

Phyletic Species Packing and the Formation of Sibling (Cryptic) Species Clusters¹

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Crozier (1977) remarked that, "... it would be big news if any widely distributed ant species were *not* to consist of siblings!" "Good" species frequently dissolve into clusters of siblings when studied closely. The pattern of cryptic species clusters is not confined to insects with a social structure. The clues may differ, and the details of speciation may change, but the final pattern seems to be widespread.

In North America the biogeographic distribution reflects several southward progressions of deserts during each ice age, each followed by a northward recession. With each progression species were compressed into the same habitat in a small region in central Mexico, and with each recession some moved northward. The Sierra Madre Occidental in the west and the Sierra Madre Oriental in the east (with the central Chihuahuan Desert) formed a wedge, and most populations moved northward along the coastal plains of the Pacific Ocean and Gulf of Mexico.

The climatological and ecological patterns also propagated a phylogenetic pattern. It is common to find overlapping distributions of very closely related sibling, often cryptic, species of insects sharing habitats. A pattern of speciation may be seen that reflects the compression and

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relaxation of species packing in the community, and, with favorable material can be deciphered into phylogenetic lineages. However, one must be studying the actual breeding patterns and the modes of adaptation of a "species" under natural conditions to detect many of the overlapping ranges of cryptic species. The *repleta* group of *Drosophila* has been the most extensively studied insect in this region, and is, indeed, an effective evolutionary model to guide other studies, particularly those of insect taxa.

I History of Systematic Convention in *Drosophila*

The ability to differentiate species is limited by the taxonomic tools. When the only tools needed to distinguish species are our eyes, and possibly modest magnification to see external detail more easily, species are not cryptic. However, if we need to examine internal anatomy or use special analytical techniques to differentiate individuals of different species, the species are called cryptic. Mayr (1942) used "sibling species" to describe phenotypically similar, closely related species. Sibling species often are cryptic, at least until an observant taxonomist notices a subtle, but consistent difference in morphology.

When Sturtevant (1942) was building the basis for modern *Drosophila* systematics, he felt that only species which could be identified from pinned specimens warranted recognition with an official Latin name. The species thereby could be recognized by examination of paratypes and holotype specimens in a museum. However, Wheeler, Patterson, Stone, Dobzhansky, Hardy, Takada, and other *Drosophila* taxonomists have placed a greater emphasis on naming species that could be distinguished by *any* means -- mating tests, internal anatomy, and genetic analyses were their tools (Patterson and Stone, 1952). By using this approach they fostered the studies of speciation, adaptation and biogeography in *Drosophila*, as well as other insects, raising the analysis of evolutionary processes to a new level of resolution. The identification of incipient species, semispecies, and sibling species became common events, and studying the mechanisms of achieving genetic isolation and measuring genetic differentiation, with or without comparable morphological diversity, became the focus of research in evolutionary genetics. A profound change also occurred when living "paratype" cultures became important adjuncts to the preserved museum specimens. The National *Drosophila* Species

Resource Center at the University of Texas at Austin is a direct result of the need for such paratype cultures.

There are numerous examples where sexual isolation is adequate under natural conditions to allow speciation, but may be overwhelmed under laboratory tests. Crowding may prevent mate discrimination, diurnal rhythms may be upset, or habitat selection may be prevented. Sometimes individuals of different species extensively hybridize under unnatural contact. The existence of either reproductive or genetic isolation in the laboratory generally implies isolation in nature, but the reverse is definitely not true. Absence of isolation in the laboratory only indicates that the test must be conducted in nature, or at least under more natural conditions.

Initially, genetic isolation was inferred from the presence of reproductive isolation. Now often it may be observed directly, even in the absence of marked hybrid inviability or infertility. We have developed additional techniques for distinguishing cryptic species in mixtures collected in the natural habitat (Makela and Richardson, 1977, 1978; Richardson, Ellison and Averhoff, 1982). When genetically differentiated populations fail to intermate even though the opportunity exists, there will be fewer heterozygotes than if they were intermating. Electrophoretically detectable variation usually allows identification of heterozygotes, as does chromosomal analysis. Therefore, data from wild individuals derived from electrophoretic and chromosomal studies can be used to determine the pattern of mating outside the laboratory.

II Concordance of Phylogenies, Biogeographies and Ecologies

A. *Species Groups*

Throckmorton (1982) outlined the broader scale of evolution in the genus *Drosophila*, and showed that major lineages each have a characteristic habitat. At times the lineage is subdivided into Old World and New World portions, but only one habitat is involved. Major migrations across large land masses subsequently separated by continental drift did not materially affect the association between a major lineage and its habitat. However, major new lineages (species groups) typically reflect a new habitat invasion. It is especially significant that the morphological differences that were used to define taxonomic species groups ultimately have such a high concordance with habitat similarities.

From Throckmorton's overview of the evolution of the genus, it is both significant that there were major splits of lineages associated with habitat shifts, and that these patterns have remained after millions of years. The separation of major land masses, emergence of mountain ranges, major climatic changes, formation of island chains and emergence of other major taxa have not disrupted the initial direction of evolutionary trends.

Both morphological similarity and habitat similarity are concordant with phylogenetic relatedness, also determined by independent criteria, such as chromosome structure. Chromosome diversity between species groups generally is so great that constructing phylogenies becomes much more difficult. Nevertheless, there has been progress.

Where polytene chromosome detail is observable, Stalker (1972) and Yoon, Resch and Wheeler (1972) have connected the most closely related species groups. Their technique is based both on maintaining identical banding sequences and on band morphology across taxonomic gaps. Banding sequences may be disrupted by chromosomal changes, but common banding morphology represents similar patterns of gene regulation since active genes localized in bands often are associated with "puffs" in the region.

Also DNA sequence comparisons are offering some promise for phylogenetically relating species groups (Richardson and Yoon, 1977; Triantaphyllidis and Richardson, 1980; Richardson, Triantaphyllidis and Turner, unpub.). The initial studies indicate rates of genetic divergence are higher in the early stages of the formation of a new species group, in agreement with the chromosomal studies (Yoon and Richardson, 1976). A faster rate is probably expected since a new group is generally exploiting new resources in a new habitat, and greater genetic change would be anticipated for adaptation than if a new niche in the same habitat was involved.

B. Subgroups and Species Complexes

1. *The Repleta Group.* Heed (1982) has outlined the patterns of biogeographic distributions and habitats of the *repleta* group in North America, and finds the patterns still concordant with phylogenetic relationships and patterns of chromosome similarity (Wasserman, 1982). There is a characteristic V-shaped distribution, with an occasional type in central Mexico. The greatest diversity is in southern Mexico, and the ranges of several species extend north eastward and

north westward. While some types, such as *D. arizonensis*, today are restricted to the northern tips of the V-distribution, they presumably moved northward with the warming following an ice age from a once single population in the south. Those that are more generalist with respect to north-south habitat differences form a complete J- or V-shaped distribution.

Broadly ranging species overlap in the south (the angle of the V) with each other as well as with the more localized species, producing a higher number of species in the *Drosophila* community. This increased number of sympatric species constitutes a greater diversity in this community than those found in central and northern Mexico. Species diversity in this area may have been even greater at the height of the ice ages, when the species at the northern tips of the V-shaped distribution were located more to the south. The present time, between ice ages, may have less species diversity even in southern Mexico than was true for most of the history of this habitat. Most of the time climates were colder than at the present. With the shorter warmer times like the present allowing the spread of species ranges which reduce the overlap, the lowered local species diversity leaves a more loosely packed community, ripe for speciation and phyletic species packing (Richardson and Smouse, 1975).

Thus, the broad pattern outlined for species groups of the genus describes clusters of species within subgroups. Habitats are subdivided within a subgroup, and even a species complex, but still having a high concordance with phylogenetic relatedness. Usually the closely related species can be found exploiting a common taxonomic section of the cacti which share a chemical similarity as well as morphological similarity (Gibson, 1982; Richardson and Smouse, 1976). When several species use a common larval substrate, such as between columnar cacti vs. prickly pear cacti, they also tend to be phylogenetically clustered. The general pattern described by Throckmorton is seen among more closely related species, which have evolved much more recently and in closer proximity than those evolutionary splits producing the lineages of species groups.

2. *Hawaiian Drosophila*. While it is not directly a focus of this symposium, it may be instructive to briefly compare the patterns of the *repleta* group, evolving primarily on large land masses, with species endemic to the

Hawaiian Archipelago. The large scale biogeographic pattern is among islands, which have emerged as a result of volcanic activity. The age of the islands forms a linear sequence from the older islands in the northwest to the younger in the southeast portions of the chain (Carson *et al.*, 1970). Migrations and resulting speciation events have not always followed the geological ages, and several reverse migrations have occurred from younger to older islands. Nevertheless, the endemic *Drosophila* form several species groups, such as the picture wings and modified mouthparts. They tend to have different ecological trends concordant with taxonomic diversity (Yoon, Resch and Wheeler, 1972; Montgomery, 1975; Heed, 1968). The modes of species recognition create important forces providing the morphological diversity for some of the lineage names -- visual wing displays in the picture wings and tactile modes involving mouthpart contact in the modified mouthpart lineage.

A new lineage arose after the present islands were formed, probably when Maui Nui was the youngest island (Yoon and Richardson, 1976). The morphological differentiation was extensive, initially resulting in its being given generic status. From chromosomal differentiation we suggested a more rapid change initially than seen in other endemic lineages, and it has been moved back into the genus *Drosophila*. In principle the genetic dynamics leading to new species groups or genera seem to be no more complex than those leading to new sibling species clusters. The difference between the inception of a new species group or genus and a new sibling species cluster lies in the ecological circumstances.

Thus, the major Hawaiian lineages must have occupied their characteristic habitat relatively early in the radiation of the genus in the islands, and thereafter each lineage continued evolving within the framework of a particular ecological theme. Subgroups and complexes of sibling species have arisen very recently in highly restricted areas, possibly sympatrically (Richardson, 1974). Thus, evolutionary patterns in Hawaiian *Drosophila* have developed under very different circumstances of geographical separation, habitat changes, time scales, and adaptive strategies, but form a lineage pattern very similar to the *repleta* group.

C. Sibling Species Clusters

1. *North American Pattern.* There are about five clusters of sibling species in the *mulleri* complex which serve as a

model of the patterns we are considering. They are (1) *arizonensis*, *mojavensis*, *navajoa*; (2) *aldrichi*, *mulleri*, *wheeleri*; (3) *ritae* and an undescribed new species; (4) *longicornis*, *pachuca*, *propachuca*, *desertorum*; (5) *martensis*, *starmeri*, *uniseta*. The latter cluster is South American, and growing (Wasserman, 1982; Sene *et al.*, 1982). The other species are not yet defined to a sibling cluster, although they are closely related to the *longicornis* cluster. Heed (1982) has given the geographic distributions. We know of undescribed species that increase this list, since they are cryptic within one of the sibling clusters. These include one in the *longicornis* cluster (Heed, 1982) and a presumptive type related to *D. propachuca* which we have observed (Richardson, unpub.). *D. tira* has been combined with *D. ritae* (Valela, unpub.), but an unnamed sibling species is known.

When we examine the clusters of sibling species within a species complex, we see a continuation of the pattern. For example, the cluster of prickly pear breeding species, *D. longicornis*, *D. pachuca* and *D. propachuca* are indistinguishable even by internal anatomy, and *D. desertorum* differs significantly only in the male genitalia, yet they all may be cultured from one piece of rotting prickly pear cactus collected in nature (Richardson, Smouse and Richardson, 1977; Richardson, unpub.). They are genetically differentiated in some enzyme systems, and there is some reproductive isolation expressed by sterility of males in certain crosses among the three species, excluding *D. desertorum*. They share many chromosome similarities (Wasserman, 1982). In fact, initially they were mistakenly split, with *D. longicornis* removed from close phylogenetic association (Wasserman, 1962), until their molecular similarities were found by M. E. Richardson (personal communication to M. Wasserman). *D. desertorum* is differentiated by several inversions from the other three species of the cluster.

The most striking difference among these four cryptic species lies in their developmental pattern. The ability to reliably culture *D. propachuca* came only after we discovered that the pupation time was almost twice as long as the other two species, and that it was necessary to wait for the adults to eclose long after all the larvae in a culture vial had pupated. This strongly suggests that these cryptic species, often sharing a common mass of rotting cacti, have diverged in their developmental pattern, thereby reducing niche overlap to some degree. *D. desertorum* is easily cultured for a few generations as an isofemale line, but even-

tually lines must be mixed to maintain a culture. This species presumably is sensitive to inbreeding depression.

These species culture best on a cactus-supplemented medium. There is not a nutritional requirement; the effects of cactus in the medium is more subtle. While the factors are unknown, our conjecture from the work of Fogleman (1982), Kircher (1982) and Starmer (1982) is that, under natural conditions, these species may feed on different yeasts and exploit slightly different stages of the rotting tissue. Diversity which might separate cryptic species might be expected to have been important adaptations in the evolution of their niche at the time they were speciating.

From southern Mexico most species of the *mulleri* complex have a characteristic V-shaped distribution. The greatest diversity is in southern Mexico, and the ranges of several species extend north eastward or north westward. While they once formed a single population in the south, once separated to the north, genetic divergence commonly results. For example, *D. aldrichi* often shows male sterility of hybrids between strains from Sonora and from Texas, suggesting an incipient species-level diversity. There also is a difference in mating speed between these two subspecies, but no consistent discrimination was shown (Richardson, unpub.). *D. wheeleri*, the closest relative to *D. aldrichi*, seems to have arisen in the northwestern extreme of the range of *D. aldrichi*, and shows a similar pattern of reproductive isolation to both eastern and western subspecies of *D. aldrichi*. There may be a region of sympatry of the eastern and western types of *D. aldrichi* in the state of Hidalgo. If this were studied, it would allow a test for genetic isolation under natural conditions. Should they be isolated in sympatry, we can formally separate *D. aldrichi* into two species, much like *D. arizonensis* and *D. mojavensis* in Sonora.

Even *D. arizonensis* from eastern Mexico inhabits a different rotting cactus than when found in western Mexico, and they are genetically differentiated as well (Richardson, Smouse and Richardson, 1977). There is no detectable reproductive isolation in the laboratory tests. Therefore, we cannot determine whether they are actually different species until they become sympatric and can express any intrinsic genetic isolation.

Adults are physiologically responsive to their microhabitats and have highly differentiated niches comparable to larvae. Eckstrand (1979) examined the ability of several cactus breeding species to physiologically regulate the loss

of water from their body. Most were similar at high humidities, but species from dry habitats were able to regulate the loss of water at lower humidities. In one case, we found greater diversity in water balance between two sibling

Hawaiian *Drosophila* species in a relatively moist habitat (Eckstrand and Richardson, 1981) than between one of them and *Drosophila* in the desert habitat (Eckstrand, 1979). The microhabitat difference is the central factor determining the physiological diversification of sibling species. Of course, each species is sufficiently mobile to traverse several microhabitats each day. Habitat selection concentrates their exposure in a particular microhabitat. In the case of the Hawaiian sibling species, one member of the sibling pair occupies a microhabitat of deep shade, often on the underside of leaves, while the other's microhabitat is open shade, and often the individuals are on the upper (exposed) side of the leaves. The distance between these microhabitats, however, is only a meter or two (Richardson and Johnston, 1975). We are still unravelling the microhabitats of desert *Drosophila*, but Johnston and Templeton (1982) report some new findings relative to dispersal patterns.

2. *South American Pattern.* In 1972 when plans were being made that M. E. Richardson and I visit the University of Sao Paulo, Brazil, there was some concern expressed when I indicated a desire to use the *repleta* group as a model. Based on earlier surveys by Theodosius Dobzhansky and his colleagues, only those species of the *repleta* group that were more associated with humans had been found. There was no evidence that a complex evolutionary process had occurred such as we had been studying in North America. Nevertheless, Drs. Edmundo Magalhaes and Crodowaldo Pavan agreed that I could reexamine some of these species. Dr. Magalhaes returned and encouraged Dr. Sene and others to work in the *repleta* group until I arrived in order to establish some stocks and gain some preliminary experience.

Soon after we arrived in Sao Paulo early in 1974 Dr. Sene and I visited the cactus nursery at the University, and found some rotting *Opuntia* with empty pupae cases and larvae. We took this rot into the lab, and reared a new species from it. Over the next several weeks we collected flies and rotting cacti in several areas in Brazil. We found still other new species. We characterized them by differences in male genitalia as well as their allozyme profiles. They are now known as *D. serido* and *D. borborema*. At this time it was apparent that there was a lot of exciting work

to be done in the evolutionary study of the *repleta* group in South America.

We visited several people who could tell us more about the paleoclimate and cactus distributions, and we began to formulate models of how the radiation in South America might have occurred. Of course, the ideas from studies in North America greatly influenced our thinking. It is, indeed, gratifying to have these hopes beginning to become realized as reported by Sene *et al.* (1982) and Fontdevila (1982).

The complexity of *D. serido* reported by Sene and Fontdevila suggests that a cryptic species cluster exists. From the differences in metaphase chromosomes shown by Sene, there might be as many as six different species that have been collected, and most of the continent has not been collected! Much work remains to organize these species into more complete phylogenies, but Wasserman (1982) has made an initial advance, relating these species to others he has included in the *mulleri* complex. While it now appears that the radiations in North America and South America were mostly independent, they are connected phylogenetically. When the cacti are better known, it may be possible to determine the relationships of these two radiations in the *mulleri* complex, and also relate the origin of this complex which lives in the cactus habitat to others that are found in more moist areas, such as the *fasciola* subgroup.

3. *North American Clusters of Cryptic Species in Screwworm Flies.* It is noteworthy that *Drosophila* species of the *repleta* group in general, and the *mulleri* complex in particular are characterized as "cactus breeders," in parallel to the new species of *Cochliomyia* (Richardson, Ellison and Averhoff, 1982) which are "warm blooded animal breeders." In this genus there is comparable morphological diversity among about nine groups, and possibly almost this many species, as there is among the four species of the *longicornis* cluster. Male genitalia can be used to separate adults in some cases, but generally the identification depends on the detailed analysis of the metaphase chromosomes. They share a larval habitat much like the prickly pear cactus breeding species in that more than one may inhabit a single wound, and superficially all are in a wound of a warm blooded mammal. Gassner and Brommel (personal communication) found important differences in the microbial community in the wounds correlated with the presence of certain types of bacteria. More recently, Foss and McDonald (personal communication) have found electrophoretically

identifiable groups of *Proteus rettgeri* from screwworm larvae that differ in wounds of sheep from those found in wounds in either horses or cattle. Microbial diversity among host species parallels that of the yeasts found in different cacti (Starmer, 1982). In addition, these types of screwworms form a biogeographic pattern similar to the species of the *mulleri* complex -- a V-shaped overall distribution, with different species tending to be isolated east to west in the north, but with extensive southern overlap. Although fertile hybrids may be obtained in the laboratory, there is no effective gene flow among them in nature.

III Significance of Cryptic Species

A. *To Speciation and Biogeographic Problems*

Divergence in similar microhabitats appears to be typical for the cryptic species clusters. The products of the divergence, the cryptic species, often overlap extensively in their ranges. Superficially these patterns seem to suggest sympatric speciation is a common mode.

While sympatric speciation may be the mode in many of these cases, two features must be considered before the case is firmly made. The species may be ancient, and their place of origin may be some distance from the present range. A detailed reconstruction of the habitats in geological history generally becomes necessary to infer the likely ranges at times when speciation occurred.

The other feature of their ranges requires examination on a smaller scale -- the "grain" of their habitat. If the grain is large, populations in one area (grain) may not have extensive gene flow with populations occupying other grains for long times. The community composition in different grains, even with similarity of microhabitats, may differ and allow divergence, and possible fortuitous genetic isolation may arise. As Templeton (1980) has shown, speciation may be rapid when there is a major reorganization of the genome, and speciation may occur in a diverse, large grain habitat.

There is no easy way to determine if sibling species arose sympatrically or allopatrically. The weight of the evidence must be the guiding factor. However, the process of speciation now appears to be much less time consuming than it once did, and we know that the effects of genetic inter-

actions, particularly those regulating genes, may have almost immediate effects that could result in considerable genetic isolation (e.g., Templeton and Rankin, 1978; Templeton, 1980). Reproductive isolation (e.g., hybrid inviability) is not as important as once thought for effective *genetic* isolation. Therefore, the theoretical feasibility of sympatric speciation is increasing. In some instances semi-species or sibling species may be of sufficiently recent origin to allow better evaluations of the roles and circumstances for sympatric and allopatric speciation dynamics. The ability to detect populations that are sympatric and exhibiting significant genetic isolation is crucial to the study of speciation.

B. To Paleontological Problems

Speciation requires (1) a potential niche, and (2) a genetically adapted type isolated from other populations in the community. To pack another species into a community, a colonizer may be from outside the habitat (traditional view) or from speciation inside the habitat ("phyletic species packing" (Richardson and Smouse, 1975)). In the latter case the speciation might be sympatric, or allopatric if the habitat were coarse grained. The divergence might be behavioral or physiological, for example, and not greatly modify external morphology, so that eventually the two diverged populations may come to occupy a single grain and have adequate genetic isolation to be sympatric sibling (and cryptic) species. Coming from inside the habitat, both species would be preadapted in many ways to all the grains (i.e., to the habitat). When a population colonizes a new grain, it would have a very much greater chance of becoming established than would an unrelated type, adapted to a different habitat.

Habitat diversity and species packing is the mode of natural selection acting in species selection (Wright, 1967; Stanley, 1975). It follows then that punctuated evolution (Gould and Eldredge, 1977) is the track of potential niches that were realized, and this track is the latent image of the habitat diversity written into the fossil record through the *morphology* of the species. When a habitat is stable, phyletic species packing can replace lineages that become extinct, and maintain an appearance of morphological stability (recorded as a single species, but most probably a cryptic sibling species complex). When the habitat shifts or suitable new ones form, the phyletic niche track shifts and

punctuates the morphological record. Thereby, one might view punctuated evolution as punctuated habitat diversity.

The examination of species groups in *Drosophila* shows greater morphological diversity associated with major shifts in habitat, and the morphological diversity observed at the level of the speciation process often is very limited. The pattern of morphological diversity more closely reflects the differences between the niches of the species than the actual incidence of speciation. As other taxa have been examined, a similar pattern is revealed, although there may be differences between taxa in the morphological expression of niche diversity.

The ice ages almost certainly contributed to the dynamics of speciation in the *repleta* group. If the rate of speciation was high when the deserts were expanding as the climate warmed, and the community was becoming more subject to invasion ("loosely packed"), then these were punctuations in the phyletic history. However, the punctuations related to such activity did not necessarily (nor even usually) appear with sufficient morphological differentiation to be detectable if one were examining a fossil record. Furthermore, the origin of the endemic groups of Hawaiian *Drosophila* would be observable if fossilized, but the rates were probably determined by the geological and botanical dynamics of the islands -- punctuations of the *Drosophila* habitat. The morphological diversity is not proportional to the genetic diversity, and the evolutionary dynamics are not proportionally reflected in the morphological pattern.

Speciation in times of greater environmental stability may be at a comparable rate, but with less chance of being reflected in the fossil record. It is impossible among related taxa to separate roles of genetic variation and mechanisms of adaptation from the historical sequence of habitat changes reflected by the niches that were developed during the successful exploitation of the resources by the lineages. This evolutionary conundrum is shared by somatic development, and also has created extensive confusion. "Nature" cannot be separated from "nurture" in the differentiation of cell lineages (nor IQ, nor other phenotype) in the development of an individual any better than can the nature of the genetic system be separated from the nurture of ecological diversity in morphological differentiation of phylogenetic lines.

C. To Ecological and Economic Problems

I once had a vertebrate ecologist tell me that he did not think that identifying cryptic species was an important problem in biology, particularly since he had not had to contend with any in his work with lizards. Another time I spent several hours with another vertebrate biologist with a different point of view. I was intrigued by his description of watching a slow progression of the parthenogenetic form of a species of lizard move across a region of Brazil. It was interesting how he related collecting with a slingshot while waiting for an airplane at a remote airport, and from one year to another the sexual form had been replaced by the asexual form. The sex ratio, of 1:1 for the sexual forms and only females in the asexual form, was the conspicuous feature of change that alerted him to the diversity. The asexual and sexual forms are cryptic species because individual females could not be categorized without examination of their mode of reproduction, such as by a progeny test. I think the difference between these two biologists' perspectives on the genetic diversity is significant. One person considered genetic diversity more of a nuisance and the breeding details as inconsequential. The competitive interactions among clearly different (morphologically distinct) species was the focus of his attention. The other person was, among other things, focusing on speciation and biogeography.

We have been working on insects recently with much the same difference in perspective between ourselves and our associates in the U.S. Department of Agriculture. *Cochliomyia hominivorax* has been considered to be one species throughout the Western Hemisphere. Memory is short. A few decades ago the saprophytic blowfly, *C. macellaria*, was considered the same species as the parasitic form. It is now important to recognize the presence of isolation among wild types, since the parasitic form is being eradicated from most of Mexico by the release of sterile flies. While some behavioral isolating barriers may be overwhelmed by releasing more sterile flies, it is inefficient (and thereby very expensive), and some matching between natural populations and released sterile flies may be necessary to do a complete job.

The taxonomic recognition of cryptic species thereby becomes critical for identifying differences in habitat selection, measuring species diversity, and for outlining geographic ranges. One can argue that logically the evaluation of competitive relations also depends on a full ac-

counting of all species, since we know there are important differences among the *Drosophila* species we have studied. While most ecological studies do not address the problem of counting cryptic species in a community, it seems important in most cases to be sure the community composition is truly as described on the species checklist.

In the case of screwworms, preliminary results clearly show how elimination of one member of a species complex "releases" others (Richardson, Ellison and Averhoff, 1982). Although the competitive interactions are unknown, two species increased dramatically in relative frequency when the most common species was eliminated. The net result was little or no change in parasite load, but the community complexity was reduced by one species.

The taxonomy, based on a biological or evolutionary species concept, must be accurate for many biological pest control programs. The work on screwworms is but one example. Malaria control in Europe was dependent on the recognition of cryptic species of mosquitos, only some of which were vectors. Pheromone attractants are effective only on some types (actually different species) of moths. The list is extensive and growing. The patterns we expect from our studies of *Drosophila* predict that simple monospecific communities based on the external morphology are typical only in recently colonized areas, and the general pattern is for there to be clusters of closely related, often cryptic, species in any "mature" population. While such cryptic diversity makes the systematics more challenging and the study of evolutionary processes more exciting, the problems of pest control are greatly complicated and such diversity is potentially the bane of pest management.

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