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THE ROLE OF HYBRIDIZATION AND INTROGRESSION IN THE DIVERSIFICATION OF ANIMALS

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ABSTRACT

Although hybridization and introgression have been considered important in generation of plant diversity, their role in evolutionary diversification of animals remains unclear. In this review, we reconsider the significance of introgressive hybridization in evolution and diversification of animals to determine if the generally negative assessment of these processes is warranted. Unlike the situation for plants, hybrid animal taxa appear to be relatively rare. This could, however, be due to negative attitudes toward hybridization and difficulty in detecting such forms. Hybridization has been responsible for instantaneous creation of several unique complexes of polyploid and unisexual animals. Allopolyploidy has allowed for diversification, whereas unisexual taxa have acted as conduits of gene exchange among related sexual species. Many instances of diploid, bisexual taxa of hybrid origin have been put forward, but few have been carefully tested. Changing attitudes toward hybrids and technological advances should allow for careful consideration of hypothesized hybrid taxa and will undoubtedly increase the number of known animal hybrid taxa.

INTRODUCTION

Around the time of the neo-Darwinian synthesis, considerable effort was directed toward understanding the origin of taxonomic diversity. This work led to several central principles, such as the importance of geographic isolation (82, 83) and selection for reproductive isolation (33). Several of these tenets have since come under scrutiny (e.g. 15, 19, 40, 63, 77, 91, 156), leading

to renewed interest in the processes generating and maintaining organismal diversity. Gene exchange among animal species has been more common than previously believed, opening the door to several new avenues of evolutionary research. Hybrid zones have been used for study of evolutionary processes (54, 55, 59), providing insight into processes responsible for patterns of geographic variation among taxa and maintenance of their distinctiveness. The genetics of reproductive isolation is still poorly understood, but experimental hybridization studies have allowed for identification of specific genetic changes responsible for species differences and reduced fitness of hybrids (25, 114, 158).

While hybridization and introgression have been deemed important by botanists (7a, 113, 114), zoologists have not seriously considered the significance of these factors in the evolutionary process. Anderson & Stebbins (6) summarized views toward the significance of hybridization in plant evolution. They hypothesized that introgression and hybridization could transfer blocks of genes among stabilized, adapted groups, permitting rapid reshuffling of varying adaptations and complex modifier systems. In this way, levels of variation would be greatly increased, and selection would be able to act upon segregating blocks of genic material derived from different adaptive systems instead of one or two new alleles generated by mutation. This set of circumstances would be particularly advantageous where new ecological niches are created by changing environments, allowing evolution to proceed at "maximum rate."

One possible outcome of horizontal transfer of genetic variation among lineages would be creation of taxonomic diversity. Although this process has been considered important in generation of plant diversity (53), the role of hybridization in evolutionary diversification of animals remains unclear. Grant (53) noted that "several generations of zoologists have concluded that hybridization does not play an important role in animal evolution," with this perspective based upon "a store of background knowledge that should not be dismissed lightly" (p. 161).

With this caution in mind, we reconsider the significance of introgressive hybridization in the evolution and diversification of animals to determine if the generally negative assessment of these processes is warranted. This is achieved by placing perceptions of hybridization and introgression in historical perspective, followed by an assessment of hybrid origins of animal taxa and evaluation of the potential role for these factors in evolutionary diversification. It is impossible for such a review to be exhaustive because many suggestions of hybrid origin are presented as digressions in papers dedicated to taxonomic treatments or studies of hybridization. Therefore, we address conceptual issues to stimulate further consideration of the role for hybridization in the diversification of animals.

DEFINITIONS

We choose to focus on hybridization and introgression as processes, bypassing conceptual difficulties associated with defining categorical units (e.g. species) involved (139). Hybridization is defined as “the interbreeding of individuals from two populations, or groups of populations, which are distinguishable on the basis of one or more heritable characters” (55, p. 5), and introgression is “the permanent incorporation of genes from one set of differentiated populations into another, i.e. the incorporation of alien genes into a new, reproductively integrated population system” (115, p. 71).

Definition of hybrid taxa is difficult, as selection of criteria for placing groups into specific taxonomic categories (e.g. subspecies, species, genera) will suffer from the same difficulties associated with nonhybrid species, reflecting the bias of the user in determining the quantity and type of differences necessary for taxonomic recognition (40). This is particularly problematic for hybrid taxa as boundaries defining species are semipermeable (54), and the extent and persistence of introgression may vary among genes. In addition, recent technological advances (61) allow for fine-scaled examination with many loci, identifying unusual patterns of introgression (e.g. 7a, 36, 42, 79, 115). Therefore, the extent of introgressive hybridization at any locality might occur anywhere along a continuous distribution of possibilities, ranging from introgression at one locus [e.g. mitochondrial DNA (mtDNA)] to enough loci that populations be recognized as distinct taxonomic entities.

Given these difficulties, we define hybrid taxa in terms of the processes generating them: the derivation of features by horizontal transfer from multiple independent lineages at some point in their history. Under this guise, a hybrid taxon is an independently evolving, historically stable population or group of populations possessing a unique combination of heritable characteristics derived from interbreeding of representatives from two or more discrete units (e.g. races, subspecies, species, etc). Historical stability implies that the mosaic of characters inherited from independent lineages is retained in the population, passed on from parent to offspring.

Stability and evolutionary independence are essential for distinguishing taxa of hybrid origin from instances of ongoing hybridization among taxa. Unfortunately, these features are difficult to evaluate. Stability can be based only on human perceptions of longevity, typically from collections that cover 300 years at most. Where taxa are allopatric, evolutionary independence is often based on degree of divergence. Thus, these criteria are open to subjective interpretation, producing a situation analogous to evaluation of specific status for allopatric forms.

HISTORICAL PERSPECTIVE

The significance of hybridization and introgression for animals has not been the subject of any major review; however, the topic has received cursory coverage in a variety of texts and articles (e.g. 15, 113). This limited coverage seems to result largely from the ideas and perspectives of prominent researchers working at the time of the modern synthesis. This sentiment is summarized by Fisher (44): "The grossest blunder in sexual preference, which we can conceive of an animal making, would be to mate with a species different from its own . . ." (p. 144).

Dobzhansky (32) recognized the importance of allopolyploidy (i.e. elevation of chromosome numbers due to hybridization of two or more species) to evolution, but he noted that the rarity of allopolyploids "constitutes the greatest known difference between the evolutionary patterns in the two kingdoms" (32, p. 219). Introgressive hybridization was considered to occur more frequently in plants than in animals, possibly due to greater attention paid to this problem by botanists. He also noted that "hybrid swarms" may reflect inheritance of shared polymorphism from a variable common ancestor, not exchange of genes among species. In a later work, Dobzhansky (34) discussed reasons for differences in the frequency of introgressive hybridization between plants and animals. Vegetative and asexual reproduction found in many plants provides for longer life and increased spreading capacity of individuals (or clones), whereas sexual reproduction maintains evolutionary plasticity. In addition, the greater complexity of tissues and organ systems in animals may require that the adaptive value of genotypes depends upon integration of a larger constellation of genes than for plants (with their simplified tissues and open systems of growth). These features would constrain the number of adaptive recombinants in animals, reducing the frequency of hybridization and increasing the importance of reproductive isolation.

One of the most outspoken and influential opponents of a significant role for hybridization and introgression in evolution was Mayr (82, 83). He acknowledged that animal species could arise instantaneously through allopolyploidy, but the rarity of hybridization in animals made this process much less important than for plants. Transformation or fusion of species by introgression was also viewed as implausible, especially when the parental species continue to exist. Since hybrids would exhibit less reproductive isolation than their progenitors, they would have to remain geographically isolated until they could maintain their integrity. In light of this perspective, Mayr argued that combinations of characters from putative parental species and morphological intermediacy are inadequate for identification of hybrid species because of both the polygenic nature of these characters and the developmental stability of interactions among

genes resulting in the phenotype. A more plausible explanation was the evolution of such intermediate forms from a single, polymorphic ancestor.

Mayr also provided several objections to the view that introgression significantly increased genetic variability in animal populations. Hybrid animals are rare in nature, even in groups that have been extensively studied. Where F_1 hybrids occur, they tend to be sterile or to exhibit reduced fertility. Hybrid and backcross individuals would also suffer reductions in fitness because gene exchange breaks up "internally balanced chromosome sections," resulting in elimination of these individuals and "severe selection against introgression." In his view, "the total weight of the available evidence contradicts the assumption that hybridization plays a major evolutionary role among higher animals" (83, p. 133).

Recently, some zoologists have become more open to a significant role for hybridization in the evolutionary process, including the formation of new species. Stebbins (140) contrasted the variation in perceived significance of hybridization in the evolution of plants and animals. Because the proportion of successful progeny segregating from hybrids is much lower for animals (due to complex patterns of development controlled by more intricate and integrated complexes of genes than found in plants), zoologists have downplayed the significance of introgression. Stebbins noted that rare gene combinations can establish rapidly; therefore, hybridization may have played a larger role in the evolution of animals than is recognized.

In his evaluation of mechanisms of speciation, Templeton (143) contemplated the production of new species by hybridization. Genetic and structural incompatibilities associated with unisexual reproduction and polyploidization were considered important means for maintenance of hybrid taxa. Conditions for stabilization of hybrid recombinants were also described. Under his scenario, hybridization is followed by inbreeding and hybrid breakdown. If recombinants with the greatest viability and fertility are able to survive, they could become reproductively isolated from both parental forms and become distinct entities. Hybridization followed by inbreeding could enhance mutation rates in recombinants, leading to increased divergence from parental forms, especially where the population of recombinants is geographically isolated. Divergence is required for coexistence; otherwise the new form could be swamped out by gene flow or eliminated through competition. On the basis of several experimental studies, Templeton suggested that this mode of speciation can occur and does not require the evolution of postmating barriers between recombinants and parental taxa.

The potential significance of introgressive hybridization in animal evolution was supported experimentally by Lewontin & Birch (73). They hypothesized that dramatic range expansion of an Australian fruit fly (*Dacus tryoni*) occurred

through adaptation to extreme temperatures, with genetic variation obtained through introgression with a closely related species, *D. humeralis*. This possibility was tested by maintaining “pure” and “hybrid” populations initiated from *D. tryoni* and F_1 hybrids between *D. tryoni* and *D. humeralis*, respectively, at a series of optimal and extreme temperatures. Hybrid populations initially produced fewer pupae than did pure lines of *D. tryoni*, but there was no difference in this feature or morphological characteristics by the end of the experiment, around two years later. Despite these similarities, hybrid lineages were found to increase more rapidly at higher temperatures, indicating that introgression of alleles allowed for adaptation to extreme warmth. As Lewontin & Birch note, these results do not prove that *D. tryoni* became adapted through introgressive hybridization, only that such a series of events could have been involved.

Several ornithologists have indicated that introgressive hybridization has been important in avian evolution. Estimates of hybridization among bird species range from 9% worldwide (50) to 15% for the Nearctic fauna (126). Short (125) noted that introgressive hybridization preserved genetic variation of each progenitor in hybrids, making “such forms ‘preadapted’ by virtue of introgressive hybridization.” In most instances dispersal has made it difficult to ascertain the fate of hybrids; however, detailed studies of Darwin’s finches allowed Grant & Grant (51, 52) to conclude that introgressive hybridization played a greater role in the evolution of animals than previously believed.

MODES OF HYBRID ORIGIN

Both hybridization and introgression have been hypothesized to enhance animal diversity, but differences between these processes require they be considered separately. Hybridization may directly produce distinct taxa, either through polyploidization or generation of clonally reproducing unisexual lineages. Alternatively, introgression could eventually lead to stable, independent lineages definable by unique combinations of characteristics. In either case, taxonomic diversification is best viewed as an incidental by-product, resulting from accumulation of genetic differences that confer distinctiveness and evolutionary independence.

Given problems associated with defining taxa of hybrid origin, assessment of a possible role for hybridization and introgression in the generation of taxonomic diversity is difficult. Nevertheless, reticulate origins have been invoked for many taxa, and it is important to determine the extent to which gene exchange has played a role in generation of taxonomic diversity.

Diversification by Hybridization

Hybridization can instantaneously produce distinct animal taxa in two ways, through increase in chromosome number (allopolyploidy) or through conversion

to an essentially all-female (unisexual) mode of reproduction. These two pathways can be difficult to separate as most animal allopolyploids are hermaphroditic or unisexual while many all-female complexes include polyploids.

All-female reproductive systems occur in three general forms, parthenogenesis, gynogenesis, and hybridogenesis (27). In parthenogenesis, females reproduce progeny essentially identical to themselves (barring mutation) without involvement of males. Gynogenetic and hybridogenetic forms require sperm to initiate egg development. In gynogenesis, fertilization only serves to stimulate development, with sperm nuclei excluded. In hybridogenesis, true fertilization occurs and paternal genes are expressed; however, only the maternal lineage is transmitted to the next generation.

Hybrid lineages have typically been identified by morphological intermediacy, increased heterozygosity at nuclear gene loci (usually allozymes), and/or excess amounts of DNA in multiples of the standard complement (e.g. 3N, 4N, etc.) obtained through standard karyotypic methods or measurement of DNA content. Mitochondrial DNA variation has been used to identify maternal lineages; however, it does not allow for recognition of hybrids unless applied in conjunction with other characters (e.g. allozymes, karyotypes, morphology). Application of these methods has provided a number of excellent examples in many groups of animals, each with their own unique features. Instead of recounting extensive reviews of polyploid and unisexual taxa (11, 14, 29, 76, 122, 156), important concepts are summarized below and new cases and updated references are provided in Table 1.

THEORETICAL CONSIDERATIONS The role of hybridization in the production of polyploid animal lineages has sometimes been difficult to determine. Allopolyploids have typically been distinguished from autopolyploids (in which multiple sets of chromosomes are derived from the same ancestral species) by the lack of multivalent sets of chromosomes or disomic inheritance of allozymes. Unfortunately, the distinction between these categories is not always clear. White (156) noted that multivalents, e.g. structures formed by association of more than two chromosomes during meiosis, have been identified in diploid organisms, possibly due to translocation heterozygosity. In addition, autotetraploids become functionally diploid over time (105). Therefore, older autopolyploids could exhibit fewer multivalents (11) and multisomic loci than expected; however, salmoniform fishes are ancient autotetraploids that have not become diploidized (4). Conversely, one could imagine a scenario in which hybridization among closely related but distinct taxa could result in polyploids that form multivalents and have multisomic inheritance, reducing the effectiveness of these characteristics for discriminating among these modes of origin.

Allopolyploid plants have been thought to be more common than autopolyploids because of increased fitness attained through their hybrid constitution,

Table 1 Hypothesized examples of asexual and polyploid taxa of hybrid origin

Taxonomic complex	Ploidy	Mode of reproduction ^a	References ^b
Platyhelminths			
<i>Paragonimus westermani</i>	3N, 4N	?	1, 3
<i>Fasciola</i> sp.	2N, 3N	P	2
Mollusks			
<i>Lasaea</i> species complex	3N-6N	G	104
<i>Bulinus truncatus</i> complex	2N, 4N, 8N	P or S?	47
<i>Campeloma decisum</i>	?	P	66
<i>Ancylus fluviatilis</i>	4N	P or S?	138
Insects			
<i>Bacillus</i> species complexes	2N, 3N	P, H	13, 145
Curculionidae	2N-10N	P, G/H?	101, 120
Simuliidae	3N	P	118
Crustaceans			
<i>Daphnia pulex</i> complex	2N, 4N	P	30
<i>Cyprinotus incongruens</i>	3N	P	146
<i>Trichoniscus pusillus pusillus</i>	3N	P	144
Fishes			
<i>Fundulus heteroclitus</i> X <i>diaphanus</i>	2N	G	28
<i>Phoxinus eos-neogaeus</i> complex	2N, 2N/3N, 3N	G	45, 46
<i>Poecilia</i> complex	2N, 3N	G,?	9, 121, 132
<i>Poeciliopsis</i> complex	2N, 3N	G, H	109, 152
<i>Rutilus alburnoides</i> complex	2N, 3N	?	5
Family Catostomidae	4N	B	128, 147
<i>Cobitis</i> complexes	3N, 4N	G	124, 148, 149
Amphibians			
<i>Ambystoma</i> complexes	2N-5N	G?, H?	58, 69, 70, 134, 135
<i>Bufo danatensis</i>	4N	B	88
<i>Hyla versicolor</i>	4N	B	80, 108, 112, 116
<i>Rana esculenta</i> complexes	2N, 3N	H	62
Reptiles			
<i>Cnemidophorus</i> complexes	2N, 3N	P	20, 96, 127, 154
<i>Gymnophthalmus underwoodi</i>	2N	P	21, 22, 160
<i>Hemidactylus garnotti</i>	3N	P	94, 111
<i>Heteronotia binoei</i>	3N	P	92
<i>Kentropyx borckiana</i>	2N	P	23
<i>Lacerta</i> complex	2N, 2N/3N, 3N	P	95
<i>Lepidodactylus lugubris</i>	2N, 3N	P	94, 110, 111, 150
<i>Nactus pelagicus</i>	2N	P	35

^aAbbreviations for modes of reproduction are: G, gynogenetic; H, hybridogenetic; P, parthenogenetic; S, self-fertilizing hermaphrodite; B, bisexual; ?, uncertain.

^bAdditional references may be found within those cited.

allowing for adaptation to a wider range of environments provided by multiple sets of genes. Using this information, White (156) reasoned that allopolyploid animals were also more likely to establish than autopolyploids. In any case, he concluded that polyploids are far less common in animals than plants.

The rarity of allopolyploid animals has been attributed to their systems of sex determination, with polyploidization directly interfering with sex determination (97) or indirectly affecting fitness through disruption of dosage compensation of sex-linked genes (106). White (156) concluded that the occurrence of polyploidy may also be constrained by modes of reproduction, particularly in those groups not exhibiting heterogametic sex determination. Many animals are obligate outcrossers, with polyploid progeny of hybridization events typically tetraploid. Such hybrids would most likely mate with diploids, producing sterile triploids. Therefore, polyploidy would be most likely found in groups exhibiting hermaphroditic or all-female modes of reproduction.

White (156) estimated that only 1 of every 1000 "species" of animals possessed all-female reproductive systems, many of which resulted from hybridization. The relative infrequency of hybrid asexual taxa has been attributed to severe ecological and genetic constraints on the origin and maintenance of such lineages. Moritz et al (93) argued that the chance of a hybrid founding a unisexual lineage is determined by a balance of genetic factors affecting the disruption of meiosis and the remainder of the developmental program, reducing the window in which hybrids can become unisexual lineages. As parental taxa diverge, genes regulating meiosis change. Combination of different alleles in F_1 hybrids may result in disruption of meiosis, increasing the proportion of unreduced ova generated in these individuals and possibly allowing for unisexual reproduction. At some point, parental taxa become too divergent, with genetic changes dramatically reducing fecundity and viability of hybrid offspring and also reducing the likelihood of establishment of unisexual lineages.

Once unisexual hybrids surmount genetic barriers to formation, a variety of genetic, ecological, and evolutionary constraints must be overcome (151, 152). Clonal transmission will result in accumulation of deleterious mutations (98) leading to "mutational meltdown" and relatively rapid extinction of such lineages (78). Pseudogamous (i.e. gynogenetic, hybridogenetic) taxa require contribution of sperm from compatible host taxa. Since these lineages are clonal, unisexual populations will be locked into certain niches that may place them at risk through competition with their bisexual progenitors or an inability to adapt to changing environments.

INFERENCE FROM DIPLOID AND POLYPLOID UNISEXUAL LINEAGES Polyploidy is typically associated with asexual reproduction and self-fertilization, especially in invertebrates (76, 156), likely due to increased probability of

establishment for such forms. In vertebrates, virtually all unisexual taxa have documented hybrid origins (153). Polyploid and unisexual lineages are often more widely distributed than their parental taxa, possibly indicative of advantages provided by their increased variability and mode of reproduction (151).

Allopolyploid and hybrid unisexual origins are more common than previously believed. Molecular methods have documented multiple origins for many polyploid and unisexual lineages, indicating that these phenomena are not accidents but reflect some general aspects of the interaction of parental genomes. Multiple origins are often attributable to several hybridization events, and reciprocal crosses may produce different results. Hybridization of male *Daphnia pulicaria* and female *D. pulex* produces diploid parthenogenetic lineages, whereas tetraploid parthenogens are produced by the reciprocal cross (38a). In some instances, only one species may serve as the maternal parent, indicating specific combinations may be necessary for production of such lineages.

Diverse complexes of clonal lineages often develop, due to genetic differences among bisexual parents. Hybridization of polyploids or unisexuals with bisexual diploids (sometimes a third taxon) has led to variation in ploidy level and/or mode of reproduction as well as allelic differences (e.g. *Bacillus*, *Bulinus*, *Cobitis*, *Phoxinus*, *Ambystoma*, *Cnemidophorus*). This diversity is likely to increase the probability of establishment and persistence as demonstrated by studies of unisexual forms of topminnow, *Poeciliopsis* (151, 152). This complex includes diploid hybridogenetic and triploid gynogenetic groups of clones produced by a variety of hybridization events involving *P. monacha* and some combination of four other species: *P. latidens*, *P. lucida*, *P. occidentalis*, and *P. viriosa*. Genetically distinct clonal lineages have different life-history, physiological, and ecological characteristics, allowing multiple clones to coexist and occupy at least part of the potential niche of the sexual species.

In some cases, hybrid origins have been attributed to other factors. Johnson (66) examined the evolution of parthenogenesis in the hermaphroditic snail *Campeloma decisum*. Unisexual reproduction was thought to have evolved spontaneously in some populations due to a parasitic trematode that ingests or blocks sperm. Fixed homozygosity at 19 allozyme loci supported this hypothesis for a subset of populations; however, all individuals from several localities were heterozygous at six loci that were fixed or nearly fixed allelic differences between eastern and western populations, implicating a hybrid origin for a subset of parthenogenetic populations. Dufresne & Hebert (38a) found that homozygous parthenogenetic clones of *Daphnia pulex* thought to be autopolyploid possessed mtDNA of *D. middendorffiana*. They concluded that these clones originated through hybridization with expulsion of the nuclear genome of the female parent while retaining mtDNA.

Asexual lineages have been considered dead-ends, not persisting long enough to contribute to the evolutionary process; however, recent studies have called

this view into question. DNA variation has been used to suggest that several unisexual lineages are older than previously believed (e.g. 58, 109, 134). Unfortunately, difficulties in accurate dating of divergence have an impact on the utility of such estimates. Failure to include the maternal progenitor will inflate estimates, requiring extensive samples to maximize chances of including the maternal parent and accurate characterization of geographic variation. For mtDNA, most estimates of divergence time are based upon a standard calibration. These are not likely accurate due to tremendous variation in rates of evolution across groups (e.g. 8, 80). Worst of all, divergence of alleles could predate (or postdate) speciation events (100), reducing the utility of such estimates.

The most significant contribution of unisexual lineages may be their ability to act as conduits for gene exchange among bisexual forms (e.g. *Ambystoma*, *Bacillus*, *Phoxinus*, *Rana*). Some members of the *Phoxinus eos-neogaeus* complex exhibit unusual modes of reproduction that could lead to gene exchange among parental taxa (46). The two triploid individuals examined produced haploid eggs that were fertilized by *P. eos*. Progeny were indistinguishable from *P. eos* on the basis of allozymes and external morphological traits, but mtDNA of all (KA Goddard, personal communication) and gut morphology of some was like *P. neogaeus*. Sex ratios of resulting progeny were approximately 1:1, and males appeared normal. Unfortunately, their ability to successfully reproduce was not determined. If such males are fertile, their contribution could lead to increased genetic diversity in the bisexual species.

Bogart (12) discussed evidence for transfer of alleles among four species of *Ambystoma* and reconstitution of parental forms. The existence of certain genotypic combinations was consistent with reconstitution; however, analysis of such individuals from a single egg mass indicated reconstituted individuals may suffer from increased mortality due to karyotypic anomalies (142). Bogart concluded that circumstantial evidence supported a potentially significant role for unisexuals in the evolutionary process. Unisexuality increases the opportunity for selection to act upon various recombinant gene combinations by maintenance of these variants for longer periods of time than otherwise possible. He further hypothesized that the ultimate outcome could be a population of bisexuals with mosaic genotypes superior to the parental and hybrid forms. This prediction has come to fruition in *Poeciliopsis*, in which a clone of the hybridogen *P. monacha-occidentalis* has reverted to sexuality. This new bisexual species contains a mosaic of genetic features from its parental contributors and occupies a unique niche (152), implicating a significant role for unisexual taxa in the evolutionary process.

INFERENCE FROM BISEXUAL POLYPLOID LINEAGES Despite expected difficulties of formation associated with outcrossing, several bisexual polyploid lineages have been generated by hybridization. Identification of polyploid lineages

has not always been simple, and some hypothesized cases have been controversial. White (156) rejected most instances of polyploidy in obligate sexual lineages, indicating that the best examples are provided by fishes and anurans. Among fishes, bisexual polyploids have been reported from five orders, with two extensively studied (16, 122). While salmoniforms are considered autotetraploid (4), allopolyploidy has been hypothesized for three cypriniform families: Catostomidae, Cobitidae, and Cyprinidae. The catostomids are a widely distributed group of more than 60 tetraploid species exhibiting disomic inheritance (41, 128). Their success has been obtained through diversification and adaptation to a variety of habitats, with representatives found in most streams, rivers, and lakes of North America and parts of Asia. Uyeno & Smith (147) hypothesized that, given the extent of polyploidy, the entire family descended from a cyprinid-like lineage approximately 50 Mya.

In cobitids, tetraploids are found in three separate groups, but only indirect evidence supports their hybrid origin (149). Ferris & Whitt (43) theorized that, based on levels of duplicate gene expression in tetraploid cobitids from the genus *Botia*, the polyploidization event was likely more recent than that giving rise to the catostomids. In their review of cyprinids, Buth et al (17) noted that 52 taxa were polyploid. Most of these are members of the subfamily Cyprininae, identified through analyses of karyotypes and genome sizes. Chromosome counts in nearly all cyprinid polyploids occur in multiples or combinations of the most common karyotypes (48 or 50 chromosomes); thus it was speculated that tetraploids (96, 98, or 100 chromosomes) and hexaploids (148 and 150 chromosomes) arose through hybridization involving pairs of diploid taxa or diploid and tetraploid taxa, respectively.

Smith (128) identified several morphological characters uniting catostomids and cyprinines, consistent with a single origin of tetraploidy for these two groups. Collares-Pereira & Coelho (24) used evidence of polyploidy in all three families to suggest that the entire order was derived from a single polyploid ancestor; however, this is inconsistent with the distribution of polyploidy throughout the families and relative timing of events obtained from levels of duplicate gene expression.

The only amphibian bisexual polyploids (3N-8N) are anurans, with incidence more phylogenetically restricted than for fishes (11). Hybridization has been implicated in several instances, but not without debate. A prime example of this difficulty is provided by North American tree frogs. Diploid *Hyla chrysoscelis* is subdivided into eastern and western populations by the tetraploid *H. versicolor*. These two species are generally allopatric, but co-occur in several narrow contact zones throughout the eastern United States. *Hyla versicolor* has been considered autopolyploid due to the presence of quadrivalents (11) and lack of allozymic variation consistent with specific status of the presumed

progenitors, eastern and western *H. chrysoscelis* (112, 116); however, immunological and allozymic data have also been used to support a hybrid origin (11, 81). Ptacek et al (108) provided mtDNA evidence supporting multiple origins of *H. versicolor*; thus, available evidence is not consistent with hybrid origins for this form.

Diversification by Introgression

Formation of new taxa by introgressive hybridization involves different circumstances than those described above. Gene exchange among taxa produces groups of recombinant individuals that eventually stabilize to form an evolutionarily independent, sexually reproducing taxon. This process has been hypothesized to include a variety of geographic scales, ranging from complete fusion of taxa to stabilization of local hybrid populations. Diversification is not instantaneous as recombinant lineages must be geographically isolated for long enough to evolve genetic differences that maintain independence and allow coexistence with parental forms.

Stable recombinant taxa have been hypothesized on the basis of several types of characters, including morphology, chromosomes, allozymes, and DNA. Hybrids have been expected to be intermediate to parental forms for complex features such as morphological variation. However, F_1 hybrids are not always morphologically intermediate between their progenitors (99, 117), whereas not all morphological intermediates are hybrids (156, 157). For example, morphological characteristics of recent year classes of the endangered sucker *Chasmistes cujus* were intermediate between older fish and *Catostomus tahoensis*, leading to concerns over human-induced hybridization. Analysis of allozymic variation failed to detect introgressed alleles in the younger *C. cujus* or to identify significant differences among younger and older representatives of this species, indicating that morphological differences reflect ontogenetic variation (18).

For more simplistic characters, (e.g. allozymes, karyotypes), the population should consist of an equilibrium distribution of variants contributed by all parental forms. Because the proportion of specific variants will be influenced by selection and drift, parental contributions may not persist for all character sets but could be represented by fixation for different diagnostic traits (e.g. alternate diagnostic alleles at two or more allozyme loci, mtDNA from one parental taxon and allozymic variants from the other). Therefore, hybrid taxa are most easily identified by examination of multiple independent character sets. Tests of hybrid origin are most readily obtained through phylogenetic analysis of each set of characters (e.g. morphology, allozymes, mtDNA, nuclear loci), with reticulate origins indicated by discordance among resulting topologies. Arnold (7) demonstrated the general utility of this approach, implicating introgressive hybridization in several animal and plant groups.

Technological advances have simplified identification of mosaic distributions of characters. Since primers for amplification and sequencing of many mitochondrial and nuclear genes have been developed, it is possible to closely examine patterns of genetic variation for a variety of independent loci. This approach has advantages over use of phenotypic characters such as morphology or allozymes because it allows for phylogenetic assessment of the source taxon for each allele. Careful examination of results derived from each data set is critical because most parsimonious topologies obtained from different character sets or loci may appear inconsistent when they are actually not well supported. Methods for assessment of phylogenetic trees are considered by Hillis et al (60) and Swofford et al (141).

THEORETICAL CONSIDERATIONS Previous objections to hybrid taxa may have been influenced by misconceptions concerning geographic scale and the structure of hybrid zones. Traditionally, gene flow has been considered to be strong enough to maintain cohesion of each species (39), and hybridization was thought to occur in continuous zones in which characters graded clinally from one form to the other. Under such circumstances, formation of hybrid taxa would be severely constrained by constant gene flow from parental taxa, preventing populations of recombinants from stabilizing and establishing independence.

Studies of population structure and hybrid zones, however, have indicated that this view of geographic structure and hybridization is oversimplified (39, 56). Organisms have a tendency to track specific favorable environments, fragmenting distributions. Because of this behavior, hybridization is often found in tracts of intermediate habitat or where conditions favoring two taxa are found in proximity. Since such conditions tend to be patchily distributed, hybridization is often better represented as a mosaic of potentially distinctive interactions among taxa, each proceeding along an independent evolutionary trajectory. In addition, environments are not stable, with resulting changes in selection pressures causing temporal shifts in the genetic composition of populations. Environmental heterogeneity and temporal instability are conducive to formation of hybrid taxa, especially where patches of hybrids have become isolated from both parental species.

Rarity of recombinant animal taxa has also influenced perceptions of significance. Difficulty detecting such forms is partly responsible for their rarity, with probability of successful identification dependent upon a variety of factors. Production of hybrid taxa should exhibit a negative correlation with levels of divergence among parental forms, with more divergent forms more likely to produce inviable or sterile hybrids. When the level of divergence among parental taxa is low, horizontal transfer will be difficult to discriminate from ancestral polymorphism. In origins involving gene exchange between common

and rare taxa, as is often the case (64), there are two potential difficulties. Influence of the less frequent taxon may be difficult to detect because it contributes proportionally fewer alleles to the recombinant taxon. In addition, rare taxa are more likely to go extinct, making it impossible to identify the source of some variants.

Probability of detection will also be reduced by time since origin of recombinant lineages. Soon after initiation, recombinant taxa are readily identifiable by mosaic combinations of character states. As time passes, however, such taxa will evolve their own unique characteristics, making it more difficult to discriminate between horizontally transmitted and convergent character states. Over time, internodal branches become relatively shorter and recombination among parental alleles becomes more likely, making ancient events more difficult to resolve with allele phylogenies.

Given all of these factors, only a subset of hybrid taxa will be detectable. Unfortunately, it is not possible to estimate probabilities of origination and detection, but it seems likely that these factors will severely limit identification of hybrid origins, making stable recombinant taxa appear much more rare than they actually are.

INFERENCE FROM STABILIZED RECOMBINANT LINEAGES The frequency of diploid bisexual taxa of hybrid origin is difficult to assess. Hypothesized instances of hybrid origin are often included as anecdotes in systematic studies and are not amenable to recovery with standard library search procedures, whereas many others have not been published and are known only to specialists. Of those cases identified (Table 2), many have not been examined with multiple sets of characters and remain conjecture based on morphological intermediacy. Additional instances of reticulate evolution have been identified (e.g. 7, 7a, 37, 102a); however, taxonomic implications have not been considered.

Tests of hybrid origin can fail to discriminate among alternate hypotheses. Smith et al (130) proposed a hybrid origin for the sucker *Catostomus (Pantosteus) discobolus yarrowi* on the basis of allozymic and morphological variation. Crabtree & Buth (26), however, found only limited evidence for contribution from one of the putative parental taxa, *C. plebius*. Morphological evidence was interpreted to represent shared primitive traits retained in *C. d. yarrowi*, and it was considered a distinctive form of the other putative progenitor, *C. discobolus*. Based on intermediacy of morphological and allozymic characters, Menzel (87) proposed that *Luxilus albeolus* was a taxon generated by hybridization of *L. cornutus* and *L. cerasinus*. Meagher & Dowling (85) examined morphological, allozymic, and mtDNA variation for these three taxa to test this hypothesis. Allozyme alleles supposedly contributed by *L. cerasinus* to *L. albeolus* were also found in local allopatric populations of *L. cornutus*,

Table 2 Hypothesized examples of bisexual diploid taxa of hybrid origin

Taxon	Evidence ^a	Reference ^b
Mollusks		
<i>Mercenaria campechiensis texana</i>	M, A, mt	103
<i>Cerion</i> "columna"-like	M, A	49, 50
<i>Cerion</i> "rubicundum"-like	M	49
Insects		
<i>Andrena montrosensis</i>	M	71, 72
<i>Papilio joanae</i>	M, mt	133
<i>Papilio brevicauda</i>	M, mt	133
Crustaceans		
<i>Bosmina coregoni/longispina</i>	M	74
<i>Daphnia wankelatae</i>	M, A	57
<i>Daphnia cucullata procurva</i>	M, A	75, 123
Fishes		
<i>Brachymystax</i> sp.	M, A	90, 107
<i>Catostomus discobolus yarrowi</i>	M, A	26, 130
<i>Chasmistes brevirostris</i>	M	89
<i>Chasmistes liorus mictus</i>	M	89
<i>Gila robusta jordani</i>	M, A, mt	37
<i>Gila seminuda</i>	M, A, mt	31, 131
<i>Luxilus albeolus</i>	M, A, mt	85, 87
<i>Mimagoniates microlepis</i>	M	86
<i>Pararhynchichthys bowersi</i>	M, A	48, 136, 137
Amphibians		
<i>Ambystoma tigrinum stebbinsi</i>	M, A, mt	68
Reptiles		
<i>Pseudemoia cryodroma</i>	M, A	65
Birds		
<i>Passer italiae</i>	M	67
Mammals		
<i>Canis rufus</i>	M, A, mt, u	119, 155
<i>Mus musculus molossinus</i>	M, A, mt	159

^aAbbreviations for character sets are: A, allozymes; M, morphology; mt, mtDNA; u, microsatellites.

^bAdditional references may be found within those cited.

preventing discrimination of hybrid origin from convergence of allozyme alleles or shared ancestral polymorphism. Reconstruction of allele phylogenies will provide more power for discrimination among these alternatives.

Analysis of proposed hybrid taxa has also yielded support for hybrid origins. DeMarais et al (31) used morphological, allozymic, and mtDNA data to examine the hypothesized hybrid origin of the minnow *Gila seminuda* (131). Taken individually, each character set yielded well-resolved differences between the

putative parental taxa, *G. elegans* and *G. robusta*. *Gila seminuda* was intermediate to *G. robusta* and *G. elegans* in phylogenetic analysis of morphological and allozymic characters, but it exhibited mtDNA essentially identical to *G. elegans*. Phylogenetic analysis of additional *Gila* species (37) identified conflict between allozymic and mtDNA topologies, patterns best explained by past episodic introgression.

Several groups of fishes from the western United States exhibit evidence of past introgression (31, 37, 129), implicating a general causative factor. Ecosystems of this region have gone through dramatic environmental change, including considerable tectonic activity and progressive aridification (10). These changes had a severe impact on aquatic ecosystems, likely producing cycles of isolation and sympatry. Divergent, isolated forms would have been forced together by desertification, allowing for gene exchange. Later periods of isolation would allow for stabilization and independent evolution of hybrid derivatives, resulting in taxonomic diversification.

The fossil record has provided historical perspective of introgressive origins for several taxa. Variation in *Cerion*, a speciose group of West Indian pulmonate land snails, has long perplexed taxonomists and evolutionary biologists (50). Goodfriend & Gould (49) described two cases in *Cerion* where introgressive hybridization has yielded temporally stable, morphologically distinct populations of hybrid origin on Great Inagua, Bahamas. In the first, a snail with a distinctive flat-topped morphology (*C. dimidiatum*) invaded over 13,000 ya ago, followed by subsequent transition of the local population to a morphology intermediate to the invader and the native species, *C. columna*. Morphological and genetic analysis of the extant population (50) indicates that the influence of introgression has been retained long after the disappearance of *C. dimidiatum* from the fossil record. A second, older introgression event between invading *C. rubicundum* and native *C. excelsior* produced snails with intermediate morphotypes (49). A series of dated fossil shells identified progressive shifts in morphotype for over 13,000 ya, changing from intermediate to that of *C. rubicundum*. Although morphological characters are good indicators of hybridization, they do not always retain evidence of past introgression. These populations are indistinguishable from *C. rubicundum*, but evidence of past hybridization likely persists at the genetic level.

Not all cases of hybrid origin are simple to interpret. Cladocerans hybridize extensively, yielding complexes of intermediate and parental morphotypes (123). Because of their ability to reproduce asexually as well as sexually, hybrid populations can be established in isolated ponds from small numbers of individuals. Distribution of such populations has been attributed to postglacial vicariant events or recent dispersal, making identification of such populations as distinct taxa controversial.

Humans have induced introgressive hybridization among taxa, directly through introduction of exotic species (e.g. *Felis concolor coryi*) or modification of habitats (e.g. *Chasmistes liorus mictus*). While the impact varies from case to case, sometimes sufficient introgression occurs to change entire taxa. It can be difficult, however, to discriminate human influence from natural effects. For example, the red wolf (*Canis rufus*) has been hypothesized to have originated through hybridization between grey wolf and coyote, stimulated by human agricultural activity (119, 155). However, available data are equally consistent with an earlier origin, possibly due to habitat changes associated with the Pleistocene glaciation.

While not hypothesized to be hybrid taxa, Darwin's finches provide a strong example of the significance of introgressive hybridization for evolution and diversification (51, 52). Long-term field studies of life-history parameters of entire island populations are possible due to their isolation, allowing for assessment of the frequency of hybridization among species, fates of hybrid individuals, and their contribution to future generations. In the case of hybridization among *Geospiza fortis*, *G. scandens*, and *G. fuliginosa* on Daphne Major, one cohort of F₁ hybrids and backcrosses analyzed over a four-year period was found to have higher average fitnesses than parental types. Because climatic stochasticity in the Galapagos Islands causes large population fluctuations in these finches, Grant & Grant (51, 52) hypothesized that hybridization could introduce genetic variation and reduce inbreeding depression during periods of small population size. Fitness of hybrids likely fluctuates with normal variation in climatic conditions, resulting in a long-term balance between hybridization and selection. Introduction of new variation by hybridization may allow selection to shift finch populations among adaptive peaks (52). The outcome of hybridization among isolated islands could vary, with each having its own local complex of interacting species.

CONCLUSIONS

Incidence of Hybrid Taxa

Hybridization and introgression increase genetic diversity through production of new recombinant genotypes, probably more rapidly than is possible by mutation. Enhanced levels of variability could allow organisms to more readily track environmental change, leading to increased rates of evolution. A possible outcome of these processes would be origination of new species through combination of preexisting characters in other taxa.

Despite the rationale of this perspective, animal hybrid taxa appear to be relatively rare. Misperception and negative attitudes have contributed to an apparent

scarcity. Bullini & Nascetti (14) noted that many invertebrate hybrid taxa were not recognized, with parthenogens and polyploids assumed to be derivatives of bisexual species even when hybridization provided a more parsimonious explanation. Such attitudes likely stem from the fact that generations of zoologists have been taught that hybridization disrupts coadapted gene complexes, yielding inferior progeny. Thus, natural selection will favor those individuals that do not hybridize, with the final stage of speciation requiring perfection of mechanisms that prevent the wastage of gametes. The inferiority of hybrids and reinforcement of reproductive isolation have recently been called into question (e.g. 7a, 19, 91), casting doubt on the negative assessment of hybridization and introgression.

Rarity is also partly due to difficulty of detection. Identification of hybrid taxa requires examination of several sets of characters, with some of the best approaches only recently technologically accessible. Even the best technology available may not allow for discrimination among alternate hypotheses as probability of detection is limited by factors beyond scientific control. To distinguish spontaneous from hybrid origins (e.g. *Hyla versicolor*) for polyploid and unisexual taxa, progenitors must be sufficiently different to increase levels of variation in hybrid progeny. Hybrid origin of bisexual diploid taxa is likely even more difficult to verify. Events must be recent enough to exclude convergence as an explanation for observed patterns of variation, and parental taxa must be sufficiently divergent to rule out ancestral polymorphism (e.g. *Catostomus discobolus yarrowi*, *Luxilus albeolus*).

Rarity of hybrid species could also result from differences in modes of production, with the pathway to evolutionary independence for hybrid taxa possibly more difficult than those taken by typical species. While hybrid unisexual and polyploid taxa are instantaneously isolated from their progenitors, they must surmount major barriers to formation and establishment. Production of chromosomal and meiotic conditions that give these forms autonomy will develop only under a limited set of conditions (93). Once produced, these forms must survive genetic and ecological constraints such as the accumulation of deleterious mutations, inability to find appropriate mates, and competition with progenitors (151, 156).

Bisexual taxa of hybrid origin do not face the same limitations; however, evolution of independence will likely be constrained by the homogenizing effects of gene exchange with progenitors (83). Production and stabilization of recombinants require a set of conditions that seem best exemplified by patchy and fluctuating environments (6). In such circumstances, species forced together in patches may hybridize due to rarity of mates (64) or breakdown of premating isolation, and resulting progeny may be as fit as parental taxa (7a).

In these isolated pockets, populations will evolve unique features through combinations of characteristics inherited from both parental taxa, and, if isolated long enough, attain evolutionary independence.

Implications

Even if hybrid taxa are uncommon, rarity should not be equated with insignificance of hybridization and introgression in the evolution and diversification of animals. Unisexual taxa have acted as conduits of gene exchange among related sexual species and may allow for reconstitution as new sexual taxa. Allopolyploidy has been important in diversification, as exemplified by diversity of catostomid fishes. Bogart (11) noted that perceptions of unisexual and polyploid hybrids are changing, with such taxa proving to be more significant for speciation than previously believed.

Stabilized recombinant taxa are indicative of a more significant role for gene exchange in the evolutionary process than generally believed. Introgressive hybridization among taxa will quickly increase levels of variation, allowing for rapid response to environmental change. The potential impact of gene exchange, however, will be limited by levels of premating reproductive isolation and reduction in fitness of recombinants relative to progeny of homospecific matings. The balance of these factors will provide a subset of circumstances under which introgressive hybridization will be important, likely determined by the degree of temporal and spatial variability of the biotic and abiotic environment and levels of divergence among taxa.

While it is difficult to predict the association between levels of divergence and fitness of hybrids, variability in habitat is readily observable. Extensive introgressive hybridization is often associated with habitats disturbed by anthropogenic activity (6, 64). More dramatic environmental changes occurred prior to human influence that would also have been conducive to introgressive hybridization (10) as indicated by evidence for extensive introgression in the evolution of several groups of western fishes (31, 37, 129). Association between habitat and reticulate evolution could be tested, with hybrid taxa expected to be more common in areas with a history of disturbance.

Several ancillary effects of introgressive hybridization require consideration. Events leading to hybrid taxa can be very difficult to reconstruct as genes will have different phylogenetic histories. These problems can extend to phylogenetic analyses involving hybrid and nonhybrid taxa, reducing resolution (129) especially where progenitors of hybrids are not closely related (84). Estimates of divergence time will also be compromised, providing dating of alleles and not taxonomic diversification (129).

Increased concern over biodiversity requires consideration of the role of hybridization in evolution. Extensive introgressive hybridization involving

introduction of exotic species and habitat disturbance indicates how humans can influence the natural balance. Instead of simply viewing hybrids as detrimental and expendable, the impact of introgression must be appraised on a case-by-case basis (38, 102). Careful consideration should be provided to biological systems in which hybridization has played a key role in the evolution of a taxonomic complex (e.g. *Gila*). Such systems are not readily amenable to captive propagation and reintroduction and will require creative management solutions to preserve this mode of evolution.

While many zoologists have come to appreciate the potential significance of such events for adaptation, few have considered hybridization and introgression as creative forces. Unlike the situation for plants, it is still too early to evaluate the actual incidence of hybrid animal taxa. Many instances have been put forward, but few have been carefully tested, particularly those involving bisexual diploid populations. Closer examination of insects has led Bullini & Nascetti (14) to conclude that hybrid speciation has been more common than previously believed. Changing attitudes toward hybrids and technological advances should allow for careful consideration of hypothesized hybrid taxa and will undoubtedly increase the number of known animal hybrid taxa.

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