Beginning of record displayed.

ILL il:9106575   Record 1 of 1

▶ :ILL: 9106575   :Borrower: TXA   :ReqDate: 20030914 :NeedBefore: 20031014
  :Status: SHIPPED   :RecDate: :RenewalReq:
  :OCLC: 14100627   :Source: OCLCILL   :DueDate: N/A   :NewDueDate:
  :Lender: *ORE,DHU,DHU,FXG,RRR   ¶
▶ :CALLNO: *Lender's OCLC LDR: 1- 1986- At Marine Science Center ¶
▶ :U TITLE: Trends in ecology & evolution (Personal ed.) ¶
▶ :TITLE: Trends in ecology & evolution. ¶
▶ :IMPRINT: Amsterdam [Netherlands] : Elsevier Science Publishers B.V.
[(Biomedical Division)], c1986- ¶
▶ :ARTICLE: Hewitt G M: Hybrid zones: natural laboratories for evolutionary
studies ¶
▶ :VOL: 3   :NO: :DATE: 1988   :PAGES: 158-167   ¶
▶ :VERIFIED: <TN:271693>OCLC ISSN: 0169-5347 [Format: Serial] ¶
▶ :PATRON: pinto, maria ¶
▶ :SHIP TO: Interlibrary Services/TAMU Libraries/5000 TAMUS/College Station,
TX 77843-5000 ¶
▶ :BILL TO: SAME...FEIN 746000531 ¶
▶ :SHIP VIA: Ariel 165.91.220.14   :MAXCOST: $50ifm   :COPYRT COMPLIANCE: CCL ¶
▶ :FAX: (979)862-4759; ARIEL 165.91.220.14 ¶

Please copy & Ariel

p. 158-167

Thank you!

Reduce to 94%

Hybrid Zones – Natural Laboratories for Evolutionary Studies

Godfrey M. Hewitt

Hybrid zones are currently of interest because they offer experimental material for studies of the characters and processes involved in divergence and speciation. Parapatric subspecies and races may differ for a whole range of genes and characters, from short DNA sequences through enzymes and chromosomes to morphology and behaviour. An understanding of the origins, evolution, dynamics and fates of these hybrid zone patchworks requires information from a multitude of lines of enquiry, including taxonomy, genetics, molecular biology, ethology, ecology, biogeography and palaeoclimatology.

Within each biological species[1] there may be distinct subspecies, geographical races, ecotypes and forms. These are the various products of evolution where genetic divergence has proceeded to different extents along various pathways. There is much debate about which of these routes may ultimately lead to speciation, and authorities differ in the importance they place on various causal factors[2–7].

Sometimes, in fairly continuous parts of its distribution, a species may clearly form a patchwork comprising several parapatric races or subspecies. Hybrid zones may be found where these different forms meet, mate and produce hybrids. These zones can be less than a kilometre wide and yet run for hundreds of kilometres across the species' range.

The size of the problem

Occasional reports of hybrid zones have accumulated for several decades, and many cases are now known for some groups of organisms. This is true in birds, for example, which are fairly obvious and have various aesthetic and gastronomic attractions encouraging their observation[8–9]. Indeed, simply leafing through the two excellent folios on African birds[10,11] reveals a surprising number of parapatric distributions, and it makes one wonder just how widespread this

Godfrey Hewitt is at the School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK.

phenomenon really is. Several other groups contain a good number of examples – particularly small mammals, salamanders, frogs and grasshoppers. A recent survey reported over 150 hybrid zones on which there had been some research[12]; over 20 more have appeared since then. As in many disciplines, most detailed studies of hybrid zones have been with animals from temperate regions. Plants are much neglected, and this uneven cover both of groups and the globe makes geographical and taxonomic frequency comparisons unreliable.

Different races and subspecies have usually been distinguished by obvious morphological criteria such as plumage, pelage or skin pattern. However, the classic work on Australian morabine grasshoppers[4,13] demonstrated extensive chromosomal parapatry (Fig. 1), and the same has recently been reported in British shrews[14]. The male calling song of frogs has likewise revealed many hybrid zones[15]. Recent studies have shown that these zones include protein and DNA sequence differences[16,17]. Clearly, chromosomal rearrangements and DNA sequence changes may not produce any obvious morphological difference, but may well modify inheritance, physiology or behaviour. These changes will be more cryptic, and the considerable number of hybrid zones already found may represent just the tip of an enormous iceberg.

Why are hybrid zones of interest?

Parapatric races and their hybrid zones may be seen as representing stages in the divergence of populations up to the level of full species. They have featured in several major models of speciation[2–4,18–20], in which they sometimes play a fundamental part. Furthermore, they have considerable experimental potential for studies of the characters and processes involved in divergence and speciation. Because hybridization occurs, the genetic basis of the differences may be determined and the number of genes and their control of

various fitness and reproductive characters will reflect the mode of divergence and may discriminate between competing theories of speciation[21–25]. Parapatric races and hybrid zones may tell us how new genes and new genomes become established[7], how much gene flow there is between them and how they spread[26].

Hybrid zones also have advantages for the study of processes not directly connected with divergence or speciation. They may comprise many interacting characters, and highly recombined genotypes can become available without prolonged laboratory crossing. Topics currently attracting interest include the distribution of rare alleles[27], morphological asymmetry[28], testicular dysfunction and gene expression[29,30], density-dependent regulation[31], genetic basis of courtship and mate preference differences[32], measurement of dispersal rate from linkage disequilibrium[33], population size[34] and patchiness[35] and the effects of parasites[36].

Origins and age of hybrid zones

The term 'hybrid zone' has been used in a variety of ways, sometimes confusingly. Fundamentally, a hybrid zone is a cline or set of clines between two parapatric hybridizing taxa for genes and the distinguishing characters they determine[12]. In principle, these clines may originate in two ways: primarily or secondarily[2]. A primary zone is one in which the differences have evolved in a continuous distribution, and where the entire distribution has remained intact subsequent to differentiation. For example, a gradient in the environment favouring different alleles on either side will produce a gradual cline; this could be progressively sharpened by selection for modifying genes until it becomes a narrow hybrid zone between two internally co-adapted genotypes[37,38]. A secondary zone is one in which the differences evolved while the two populations were geographically isolated, so that when their ranges altered and met, a steep cline formed as they hybridized.

While there is clear experimental evidence that sharp environmental changes can produce dramatic

primary clines[39,40], secondary contact is more favoured as the proximate origin of most hybrid zones[4,13,41,42]. Most zones in temperate latitudes are readily explained by secondary contact that occurred as ranges expanded following the last ice age; indeed, several well-known examples exist in mountain regions of Europe and North America (Table 1). Also, the post-glacial climatic optimum (~7500–5000BP) would have raised the lower altitudinal limit of the distribution of currently montane species, restricting them in places to several peaks. If the isolates differed genetically, they would then form hybrid zones in the intervening cols as the climate deteriorated again and their distributions expanded downwards. This seems particularly likely for the lizard *Sceloporus grammicus* in the central Mexican mountains, the grasshopper *Podisma pedestris* in the western Alpes Maritimes of France (Fig. 2), and lizards and small rodents in South West North America[12,43].

Even though a zone may have formed after the last climatic distribution change, the differences between the forms could have arisen by primary or secondary means at any time in the prior history of the species. There is growing evidence for relatively slow rates of evolutionary change in biochemical and chromosomal characters[44,45], and thus it may have taken many changes in environment and distribution to produce the considerable differences that exist between some parapatric subspecies. For example, the eastern fire-bellied toad (*Bombina bombina*) meets the western yellow-bellied toad (*B. variegata*) to form a hybrid zone down through central Europe; this involves many behavioural, reproductive, morphological and biochemical characters (Table 2). Biochemical and palaeontological data suggest a divergence of the two taxa several million years ago in the Pliocene[46]. Since then they will have experienced many distributional and ecological variations, providing many opportunities for both allopatric divergence and ecological differentiation with or without gene flow. A similar case can be made for the mouse (*Mus musculus/*
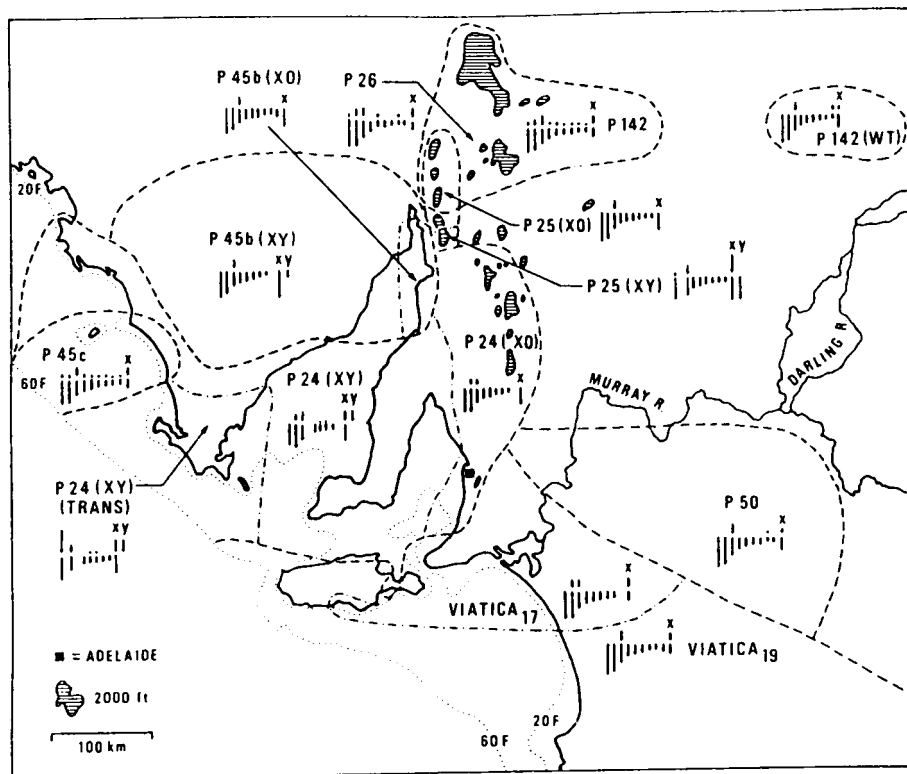

Fig. 1. The distribution of chromosomal races and species of *Vandiemenella* (*Warramaba*) *viatica* grasshopper complex in south Australia. The names and numbers are provisional identifications for the taxa by Key and White until they are formally described, and their ranges are shown by dashed lines. The coast line during the ice ages is indicated at 20F and 60F. Karyotypes are shown as haploid for the autosomes; the sex chromosomes are shown as X and Y. *Data by courtesy of Michael White, Ken Key, Graham Webb and Margaret Mrongovius.*

domesticus) hybrid zone, for which protein and mitochondrial DNA differences indicate divergence taking place for the last one million years[47,48].

The current surge of molecular investigation may provide additional evidence on these questions. At present it appears that subspecific differences may have accumulated over a considerable period, but that many extant hybrid

Table 1. Examples of hybrid zones in Northern Old World and New World that occur in regions once covered by ice or periglacial

Old World

Bombina bombina/variegata (toad)	Poland
Chorthippus parallelus/erythropus (grasshopper)	Pyrenees
Corvus corone/cornix (crow)	Scotland
Erebia cassioides/tyndarus (butterfly)	Alps
Mus musculus/domesticus (mouse)	Denmark/Germany
Natrix natrix/helvetica (snake)	Holland
Podisma pedestris XO/XY (grasshopper)	Alps
Rumex acetosa/thyrsoides (sorrel plant)	France
Sorex araneus – centric fusions (shrew)	Britain/Sweden
Triturus cristatus/marmoratus (newt)	France

New World

Bufo americanus/hemiophrys (toad)	Manitoba
Chilocorus tricyclus/hexadactylus (beetle)	N. Rockies
Dendroica coronata/auduboni (warbler)	N. Rockies
Geomys bursarius/lutescens (pocket gopher)	Nebraska
Gryllus pennsylvanicus/firmus (cricket)	Connecticut
Hyalophora euryalis/gloveri (moth)	Sierra Nevada
Icterus galbula/bullockii (oriole)	Nebraska
Rana pipiens/blairi (frog)	S. Dakota
Spermophilus richardsonii/aureus (ground squirrel)	Montana
Thomomys talpoides – chromosome races (pocket gopher)	Rockies

Many other cases of probable range changes occur here and elsewhere. The second binomial may be specific or subspecific.

zones have formed by secondary contact following some recent major environmental change.

Types of hybrid zone

Most well-studied hybrid zones comprise many character differences[12] (Table 2); they are multiple coincident clines for many DNA sequence variations controlling a range of phenotypes. Each of the individual gene clines could depend on one of six main genotype fitness relationships, as follows:

(1) homozygotes and heterozygotes equally fit;

(2) one homozygote fitter than the other genotypes;

(3) heterozygotes less fit than homozygotes;

(4) each homozygote fitter at higher frequency – positive frequency dependence;

(5) each homozygote fitter in a different environment;

(6) heterozygotes fitter than homozygotes in the zone.

(Other genotype fitness combinations are, of course, possible.)

In addition, when the taxa differ in a character produced by the interaction of several genes, the recombination between them may produce less fit hybrid genotypes, and

the clines will have properties of hybrid disadvantage (i.e. type 3). Evidence has been presented for all of these fitness types, but a careful survey indicates that some are more important than others in hybrid zones.

Neutral diffusion

When the alleles for which the races differ are equally fit in combination with either parental genome, they will diffuse into each other, producing a progressively shallower cline. This is most readily envisaged following secondary contact; the width of the clines will be a product of the organisms' dispersal rate and the square root of the number of generations since contact[38]. While neither of these parameters is easy to measure accurately, it is possible to place a reasonable contact date on the zones in glaciated and Northern temperate regions and to obtain tolerable mark–recapture estimates of dispersal for some organisms. The width of many hybrid zones is one hundred times the estimate of dispersal for the individual organisms; this suggests that neutral diffusion may be occurring for the genes controlling the characters involved (see Fig. 3 in Ref. 12). Although this conclusion seems fairly robust, the dispersal rate is likely to vary considerably with differing population density, structure and patchiness as determined by the environment. More work is needed here.

Advancing wave

If one allele is advantageous over the other it will spread as a wave front through the range, replacing the disadvantaged allele. This type of process has been observed for Warfarin resistance in rats[49], and spread can be quite rapid (even though here the heterozygote is most fit). It is not surprising that there is little evidence for this phenomenon in well-studied hybrid zones. Such advantageous alleles are likely to have spread through the zone already; one would be lucky to catch one in progress. There are a few reports of moving zones, e.g. in the grackles *Quiscalus quiscalus* in Louisiana[50], the warblers *Vermivora pinus/ chrysoptera* in New England[51] and
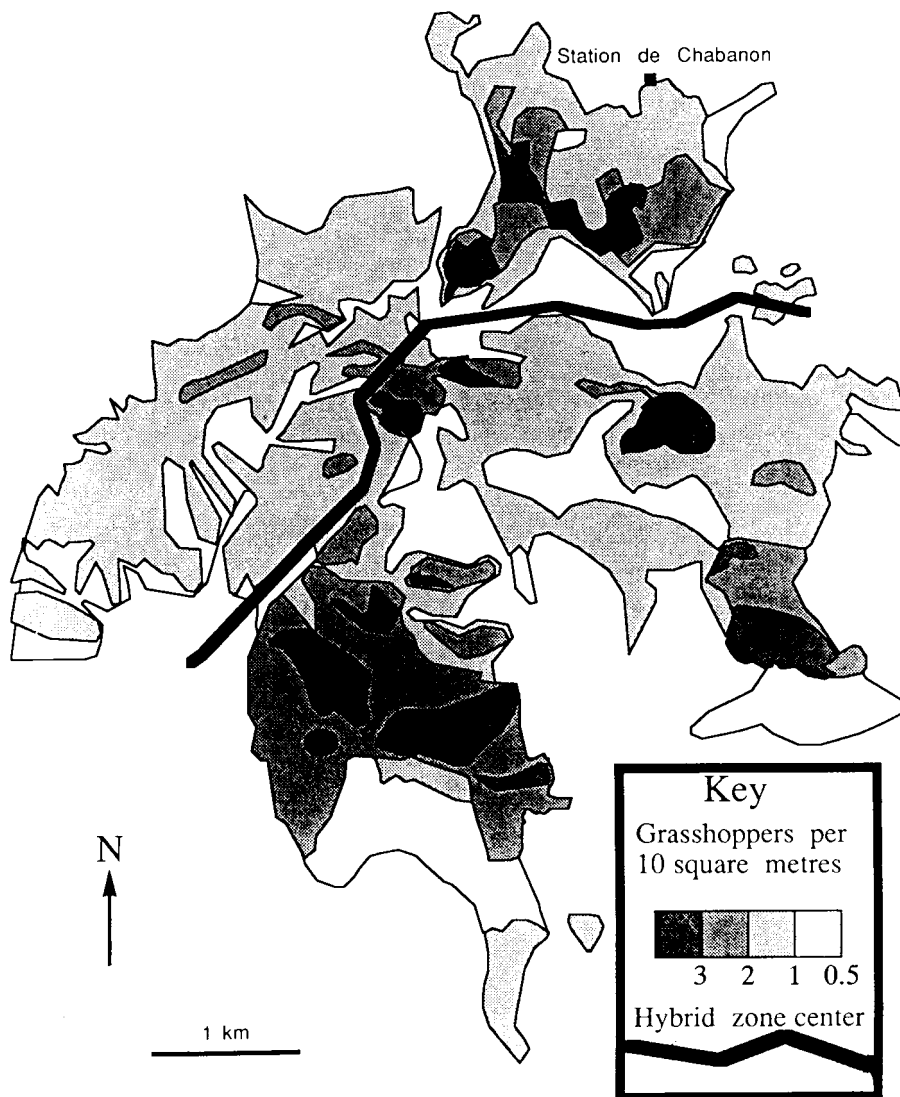

Fig. 2. A contour map of *Podisma* density in the area near Seyne-les-Alpes where a hybrid zone occurs. The centre of the sex chromosome cline is shown and the density per 10 square metres is given. The region consists of high domed mountains and several areas of high density were probably refugia in the climatic optimum.

Table 2. Six contrasting hybrid zones and a guide to their characteristics

Organism and location	Differentiating characteristics		Width of cline	Dispersal per generation	Hybrid unfitness	Location of zone	Comments	Refs
Bombina bombina/variegata (toad), Poland – Bulgaria	Alloz.[a]	39:0:14(2)[a]	5–7 km	0.4–0.9 km	Hybrids inviable Morph. aberrations	Habitat altitude correlation Permanent and temporary water pools	Many differences mating preference	33,46
	Chrom.	none noted						
	DNA	mitochondrial	5–7 km	crawls and swims				
	Morph.	skin, vocal sac, devel. rate, fecundity	5–7 km				W and E refugia Diverging 5 m yrs 2° contact 8000BP rare alleles	
	Behav.	call, territory	5–7 km					
Caledia captiva races (grasshopper), E. Australia	Alloz.	23:3:0(5)	0.35 km	0.01–0.1 km	F1 viable F2 inviable	Climatic regime changes	All chromosomes differ	55,71
	Chrom.	inversions and C bands						
	DNA	ribosomal, repeated DNA	(displaced)		backcross 50%		F2 recombinants unfit	
	Morph.	? subtle		can fly			disequilibrium changes rDNA uncoupled rare alleles	
	Behav.	none noted						
Chorthippus parallelus parallelus/erythropus (grasshopper) Pyrenees	Alloz.	19:11:0(3)	varies ~15 km	0.03–0.1 km	F1 testicular dysfunction	Franco–Iberian	Haldane's Rule	29,30,32
	Chrom.	fluoresc.-bands				Along ridge of mountains below 2000 m	Mating preference	
	DNA	nucleolar organizers	0.6 km	can't fly	ccbackcross–small testes		SW and SE refugia	
	Morph.	stridulatory pegs and ovipositor length	4.1 km		Females normal		2° contact 10 000–8000 BP	
	Behav.	song courtship calling syllable echeme interval	2.1 km 19 km 1.4 km					
Gaillardia pulchella races (composite weed), Texas	Alloz.	13:7:0(4)	Varies between transects and loci	'restricted'	F1 50–75% less stainable pollen	Carbonate rich/poor ecotone	Recent man made?	68
	Chrom.	structural?				roadside and pastures	clines non-coincident, width varies ecotonally	
	Morph.	ray colour (RCI)	MEF 16 m–503 m	insect pollinated passive seeds				
	Physiol.	soil adaptation	MES 41 m–333 m RCI 167 m–1180 m PGM 200 m–large					
Mus musculus/domesticus (commensal mouse), Denmark–Black Sea	Alloz.	41:17:13	20 km	0.1–3.0 km	None noted	Climatic? in Denmark	Many differences diverging 1m yrs W and E refugia 2° contact 6000 BP rare alleles	48,80
	Chrom.	Y chrom sequence	2 km					
	DNA	mitochondrial	2–20 km	runs and is man assisted				
	Morph.	pelage colour	20–40 km					
	Behav.	habitat choice						
Pinus muricata-N/S (bishop pine) California	Alloz.	26:8:1	~2 km	1–10 km long distance pollen dispersal	Seedlings≠Adult in allozyme frequency	No obvious environmental gradient	Assym. gene flow Flowering time displaced glacial refugia 2° contact after Xerotherm	56
	Chrom.	not noted						
	Biochem.	xylem resin						
	Morph.	foliage colour						
	Behav.	flowering time						

[a]Allozyme notation: 39:0:14 (2) denotes 39 loci: 0 polymorphic: 14 fixed differences: 2 frequency differences.

the lizard *Pholidobolus montium/ affinis* in Ecuador[52], but these instances may be due to human activities.

Tension zone

Hybrid unfitness due to either heterozygote disadvantage at an individual locus or maladapted hybrid recombinants between the racial genomes produces a particular type of hybrid zone that has been called a tension zone[53]. This phenomenon has interesting properties. Because the heterozygotes or hybrid recombinants leave fewer offspring, these genotypes tend to be removed from the population by natural selection, leaving pure parental genotypes. Dispersal of an individual amongst the other types means that when it mates it is more likely to produce inferior hybrid offspring. The two parental types retain their purity, and the width of the zone (w) is determined by balance between dispersal (σ) and selection (s) against hybrids ($w \sim \sigma^2/s$).

Since tension zones are caused by genetic incompatibilities they are not necessarily related to ecological differences and ecotones. They have the potential to move whilst maintaining their internal structure and tending to minimize
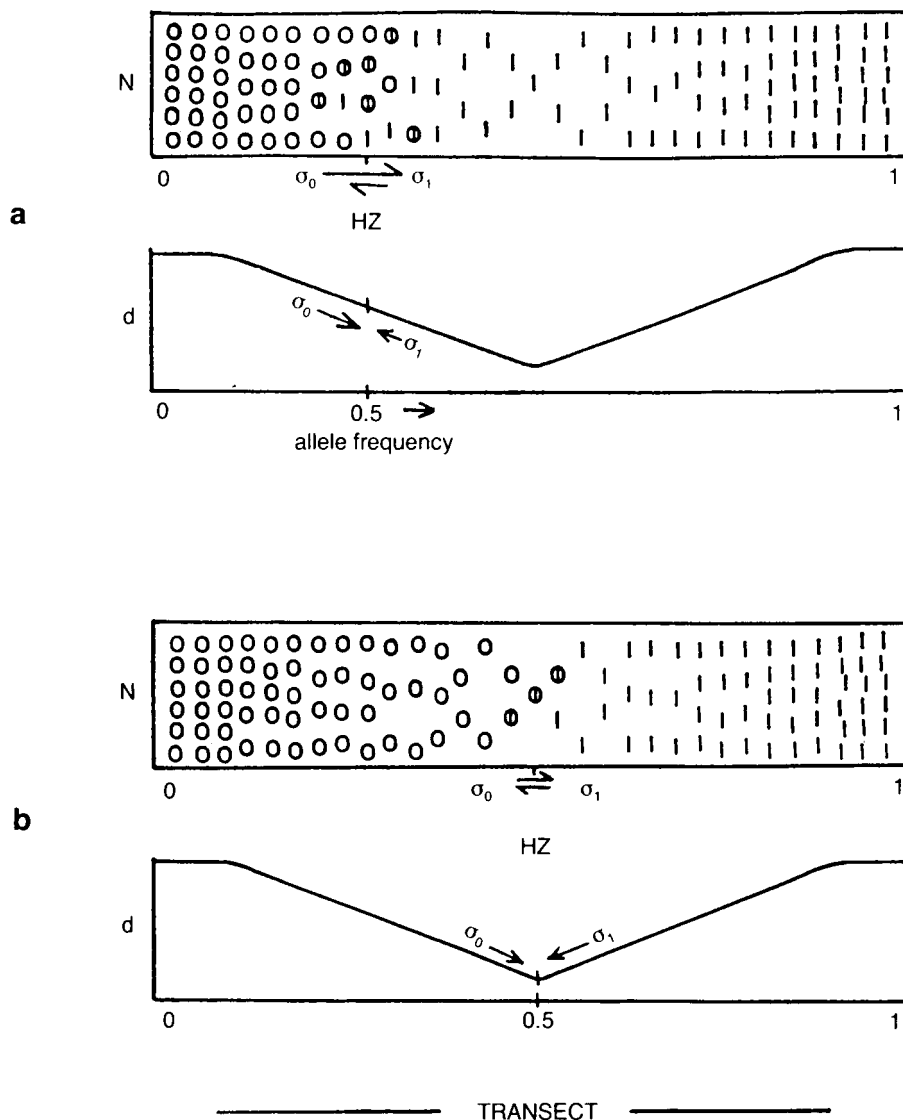
Fig. 3. A simple diagram of a transect through a region of lower density (d) of individuals (N) of three genotypes in a hybrid zone viz.–I, one homozygote; $\oplus$, heterozygote; O, other homozygote. The dispersal in each case is shown as σ. (a) the zone is on a density slope and will move because $\sigma_0 > \sigma_1$ until (b) the zone is at an equilibrium $\sigma_0 = \sigma_1$ in a density trough.

and a dispersal of 20 m per generation should produce a zone only 28 m wide. The fact that the inviability zone is some 350 m wide demonstrates that many gene differences (~150), each of small effect, are involved in producing the hybrid unfitness. Thus the two races differ by a significant proportion of their genome[62] – an unexpected conclusion given the similar karyotype and morphology of the two races. This combination of detailed ecological and genetical experimentation is proving particularly fruitful in disentangling the factors involved in hybrid zones.

Homozygote frequency dependence

Genic heterozygote disadvantage produces frequency-dependent selection, where the rarer form reduces in frequency in each generation, thus creating a tension zone. Phenotypic frequency dependence, as in Müllerian mimicry in *Heliconius* butterflies[65], also generates a tension zone having the same properties as a heterozygotic tension zone. The difference between these types of zone is simply the stage at which selection operates: the rare homozygote butterfly is immediately at a disadvantage when it strays into the other model's territory, while heterozygote disadvantage is effective after the migrant has reproduced. This relationship has not always been clearly appreciated. Such homozygote frequency dependence may maintain zones in many other warningly-coloured butterflies, and many other interactions between forms, such as shell coiling in the Moorean snail *Partula*[66,67]. Of course, heterozygote disadvantage may also be involved.

Environmental clines

Sharp clines can exist between two different environments, where each favours a different allele or set of alleles. Indeed, at least a quarter[43] of hybrid zones are found at or near an environmental transition, and the races may have alleles suited to different conditions. Such environmentally determined clines are expected to follow the course and shape of the ecological change. One would also expect clines for different loci not to be coincident. This is because the null point for selection between

their length. Many hybrid zones show evidence of some form of hybrid unfitness; examples include the toad *Bombina*[54], the Australian grasshopper *Caledia*[55], the meadow grasshopper *Chorthippus*[29], the Californian pine *Pinus*[56], the alpine grasshopper *Podisma*[57], the leopard frog *Rana*[58], the Mexican lizard *Sceloporus*[59], the mole rat *Spalax*[60], the pocket gopher *Thomomys*[61] and the eumastacid grasshoppers *Warramaba*[4].

The evidence for *Podisma pedestris* is particularly clear. Reduced hatching and survival of hybrids between two chromosomal races has been demonstrated in the laboratory[62], and hybrid populations in the field also show reduced hatching and development rate[31,63]. The field results

have been achieved by careful vegetation analysis (to allow matching of habitats) coupled with extensive quadrat estimates of insect age and density through the season in a range of sites inside and outside the zone. There is no evidence for ecological difference between the habitats of the two races; indeed, the zone runs for 140 km along the length of the Alpes Maritimes from Seyne in the west to Tende in the east with no indication of following an ecotone[57,64]. Detailed sampling and breeding has also allowed an accurate determination of the width of the zone in several places for sex chromosome type and hybrid inviability; and several mark–recapture estimates of dispersal have been made. A hybrid disadvantage of some 50%

er-
ily
in-
de
lif-
all
ng
wo
or-
ex-
lar
he
le-
cal
cu-
he

in-
en-
rer
ch
on
en-
in
er-
he
tic
le-
oly
er-
fly
ge
d-
ite
he
e-
en
io-
ay
ier
nd
en
he
Of
ge

en
re
et
a
nd
n-
ve
n-
e-
to
ne
so
ot
se
en

two alleles along an environmental gradient will probably be different for each gene; the products of various genes and their control of cellular reactions will be different and any particular environmental factor, be it temperature, humidity, predators or parasites, will not favour change of all these functions in the same place. There are a few zones that provide this type of evidence; the winter annual composite *Gaillardia* in Texas[68] is a particularly good example (Table 2) and there are indications of a similar phenomenon from the titmouse *Parus* in Texas[69] and the meadow lark *Sturnella* in the Great Plains[70].

While we may be able to decide between an environmental cline and a tension cline at the level of the single gene, the distinction between environmental and tension zones may be illusory. If an organism adapts to two different environments, many genes will be fixed for different alleles. These loci will interact and selection will produce co-adaptation. Some may also be linked. So, when hybridization occurs the recombinants will have reduced fitness and the zone will have the properties of a tension zone. The ecological differentiation will remain and the result is a tension zone with alleles suited to different environments locked in.

Two ecological races may also differ for alleles showing heterozygote disadvantage. There is evidence of this mixed nature in several zones, for instance the very well studied zone in the Australian grasshopper *Caledia*[55,71], the meadow lark *Sturnella*[70] and the newt *Triturus*[72]. The crickets *Gryllus firmus* and *G. pennsylvanicus* form a long, broad, patchy hybrid zone down the north east USA[73–75]. They show a general concordance of mtDNA with nuclear differences, and in some populations around New Haven, Connecticut, each genome is associated with a particular soil type. Since the *G. firmus* ♀ × *G. pennsylvanicus* ♂ cross is infertile, this is a mixed ecological/tension zone where the distribution of soil types allows a mosaic intermingling.

Hybrid superiority

It is theoretically possible that a hybrid zone could exist in which a heterozygote or hybrid genotype is fitter than either homozygote in a narrow region between two environments each favouring one or other race. This explanation has been strongly advocated for some vertebrate zones[76–79], and has been called the 'geographically bounded hybrid superiority' model. However, even in these cases the available evidence does not allow this model to be distinguished from other explanations, particularly tension zones (type 3) and environmental zones (type 5). Under this model one would expect the ecotonal region with a particular environment where the hybrid was favoured to vary in width and be more likely to have a broken patchy distribution. One would also expect that only a few particular hybrid genotypes would be favoured over the others in the zonal environment. This would produce clines which were neither smooth nor coincident. Most hybrid zones are, in fact, highly polymorphic for racial alleles (e.g. allozymes) and they are usually smooth and coincident.

To determine the fundamental causes of any hybrid zone, one needs detailed estimates of fitness over the life cycle coupled with reliable estimates of dispersal, since, as shown above for tension zones, relatively low selection can produce a fairly narrow zone when genetic dispersal is not great. A neutral diffusion zone may not be very wide either, when dispersal is effectively low. In two of the cases where the hybrid superiority model has been preferred there are, in fact, clear suggestions of some hybrid inferiority; in the pocket gophers *Geomys* of Nebraska the two hybrids had a lower number of embryos and uterine scars than the seven homozygotes examined[78], and in the Northern Flicker *Colaptes* from Platte River in Nebraska/Wyoming there are strong indications that the hybrid males have a lower brood size both early and late in the season[79]. Furthermore, in both these cases the suitable environment is not continuous. The actual genic dispersal needs to be determined before a proper distinction between causes can be made. Nevertheless, superiority of particular hybrid genotypes may occur where populations produced by occasional hybridization are separated for some time from parental types, and this may be the case in some plants[3]. This depends on spatial separation more than heterozygote advantage or superiority of a wide range of hybrids.

Multiple zones

The six types of cline may be combined together in various ways. As already emphasized, most hybrid zones when investigated in detail prove to comprise multiple differences and each gene may be under different selection pressures. The combination of both ecological and tension clines has been mentioned; several zones probably contain neutral diffusion clines as well. Clines due to diffusion will be wider than tension or ecological clines maintained by selection and when heterozygote disadvantage is particularly strong the cline may be very narrow indeed. In the grasshopper *Chorthippus parallelus*[30], some song component and enzyme clines are 15–20 km wide, while the cline for nucleolar organizing regions is about 0.5 km. Similarly, in *Mus musculus/domesticus*, morphological and enzyme clines are 20–40 km wide while clines in mtDNA and Y chromosome sequences may be only 2 km wide[48,80].

Density troughs and traps

The evidence clearly suggests that most zones contain some element of hybrid unfitness or frequency dependence and thus are in part tension zones. Tension zones have the interesting property that they are mobile but tend to come to rest in regions of low population density. This stems from the fact that if more homozygotes of one race are dispersing in from one side, the centre of the cline will be moved towards the region of lower density[64] (Fig. 3). Such low density troughs can be powerful traps[57,81] and even zones where one race has a significant fitness advantage will be prevented from advancing through the species' range by relatively small reductions in density.

Since environmental features like valleys, rivers, ridges and woods cause density to vary over orders of magnitude, we can expect hybrid zones to be trapped for some time in density troughs. Quite

a number of zones do appear to lie in such places[43], and detailed plotting of density of the grasshopper *Podisma pedestris* in the Alpes Maritimes clearly supports this expectation[35,62] (Fig. 2). The later study at Seyne also nicely illustrates how a zone may be pinned by two regions of very low density and pass through a high density region in between – a situation that is produced repeatedly and dramatically when two races are separated by a ridge of mountains and meet and hybridize through lower passes and foothills. This is seen in *Podisma*[62,64] and *Chorthippus*[30,32]. Computer modelling of the *Podisma* zone in the higher density region at Seyne, using measured population and fitness parameters, shows that the zone is running just where expected from a balance between selection, dispersal and density[35]. Such detailed measures show that a zone's particular course can be held by quite small changes in density; this has major implications for genome and racial expansion.

The existence of stable density troughs caused by factors like mountain ridges, river valleys or soil composition means that tension zones should not move far. The continuation of hybrid zones on to islands such as Kangaroo Island off south Australia (Fig. 1) (*Warramaba viatica*) or isolated mountain blocks such as Seyne in the Alps (Fig. 2) (*Podisma pedestris*) clearly argues for long term stability of hybrid zones, probably since secondary contact after the last ice age.

Range contraction and expansion

It has been argued that many zones were formed by secondary contact following post-glacial expansion, even though the differences between them may well have evolved over much longer periods of time. During this time there have been several ice ages causing major range changes, and many minor ones have occurred in between. Consequently the differences previously accumulated between populations in two refugia will expand together and meet to form many coincident clines (Fig. 4). These clines may be for hybrid unfitness, ecological adaptation or neutral differences. Repeated contraction and expansion will cause more differences to accumulate[43,57]. It is difficult to escape this conclusion for temperate regions and it provides the most tenable explanation for the multiple nature of hybrid zones.

There is currently some debate about the extent and nature of ice age refugia in the tropics and their role in producing diversification[82–84]. In particular, the discussants use evidence from the width and position of contact zones in birds and butterflies from Africa and South America. A distinction between the various hypotheses would be easier if we had better information on the zone widths, location in inhospitable regions, the dispersal of the species, and particularly the degree of hybrid unfitness and frequency dependence – which will affect the zone width. Some excellent work is in progress on tropical butterflies[65], but more is needed.

Speciation by hybrid zones

Range contraction and expansion can reduce a widely distributed taxon containing several variants into a small refugium and then can spread one surviving combination of genes over a large area, juxtaposing it with another[43] (Fig. 4). The differentiation of these two genomes may proceed by selection or drift within the species' range largely independently of this geographic reorganization – although the small populations at the edge of a range may offer variants a greater chance of establishment[26]. Repeated range change can lead to the accumulation of these differences in a major zone, so that after several cycles gene flow may be so reduced as to produce two species. Some hybrid zones are very strong barriers to gene flow[85] and the two taxa may be designated as full species, e.g. *Bombina bombina/variegata*[33,46].

One might think of this as 'speciation by accumulation'; even so it is still necessary to explain the origin of the crucial differences causing reproductive isolation. Certain organisms seem particularly likely sources of valuable information on these processes. For example, the pocket gopher *Thomomys bottae* has some 215 races in California; detailed studies of its genetic and morphological relationships suggest how an adjacent sister species, *T. townsendi*, may have arisen by peripheral allopatry[86–88]. The plethodontid salamanders also seem to be remarkably rich in cryptic sibling species[89–91], and the comprehensive study of a classic 'ring species' in one of them, *Ensatina eschscholtzii* from California, is revealing several stages of divergence and speciation[92–94].

Stasipatric speciation was proposed[13,20] as a result of work on the extensive parapatry of chromosomal races in the Australian grasshopper *Warramaba viatica* complex (Fig. 2). This research envisages a novel karyotypic change becoming established in the interior of a species range and spreading out behind a hybrid zone, which (because it is a barrier to gene flow) ultimately allows speciation. However, there are several difficulties with this model[42], the greatest perhaps being the apparent immobility of hybrid zones, whether they enclose a small bubble of a new mutant or a widely distributed race. The initial fixation of negatively heterotic mutants is also a problem, although recent theoretical work suggests how this may occur in a continuous population as well as in a small one[7,95].

Probably the major influence of hybrid zones on theories of speciation has been the development of the idea of reinforcement. Since hybrids in the zone are less fit, there is selection for genes for assortative mating within each race; it has been claimed that this would lead to the evolution of pre-mating isolation[96,97]. However, there are severe problems with this proposal[42,98] and little, if any, evidence for its occurrence[99]. Theoretical modelling[100–102] shows that for reinforcement to occur there needs to be strong selection against the heterozygote for the fitness gene, strong assortative mating produced by the mating locus, and tight linkage between them. Contrary to this, we have seen that in a hybrid zone unfitness is usually caused by many genes of small effect spreading throughout the genome. Furthermore, even in those hybrid zones involving be-
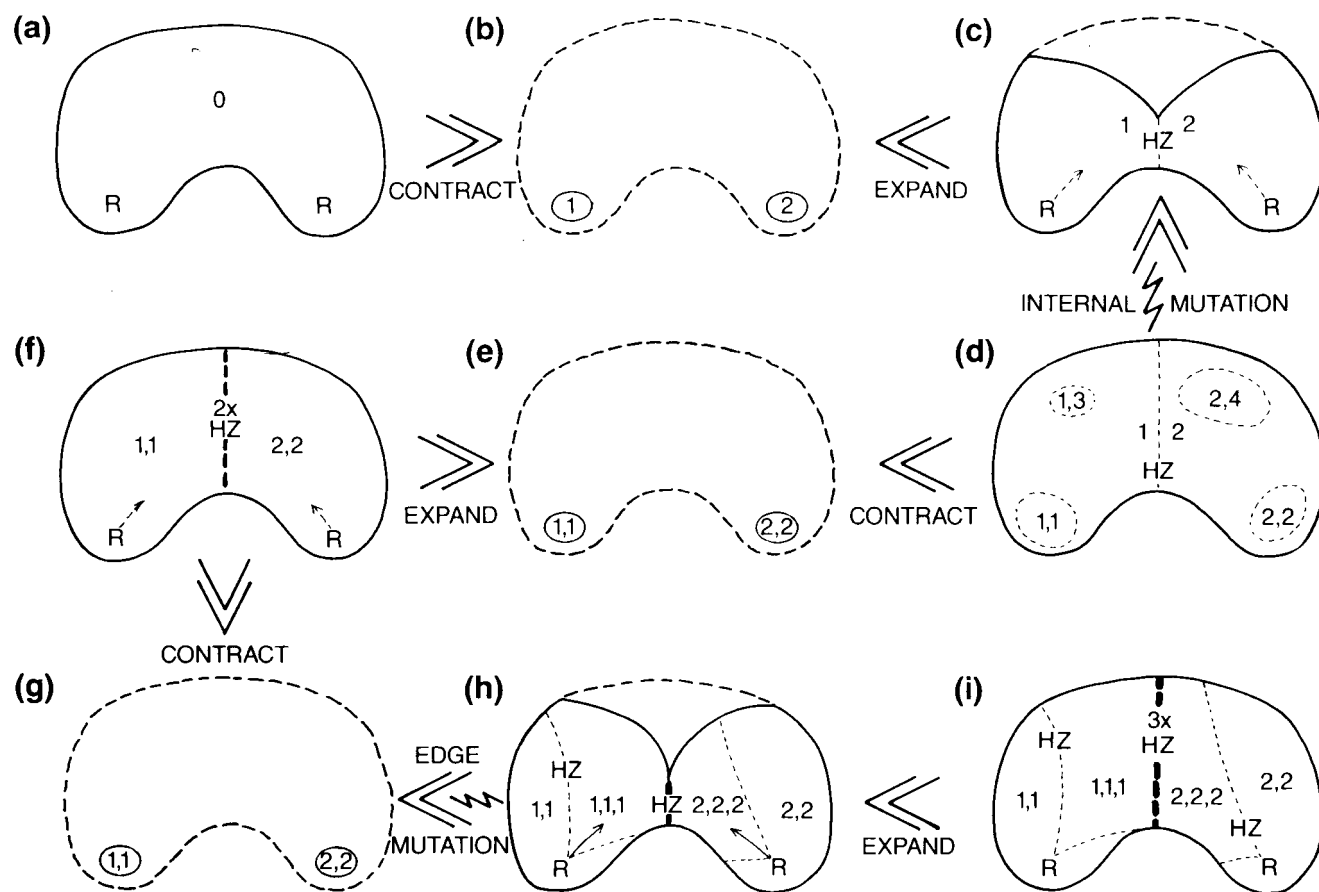
Fig. 4. A series of range contraction–expansion cycles for an organism originally with genotype 0 (a), two refugia are marked R. Mutations 1–4 occur, causing changes in the genotypes; these may be in the refugia (b), within the species range (d) or at the expanding edge of the range (h). When contraction into refugia occurs only certain modified genotypes survive; when these expand and meet a hybrid zone forms (HZ). After several cycles a strong multiple zone can be produced (3× HZ).

havioural differences, support for reinforcement is weak at best, and usually the data are insufficient[103].

The Polynesian snail *Partula suturalis*[66], where dextrally and sinistrally coiled shell types mate assortatively and avoid mating with sympatric species, is the most promising example for further study – but even here the barriers to gene flow are ineffective[67]. There is evidence from sympatric *Drosophila* species that pre-mating isolation may evolve faster than post-mating isolation[104], and it may be possible for reinforcement to occur rapidly on occasions when the genetic architecture, behaviour and population dynamics of the organisms meet the necessary conditions. It is important to improve our poor understanding of the genetics of differences in the mate recognition system[103], especially if we hope to explain clusters of behaviourally isolated species such as those in the bewildering complexity of acoustic taxa in the crickets of Hawaii[105].

The hypothesis of speciation by reinforcement has been applied not only to tension zones and environmental clines but also to sympatric speciation by adaptation to a heterogeneous environment. Recent work on host-specific insects suggests how sympatric speciation may occur[106].

While reinforcement of hybrid zones has received a great deal of attention, its converse – amelioration by selection for beneficial modifiers of heterozygote unfitness – is rarely addressed. Crosses between *Chorthippus parallelus parallelus* and *C. p. erythropus* produce sterile males, yet the males in the hybrid zone appear quite normal[29,30]. Similarly, assortative mating in *Bombina bombina/variegata* is stronger outside than inside the zone[33]. In the shrew *Sorex araneus*[107], meiotic problems of metacentric chromosome hybrids are ameliorated in the zone by the presence of unfused acrocentrics. In *Chorthippus* and *Bombina*, amelioration may simply

be due to segregation and recombination of racial alleles in the zone as a result of generations of hybridization, so that the chance of an F1 hybrid genome is vanishingly small; this would not explain the zonal acrocentrics in *Sorex*, which seems to require selection for a particular karyotype. However, even if amelioration has occurred in these cases, the zones are still narrow, and their positions have apparently been stable since the last ice age.

Conclusion and prospect

The last few years have produced considerable advances in our understanding of hybrid zones, and this is due in no small part to the interplay of several lines of enquiry. Basic genetical ideas of selection and gene flow, when developed mathematically, lead to more sophisticated determinations of zone dynamics, involving detailed field ecology and laboratory genetics. This, in turn, required computer modelling of small scale

population dynamics and genetics to explain interactions over a few metres, and a consideration of Pleistocene biogeography for the distribution of zones and taxa over continents.

We now know that hybrid zones divide up the ranges of many species, in some cases producing a complex patchwork of subdivision. Many zones comprise clines for many genes affecting all sorts of characters, with a large proportion involving hybrid disadvantage of some sort. Such tension zones may be immobile because of low density traps, negating stasipatric models of speciation. They also appear fairly stable and show no signs of reinforcement leading to speciation. While hybrid zones constitute semipermeable barriers to gene flow, there often appears to be little gene exchange between the several genomes into which many species are divided. In temperate regions, and arguably also in the tropics, the proximate origin of hybrid zones is secondary contact after the last glaciation, but the initial genetic divergence probably began millions of years ago and the distributions have been through several cycles of contraction and expansion, leading to the accumulation of differences.

A multitude of questions remains. How subdivided are species genomes – are there zones within zones? What are the effects of population structure and patchiness on dispersal and gene flow between populations, races and subspecies? What is the genetic control of character differences and how do they become established?

These are just a few of the many questions that further study of hybrid zones may help resolve. The recent flowering of molecular techniques has already produced new approaches to their study[46,47,71]. These techniques, along with mathematics and computing can contribute much to this already fertile interaction of ecology and genetics. This prospect is paticularly exciting for groups where the phylogenetic and biogeographic settings are well studied.

References

1 Key, K.H.L. (1981) Syst. Zool. 30, 425–485
2 Mayr, E. (1970) Populations, Species and Evolution, Harvard University Press
3 Grant, V. (1971) Plant Speciation, Columbia University Press
4 White, M.J.D. (1978) Modes of Speciation, Freeman
5 Templeton, A.R. (1981) Annu. Rev. Ecol. Syst. 12, 23–48
6 Wright, S. (1982) Annu. Rev. Genet. 16, 1–20
7 Barton, N.H. and Charlesworth, B. (1984) Annu. Rev. Ecol. Syst. 15, 133–164
8 Short, L.L. (1969) Auk. 86, 84–105
9 Short, L.L., Schodde, R., Noske, R.A. and Horne, J.F.M. (1983) Aust. J. Zool. 31, 517–531
10 Hall, B.P. and Moreau, R.E. (1970) Atlas of Speciation in African Passerine Birds, British Museum Natural History
11 Snow, D.W. (1978) Atlas of Speciation in African Non-Passerine Birds, British Museum Natural History
12 Barton, N.H. and Hewitt, G.M. (1985) Annu. Rev. Ecol. Syst. 16, 113–148
13 White, M.J.D. (1968) Science 158, 1065–1070
14 Searle, J.B. in Kew Chromosome Conference III (Bennett, M. and Brandham, P. eds), HMSO (in press)
15 Littlejohn, M.J. and Watson, G.F. (1985) Annu. Rev. Ecol. Syst. 16, 85–112
16 Hunt, W.G. and Selander, R.K. (1973) Heredity 31, 11–33
17 Ferris, S.D., Sage, R.D., Huang, C.M., Nielson, J.T. Ritte, V. and Wilson, A.C. (1983) Proc. Natl Acad. Sci. USA 80, 2290–2294
18 Dobzhansky, T. (1970) Genetics of the Evolutionary Process, Columbia University Press
19 Bush, G.L. (1975) Annu. Rev. Ecol. Syst. 6, 339–364
20 White, M.J.D. (1978) Syst. Zool. 27, 285–298
21 Gold, J.R. (1980) Genet. Res. Camb. 35, 157–164
22 Templeton, A.R. (1982) in Mechanisms of Speciation (Barigozzi, C. ed.), pp. 105–121, Liss
23 Lande, R. (1983) Heredity, 50, 47–66
24 Coyne, J.A. (1985) Genet. Res. Camb. 46, 169–192
25 Coyne, J.A. (1986) Genetics 114, 485–494
26 Hewitt, G.M. (1988) in Speciation and Adaptation (Otte, D. and Endler, J. eds), Academy Natural Sciences Philadelphia (in press)
27 Woodruff, D.S. Biol. J. Linn. Soc. (in press)
28 Mitton, J.B. and Grant, M.C. (1984) Annu. Rev. Ecol. Syst. 15, 479–500
29 Hewitt, G.M., Butlin, R.K. and East, T.M. (1987) Biol. J. Linn. Soc. 31, 25–34
30 Hewitt, G.M., Gosalvez, J., Lopez-Fernandez, C., Ritchie, M.G., Nichols, W. and Butlin, R.K. in Kew Chromosome Conference III (Bennett, M. and Brandham, P. eds), HMSO (in press)
31 Nichols, R.A. (1985) in Orthoptera I (Gosalvez, J., Lopez-Fernandez, C. and Garcia de la Vega, C. eds), pp. 55–83, Fundacion Ramon Areces
32 Butlin, R.K. and Hewitt, G.M. (1985) Biol. J. Linn. Soc. 26, 269–285
33 Szymura, J.M. and Barton, N.H. (1986) Evolution 40, 1141–1159
34 Barton, N.H. and Hewitt, G.M. Genetics (in press)
35 Nichols, R.A. and Hewitt, G.M. (1986) Biol. J. Linn. Soc. 29, 301–316
36 Sage, R.D., Heyneman, D., Lim, K-C. and Wilson, A.C. (1985) Nature 324, 60–63

37 Clarke, B.C. (1966) Am. Nat. 100, 389–400
38 Endler, J.A. (1977) Geographic Variation Speciation and Clines, Princeton University Press
39 Snaydon, R.W. and Davies, M.S. (1972) Evolution 26, 390–405
40 McNeilley, T. and Antonovics, J. (1968) Heredity 23, 205–218
41 Carson, H.L. (1975) Am. Nat. 109, 83–92
42 Barton, N.H. and Hewitt, G.M. (1981) in Evolution and Speciation (Atchley, W.R. and Woodruff, D.S., eds), pp. 109–145, Cambridge University Press
43 Hewitt, G.M. (1985) in Orthoptera I (Gosalvez, J., Lopez-Fernandez, C. and Garcia de la Vega C., eds), pp. 15–54, Fundacion Ramon Areces
44 Kimura, M. (1983) The Neutral Theory of Molecular Evolution, Cambridge University Press
45 Wilson, A.C. (1985) Sci. Am. 253, 164–173
46 Szymura, J.M., Spolsky, C. and Uzzell, T. (1985) Experientia 41, 1469–1470
47 Wilson, A.C., Cann, R.L., Carr, S.M., George, M., Gyllensten, U.B., Helm-Bychowski, K.M., Higuchi, R.G., Palumbi, S.R., Prager, E.M., Sage, R.D. and Stoneking, M. (1985) Biol. J. Linn. Soc. 26, 375–400
48 Sage, R.D., Whitney, J.B. and Wilson, A.C. (1986) Curr. Top. Microbiol. Immunol. 127, 75–85
49 Greaves, J.H., Redfern, R. and Ayres, P.B. (1977) Genet. Res. 30, 257–263
50 Yang, S.Y. and Selander, R.K. (1968) Syst. Zool. 17, 107–143
51 Gill, F.B. (1980) Auk 97, 1–18
52 Hillis, D.M. and Simmons, J.E. (1986) J. Herpetol. 20, 85–87
53 Key, K.H.L. (1986) Syst. Zool. 17, 14–22
54 Szymura, J.M. and Farana, I. (1978) Biochem. Genet. 16, 307–319
55 Shaw, D.D., Wilkinson, P. and Coates, D.J. (1982) Chromosoma 86, 533–547
56 Millar, C.V. (1983) Evolution 37, 311–319
57 Hewitt, G.M. and Barton, N.H. (1980) in Insect Cytogenetics, Symp. R. Entomol. Soc. (London) 10, 397–436
58 Kocher, T.D. and Sage, R.D. (1986) Evolution 40, 21–33
59 Hall, W.P. and Selander, R.K. (1973) Evolution 27, 226–242
60 Nevo, E. (1986) in Evolutionary Processes and Theory (Karlin, S. and Nevo, E. eds), pp. 439–474, Academic Press
61 Thaeler, G.S. (1974) Syst. Zool. 23, 343–354
62 Barton, N.H. and Hewitt, G.M. (1981) Heredity 47, 367–383
63 Nichols, R.A. and Hewitt, G.M. (1988) Ecol. Entomol. 13, 39–49
64 Hewitt, G.M. (1975) Heredity 35, 375–385
65 Mallet, J. (1986) Heredity 56, 191–202
66 Murray, J. and Clarke, B. (1980) Proc. R. Soc. London Ser. B. 211, 83–117
67 Johnson, M.S., Murray, J.W. and Clarke, B. (1986) Heredity 56, 319–327
68 Heywood, J.S. (1986) Evolution 40, 1132–1140
69 Dixon, K.L. (1955) Univ. Calif. Publ. Zool. 54, 125–206
70 Rohwer, S.A. (1972) Trans. Kansas Acad. Sci. 75, 1–19
71 Arnold, M.L., Shaw, D.D. and Contreras, N. (1987) Proc. Natl Acad. Sci. USA 84, 3946–3950
72 Schoorl, J. and Zuiderwijk (1981) Amphibia–Reptilia 3/4, 235–252
73 Harrison, R.G. (1986) Heredity 56, 337–350

74 Harrison, R.G., Rand, D.M. and Wheeler, W.C. (1987) *Mol. Biol. Evol.* 4, 144, 158
75 Harrison, R.G. in *Speciation and Adaptation* (Otte, D. and Endler, J. eds), Academy Natural Sciences Philadelphia (in press)
76 Moore, W.S. (1977) *Q. Rev. Biol.* 52, 263–277
77 Moore, W.S. and Buchanan, D.B. (1985) *Evolution* 39, 135–151
78 Heaney, L.R. and Timm, R.M. (1985) *Biol. J. Linn. Soc.* 25, 301–317
79 Moore, W.S. and Koenig, W.D. (1986) *Auk* 103, 42–51
80 Vanlerberghe, F., Dod, B., Boursot, P., Bellis, M. and Bonhomme, F. (1986) *Genet. Res. Camb.* 48, 191–197
81 Barton, N.H. (1979) *Heredity* 43, 341–359
82 Benson, W.W. (1982) in *Biological Diversification in the Tropics* (Prance, G.T. ed.), pp. 608–640, Columbia University Press
83 Endler, J.A. (1982) in *Biological Diversification in the Tropics* (Prance, G.T. ed.), pp. 641–657, Columbia University Press
84 Mayr, E. and O'Hara, R.J. (1986) *Evolution* 40, 55–67
85 Barton, N.H. and Hewitt, G.M. (1983) in

Protein Polymorphism: Adaptive and Taxonomic Significance (Oxford, G.S. and Rollinson, D., eds), pp. 341–359, Blackwells
86 Patton, J.L. (1973) *J. Mammal.* 54, 561–584
87 Smith, M.F. and Patton, J.L. (1984) *Evolution* 38, 1079–1087
88 Patton, J.L. and Smith, M.F. in *Speciation and Adaptation* (Otte, D. and Endler, J. eds), Academy Natural Sciences Philadelphia (in press)
89 Highton, R. and Larson, A. (1979) *Syst. Zool.* 28, 579–599
90 Larson, A. (1984) *Evol. Biol.* 17, 119–218
91 Larson, A. in *Speciation and Adaptation* (Otte, D. and Endler, J. eds), Academy Natural Sciences Philadelphia (in press)
92 Wake, D.B. and Yanev, K.P. (1986) *Evolution* 40, 702–715
93 Wake, D.B., Yanev, K.P. and Brown, C.W. (1986) *Evolution* 40, 866–868
94 Wake, D.B. in *Speciation and Adaptation* (Otte, D. and Endler, J. eds), Academy Natural Sciences Philadelphia (in press)
95 Rouhani, S. and Barton, N.H. (1987) *J. Theor. Biol.* 126, 51–62
96 Dobzhansky, T. (1951) *Genetics and the Origin of Species*, Columbia University Press

97 Dobzhansky, T., Ayala, F.J., Stebbins, G.L. and Valentine, J.W. (1977) *Evolution*, Freeman
98 Paterson, H.E.H. (1978) *S. Afr. J. Sci.* 74, 369–371
99 Butlin, R.K. (1987) *Trends Ecol. Evol.* 2, 8–13
100 Maynard Smith, J. (1966) *Am. Nat.* 100, 637–650
101 Caisse, M. and Antonovics, J. (1978) *Heredity* 40, 371–384
102 Felsenstein, J. (1981) *Evolution* 35, 124–138
103 Butlin, R. in *Speciation and Adaptation* (Otte, D. and Endler, J. eds), Academy Natural Sciences Philadelphia (in press)
104 Coyne, J.A. and Orr, H.A. in *Speciation and Adaptation* (Otte, D. and Endler, J. eds), Academy Natural Sciences Philadelphia (in press)
105 Otte, D. in *Speciation and Adaptation* (Otte, D. and Endler, J. eds), Academy Natural Sciences Philadelphia (in press)
106 Wood, T.L. and Guttman, S.I. (1983) *Science* 220, 310–312
107 Searle, J.B. (1986) *Proc. R. Soc. London Ser. B*, 229, 277–298

Gut Fungi

I. Brent Heath

Herbivores consume large quantities of cellulose and other plant cell wall (fibre) carbohydrates yet generally lack the enzymes to digest them. This has led to the evolution of specialized portions of the gut, such as the rumen and caecum, which contain large populations of digestive anaerobic microorganisms. Diverse bacteria and protists from this environment have been studied for over a hundred years but it is only recently that a significant population of highly specialized flagellate fungi have been identified. These fungi are important in fibre digestion. Their diversity, properties, activities, phylogeny and possible economic significance are the subjects of this review.

One of the more remarkable features of evolution is that, whilst herbivory is widespread in both vertebrates and invertebrates, and plant-derived cellulose is one of the most abundant organic molecules on earth, few herbivores have evolved the ability to synthesize cellulose digesting enzymes. Instead, most organisms have evolved symbiotic associations with assorted microorganisms. The best-known example of this strategy is the rumen, a fore gut fermentation chamber containing an enormous population of micro-

I. Brent Heath is at the Biology Department, York University, 4700 Keele Street, North York, Ontario, M3J 1P3, Canada.

organisms vital to the nutrition of the ruminants. Functionally similar populations occur in variously specialized parts of either the fore or hind gut of most herbivores.

Partly because of their obvious economic importance, the rumen populations have been studied extensively for over a hundred years. One of the most remarkable features of this work is that we now know that large numbers of fungi, which have been estimated[1] to constitute as much as 8% of biomass, occur in these populations, yet they remained totally unrecognized as fungi until about 12 years ago. I shall review the fascinating characteristics of these fungi by citing selected key references; further references can be found in the 1988 volume of *BioSystems*. Some less common terms used in this paper are defined in Box 1 and relevant aspects of fungal taxonomy are outlined in Box 2.

Historical perspective

In 1910 Liebtanz[2] described a group of uniflagellate rumen-inhabiting cells as flagellates. A little later Braune[3] named a polyflagellate rumen inhabitant, *Callimastix frortalis*. Both authors felt that these cells were indeed

zooflagellates. In subsequent years the uniflagellates were largely forgotten but the host range and species complement of *Callimastix* was extended considerably. In 1966 an analysis of the ultrastructure and life cycle of a copepod-inhabiting species of *Callimastix* showed that it was most probably a chytridiomycete fungus. Vavra and Joyon[4] suggested the generic name *Neocallimastix* for the rumen-inhabiting species which they still believed to be zooflagellates.

It was not until 1975 that Orpin[5] first recognized that the rumen inhabitant then known as the zooflagellate, *Neocallimastix frontalis*, was also the zoosporic stage of a fungus that he was able to isolate and culture. He went on to show that the sheep rumen also contained other fungi which produced uniflagellate zoospores[6,7]. Because the taxonomy and phylogeny of the zoosporic fungi is now largely based on zoospore ultrastructure[8], it was not until such data became available[9,10] that some attempt at formal taxonomy could be made. *Neocallimastix* was assigned to a new family (Neocallimasticaceae) in the Spizellomycetales of the Chytridiomycota[10] and subsequently it became clear that the