

*ments of Botany and of Ecology and Evolutionary Biology, University of
Knox*

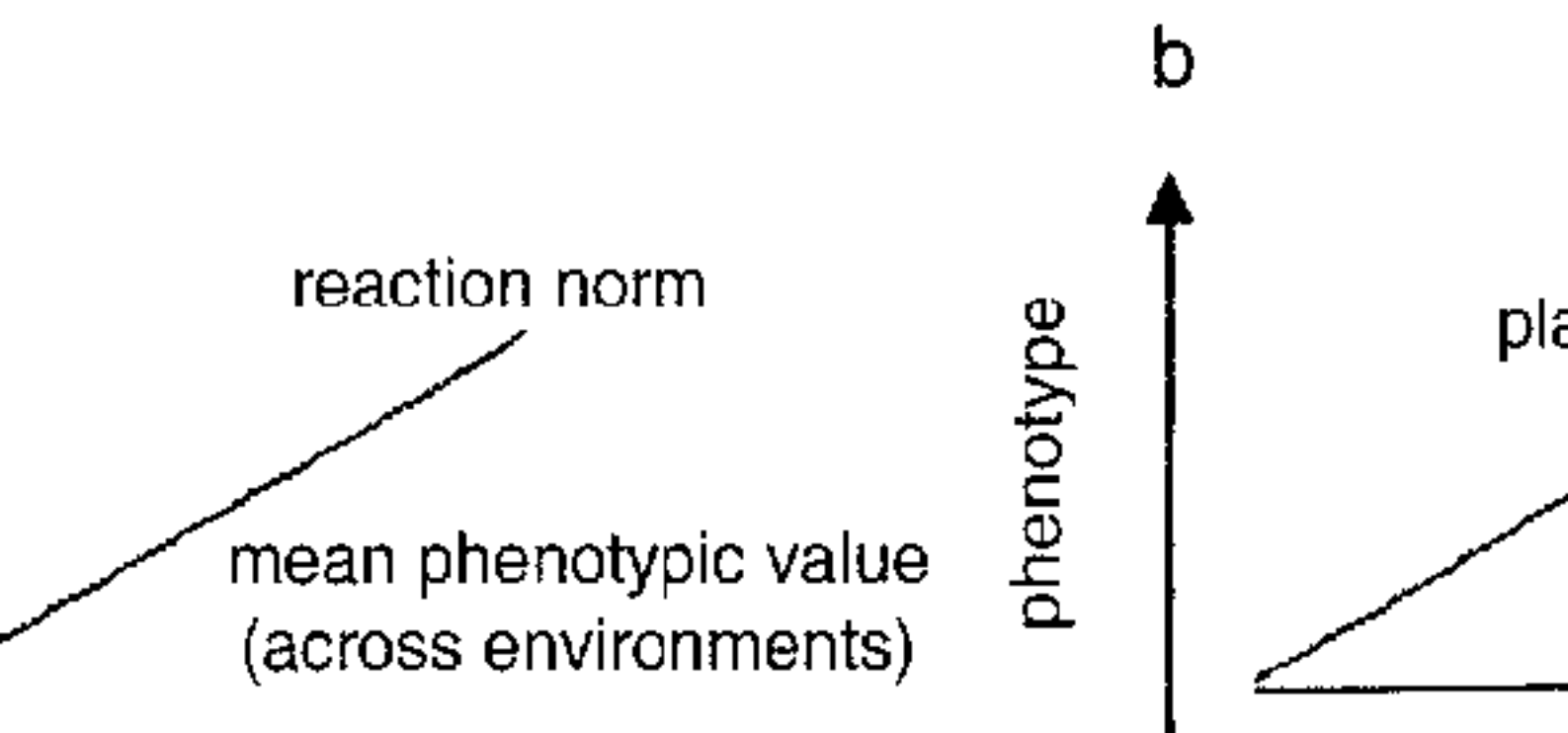
TERS AND ENVIRONMENTS: THE C TION NORMS

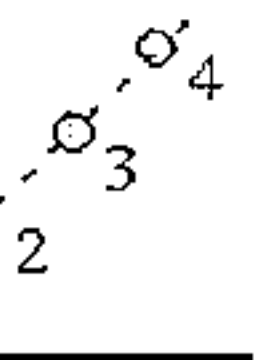
biologists speak of a given “character,” they usually
A character can be continuous or discrete

evolutionary biologists.

son for such a dearth of consideration is that need for a long time simply denying the existence (or a of phenotypic plasticity (Schlichting and Pigliucci, 1998). Darwinian synthesis was the unification of classical nat with modern genetics (especially population gene and Provine, 1980; Mayr, 1993). Ecology barely ente ding the important work of Clausen, Keck, and Hiesey (Clausen *et al.* (1940); Clausen and Hiesey, 1960; and of the environment was thought of as a "problem" and a combination of genetics and natural selection wo (Lewontin, 1978; Levins and Lewontin, 1985). An eloped during that time perhaps best embodied the att thought that they could minimize the effect of a phenotypes by growing different genotypes und conditions. The reasoning behind these "com was that any observed variation would have to be a *the important* component from an evolutionary standpo would have been kept in check. That is true enough alized that the results are going to be dependent on v one chooses. Furthermore, many common envi d misleading outcomes because they represent novel for the genotypes being studied. The phenotype ex den conditions, therefore, may not reflect what we wo d in the selective environments historically experienc (Service and Rose, 1985; Holloway *et al.* 199

an increase in the value of the environmental factor
can be plastic or nonplastic (Fig. 1b), which means
norms *are not* synonyms, contrary to a widespread

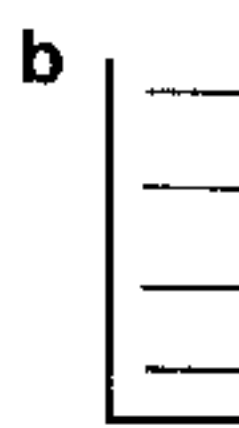




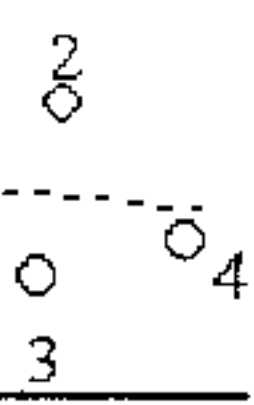
Environment 1

$$r_{ae} = +1$$

genetic variation
 no plasticity
 no variation for
 plasticity



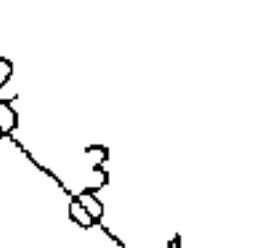
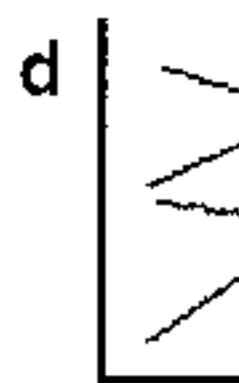
envi



Environment 2

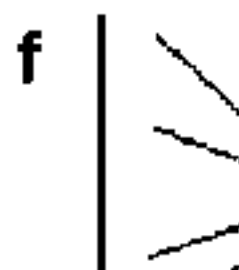
$$r_{ae} \sim 0$$

genetic variation
 plasticity
 variation for
 plasticity



$$r_{ae} = -1$$

no genetic variation
 no plasticity
 variation for



ment means (not shown). Finally, there can be interaction for the mean or mean plasticity. This latter one is intriguing and counterintuitive. The way such a population reaction norm diagram is a series of lines diverging at one extreme of the environmental gradient, while converging at the other. Furthermore, the slopes of some reaction norms would be positive (Fig. 2f). While an analysis could show no genetic variation (for the mean) and no (overall) phenotypic variation, all genotypes would be plastic (but in different fashions) and there would be genetic variation for plasticity (because of the divergence of the reaction norms). Obviously, any combination of the three fundamental components (genetic variation, plasticity, and variation for plasticity) can occur, and does occur, in natural populations of plants and animals.

INTERENVIRONMENT GENETIC CORRELATION

Another way of looking at reaction norms, which makes the relationship between characters and environments even more intuitive, is to plot phenotype functions in environment-phenotype space, and to represent genotypes as points in environment-environment space. One can think of the expression of the same trait in two environments as two distinct traits (in environment one and environment two). The genetic correlation that can assume any value between -1 and 1 is the environment genetic correlation (r_{ac}) is close to either 1 or -1. The simplest interpretation is that the same genes affect

what a character is, how it is controlled, and how it changes (Scheiner, 1993b; Schlichting and Pigliucci, 1998). Graphically, of course, it becomes difficult to represent character states as soon as the number of environments becomes more than three. More importantly, however, I have argued (Pigliucci, 1996b) that both approaches suffer from the simple fact that they are *representations* of the underlying biology. As such, they do not tell us about the molecular biology, developmental mechanisms, or physiological processes that produce these patterns and that, in fact, are the main focus of research understood in studying the evolution of characters.

PLASTICITY INTEGRATION: CORRELATIONS AMONG CHARACTERS AND PLASTICITY OF CORRELATIONS

Characters tend to covary across environments. This phenomenon has been called "plasticity integration" by Schlichting (1986, 1989a), and has been documented in a number of plant and animal systems (e.g., Mazer and Levin, 1993; Newman, 1994). To date, however, few studies have addressed plasticity integration, in part because of the necessary experiments. However, plasticity integration is important to our understanding of character evolution. If characters covary within a given environment, but across the range of environments, this calls for models of phenotypic evolution that are more sophisticated than the ones produced so far (van Tienderen and Koelewijn, 1994).

g. 3. Schlichting and Pigliucci (1995b) compared the integration (i.e., the character correlations) of several populations of *Monardella*, finding that populations could be grouped by their correlation structures. However, such grouping depends on the environment in which the plants were growing (once the genetic differences are accounted for). For example, while populations from Jayton always belong to the same branch on the phenogram, the phenogram for Jayton is quite different under the low nutrient environment and when these are compared to the other environments. This raises not only interesting evolutionary and ecological questions but also a new perspective on an old problem of systematic classification conducted at lower taxonomic ranks. In a study on *Monardella* (Liliaceae), for example, I have demonstrated that the relationship between the way in which the multivariate phenotypic variation responds to environmental stress and the subspecific classification is highly dependent on such a simple parameter as water availability (Pigliucci *et al.*, 1991b). In other words, if one were to classify populations as belonging to one subspecies or another based on a trait highly dependent on such a simple parameter as water availability, the result would be highly dependent on such a simple parameter as water availability. Therefore, a "common garden" approach would not solve the problem. In fact it may very well make it worse. Common gardens are intended to provide a relatively benign environment to the plants. However, if definite phenotypic differences evolve they are a response to stress or locally different conditions. The benign environment of a greenhouse may obliterate any biologically significant differences (the "silver spoon effect" quoted in Sultan, 1990).

ANOTHER DIMENSION TO THE PROBLEM: THE INTERACTION OF DEVELOPMENT AND PLASTICITY

Genetic plasticity is not just an environmental phenomenon, but the result of complex genotype–environment interactions. However, these interactions do not occur at one point in time. Rather, phenotypic plasticity is a continuous process, and the reaction norms that we usually measure at reproductive maturity, are in fact the result of interactions between environments and genes throughout the ontogeny (Lewontin, 1949; Smith-Gill, 1983; Pigliucci and Foster, 1998).

The literature on developmental plasticity is assuming an increasingly important role in shaping our thinking about plasticity in particular, and evolution in general. Clear empirical examples of how phenotypic plasticity is shaped by the interaction between development, genotype, and environment have been published especially, but not uniquely, in plants (e.g., Schaffer and Gadgil, 1975; Martin-Mora and James, 1995; Schaffer and Gadgil, 1975; Brakefield *et al.*, 1996; Bruni *et al.*, 1996; Ghalambor *et al.*, 1997).

The emerging picture from all these studies is that adult phenotypic plasticity is largely shaped by the way genetic instructions are expressed in response to the environmental milieu. This is far from being a vague statement. It involves tracking the differential expression of genes at different developmental stages, in different tissues, and in response to distinct environmental conditions.

the question of what exactly we consider an “environment” to measure it. This is one of the most important and deceptive aspects of the problem of how phenotypic plasticity changes organisms and their characters.

IS THE ENVIRONMENT?

One of the most fundamental problems with ecology is how to propose to study the effects of environments on organisms. It is when it comes down to pinpoint the biological aspects of an organism's milieu. This is true notwithstanding the varying physical and biological aspects of the environment. One approach to answer this question has been taken, for example, by Bell and Lechowicz (1991; Lechowicz and Bell, 1991). In that series, these authors argued that there are fundamental aspects that can be used to study environmental heterogeneity. The most intuitive and is based on actual measurements of environmental conditions which plants and animals live. The problem is, as an ecologist, the amount of variance detectable even on small spatial scales. Temperature, humidity, and nutrient availability is significant. In addition, one has to add that such measurements are also difficult to take because of both seasonal and short time fluctuations. This is what Bell and Lechowicz term direct. This comes from using the organisms themselves as indicators of the quality of the environment through the use of bioassays. Unfortunately there

ng that the environments considered in the study
l spatial scales (i.e., they are fractal). The indirect
ampling 555 points in the same grid and measuring
K⁺ and NO₃⁻ ions (Lechowicz and Bell, 1991).
that all three edaphic measures are predictably similar
arger spatial scales the autocorrelation is negligible.
cluded that the environment varies at scales that are
and genetic neighborhood size of typical understory plants.
s finding affects our understanding of the relationship
nvironment as perceived by the organism and the macro-
on and, therefore, the response to selection in natural populations.
(1994) and Stratton and Bennington (1996) have
he relationship between character expression, fitness, and
attern of environmental heterogeneity. In a study (Stratton
on, 1994, 1995) Stratton planted plants at 630 locations to
directly measure environmental effects. The experimental
es with clearly identifiable phenotypic markers so that the
genotype of the plant by sight. The results indicated that
by environment interaction is observable at the smallest scale
, with reversals in the relative fitness of different genotypes
this same scale. Stratton therefore concluded that the
ly induced pattern of spatial heterogeneity in relation to
e of the next generation of plants, which mostly dispersed
f environments.⁴ However, when he attempted to correlate
with indirect measurements of soil nutrients and percent
... found that only 10% of the

controlled laboratory studies focusing on one of the most likely candidate factors are the only method to address the causality question. However, manipulation experiments and findings in order to make them relevant to natural conditions. The large range and number of possible environmental variables in the field (Bell 2) elegantly summarized what we know of environmental variance in his list of five attributes of environmental variance is relatively large. By "relatively," he referred to either genetic or genotype-by-environment variance. In a variety of traits in crop plants (our largest database to date), the environmental variance explains close to 80% of the total variance of a given character. Therefore, geneticists are advised to pay attention to what was once considered "noise" (Sultan, 1992). Second, the environment is constantly changing in space and time. Bell and Lechowicz's own data discussed above support this point. As a consequence, Bell argues, the success of genetics has been so successful in genetics may turn out to be less successful in ecology (contra some current trends in the field). The decoupling of organisms to the environment is indefinitely inconsistent with the idea that the ranking of performance of different organisms is determined by their phylogeny. This is another factor decoupling ecology from genetics. Phylogenetic diversity cannot be explained by (i.e., is not a function of) environmental diversity. This decoupling is also consistent with the idea that genetic information is conserved throughout a phylogeny (because new species arise from their immediate ancestors or sister groups), while environmental conditions are constantly changing.

that keeps shifting away.

Another component to environmental variation and its characteristics that is not part of Bell's classification is the reaction of an organism to an environmental factor we use a biologically relevant range of that factor. For example, we refer to "temperature" or "water," meaning the range covered by the factor (e.g., Huey *et al.*, 1990; Dählhoff and Somero, 1991; Somero *et al.*, 1994; McMichael and Burke, 1994; Schrag *et al.*, 1994; Somero and Lenski, 1997; Brakefield and Kesbeke, 1997; Somero *et al.*, 1998), or drought to flood (Pigliucci *et al.*, 1991b; Somero, 1994; Voesenek and Veen, 1994; Bruni *et al.*, 1996; Kiesecker *et al.*, 1996). Of course, some of these studies are conducted along an environmental gradient, but still most of the current studies are studies of response to the whole gradient (as in "the reaction of *Ambystoma macrodactylum* to temperature..."). I make the suggestion that the response of the gradient are likely to be more different from each other (i.e., organismal response or perception) than either is to the extreme of the gradient. In other words, it may be that the response to low water is more similar to the response to low water (since the response to high water is coupled) than the reaction to high temperature is to the response to high temperature.

These ideas are supported out by the molecular literature. Evidence is accumulating that the molecular machinery necessary to respond to drought (e.g., Somero, 1994; Welin *et al.*, 1994; Jagtap and Bhargava, 1995; Somero and Somero, 1995; Naguchi-Shinozaki *et al.*, 1995) is different from the machinery necessary to respond to flooding (Armstrong *et al.*, 1994; Huang and Kao, 1994).

tence of phenotypic plasticity affects another major area of evolutionary biology of characters: the idea of homology. The concept of homology is older than evolutionary biology itself, but has undergone several dramatic redefinitions in recent times (Wagner, 1994). The distinction between interorganismic and intraorganismic homology (1994). The first is found when we compare across species different evolutionary histories, such as the bird's wings and the bat's wings (Gatesy and Dial, 1996a). The second type of homology is the convergence and specialization of the same ancestral structure (as seen in insects: Carroll *et al.*, 1995; Osorio *et al.*, 1995). The third type is that genotypes have to produce different character states in different environments. This may constitute a third category of homology, interenvironmental homology.

Interenvironmental homology is related to the fact that different environments can be related to each other. It is very reasonable to consider interenvironmental homology as related to intraorganismic homology. In fact, organisms can in part or modify through evolutionary time the representation of their ancestors. For example, intraorganismic homologous structures, such as body segments in insects and their relatives are clearly related to interenvironmental homology of the same body segment across individuals (Wagner, 1994). Intraorganismic homology can be related to an interenvironmental homology (possibly vice versa, see later). A particularly clear example is the relationship between intraorganismic and interenvironmental homology in heterophylly, the production of entire or dissected leaves in response to environmental conditions such as water level fluctuation.

and wing dimorphism would directly provide in homology.⁵ In fact, Winn (1996a,b) has emphasized the distinction between phenotypic plasticity and environment-induced variation in the morphology of the same structure. In his review of the homology concept invoking comparative approaches to unravel the problem of how the individual is canalized developmentally and how it emerges during ontogeny, he stressed the role of phenotypic plasticity in the evolution of homology (Winn-Eberhard, 1989; Schlichting and Pigliucci, 1998; see also Schlichting, 1996). A system in which to apply both the experimental and comparative methods to tackle the intimately related problems of homology and phenotypic traits.

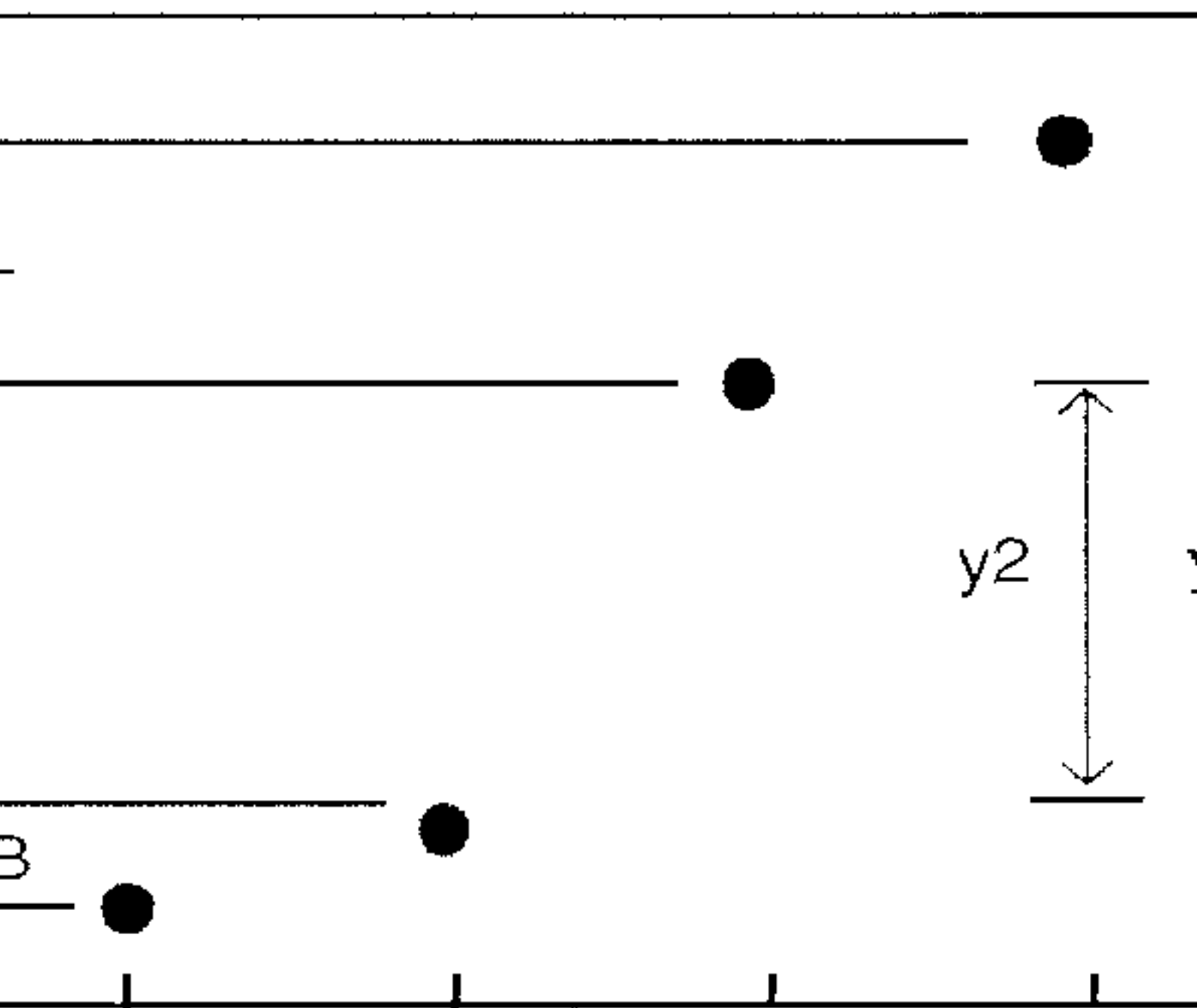
Of phenotypic plasticity, and in particular the canalization of genetic correlations cited earlier, can also shed light on the concept of homology. According to both Van Valen (1982) and Schlichting (1996) homology is a "correspondence caused by a continuity of inheritance". That is, the homology of two structures is an unbroken connection throughout evolutionary time. According to Van Valen (1982) this connection does not have to be based on the similarity of the two traits. What Roth later termed "genetic piracy" (Roth, 1996) as well. Sometimes clearly homologous structures from different viewpoints are actually under the influence of different genes. Van Valen would still consider these traits homologous. He would suggest that this is an example of genetic piracy, in which a new gene (or genes) takes over the role previously held by a different gene.

different paces and in different manners. How, then, can living organisms not be a matter of degree?⁶ In the case of the phenomena of genetic piracy and interference, it is clear that the information underlying homologous characters, through time, culminating in the possibility of no similarity whatsoever between two homologous characters. By analogy, we can tell that two extant structures are definitely homologous, like the stem and dissected leaves of a heterophyllous plant, or the wing- and leg-bearing segments in insects (e.g., the leaves and wing- and leg-bearing segments in insects), or probably homologous (e.g., the leaves and wing- and leg-bearing segments in insects). We can imagine that at one point both the informational base and the expression of two characters will diverge enough through time that it is difficult for us to recognize their ancestral homology. Characters that are still clearly homologous evolve into structures that are an integral part of them but were not present in the ancestor. Should we not consider these as examples of partial homology?⁷ The discussion so far has moved from a consideration of the expression of a character in extant populations (a microevolutionary level) to broader implications on homology and character evolution (a macroevolutionary level). The last, but certainly not least, the relationship between environments and characters (a new, albeit not at all new) way of looking at macroevolution it

**CHARACTERS, PHENOTYPIC NOVELTIES, AND
ON**

ology requires no initial change in the genetic system. If a phenotype happens to be advantageous, selection will favor it. Whatever genetic modifiers stabilize the phenotype reduce its fluctuations. This idea is not new. As Schlichting and Armbruster pointed out, it is a reformulation of Waddington's (1942, 1952, 1960), in itself not different from Baldwin's (1949) "stabilizing selection," or even from Baldwin's "evolution," and closely related to Goldschmidt's (1941) "saltation."

To a large extent, the reason why the role of phenotypic plasticity (and genetic assimilation) has not been taken seriously even in the modern synthesis is that environmental influences have been regarded as a "nuisance" to be dealt with in practice, but certainly not in theory (Armbruster, 1992). Therefore, classical evolution by gradualism has for all effective purposes been the only game in town. The particularly inefficient explanatory frame at best, relying on unexplained phenomena as "preadaptation" (Futuyma, 1997), that biologists are faced with increasing pressure to admit to the existence of two more mechanisms. On the one hand, the effect of developmental effects (Gottlieb, 1984; Doebley *et al.*, 1993; Dorweiler *et al.*, 1993; Wagner *et al.*, 1994; West-Eberhard *et al.*, 1996; Schluter, 1996; Sordino and Duboule, 1996; West-Eberhard, 1997). On the other hand, the contribution of phenotypic plasticity (West-Eberhard, 1989; Smith, 1990; Schlichting and Armbruster *et al.*, 1994; Whiteman, 1994; Janzen, 1995; Brakefield *et al.*, 1997) and its interactions with major developmental effects (notably



Benthic
Worms

Benthic
Plankton

Limnetic
Worms

Limnetic
Plankton



the hypothesis is that a simple change in diet, circumstances, created a partially new morphology of the bone developmental system. This allowed them, under suboptimal conditions, in the new environment, selection for gene substitutions would gradually increase the genotype and the environment. The advantage of this way with the idea of preadaptation. No preexistence is necessary because the new morphology is a by-product of a reaction norm. Not even mosaic evolution is necessary (in parallel) because the plasticity of the developmental system allows characters simultaneously, not one at a time [see Weidner's example of this].

Finally, examples like these are hard to find in the literature because of the previously mentioned lack of expectation that phenotypic plasticity play a major role in macroevolution. In part, however, due to the experimental difficulty of investigating the fixation of a new mutation. After all, it may take very few generations of modifiers to bridge the gap between one stable morphology and another. In fact, the "signature" of genetic assimilation would be the absence of such a gap. Of course, this is equally true of the classical theory of preadaptation. However, such is the case with any scientific paradigm (Kuhn, 1970). As in the case of any theory, this one also needs to be investigated by the same method (Harvey and Purvis, 1991). However, the substitution-only theory, evolution by phenotypic plasticity

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