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SEARCHING FOR THE EVOLUTIONARY ROOTS OF CLADISTICS (A SIMPLIFIED CONSPECTUS OF HOLOGENETIC THEORY)

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'Modern evolutionary mechanics prefers to deny a causal relationship between phylogeny and ontogeny. What else? The very importance of embryology in tracing anatomical homologies is subordinate to comparative anatomy. Nowadays the same organ may originate phylogenetically from entoderm and ontogenetically from ectoderm... Nonetheless all this is good; oh how these doubts which now affect and divide the students of evolution are better than that unconscious security with which once they used to think that invoking natural selection, heredity, and adaptation one had to solve all problems'.

So wrote Daniele Rosa (1857 - 1944) to his former student Giuseppe Colosi in 1939, at the age of 82 and half blind for over 30 years (Colosi 1961).

I take as demonstrated that Rosa in his book on 'Hologenesis' (1918) wrote one of the best pieces of hypothetico-deductive reasoning in biology. In it he introduced and clearly described for the first time (Baroni Urbani 1977), among other things, the dichotomous path of speciation, the resulting asymmetry of

the two sister branches in phylogeny as plesiomorphic and apomorphic, and the idea of the biogenetic law. Yet these ideas had virtually no impact on the scientific milieu of his time.

Rosa had a difficult character and a mean reputation in the Italian academic world. A significant example of this is given by Colosi (l. c.). At that time professorships in Italy were attributed by marks (50 points was the maximum score) and the amount of marks of a candidate - it could remain stationary but not regress - was decided by a national board of full professors evaluating his published record. At the end of the last century Daniele Rosa - a very young, enthusiastic, and starving scientist - was continuously applying for every position in zoology, yet never reaching a reasonable score. Finally, he decided to make a particular effort in order to reach his target (he was already in his early forties). In 1899 he published his most famous paper on the progressive reduction of variability during evolution, a paper which already contained the premises of hologenesis and which was translated later into French and German. Armed with this new weapon in his repertory, he applied for the chair of zoology at the University of Messina, only to see his application returned. Moreover the addition of the last monograph to his record had advanced his score by only 0.02 points! Rosa received few national and only one international honour: the membership of the Society of

Friends of Natural Sciences in Moscow, in 1889, for his distinguished contributions to the classification of earthworms.

In a previous paper (1977) I underlined some baffling similarities between Rosa's work and the work of Willi Hennig. It is legitimate to assume that these similarities are due to something other than chance alone and this hypothesis has been recently confirmed by Prof. Benedetto Lanza of the Zoological Museum of the University of Florence who still remembers details of a visit of Hennig to Colosi in Florence to discuss and to read Rosa's papers at the Institute Library (B. Lanza, oral communication, March 1988). In spite of the congruence among the works of the two scientists, at least one major difference in trend must be stressed: Hennig dealt with classification only and Rosa was concerned by evolution alone. For this reason the homology concept is rarely used in the book by Rosa and is simply an instrument to explain some examples. It is not a dominant idea in his reasoning. His leading idea was to explain the origin, distribution, and extinction of species. This seems the most important argument justifying a study and a re-evaluation of the work of Rosa.

All this, however means not that Rosa was right in everything he said. Nonetheless, I am convinced that Rosa accomplished one of the best performances of his time, exactly as, before him, Darwin, Lamarck, and Buffon had done. Today, thanks to the progress of scientific knowledge, we should all have a deeper understanding of evolutionary problems than our famous forerunners who justly deserve a leading position in the history of scientific thought. Rosa's book, additionally, shows another objective drawback: it is written in a way very different from what is expected in a textbook today. His long sentences, with symmetrically distributed adverbs and adjectives in order to have the desired effect after a grading of nuances, may possess some kind of 'art nouveau' literary flavour. However they are often difficult to follow, even for an Italian. These difficulties are only in part overcome in the French edition of this book (1931) which I am inclined to regard as Rosa's main fault: this is barely more than a translation of the 1918 original and 13 important years of developing biological thought and discoveries are completely excluded from it.

Given the broad consistency between cladistic methods and hologenetic evolutionary thought it may be worth summarising here the main conclusions attained by Hologenesis and the way in which they have been reached. Their truth or falsifiability can be subject to personal interpretation but what is important is that there is overlap between the two

approaches, and that there are reciprocal implications for each discipline.

The purpose of the present paper is not to reaffirm the whole or parts of Hologenesis as the true or better explanation of evolution (which I ignore myself), but just to show how much of the work of Daniele Rosa can still fit the thinking of his detractors, or the one of those who surpassed them and elaborated again very similar reasonings.

The premises of hologenesis

The hologenetic reasoning begins with some necessary starting hypothesis and, in order to flow in a way as credible as possible, these hypotheses have been limited to the minimum necessary. The whole theory relies on three initial assumptions only. Actually, a fourth, non declared, necessary, assumption is that evolution exists.

The three assumptions of hologenesis are as follows:

1. Evolution depends on endogenous and exogenous factors but the first are more important than the latter ones.

Rosa gives reasonable evidence that this hypothesis was not new but borrowed from Nageli (1865, 1884) and in part from Lamarck (1809) as well. The exact meaning of this hypothesis is explained as follows. The observed course of evolution obviously depends on environmental constraints as much as lungs have been developed when marine organisms colonized the land. But if, in a hypothetical experiment, these organisms could have been kept under perfectly constant laboratory conditions during the same amount of time, they would have evolved anyway in some direction instead of remaining unchanged as implied by Darwinist theory, and as clearly stated by Weismann (1875).

2. The direction in which evolution proceeds is also independent of variation resulting from exogenous factors.

This second hypothesis is also credited to Nageli, but improved and made more rigorous by pruning the concept of 'stimulating action' in which Rosa recognizes erroneous Lamarckian remains. Organic evolution is compared to the developmental capacity of an embryo which is destined to undergo transformation anyway, provided food is available and environmental conditions permit survival. The main consequence of this is that individual variations are permitted but the major evolutionary trends are already implicit

within the organisms and, hence, the same species is constrained to undergo evolution (or extinction) roughly in the same way, at the same time, and on its whole area of distribution. Although Rosa's formulation is unique and more precise, I see no fundamental differences between this hypothesis and the implications of what, in modern evolutionary literature, is commonly understood as 'prime movers' of evolution or, even more clearly, 'specific preadaptations'.

3. In spite of this [preadaptation], evolution is not linear but dichotomously branched through differential divisions of the specific idioplasma which are determined by the evolutionary level already attained.

This last hypothesis is regarded by Rosa as his only original contribution to the premises of hologenesis. The term 'idioplasma', was considered 'virtually meaningless' by Simpson (1978). Rosa gave his own literal definition of idioplasma in a footnote to page 2 of his book:

"*Specific idioplasma*" is simply the translation of the term "*Artiplasma*" already used by Fick (1901) as opposed to "*Individualplasma*". The concept of *Artiplasma* is regarded as correct even by Haecker (1911) and is similar to the "*Artzelle*" concept introduced by O. Hertwig (1899) which implies that all cells of a species are different from the cells of another species'.

Considering that this was written in 1917, it might reasonably represent what we call alleles today.

The dichotomy of evolution, for Rosa, is justified by the necessity to avoid unlimited linear evolution from all conceivable ancestors (in contrast with our knowledge) and by analogy between ontogeny and phylogeny. Dichotomies could be considered both cases of a species A giving rise to two species B and C and even the case of A giving rise to B while remaining unchanged. Which one is the right view will not affect the hologenetic reasoning, but the former hypothesis is claimed to better fit the experimental evidence.

After describing the three starting hypotheses of hologenesis Rosa apologizes for their speculative nature but makes clear that no other evolutionary theory has been able to deal with these problems in a more concrete way. His main task, from then onwards, was to test if the hologenetic hypotheses allowed a better understanding of evolutionary phenomena.

The dominant methodological instrument of Rosa's book is the search for potential falsifiers at every step of his reasoning. For this reason, after formulating the three fundamental premises of hologenesis, Rosa devoted a whole chapter to discuss the meaning

of apparent cases of evolutionary stasis, involution, neoteny, etc. The difficulty for hologenesis is not very different from that of other evolutionary theories, and Rosa gives credit for reasonable solutions of the problem to several scientists ranging from Kohl (1895), his own 1899 paper, and Cuenot (1911).

The phylogenetic prospective and the progressive reduction of variability

From the fundamental propositions of hologenesis, it flows that each species is like an egg: from it only some precise pair of daughter species can originate. In this way Rosa opposes Lamarckists and Darwinists together, the latter represented essentially by De Vries (1901 - 1903) who clearly asserted the importance of cumulative mutations and the necessary freedom of variation in every direction. The universally accepted Dollo's law on irreversibility of evolution (Dollo 1893) is clearly contradictory to this view because random should imply reversibility as well. Additionally, the observed phylogenetic variation of the known species is much narrower than one would expect under the perspective of random mutation. To Dollo's law, with several concrete examples, Rosa adds another general principle: the progressive reduction of variability during evolution. Just as in an embryo each cell possesses only a given prospective value or a precise developmental fate, each species can give rise to a limited set of descendants.

As a demonstration of this, Rosa adduces the fact of progressive reduction of taxonomic rank in all plausible phylogenies, i.e. the first tetrapod gave rise to other tetrapods only, the first hominid only to other hominids, etc. The explanation of this phenomenon is a mere consequence of the fundamental propositions of hologenesis. By admitting the dichotomous pattern of evolution in which a species A gives rise to two daughter species B and C, it is clear that each daughter species will carry in itself a different and reduced part of the maternal idioplasma (i.e. phylogenetic prospective) which is, by definition, smaller than the idioplasma of A, the only one able to contain both B and C.

This point is still subject to debate today between students accepting or refusing the 'creative' power of natural selection. It may be worth recalling that, even within the most convinced neoDarwinist circles, the concept of 'phylogenetic inertia' is commonly employed to explain why, e.g., it is very unlikely to find very advanced social insects driving airplanes and constructing TV sets however long we can let natural selection at work.

Apparent polyphyly and bathyphyly

Under the term of 'apparent polyphyly' Rosa makes sense of unexplained fact that the fossil record shows nearly always rectilinear evolution. In fact, the ancestors of horses were still horses, the ancestors of insects other insects, the ancestors of different Mastodon species other Mastodon species, etc. and we do not know a real common ancestor giving rise e.g. to all members of a genus, a family, or a class.

This fact alone represents a major difficulty for orthodox evolutionary theory which is obliged to admit unchanged orthoselection during several geological epoches in spite of the continuously changing environmental conditions.

Such apparent orthogenesis is called by Rosa 'intrinsic orthoselection', i.e. selection within the phylogenetic prospective of the ancestors, as opposed to the 'extrinsic orthoselection' due to implausible constant environmental pressures as the Darwinists are obliged to postulate.

This observation could lead us to admit a large degree of polyphyly. This must, of course, be only apparent in order to avoid accepting the idea that life originated as many times as there are extant species. The most plausible explanation can be found again in the biogenetic law and in the progressive reduction of variability: the prospective potential of the ancestral forms was much greater at the early stages of life, and the true ancestors of advanced groups, like, e.g. the vertebrates, were very old and unspecialized individuals which left no recognizable fossil traces. Even dichotomous evolution, hence, was faster at the beginning of life and the most dramatic branchings are inevitable very old. Monophyly, however, is the only reasonable hypothesis, although it may prove to be impossible to demonstrate.

Rosa recognizes at this point two potential risks with his conclusions in a classificatory framework: (1) the apparent polyphyly of living beings might imply our incapacity to identify monophyletic groups as impossible to characterize, and (2) a reduced value of the homology concept, given the fact that 'really' homologous structures are very likely to be derived from an unique primitive ancestor who did not yet possess them.

The only way to define natural groups is some kind of 'overall similarity' which must be greater within the group, a position not too far, in practice, from what is called today the inductive method of homology detection. Rosa borrows from Osborn (1906) the concept of 'latent homology' to explain the common rise of similar structures within monophyletic groups from an ancestor which might not have possessed them.

Opposed to homology is, of course, analogy, but convergence in a strict sense should not exist given the continuous, divergent, branching of evolution. Real convergence can be admitted only if evolution proceeded at random and phylogenies become unrecognizable.

Systemic dichotomies and asymmetry of sister groups

In this chapter Rosa starts with a formidable display of botanical and zoological knowledge in which he shows that classification itself often already presents a dichotomous arrangement at each level. When such a dichotomy is not already available, it can be introduced with improved results. A consequence of this is that in a 'sound' classification all categories and not only species can claim a similar degree of naturalness. The objection that some evolutionary branches may have undergone extinction without leaving (known) fossil remains is overcome by the nature of dichotomy itself: each branch must inevitably appear as one of two sister branches even if additional, intermediate, sister branches have been wiped off from the cladogram.

A careful analysis of the dichotomous branches, whenever possible, always shows that one branch is more primitive than the other one, i.e. it has a reduced phylogenetic perspective. Rosa gives abundant examples that this asymmetry was already known, recognized, and described in the literature. The main novelty lies in its interpretation. The primitive forms cannot be interpreted as surviving ancestors of the contemporary more evolved ones and the former abundance and present extinction of several forms cannot be tribute to the struggle for life alone: a sturgeon is no less competitive than a teleostean in spite of the cartilaginous skeleton and its ganoid scales. Even if the fossil record appears to be older for the primitive forms than for the most specialized ones, this is a simple consequence of the fact that the plesiomorph branch had a faster dichotomous evolution. as a result of this, coupled with the progressive reduction of variability, it will reach extinction earlier or there will be a drastic reduction in the number of species.

The evolution of every branch, in fact, is destined to reach an apogee in which its maximum diversity can be observed, i.e. when an equilibrium between speciation and extinction is attained. Afterwards, competition and exhausted phylogenetic prospective may reduce numerically or suppress the whole branch. The other branch (the apomorphic one), by showing slower evolution can produce forms which are more complex and better adapted to the changing environmental conditions.

Both branches reach a sort of 'final' evolutionary status called paracme (Haeckel 1866) representing some kind of evolutionary *cul-de-sac* in which only minor variations are still allowed. The plesiomorph branch must, by definition, attain the paracme status before the apomorphic one. This status can often be recognized by bizarre morphology, extreme structural complexity, hyperthely, or giantism. None of these characters, however can be regarded as a sure indication of exhausted evolutionary potential. As a consequence of all this, the apomorphic branch, by undergoing more dichotomies, should also show a greater diversity than the plesiomorphic one.

The origin of species and survival of the new ones

This is obviously the central problem of every evolutionary theory. Rosa saw insurmountable difficulties in all other theories, while his own explanation flows as a direct consequence of the basic hologenetic hypotheses. Nevertheless, his explanation is admittedly finalistic (Rosa was a convinced atheist) and non falsifiable, as all other alternative hypotheses also are.

The main questions Rosa tries to answer are the following:

1 Why do organisms appear to us grouped into species and not in a continuous series?

2 How can new species get established in spite of their initial obligatory interbreeding with not yet muted individuals?

3 Even admitting that each [selected mutation] is better adapted to the environment, how can it be produced in numbers sufficient to permit its survival?

The answer usually given to all these questions i.e. geographic isolation - appears completely unsatisfactory to Rosa who observes how, for instance, all domestic races of animals and plants reached a very high degree of morphological discontinuity but still, when allowed, freely interbreed with each other. It seems moreover unlikely that each of the countless species of radiolarians, forams, diatoms, flagellates, etc. living in high population densities and complete sympatry, all originated in an isolated environment.

From the third fundamental hypothesis of hologenesis, it follows that the idioplasma (the term has a historical value, but I think that, by now, nobody should seriously object to calling it DNA), after a given number of replications is constrained to divide itself into two daughter idioplasmas by its own nature. This is the

only way in which a stem species can give rise to two daughter species in large numbers of individuals and roughly at the same time. Rosa favours this view not only for its strict adherence with his starting hypothesis, but also for offering the following concrete advantages on any other hypothesis: 1. Further inbreeding with the stem species is destined to disappear by the gradual disappearing of the stem species itself. 2. It allows for highly probable interbreeding of sexual partners carrying the same mutation. Rosa used himself the term 'internal mutation' and conceded that such internal mutations are virtually the same as that which one of his major foes - H De Vries - had already postulated and called 'premutations'.

Adaptations and the laws of evolution

Most evolutionary studies emphasized the adaptational value of new mutations to the external environment and did not consider the even greater need for a mutation to fit the intrinsic complexity of an organism.

Darwin and De Vries deserve the credit for giving a plausible physical explanation of evolution, and, given the diversity of external environments, there is some chance that a random mutation may fit one of them. On the contrary, the organism itself is only one and a random mutation may have a chance of being non-lethal only in very simple organisms. While expanding this point Rosa loses his self-control and (by pure convergence) exclaims (page 197): 'The deuce! If I add a modification "whatever" to the [still very simple] organism of my watch, for sure I must bring it back to the [blind] watchmaker'.

The sole alternative lies in the fact that the idioplasma itself must obey some kind of chemical or physical law - yet to be discovered - which permits only 'harmonic' variability, i.e. compatible with physiological survival. In order to explain this, one should suppose that the idioplasma is composed by many smaller units (the energetic equilibrium of which is necessary to life), smaller units which had already been postulated under the name of 'pangenes' (De Vries 1889) or 'determinants' (Weismann 1875). Either for personal sympathy, or for respect of priority, or just for bad luck, Rosa adopted the latter name.

Such determinants or [pan]genes must be very small particles which, all together, constitute the specific idioplasma. The characteristic of determinants is some kind of diploidy (the word is mine) in order to allow for their doubling into two daughter species.

For Rosa a determinant is never destined to true extinction but one of its two homologous parts (would it be biased to call them alleles?), i.e. the one destined to one daughter species,

has a different phylogenetic potential than the one destined to its sister species. The whole mechanism of speciation is viewed by Rosa as in Figure 1.

From this diagram Rosa demonstrates five small theorems explaining further properties of evolution which may be either trivial or irrelevant in a modern context. One of them (his 'Nota 4a') may still offer an argument for speculation today.

Assuming two simple sister species possessing two determinants only (B and C), their idioplasms can be represented as $B > C$ and $B < C$ (Figure 1). In this sense they would be symmetric. But if - as suggested in Rosa's 'Nota 3a' - complementary determinants, must have opposite value, the former inequalities became $B^+ > C^-$ and $B^+ < C^-$, which is asymmetric as supposed by Rosa for the evolution of plesiomorph and apomorph branches.

It may be worth emphasizing again that the whole discussion on the role of determinants during evolution is kept strictly in terms of combination of molecules of compound(s) unknown to Rosa and that it is in the finite number of viable recombinations of organic compounds that Rosa recognizes an additional confirmation for his law of progressive reduction of variability during evolution.

In summary, the phylogenetically most important adaptations are the internal adaptations to the ergonomics of the organism itself. These adaptations, claims Rosa, are explained only by Hologenesis. The dichotomous evolution can account very easily for the observed organic diversity; assuming the monophyly of life, after 50 dichotomous divisions of the first living being we would already have $1'125'899'906'842'624$ different species. This implies that - always for 50 hypothetical divisions only - for each known living species about one billion other species have already undergone extinction. And it is by this formidable elimination process that natural selection exercised entirely its power by eliminating several branches, some at their very appearance, others later because they were unadapted to the environmental conditions. However, the astronomic figures of the hypothetical numbers of species attained by continuous dichotomic divisions could be greatly reduced if extinction was high during the first branchings of 2, 4, 8, etc. species. But this is very unlikely, claims Rosa, because primitive organisms were very simple and with very broad adaptation capacity. As a consequence of the progressive reduction of the phylogenetic prospective. The power of natural selection, hence, increased with increasing organic diversity and complexity. Natural selection deserves a major role in evolution only after the hologenetic principles

have been admitted. Rosa's insisting on this point appears much better directed against Lamarckists and Neodarwinists; Darwin himself admitted that the important role of 'spontaneous variations' and of 'the laws of growth' may overcome the one of natural selection (Baroni Urbani 1979). Lack of natural selection (or, the other way around, production of a majority of adapted branches) is the explanation for the known cases of explosive speciation.

The last advantage of Hologenesis, for Rosa, is precisely its capacity to make natural selection more plausible. A new random mutation better fitting the changing environment has incredibly low probabilities to appear precisely in the place and at the time in which environmental conditions are changing. By internally driven evolution, such mutations will appear on the whole area of the ancestor species - an area which must be broader, the more ancestral it is. Hence at least a few demes may have a chance of being selected at the right place and at the right time.

With this reasoning, originally contained in 236 pages and which I summarized here with great simplifications, Rosa concludes his proposition of the hologenetic theory by emphasizing how it does not contradict any known physical law and how it appears to have a better predictive value than other theories.

Biogeography

After expanding the principles of Hologenesis, Rosa devotes the last, longer, chapter of his book (over 60 pages) to biogeography. In biogeography - he claims - the difference between his theory and all other theories is even greater and the hologenetic hypothesis shows a much greater predictive value. In spite of that, in this chapter, Rosa's reasoning is much more inductive than anywhere else in the attempt to find an agreement between the huge mass of information and the theoretical framework.

The first, insurmountable, difference between hologenesis and orthodox evolutionary theories is that the origin of species is polygenetic for the first (i.e. new species arise on large areas), and monogenetic for the latter (i.e. new species arise on geographically restricted centers of origin). As a corollary of this, polygeny in speciation was already admitted frequently in the literature but, either by students negating evolution, like Agassiz (1869), or by scientists concerned much more with a description of nature than with its evolutionary interpretation, like von Kolliker (1872), Engler (1879 - 1882), von Ettingshausen (1894), Briquet (1901), and Guppy (1910).

In fact, on this subject, the two points of view, i.e. the monogenetic, orthodox one and the polygenetic, hologenetic and agnostic one are diametrically opposed and irreconcilable. If the monogenetic perspective is true, we should be able to find fossil or other, presumptive evidence that the geographic distribution of living taxa was decreasingly smaller in the past up to an eventual coincidence with their centers of origin. On the contrary, if the (hologenetic) polygenetic hypothesis is right, the former geographic distributions should appear always larger than the present ones, approaching more and more the initial cosmopolitism of the stem species.

And this is precisely what we can observe: Rosa gives several examples of it ironically drawn from the work of Darwinian writers and going back up to Pfeffer (1891), Trouessart (1890), and even Wallace (1880).

Migrations and dispersal, however, are accepted by Rosa as well, but their role is supposed to be much less important than what it used to be. As a general rule, geographic distributions should be broader for ancestral and narrower for derived forms. This is confirmed, e.g. by the fact that differences between tertiary faunas and floras were smaller than the present ones and bigger than those among cretaceous ones, etc. Other facts of biogeography appear in contrast with Hologenesis, like the absence of placental mammals in Australia: under a strict polygenetic hypothesis they should have evolved there as well. Rosa noticed this difficulty and tried to overcome it by explaining this and other extraordinary discontinuities in biogeographic patterns as a consequence of the previously demonstrated bathyphyly, i.e. the great antiquity of all ancestors of most recent groups. The key factor in interpreting the taxonomic composition of terrestrial biota is the relative epoch of emersion of the land. Only the taxa still subject to dichotomous division as marine ancestors at that time had the possibility of colonizing the land from sea.

At the end of his book Rosa apologizes for trying to change so much of the established thought and justifies himself by recalling how his original contribution has been just adding one minor hypothesis to other, generally accepted, principles. After doing it, a concatenation of conclusions followed each other in an unavoidable way.

While summarizing the basic concepts of "Hologenesis" as it was proposed over 70 years ago by Daniele Rosa, I have tried to simplify his style and to add nothing of my own but the use of a more contemporary terminology. My efforts are an attempt to show that it is true that the use of terms which are virtually exclusive to, or characteristic of one or another school of thought may be regarded as

provocative. It was intentional. If, in doing so, I betrayed Rosa's spirit and ideas, this was entirely unintentional and I must apologize for having done it.

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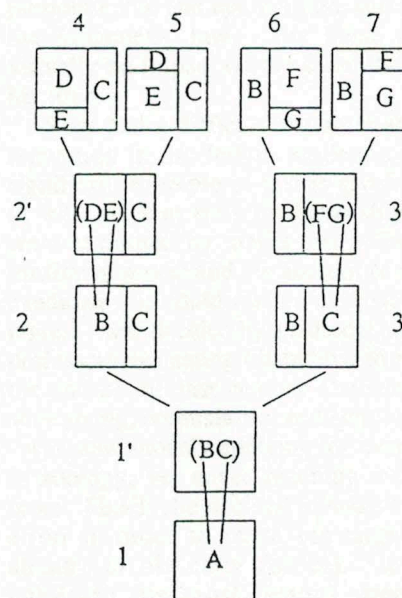


Figure 1. The mechanism of speciation as hypothesized by Rosa, with one stem species giving rise to two sister species sharing the same genetic determinants but in different proportions and possessing different phylogenetic perspectives (redrawn from Rosa, 1918, plate B).
