signals. These problems were systematically addressed since Romanes, Baldwin and Lloyd Morgan. In the 1920's a veritable revolution in ~~this~~ such directions was provided by von Frisch's studies of the "dances" by which bees ~~these~~ convey "abstract" informations on the direction and distance (or, better, flying effort) of food sources. Besides opening a new avanue to interpret the origin of abstract languages in general (see exp. Haldane, 1956), these studies alerted ecologists on the sophistication and flexibility signal systems can attain even in relatively "lowly" animals.

3) Ecological genetics and the origin of races and species.

Genetics being relatively recent and ecological genetics still more, it might seem odd that this section starts way back to the 18th century. Let me first explain a main logical reason why. Further historical resons will hopefully become apparent in due course, even to those who perfer to confine usage of the term genetics to transmission genetics (as it generally was prior to recent, more direct methods of investigation). Conventional genetics largely consisted in searching for variations through their gross phenotypic manifestations, while any other condition is held as constant as possible. The result would tell precius little as to the innate determinism of any observed trait, -- some trait can be affected by variants, usually uninteresting ones from the point of view of adaptation and evolution.

To sort out the extent in which any observed characteristic is innate, exactly the inverse procedure as in transmission genetics has been traditional -- one would start by excluding possible genetic variants ~~for~~ affecting a trait of interest, and then sort out its change in different rearing conditions. Such experiments are now standard in ethology (see Lorenz, 1965), and the only required "genetics" is whatching out for mutants which might disturb the results. One further premise is here necessary. By studing the "permanence" of traits in the way just above one can easily approach the problem of the origin of species even without reference to any theory on large scale evolution. ~~Also~~ In fact one might do so even if being a convinced creationist, as in Linneus' case. Well aware both of the existence of "mutations" and of the plasticity of plant phenotypes, Linneus maintained that new plant species could easily originate by hybridization. This theory gave rise a lively experimental tradition, eventually culminating in Mendel's classic studies (see Olby, 1979). In this light it is hardly surprising that Mendel refrained from associating his experiments with Darwin's theories, by then already very popular in Germany. Whichever ~~his~~ Mendel's real purposes might have been, he probably could do as well without any theory on evolution proper.

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With these premises, let me describe in a schematic, abstract way the most frequent results of transplant experiments. Let X be a well defined plant type as found in a general location A, and not affected by detectable mutants. When this is transplanted to a climatically quite different location, B, one might find that

i) in B, X looks exactly as it did in A;

ii) in B, X changes to a Y, not obviously similar to any native plant of B;

iii) in B some X speciemen change to a Y and some others to a Z, neither obviously close to any native plant of B;

iv) in B, X changes to a Y, indistinguishable form a native plant of B;

v) in B some X specimen continue to look as in A, while others change to a Y, indistinguishable from a native plant of B.

Here "change" might mean a number of things such as new branches of the very same transplanted individual but, more usually, it refers to the results of vegetative propagation. These, or combinations thereof, were precisely the results Gmelin was getting transplanting to his St. Petersbug garden siberian plants (see again, Guyenot, 1956) or french botanists were getting by planting alpine forms near sea level (cf. Scudo, 1976) etc..

Gmelin's interpretations are among the oldest and most influential, since he spread them through the 13th (postumous) edition of Linneus' Systema Naturae. He had studied the famous Peloria which Lineus had recognized as a "mutant" of another species, and he had found that the

only two species of Dephinium of Siberia were giving rise to five or six distinct forms in his St. Petersboug garden. Gmelin explained this last result by the same hypothesis of hybridization Linneus had finally brought up for Peloria, concluding that "the number of plants the Creator initially made up has doubled or tripled, or multiplied at no end" (as in Guyenot, op. cit. p. 370). On the other hand Wolff came to the conclusion that in cases such as ii) and iv) the true nature of the species involved had not changed at all, only their outward apparence did (see Roe, 1980). Most such observations, then, could be accounted for one way on another ~~at that~~ when performed ~~time~~. Only observations as in v) remained baffling and highly controversial, even after Piaget had provided for them the plausible explanation below (cf. Scudo, 1976).

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Possibly the most clear cut case studied by Piaget is the alpine variety of the crassulacean Sedum album, micranthum, formerly classified as a separate species. He found that micranthum from some locations would perfectly revert to the album type when grown in Geneva, while the form other locations would retain ~~its own~~ micranthum type. Piaget's now "obvious" explanation is that reverting micranthum are just a somatic modification of the type, while the non revertants are phenocopies of this somatic modification. The explanation is fully consistent with the altitudinal distributions of the two kinds, as well with the operation of natural selection on a plant with substantial vegetative reproduction, ~~limited~~ short ranging intercrossing and seed dispersal. The genetic variations which fix micranthum at harsher, higher locations would be of no use at lower ones, where either mode of growth can be more favorable depending on climatic changes. At higher, harsher stations revertant plants would be selected against, since they might occasionally produce revertants in rare milder seasons and these would be at a big disadvantage in a normal season.

Going back to animals physiological changes such as those postulated by Romanes, Gulick and Wallace were being found in increasing numbers by the turn of the century, particularly in some insect taxa. One could still doubt, however, as whether reproductive isolation form the parent form could be tight enough to prevent substantial swamping of any selective divergence. Marchal's experiments on a scale insect genus Lecanium (1908) were among the first to show that such a physiological modification could also automatically produce a very tight reproductive isolation. He was studying two closely related "species", the peach scale (L. Corni) and th black scale locust (L. robiniarum), which also present intermediate varieties in plants such as wistaria and wines. By transferring ovigeorus females form peach to black locust tree (Robinia pseudoacacia), Marchal found that their progeny did very well in the new host, where it grew as indistinguishable form L. robiniarum. On the other hand hardly any progeny from these would survive when re-transferred to peach. Since natural transfer from peach to black locust tree appeared to be very rare, and the reverse one nearly impossible, reproductive isolation between the two forms would be very tight form the outset. Incidentally the same transfer technique easily allow to sort out purely phenotypic from genotypic components in the differencies between ~~other~~ related species, as for two species of Trichograms (Marchal, 1927).

The widespread use of the term "physiological segregation" by french ecologists, and that of "Howard's host selection principle" by british ones, both refer to observations and experiments such as those by Marchal in Lecanium. These terms came into widespread use at the turn of the century, and they remained in use throughout the "Golden Age" (in France also as late as the 1960's, cf. III, 2 b). Some later studies which did not have any sizeable influence on theorists of the "Golden Age" are also worth mentioning in the present context.

Piaget's studies on Limnanea stagnalis in the 1930's are still among those best dispalying the evolution of a reflex action, both in terms of its adptens and of its genetic determinism. In nature this snail differs in elongation according to habitat, the most flattened from (lacustris) being characteristic of gravel shores of lakes. However in the same habitat one can also find individuals with elongated upper part of the shell (the lower one being as flat as the others), showing that gravel habitat can force a flattened mode of growth also on immigrants form sandy or muddy beaches. Lacustris progeny grown in the laboratory turned out to correspond to five different level of flattering, ranging from the stagnalis type to somewhat less than lacustris. Then lacustris corresponds either to the type of the species or to any of four degree of fixation of the reflex by which all snail hang to a solid substratum. Also, crosses among these five phenotype give relatively simple menelian segregations.

To conclud this sketch one should also mention how learned components in species recognition provide still another potential mechanism for the evolution of reproductive isolation, particuarly in bird species with differnt color morphs in different parts of their range. Mainardi was the first to suggest that a tendency to prefer the same morph of the parents, or of the single ~~one~~ parent which reares the progeny, would tend to maintain homozygosity for either morph at any one location (cf. 1968). Both observations such as Griffith Smith (1967) on North American gulls and more precise models such as by Matessi and Scudo (1975, see also Scudo, 1976 b) appear to strenghten Mainardi's contention. Then, at present, a detailed knowledge on several mechanisms would vindicate Wallace's theory on speciation (cf. § 1c), and also show how frail this would look not knowing these mechanisms.