Models of Speciation

New concepts suggest that the classical sympatric and allopatric models are not the only alternatives.

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The modern or synthetic view of organic evolution regards speciation as a special and perhaps usually brief stage in evolutionary divergence, during which genetic isolating mechanisms develop to a level which makes the phyletic separation of the incipient species irreversible (except for the special case of alloploidy, almost entirely restricted to plants). As formulated and extended by Mayr (*1*), this process is conceived of as occurring when the diverging populations are geographically separated and occupy different territories. It is this *allopatric* model of speciation which has frequently been presented in terms of the well-known "dumbbell" diagram (*2*, figure 5-1). Allopatric speciation has been put forward as an alternative to the now largely discredited hypothesis of *sympatric* speciation, that is, the idea that "biological" or "ecological" races of a species can coexist geographically in an area and gradually diverge genetically until they constitute distinct species.

General acceptance of the allopatric model as the *only* mechanism of speciation in animals (or virtually the only one—exceptions are sometimes admitted in the case of endoparasites and a few other instances in which ecological separation is practically equivalent to geographic separation) has been mainly due to detailed study and reinterpretation of the examples which were earlier alleged to establish the existence of sympatric speciation. When examined more closely, most of these proved to be examples of forms that had already diverged to the level of full species and might well have done so allopatrically, with subsequent range extension leading to geographical coexistence. Apart from the collapse of the case that had been used to support it, sympatric speciation also seems incompatible with ordinary principles of population genetics, since it would require genetic isolating mechanisms to be built up within a single population, by natural selection, and this implies the spread of mutations which would prevent matings occurring or render them fruitless.

For these reasons, and because there are innumerable instances that seem to support it, allopatric speciation has now been accepted by almost all vertebrate zoologists. Cases where no paleontological or cytogenetic data exist are automatically interpreted in terms of the allopatric model, even if the particular interpretation seems somewhat forced (*3*).

Lingering doubts as to the universality of the allopatric model have persisted, however, among entomologists and botanists. Some students of the "species flocks" in ancient freshwater lakes also feel that the allopatric model does not fit these cases, although others believe that even in such instances an allopatric interpretation is plausible. For some time past there seems to have been renewed pressure to find out in much greater detail what the genetic basis for isolating mechanisms really is and how it develops. And recently, almost suddenly, a number of papers have appeared that seem to open the question (which should probably have been asked earlier): are the sympatric and allopatric models really the only conceivable alternatives? Even if we admit that all speciation has a geographic basis, in the broad sense, does it necessarily follow that allopatric speciation (in the sense of the dumbbell diagram) is the only form of geographic speciation?

These questions are intimately bound up with the relative roles of "point mutations" and chromosomal rearrangements of a relatively gross kind in speciation. (The existence of intermediate categories of chromosomal changes still further clouds the issue, but will not be discussed here.) It is a matter of empirical observation that, as far as the higher animals are concerned, even the most closely related species are usually found to differ in karyotype when the chromosomes are examined under the microscope. The only sure exceptions to this generalization seem to be certain species complexes in the genus *Drosophila; D. mulleri, D. aldrichi*, and *D. wheeleri* have been said not to differ at all in the banding pattern of their polytene chromosomes (*4*), and the same is apparently true of several Hawaiian species complexes, which have been described in consequence as *homosequential* (*5*). In other groups of organisms apparent or reported cases of distinct species with indistinguishable karyotypes have been based on comparisons of metaphase chromosomes alone, banded polytene chromosomes not being available. In the sciarid, chironomid, and simuliid midges, where polytene chromosomes do occur and have been analyzed by numerous workers, homosequential species complexes have not been found and even the most closely related species seem to differ in karyotype (*6*). In the case of *Chironomus thummi* and *piger*, however (regarded by me as species, but by Keyl as subspecies), the difference in banding pattern consists in the reduplication of a number of individual bands rather than in any large-scale rearrangements (*7*). In those groups of grasshoppers and beetles that have been subjected to critical cytogenetical analysis (but only on the basis of metaphase chromosomes, since polytene elements do not exist in these groups), each species seems, in general, to be karyotypically unique (*8*).

The above facts are obviously compatible with the view that certain types of chromosomal rearrangements such as inversions and translocations of various kinds (including chromosomal fusions and dissociations, producing changes in chromosome number) may play a primary determining role in the speciation process in many groups of animals. But the existence of the homosequential species complexes referred to above proves conclusively that karyotypic changes are not a universal *sine*

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qua non for speciation. And furthermore, even in those groups where the most closely related species differ karyotypically, the prima facie evidence cannot conclusively prove that chromosomal rearrangements cause speciation —such changes could be mere epiphenomena of the speciation process. We need above all to know what part these rearrangements play in interracial and interspecific hybrids, that is, in the offspring of crosses between forms that have reached various stages of evolutionary divergence. Only then can we discuss them as possible genetic isolating mechanisms. The matter is extremely complex, because we cannot necessarily assume that a chromosomal rearrangement at the present time has exactly the same genetic properties or behaves at meiosis in the same manner as when it first arose; selection may have altered it in the course of centuries and millenia.

By and large it seems safe to accept the generalization that most point mutations have a finite and generally quite high (on the evolutionary time scale) rate of recurrence, whereas gross structural changes in the chromosomes are, in practice, unique events, since they depend on the coincidence of two or more very rare events (that is, two or more chromosome breaks at particular loci) in the same cell, followed by reunion in a new sequence. This proposition seems undeniable when we are considering chromosomal rearrangements in Diptera such as *Drosophila*, where the breakage points can be defined very precisely in terms of the banding pattern in the polytene chromosomes. In other groups of organisms, however, it is less easy to be absolutely certain—two rearrangements may look identical under the microscope, but may have slightly different end points. It is unlikely, however, that this is a serious source of error in cytogenetic analysis of evolutionary processes. Thus we may accept the general concept of a monophyletic origin for chromosomal rearrangements versus a polyphyletic one for point mutations; and this viewpoint is basic to the discussion presented here.

Mayr (*1*) has argued forcefully against all theories of species arising from single mutant individuals and has emphasized that speciation is a "population phenomenon." While the general proposition is undeniable, it is clear that all mutations arise in the first place in single individuals. If we are considering the spread of a particular point mutation throughout a population we may consider such a mutation as arising independently in a number of individuals, distributed in space and in time over many generations, each of these individuals acting as a focus from which dispersal of the altered gene occurs. In the case of a structural chromosomal change, however, we should think in terms of a single individual as the sole point of origin of the new type of chromosome. It is thus easier to conceive of an entire population changing in respect of a point mutation (complete replacement of one allele by another) because this process can be initiated spontaneously at a number of focal points of origin. In the case of a structural rearrangement, having a single point of origin, the spreading process must be on a different scale of magnitude, either in space or time, or both.

Contiguous Subspecies

Criticism of the view that all speciation is essentially allopatric seems to have developed among both zoological and botanical evolutionists recently, largely as a result of detailed studies of animals and plant distributions in space. A number of workers appear to have discovered, almost simultaneously, that in many instances closely related taxa (geographic subspecies, semispecies, or incipient species) do not overlap broadly in geographic distribution (the sympatric situation), neither do they live in entirely separate areas. On the contrary, they occupy *contiguous* areas, with an extremely narrow zone of overlap, within which hybridization is theoretically possible and may actually occur. Such situations, which have been studied in grasses (*9*), pocket-gophers (*10*), and wingless grasshoppers (*11*), have been designated *parapatric* by some authors. Geographic distribution patterns of this type are hardly likely to exist in highly mobile organisms, but may be expected to be common in ones which are sessile or exhibit a low degree of vagility. Some parapatric distribution patterns seem to depend on a sharp ecological discontinuity (for example, in soil type); but others exist in spite of an apparent uniformity of the environment.

In plants, Lewis (*12*) has distinguished two modes of speciation which he calls "gradual" and "saltational." Gradual speciation is described as due to multiple genetic changes without major chromosomal rearrangements; speciation by saltation involves multiple structural changes of the karyotype (*Clarkia franciscana* differs from its presumed ancestor *C. rubicunda* by at least three translocations and four inversions). Whereas closely related species may appropriately be designated siblings, the relationship in the case of speciation by saltation is more akin to that of parent and offspring, since one can distinguish clearly between the ancestral and the derivative species. It is characteristic of such cases that the hybrids show a high degree of sterility, as a result of the multiple karyotypic differences.

Higher plants are, of course, sessile. Their "vagility" depends on the precise pollination mechanism on which they depend. The vagility of many wingless insects and other invertebrates is probably of the same order of magnitude. On a priori grounds we might expect to find some resemblances between methods of speciation in these groups and the higher plants; by contrast, the birds, larger mammals, pelagic organisms, and animals liable to accidental dispersal over great distances might be expected to show a different pattern.

The races and species (some perhaps semispecies in the sense of Mayr) of wingless grasshoppers belonging to the *viatica* group (Eumastacidae, Morabinae; there is no valid generic name for these insects at present) show typically contiguous or "parapatric" ranges in southeastern Australia (Fig. 1). They differ in respect of certain easily identifiable chromosomal rearrangements such as fusions, pericentric inversions, and a translocation (*11*). The eastern, 19-chromosome race of *viatica* ($2n♂ = 19$, $2n♀ = 20$) has a karyotype that probably differs little from that of the common ancestor of the whole group. The western, 17-chromosome race of the same species and an unnamed species "P24" differ from *viatica* in having a fusion between a long "B" chromosome and a small chromosome "6" (the B + 6 fusion). There are three cytological races of P24: one with an acrocentric X chromosome and no Y, one with a neo-XY in the male (the result of a centric fusion between the X and autosome "1"), and a third race (also XY) homozygous for a translocation between the "A" chromosome and the B + 6 element. Species "P25" has two races, one with XO males, the other with a neo-XY mechanism (the result of a centric fusion between the X and chromosome B). Species "P45b" also has XO and XY races, but in this case the X-autosome fusion is a tandem one (that is, not a centric one) between the original X and chromosome 6. Species "P45c" has a karyotype much like the "primitive" one of *viatica,* but the short limbs of most of the acrocentric chromosomes are significantly longer than in other members of the group. Chromosome 6, which has been involved in two of the fusions, is late-labeling after tritiated thymidine autoradiography (*13*).

Wherever the ranges of two forms of this group come in contact, there is a hybrid zone, at most a few hundred meters in width. Similar distribution patterns exist in numerous other genera and species groups of morabine grasshoppers in Australia; one might say that many species groups show a mosaic distribution pattern, with little or no sympatry (approximately 220 species of morabine grasshoppers, the great majority still undescribed, are known to exist in Australia). As far as the *viatica* group is concerned, ethological isolation between parapatric forms seems to be generally absent or so weak that the production of hybrids is not prevented in the zone of overlap. Overlap zones have not been found between all the taxa we have recognized but this is undoubtedly owing in the main to destruction of the original vegetation since the introduction of agriculture, which has greatly reduced the areas suitable for supporting populations of these insects. However, four zones of hybridization have now been studied in the Australian morabine grasshoppers (three of them in the *viatica* group), and we have presumptive evidence of several more. In the case of the hybrids between the 15- and 17-chromosome races of *Keyacris scurra* (*14*) and in that of the two races of *viatica* (*15*) there is clear evidence of a significant reduction in the fecundity of male hybrids collected in nature, as a result of meiotic asynapsis or malorientation of multivalents at the first metaphase. Studies of laboratory-reared hybrids, in numerous other instances where natural hybrids have not yet been found, suggest that this is always so in the case of parapatric taxa of morabine grasshoppers (*11, 16*). The proportion of aneuploid sperms formed in this way ranges from perhaps 4 percent in hybrids between the 15- and 17-chromosome races of *K. scurra* (*14*) to over 40 percent in some of the hybrid combinations in the *viatica* group. In addition, certain male F_1 hybrids in the *viatica* group are stunted in development and their testes never develop to the stage where meiosis occurs [for example, hybrids between P45c ♂ and P25 (XY race) ♀], while in certain hybrids between the XO and XY races of P45b meiosis occurs but there is a massive degeneration of secondary spermatocytes and spermatids, so that no sperms are formed. Obviously these gross disturbances of development and spermatogenesis represent genetic isolating mechanisms that have developed subsequently to the primary (and weaker) isolating mechanisms inherent in the chromosomal rearrangements. No really adequate studies have been carried out on the meiosis of female hybrids in the *viatica* group, but there is no reason to suppose that the course of meiosis is significantly different in the two sexes (although the bivalents are more sharply stretched on the spindle of the egg), so that female hybrids probably produce aneuploid eggs in about the same proportion as the males produce aneuploid sperms.

It would hardly be profitable to discuss in a semantic manner just what taxonomic rank we should assign to the members of the *viatica* group. Obviously they represent various stages in evolutionary divergence. In a case such as this, raciation and speciation are parts of a continuous process and cannot be sharply distinguished.

Two conclusions seem to follow from these facts. The first is that some types of chromosomal rearrangements function as fairly strong, primary genetic isolating mechanisms between incipient species of morabine grasshoppers. The narrowness of the zones of overlap is evidence of strong selection against fused chromosomes in "unfused territory" and vice versa (in those cases where a fusion is involved; some pericentric inversions may have functioned in a similar manner). Naturally, the

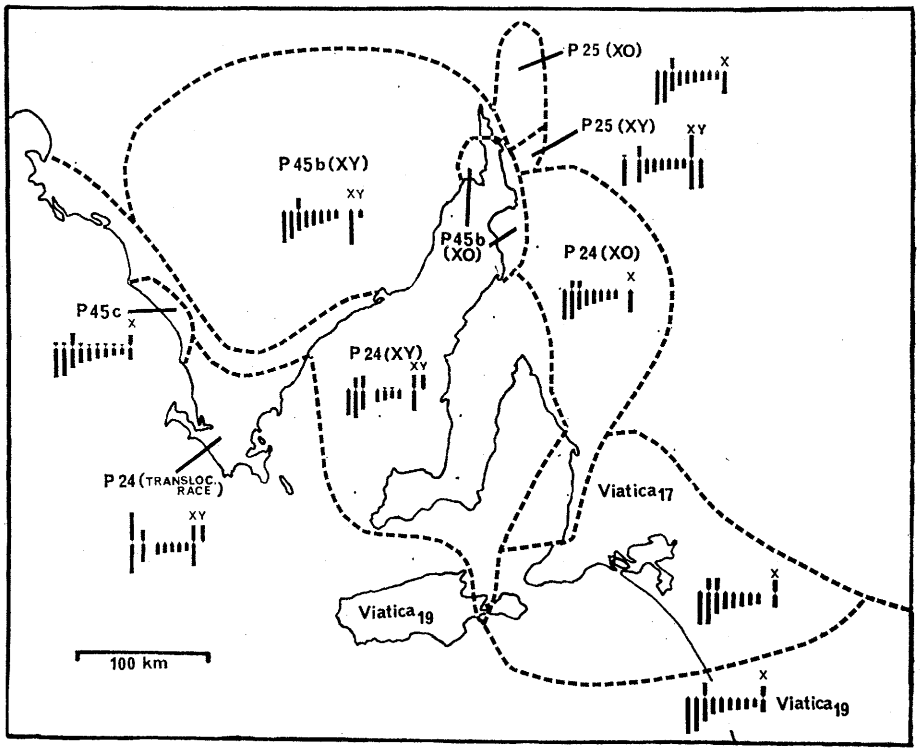

Fig. 1. Map of a portion of South Australia, showing the present distribution limits of the members of the "coastal" group of forms of the *viatica* group of grasshoppers. [Based on figure 1 of White, Blackith, Blackith, and Cheney (*11*), revised slightly.] The two "inland" species P50 (which occurs to the north of *viatica*$_{19}$) and P 26/142 (which is sympatric with the XO race of P25 but extends further north and east) have been omitted. During the Pleistocene glaciation the gulfs between the Eyre, Yorke, and Fleurieu peninsulas were dry land, and Kangaroo Island was also a part of the mainland. The ideograms show the haploid karyotypes of the various forms, with both the X and the Y included in the case of the XY races. In *viatica*$_{19}$ the chromosomes from left to right are designated A, B, CD, 1, 2, 3, 4, 5, 6, X. The karyotype of the XO race of P45b is not shown; it is not significantly different from that of the XO race of P25.

narrowness of the hybrid zone depends also on the extremely sedentary nature of these wingless insects; if their vagility was greater the hybrid zones would be much wider.

The second conclusion which we must draw from the cytogenetic and field observations is that, in spite of the strong selection against them, these chromosomal rearrangements have in fact proved highly successful in an evolutionary sense, having spread over large areas of territory. Several theoretical possibilities exist with regard to this process. We may imagine the rearrangements as establishing themselves in the first instance in a marginal colony (perhaps a small and isolated one) and then spreading out in the homozygous state into territory previously unoccupied by the species (Fig. 2A). Alternatively, the rearrangements might originate well within the existing range of the species and spread out from there (Fig. 2B). A third possibility, combining some features of the first two, would be for a rearrangement to establish itself first of all in a peripheral isolate and then spread through the existing range of the species (Fig. 2C). The first of these models is essentially an allopatric one, although different from the "dumbbell" model. The second and third are variants of what we have called the *stasipatric* model, since it involves the spread of a chromosomal rearrangement which forms the basis of a cytogenetic isolating mechanism throughout a substantial part of the range of an already existing species (*11*).

Stasipatric Speciation

As far as the *viatica* group of morabine grasshoppers is concerned, reasons have been given for rejecting the classic allopatric model (*11*). It virtually necessitates three unlikely assumptions: (i) that in addition to a B + 6 fusion, there was a subsequent B − 6 dissociation, (ii) that the B + 6 fusion occurred right at the beginning of the phylogeny of this group of species in spite of the fact that it does not seem to constitute a very effective isolating mechanism between *viatica*$_{19}$ and *viatica*$_{17}$, and (iii) that an invasion of territory by the *viatica* group took place in a northwesterly direction (presumably during the Pleistocene), whereas if any migration did take place it was probably in the opposite direction (that is, southeasterly).

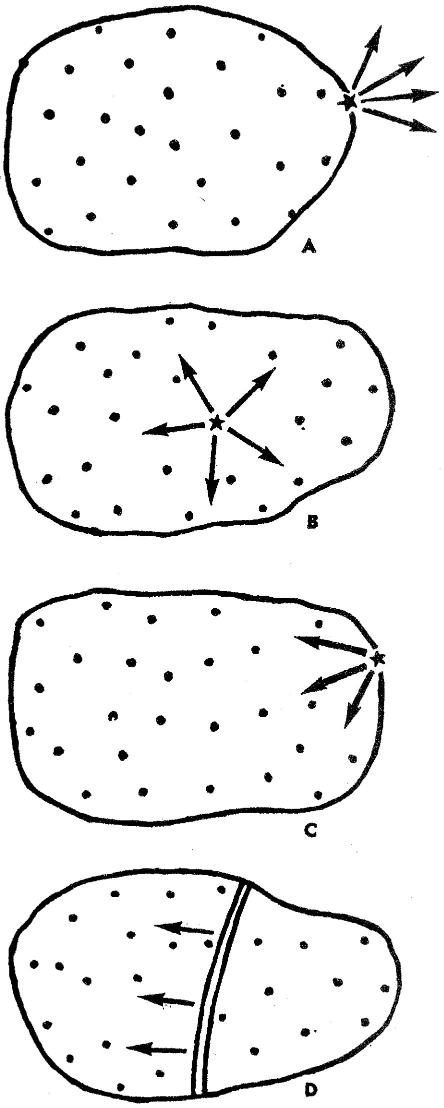

Fig. 2. Allopatric and stasipatric models of geographical speciation. (A) The chromosomal rearrangement manages to establish itself in a geographically isolated peripheral deme and spreads into territory previously unoccupied by the species (one form of allopatric model). (B) The chromosomal rearrangement establishes itself in a nonperipheral local colony and spreads through the range of the species on an advancing front (the stasipatric model). (C) The chromosomal rearrangement establishes itself in a peripheral colony and then spreads through the existing species population (modified form of stasipatric model). (D) The result of B or C: a narrow hybrid zone showing a slow secular movement across the territory occupied by the species until it is arrested in some way.

An interpretation of the cytogenetic evolution of the "coastal" forms of the *viatica* group is shown in Fig. 3. It is assumed that a widespread species which we may call *proto-viatica* became fragmented into the existing races and species as a result of: (i) a conversion of the original metacentric X chromosome into an acrocentric, presumably by pericentric inversion (stage 1A in Fig. 3), (ii) the B + 6 fusion (stage 1B), (iii) three different X-autosome fusions and a translocation (stage 3). It is not necessarily implied that stage 1A occurred before stage 1B; when both of these are superimposed we have the situation shown in stage 2, when we have the present-day species already in existence. The relation between the XO races of P25 and P45b is not clear; these taxa do not seem to differ karyotypically, but can be distinguished by a character of the external male genitalia.

It is assumed in Fig. 3 that each of the chromosomal rearrangements arose in the first instance somewhere within the territory occupied by *proto-viatica*, that is, in the manner shown in Fig. 2B (rather than as in Fig. 2C). However, neither of the two variants of the stasipatric model seem at first sight easy to accept, in view of the apparently strong selection against the new types of chromosomes as a result of the lowered fecundity of the heterozygotes. There does not seem to be the slightest possibility that the chromosomal fusions and dissociations that have established themselves in the morabine grasshoppers (and at least 36 of the former and 21 of the latter are known in the subfamily as a whole) were ever part of adaptive polymorphisms dependent on heterozygote superiority. Thus the cytotaxonomic differences between morabine species, unlike the paracentric inversion differences between dipteran species, are definitely *not* the remnants of former heterotic polymorphisms.

What, then, is the solution of this paradox? Genetic "drift" in numerous small isolated or semi-isolated demes may have played a part in the "stasipatric" process, particularly if homozygotes for the new chromosome have a considerably higher fitness than either the heterozygotes or the homozygotes for the original condition. It is difficult, however, to accept genetic drift as the sole or even the main cause for the spread of these chromosomal rearrangements, particularly since the result seems to be a relatively straight or curved "frontier" between two structurally homozygous populations, rather than a complex mosaic of demes, some homozygous for one cytological condition and some for the other.

The most plausible explanation for the "stasipatric" process shown diagrammatically in Fig. 2, B, C, and D, would seem to be that the rearrangements which have succeeded in spreading geographically, when they "should" have become extinct as a result of natural selection, are ones which have enjoyed the benefit of a segregational advantage (meiotic drive) in the egg. A cytological study of several hundred eggs from heterozygous females, in order to determine whether the "new" type of chromosome passes into the egg nucleus more frequently than into the polar body, would have to be carried out in order to test this hypothesis. It may be that the very few chromosomal rearrangements which play a critical role in speciation through their ability to generate powerful isolating mechanisms are precisely those which happen to possess a segregational advantage in the female meiosis. Meiotic drive has earlier been considered as a force which could have evolutionary consequences, but not quite in the sense considered here (*17*).

By comparison with the "saltational" model put forward for the plant genera *Clarkia, Holocarpha, Lasthenia*, and *Allophyllum* (*12*), the karyotypic differences between contiguous or parapatric species (or semispecies) of morabine grasshoppers seem to be due to single rather than multiple rearrangements. Obviously, the "saltational" model of Lewis and my "stasipatric" model are not quite equivalent, any more than the modes of life or population structures of higher plants and grasshoppers are identical. But a similarity certainly exists.

Although the stasipatric and allopatric models seem essentially different, they are not entirely antithetical, and it is therefore possible to imagine various ways in which they might be combined. Thus in the case of a chromosomal rearrangement which first establishes itself near the edge of a species distribution, one can imagine it spreading both inwards through the range of the species (stasipatrically) and outwards into previously unoccupied territory (allopatrically); in other words, a combination of models A and C of Fig. 2 is conceivable.

Although the stasipatric model was developed in the first instance to explain the pattern of evolutionary differentiation in the *viatica* group, it clearly fits the facts in some other groups of morabine grasshoppers as well, although the details have not yet been worked out fully. It would be premature to speculate just how far it applies in other groups where the cytogenetic analysis has not been pushed to the extent of determining what happens in the critical zones of contact or overlap. The case of the ladybird beetles *Chilocorus tricyclus* and *hexacyclus* in Canada seems to fall into the same category as the morabine grasshopper cases in that there is a very narrow zone of overlap, within which interspecific hybrids, whose fertility is severely reduced by cytogenetic processes, occur (*18*). The possibility that the stasipatric rather than the allopatric mechanism of geographic speciation has played a role in some groups of small mammals such as insectivores (*19*) and rodents (*20*) should certainly be considered.

The question as to which of the two variants of the stasipatric mechanism (Fig. 2B or 2C) has occurred in the *viatica* group (and, by implication, in the other groups of morabine grasshoppers) can be answered only on the basis of statistical probability. At first sight it might appear easier for a new chromosomal rearrangement to establish itself in a small isolated peripheral population (Fig. 2C). But a rearrangement which is capable of spreading through a continuous (or semicontinuous) population of a species should also be capable of initially establishing itself in the interior of a population. In other words the evolutionary success of these rearrangements *is* puzzling, but their initial establishment seems to be no more difficult to explain than their subsequent spread, if we accept the notion that populations of these insects are in any case broken up into numerous small colonies on single shrubs or groups of shrubs. There is thus no compelling reason to believe in a peripheral initial establishment. On the contrary, statistical arguments seem to strongly favor an "internal" origin for the rearrangements (Fig. 2B). The vast majority of the individuals of a sedentary species are "internal" rather than peripheral at any time. And—what is probably more important in this case—because of ecological discontinuities of the environment, the great majority of small isolated demes will be "internal." The distinction between the two models

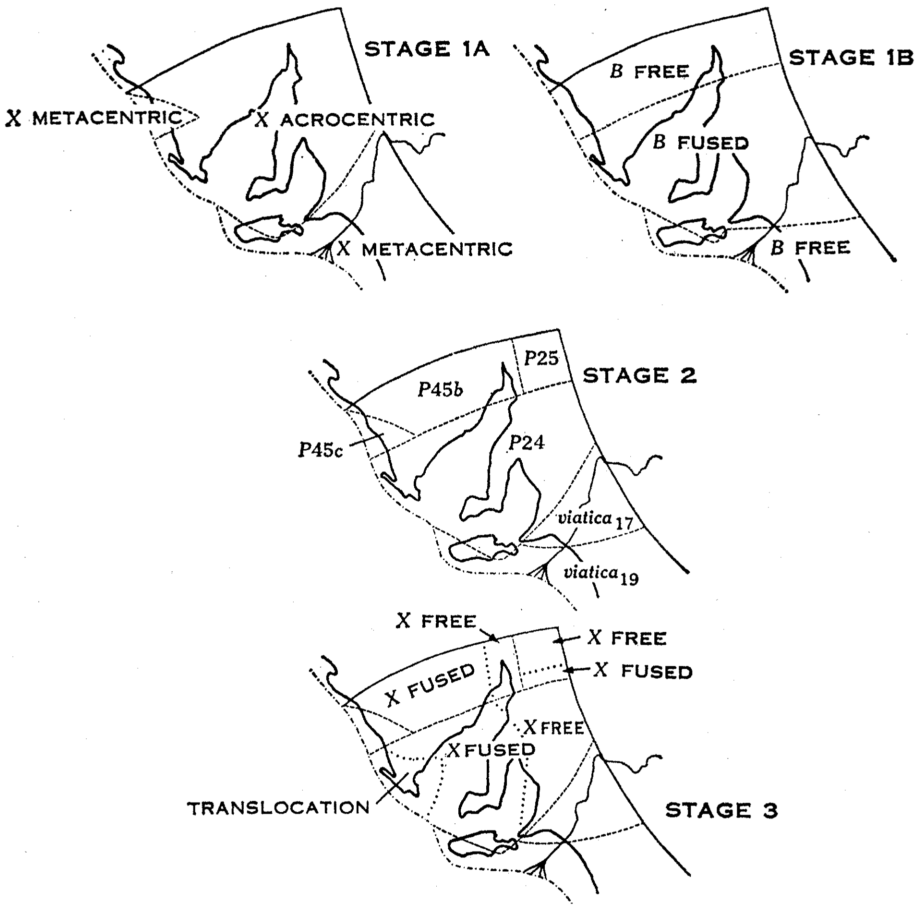

Fig. 3. Diagram illustrating the suggested mode of origin of the "coastal" species and races of the *viatica* group of grasshoppers in the state of South Australia. The dot-dash line indicates the approximate location of the Pleistocene coastline, when the sea level was about 100 meters lower than at present. [From White, Blackith, Blackith, and Cheney (*11*)]

symbolized in Fig. 2, B and C, is, however, a relatively minor one, and Fig. 2C should definitely not be considered as an allopatric model in the classical sense of the dumbbell diagram.

The concepts presented here are put forward in the hope that they may stimulate renewed interest in the cytogenetic processes involved in animal speciation. It is beginning to appear that there are more different kinds of mechanisms involved than was suspected a few years ago. Differences in modes of speciation are clearly related to differences in population dynamics and population structure; but they may also depend on differences in the genetic system.

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Sleep Disorders: Disorders of Arousal?

Enuresis, somnambulism, and nightmares occur in confusional states of arousal, not in "dreaming sleep."

Roger J. Broughton

Nocturnal enuresis, somnambulism, the sleep terror, and the nightmare are important social and medical problems. Their social impact can be appreciated from the extent to which they appear in the literature of various cultures (examples are Lady Macbeth's sleepwalking and the nightmares of Dante's Souls in Purgatory). They pose medical problems because of their frequency, their unresponsiveness to treatment, and their similarity, in certain respects, to other, more dangerous sleep disorders, especially nocturnal epileptic seizures. Recent studies have helped clarify their pathogenesis. Data are presented here which support the hypothesis that they occur independently of typical periods of dream activity, a view in direct contradiction to widespread long-standing assumptions. The results of recent investigations of their physiological and psychological mechanisms are also presented. Until these mechanisms are understood, treatment will remain empirical.

I begin with a summary of the essential features of each of the four attacks.

1) Nocturnal enuresis, or bed-wetting, is a common symptom in children and young adults. Incidences have been reported as follows: 10 to 15 percent for "nervous" children and 30 percent for institutionalized children (*1*); 1 percent for U.S. naval recruits who have been previously screened for the disorder (*2*); and 24 percent for naval recruits discharged on psychiatric grounds (*2*).

Typically the subject awakens to find himself in soaked bedclothes. An observer usually notes movement succeeded by several seconds of tranquillity, with apparent continuation of sleep, at which time the enuresis occurs. The subject is difficult to arouse, confused, disoriented even to the extent of denying that the bed is wet, and completely unable to recall any dreams.

When no organic cause (for example, pathology of the genitourinary system, epilepsy, and so on) is known, enuresis often is described as "idiopathic" or "essential." It has been interpreted as an expression of aggression, Oedipus fixation, or pathologically deep sleep (*3*). The unmotivated nature of the episode and the social ostracism incurred have been well described by George Orwell (*4*), who suffered from childhood enuresis:

> I knew that bed-wetting was (a) wicked and (b) outside my control. The second fact I was personally aware of, and the first I did not question. It was possible, therefore, to commit a sin without knowing you committed it, without wanting to commit it and without being able to avoid it.

2) In a typical attack of somnambulism or sleepwalking the individual sits up quietly, generally an hour or two after falling asleep, gets out of bed, and moves about in a confused and clumsy manner. Soon his behavior becomes more coordinated and complex. He may avoid objects, dust tables, go to the bathroom, or utter phrases which are usually incomprehensible. It is difficult to attract his attention. If left alone, he

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