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DO SUTURE ZONES EXIST?

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Abstract.—Remington (1968) argued that 13 suture zones exist in North America. Remington defined a suture zone as, “a band of geographic overlap between major biotic assemblages, including some pairs of species or semispecies which hybridize in the zone” (p. 322). Although initially controversial, the idea that suture zones exist has picked up momentum over the past decade, due largely to the phylogeographic work of Hewitt, Avise, and their colleagues. Nevertheless, the reality of suture zones has not yet been subjected to rigorous analysis using statistical and geographic information system (GIS) approaches. To test for the existence of Remington’s suture zones, we first identified 117 terrestrial hybrid zones in Canada and the United States through a literature search for the key words “cline,” “contact zone,” “hybrid zone,” and “hybridization” in articles published between 1970 and 2002. The 117 hybrid zones were mapped using a GIS approach and compared with a digitized version of Remington’s original suture zone map. Overall, there does appear to be an association between hybrid zones and suture zones, but this association is largely attributable to clustering of hybrid zones in only two of the 13 suture zones recognized by Remington. The results suggest that evolutionary biologists should retain some skepticism toward Remington’s suture zones.

Key words.—Geographic information system, hybridization, hybrid zones, range boundaries, reinforcement, spatial concentration, speciation.

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In recent years the term “suture zone,” which is used to describe an area where multiple hybrid zones exist, has begun to appear with increasing frequency in the literature of evolutionary biology (Hammond 1990; Hewitt 1996, 1999, 2001, 2004; Avise 2000; Guillaume et al. 2000; Kropf et al. 2002; Redenbach and Taylor 2002; Brunner et al. 2002). The meaning attached to this term by evolutionary biologists stands in contrast to its usage among geologists, who use “suture zone” to describe the collision of continental plates (Goudie 1985; Orme 2002). Perhaps the most well-known geological suture zone is the Himalayan mountain range formed by the collision of the Indian subcontinental plate and the Asian continental plate (Pichamuthu 1967). The definition evolutionary biologists attach to suture zones was introduced by Remington (1968), who was the first person to perform a continental-scale analysis of hybrid zone locations, the results of which led him to conclude that hybrid zones tend to cluster in certain geographic areas. Remington’s conclusions were presaged by the work of Anderson, a debt readily acknowledged by Remington. Anderson (1948, 1953) noted that dispersal from Pleistocene refugia and subsequent contact of populations would lead to a clustering of hybrid zones and

he described what Remington later called the Central Texas and the Southern Appalachian-Ozark-Ouchita suture zones. Nevertheless, Remington deserves credit for his continent-wide mapping efforts and for carefully considering the evolutionary implications of suture zones.

Remington was a strong advocate of the hypothesis of reinforcement (Dobzhansky 1940), which had a profound influence on his thinking about suture zones. First, the fact that hybridization still occurs in suture zones suggested to him that suture zones must be young, on the order of a few centuries old. If they were older, on the order of a few millennia in age, reproductive isolation would have evolved between interacting taxa due to selection against hybridization (Remington 1968). Second, it seemed to Remington that suture zones presented biologists with extraordinary opportunities to study the evolution of reproductive isolation because of the potential for comparisons among multiple interacting pairs of taxa that are all in the process of acquiring isolation.

The fact that the closely related species that made contact in suture zones represented a wide variety of terrestrial organisms indicated to Remington that these species must have been previously isolated by very significant barriers to dispersal, such as large tracts of unsuitable habitat, which had recently been modified due to climate change or to the activities of humans. The breakdown of these barriers not only

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provided an opportunity to study how contact with a close relative could drive the evolution of reproductive isolation, it presented biologists with the prospect of studying the effects of introgression on interactions within communities (Remington 1968).

Initially, Remington's paper caused little stir among evolutionary biologists. The cool reception was due, at least in part, to the strong criticism directed at the paper by Short (1969) soon after its publication. Short identified problems with some of the bird data used by Remington and he was unhappy with the paper's failure to acknowledge some of the major contemporary works concerning reinforcement (e.g., Brown and Wilson 1956; Sibley 1957, 1961; Stebbins 1959; Grant 1963; Bigelow 1965; Wilson 1965).

The resurgence of interest in suture zones has been led by Hewitt who discovered Remington's ideas in 1975, while conducting background research for a review article (Hewitt 2001). Over the course of the following 30 years, Hewitt's research on hybrid zones has led him to share some of Remington's views. In particular, Hewitt has argued that multiple hybrid zones congregate in specific geographic regions in Europe due to major biogeographic barriers and congruent postglacial biotic range expansions (Hewitt 1999, 2001). He has also demonstrated (Hewitt 1999) that a suture zone in central Europe that Remington (1968) predicted to occur seems to be real, containing multiple hybrid zones that span a broad range of taxonomic groups (e.g., *Erinaceus* spp. *Quercus* spp. *Albies* spp. and *Mus* spp).

Avise, who discovered that the Floridian suture zone mapped by Remington seems to extend into the marine environment (Avise 2000), is another prominent advocate of suture zones. Avise (2000) suggested that the same physiographic and climatic properties that are responsible for the terrestrial suture zone in Florida are also responsible for the marine suture zone. Avise's reasoning echoes that of Remington, who suggested that shallow-water marine organisms may form aquatic suture zones in locations close to terrestrial suture zones due to similar climates and physiographies.

Thus far, support for Remington's suture zones has come from visual comparisons of hybrid-zone locations with the hand-drawn map of suture zones produced by Remington (Avise 2000) or by the claim that hybrid zones exist in areas where Remington predicted they would be (Hewitt 1996, 1999). The conclusion that Remington's suture zones exist can be better analyzed through a geographic information system (GIS) approach. GIS allows researchers to input large spatial datasets into a computer, assign attributes to geographic locations in these datasets, analyze quantitative relationships among geographic locations, and precisely analyze spatial relationships (DeMers 2000). These unique capabilities of GIS have revolutionized not only the field of geography, but have benefited various biological disciplines. Surprisingly, evolutionary biology has been one of the few biological disciplines with a significant field-research component to largely ignore this powerful technology, despite pioneering efforts by Kohlmann et al. (1988), Kidd and Ritchie (2000), and Ritchie et al. (2001).

In the study reported here, we harness GIS technology to analyze the suture zones in Canada and the United States proposed by Remington (1968). Specifically, we test whether

overlap among hybrid zones that have been studied over 33 years and suture zones is greater than expected by chance alone, that is, greater than expected if hybrid zones were distributed in a random fashion across Canada and the United States.

METHODS

Literature Search

The biological literature dating from January 1970 through 2002 was searched for the key words "cline," "contact zone," "hybrid zone," and "hybridization." We began the literature search in 1970 to ensure that differences existed between our dataset and the dataset analyzed by Remington. It would not be appropriate to test the existence of Remington's suture zones using a data set with too strong a similarity to the one that he used to create his original suture zone map. Seven different article databases were used for this search: AGRICOLA, Basic BIOSIS, BioAg Index, BIOSIS, General Science Abstracts, GeoBase, and SciSearch. Of interest were articles that described terrestrial hybrid zones between full species, between subspecies, and between races in Canada and the United States. Only zones that contained at least one sufficiently georeferenced hybrid population (coordinates, towns, counties) were included in this study. Articles that described hybrid zones, but gave only vague geographic information pertaining to zone location, such as state or province, were omitted to reduce the amount of guess-work associated with the mapping process.

It is also important to note that the literature search was constrained by the key words used for the search. If authors did not use one of the four key words in the title, the abstract, or as a key word, their article would not have been sampled. Also, as stated above, we included only terrestrial hybrid zones; therefore some well-known hybrid zones that involve aquatic organisms have been excluded (e.g., *Lepomis*, *Limnoperus*, and *Nototropis*). Aquatic hybrid zones were left out of this study because Remington (1968) excluded them from his study, arguing that the location of freshwater hybrid zones, in particular, were unlikely to be influenced by the same factors that influence the location of terrestrial hybrid zones.

Suture-Zone Geographic Information System

A GIS database was created using ArcView 3.2 (Environmental Systems Research Institute, Inc. 1999) by generating map layers for each hybrid-zone. Initially, we created a map layer for each hybrid-zone population using the georeferenced locality information gleaned from the literature as described above. Next, these zero dimensional point data were converted into two-dimensional areas for our analyses.

The conversion of three or more point locations into areas has been a problem for geographers and biologists alike because of the variety of different shapes that can be drawn around point distributions (Rapoport 1982). We tested three point location to area techniques (harmonic mean, adaptive kernel, and minimum convex polygon) before deciding to use the last. We rejected the first two techniques because both enlarge areas of hybrid zones where increased sampling of

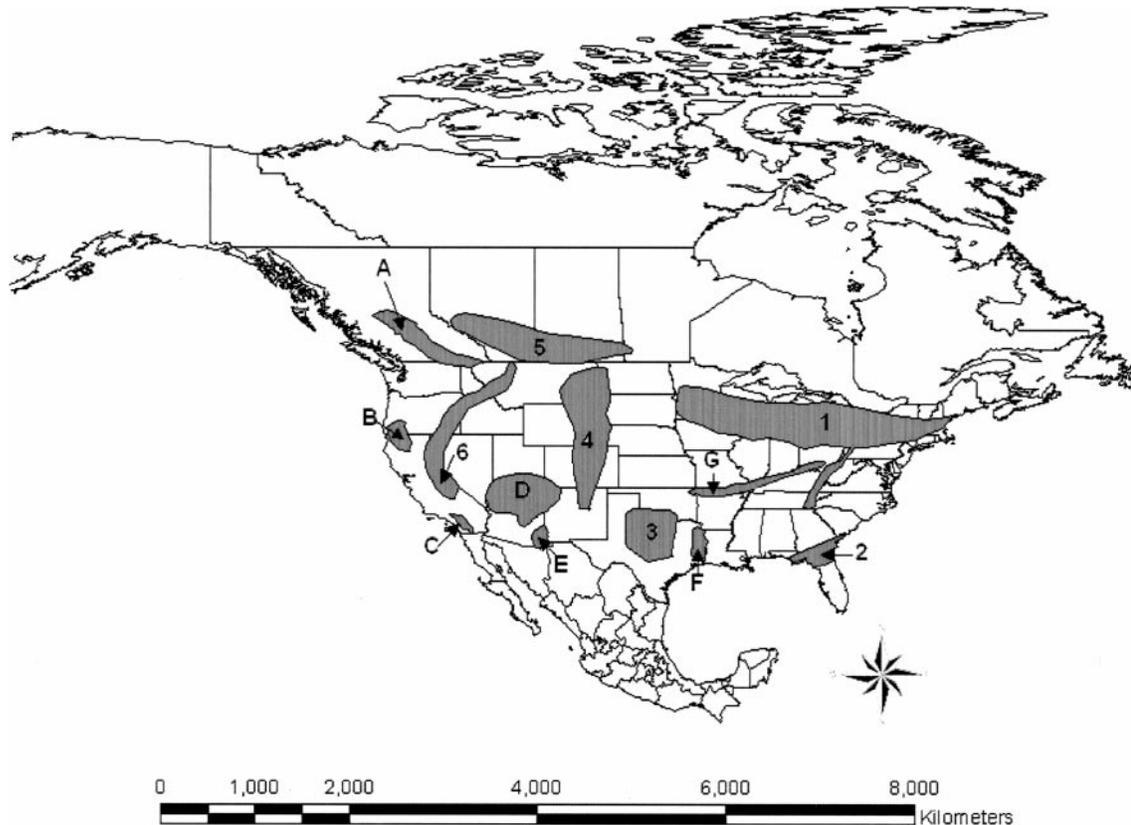


FIG. 1. Digital version of the original 13 North American suture zones mapped by Remington (1968).

populations has occurred. In contrast, the minimum convex polygon (MCP) approach, which creates polygons that have no internal angles greater than 180 degrees, does not rely on a probability distribution and therefore does not place greater emphasis on areas that are collected more heavily. Also, this technique consistently provided the most conservative estimates of hybrid-zone area. To convert hybrid zones containing three or more reported populations into polygons, we used the Home Range Extension for ArcView 3.x (Rodgers and Carr 2002).

To include hybrid zones having one or two reported populations, we used the buffering capabilities provided by ArcView 3.2 (Environmental Systems Research Institute, Inc. 1999). Hybrid zones containing only two reported point locations were converted into polygons by connecting the two points with a line and then applying a 5-km buffer to the line to give a two-dimensional shape. Hybrid zones containing only one reported point location were converted into a two-dimensional area by encircling the point location with a 5-km buffer. The 5-km buffers provided the most conservative hybrid-zone areas that could still be detected by the GIS.

The suture zone map published by Remington (1968) was digitized into the GIS (Fig. 1). An Albers's equal-area projection of North America was used to avoid areal distortion between the published paper map and the electronic map used for the analysis. The same projection was used for all overlap measurements to ensure accurate areal representations of all polygons.

The total area of each hybrid zone, suture zone, and the

area of hybrid zone/suture zone overlap were calculated within the GIS using a grid cell size of 100 m. The same grid cell size was used to compute the total area of Canada and the United States.

Statistical Analyses

We employed a contingency table χ^2 analysis to determine whether the amount of spatial overlap between suture zones and hybrid zones is greater than expected by chance. Any given area of Canada and the United States can be placed into one of four categories: (1) within both a suture zone and a hybrid zone; (2) within a hybrid zone only; (3) within a suture zone only; or (4) outside of all suture zones and all hybrid zones. The expected values of the four categories were obtained by: (1) multiplying the observed percent hybrid zone area by the observed percent suture zone area; (2) multiplying the observed percent hybrid zone area by the observed percent no suture zone area; (3) multiplying the observed percent no hybrid zone area by the observed percent suture zone area; and, (4) by multiplying the observed percent no hybrid zone area by the observed percent no suture zone area. A similar approach was used to evaluate whether any particular suture zone showed a stronger association with hybrid zones than expected by chance alone. Significance of these individual tests was evaluated in two ways, without correcting for multiple tests and by using the sequential Bonferroni adjustment (Holm 1979).

Finally, a global *G*-statistic (Getis and Ord 1992; Lee and

TABLE 1. Results of the one-tailed χ^2 contingency table analysis. Suture zone 1 and suture zone 4 have significant *P*-values. The remaining 11 suture zones were not supported by the data.

Suture zone	df	χ^2	<i>P</i> -value
1	1	4.71	<0.05
2	1	<0.01	>0.95
3	1	<0.01	>0.95
4	1	5.41	<0.05
5	1	0.28	>0.55
6	1	1.80	>0.10
A	1	1.08	>0.30
B	1	0.14	>0.70
C	1	0.02	>0.85
D	1	0.008	>0.90
E	1	<0.01	>0.95
F	1	0.05	>0.80
G	1	0.07	>0.75

Wong 2001) was calculated within the GIS database to determine whether Canadian and U.S. hybrid zones exhibit hotspots of hybrid zone clustering. This calculation gave a significant result, which led to the employment of a local *G*-statistic (Getis and Ord 1992; Lee and Wong 2001) to identify the exact location of each hotspot of hybrid zone clustering.

RESULTS

Literature Search

A total of 117 hybrid zones containing one or more reported locations that could be mapped into the GIS were uncovered by our literature search. The taxonomic composition of the hybrid zones was 14.5% ($n = 17$) amphibians, 12.8% ($n = 15$) birds, 13.7% ($n = 16$) insects, 16.2% ($n = 19$) mammals, 39.3% ($n = 46$) plants, and 3.4% ($n = 4$) reptiles.

Chi-Square Analysis

Overall, there does appear to be an association between hybrid zones and suture zones ($\chi^2 = 7.471$, $P < 0.01$, $df = 1$), but support for individual suture zones was generally weak. Only suture zones 1 and 4 exhibited a significant clustering of hybrid zones (suture zone 1, $\chi^2 = 4.718$, $P < 0.05$, $df = 1$; suture zone 4, $\chi^2 = 5.406$, $P < 0.05$, $df = 1$), prior to sequential Bonferroni adjustment. Suture zone 1 runs east-west through the Great Lakes region, while suture zone 4 runs north-south along the eastern face of the Rocky Mountains. The remaining suture zones showed little correspondence with recently studied hybrid zones (Table 1). Upon implementing the sequential Bonferroni correction, which provides a more conservative estimate of statistical significance, even suture zones 1 and 4 did not achieve significant *P*-values.

Percent Overlap of Hybrid Zones with Suture Zones

Hybrid zone areas were calculated within the GIS (see Appendix available online at <http://dx.doi.org/10.1554/04-239.1.s1>). The percent of each hybrid zone that overlaps with a suture zone was also calculated in the GIS (see Appendix available online). Of the 117 hybrid zones mapped,

46.2% ($n = 54$) had some overlap with at least one of Remington's suture zones. The percentage of overlap ranged from 100% for 17 hybrid zones (*Aquilegia* spp.–suture zone 6; *Arctium* spp.–suture zone 1; *Arphia* spp.–suture zone 4; *Claytonia* spp.–suture zone 1; *Cnemidophorus* spp.–suture zone 4; *Ipomopsis* spp.–suture zone 4; *Iris* spp.–suture zone B; *Juniperus* spp.–suture zone 1; *Limenitis* spp.–suture zone 4; *Molothrus* spp.–suture zone 6; *Myotis* spp.–suture zone A, *Peromyscus* spp.–suture zone C; *Pinus* spp.–suture zone D; *Plethodon* spp.–suture zone G; *Populus* spp.–suture zone 5; *Salix* spp.–suture zone 1; and *Typha* spp.–suture zone 1) to < 0.01 % for two hybrid zones (*Populus* spp.–suture zone 5 and *Gryllus* spp.–suture zone 1). Of the total hybrid zone area mapped, 35.7% overlapped with Remington's suture zones.

Hybrid Zone Spatial Concentrations

A global *G*-statistic analysis designed to detect the occurrence of hotspots of hybrid zone clustering in Canada and the United States yielded a significant result ($Z_g = 29.4024$, $P < 0.0001$). To determine the exact location of the hotspots, we employed a local *G*-statistic analysis and mapped all locations with $Z_g \geq 1.96$ ($P \leq 0.05$) as shown in Figure 2. In total, 23 disjunct hotspots of hybrid zone clustering were identified. Eleven of these hotspots were quite large when compared to the rest. One large hotspot runs diagonally from the coastal regions of New York inland, eventually following the Appalachian Mountains in eastern West Virginia. Three hotspots occur in the southern Rocky Mountains of Colorado and New Mexico, one of which runs north to Montana. Two large hotspots are located at the central portion of the Sierra Nevada range in California and western Nevada, while another hotspot is in northeastern Idaho. Another large hotspot is located in the Great Lakes area running from approximately Toronto, to Detroit. The final three large hotspots are located in central Alabama in the Cascade Range east of Seattle, Washington; and in southern Kentucky (Fig. 2).

DISCUSSION

Our search of the literature uncovered 117 hybrid zones in the United States and Canada for which sufficient information exists to allow mapping in a GIS framework. Fifty-four of these 117 mapped hybrid zones demonstrated some overlap with Remington's suture zones. The overlap ranged from complete (the hybrid zone was entirely contained within a suture zone) to very little (only a small percentage of the area of the hybrid zone occurred within a suture zone). About half of the hybrid zones (53.8%) fall outside of Remington's suture zones. This last finding is not consistent with the conclusions of Remington (1968), who contended that few hybrid zones would occur outside his suture zones and that those few would probably arise as a result of a breakdown of environmental barriers caused by human disturbance, a situation described by Anderson (1948, 1949) as 'hybridization of the habitat.' In contrast with this contention, human disturbance was rarely invoked as an explanation for the occurrence of the hybrid zones that we mapped outside of Remington's suture zones. Instead, the hybrid zones were seen as naturally occurring (e.g., *Rana blairi*–*R. spenocephala* Par-

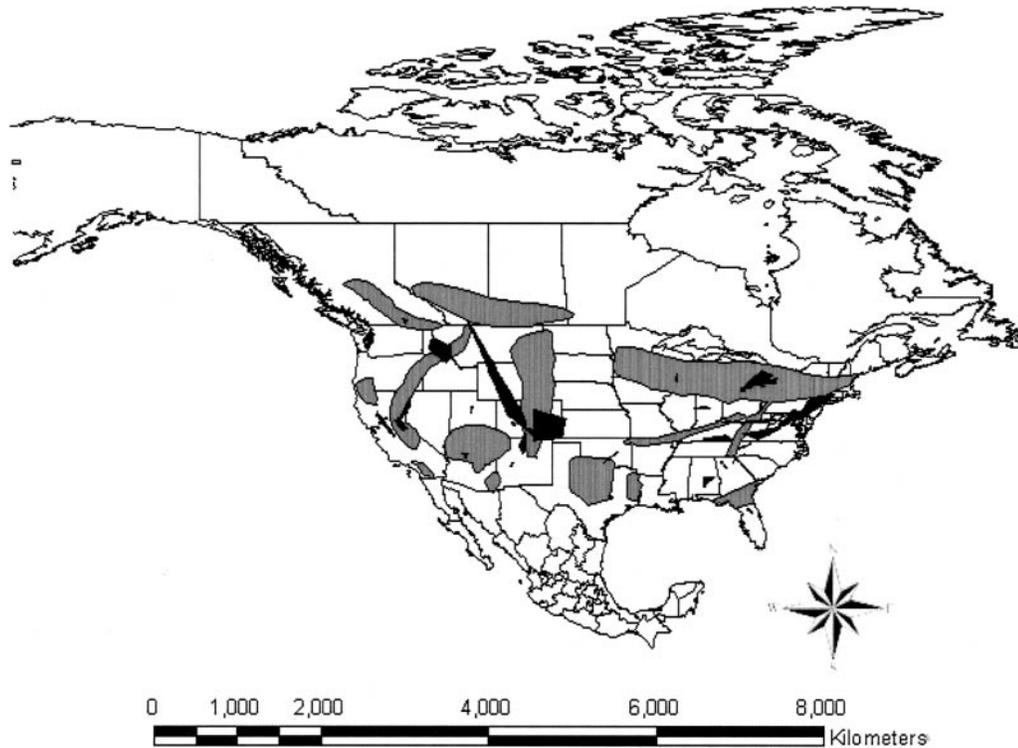


FIG. 2. Hotspots of North American hybrid zone clustering (black) mapped on top of Remington's suture zones (gray).

ris 1999, 2001; *Picea mariana*–*P. rubens* Perron and Bousquet 1997).

Not only do many hybrid zones occur outside of suture zones, most of the suture zones are not hotspots with regard to the occurrence of hybrid zones. Remington identified 13 suture zones in Canada and the U.S.—six major and seven minor. Of the 13, only two, suture zone 1 (Northeastern–Central suture zone) and suture zone 4 (Northern–Rocky Mountain suture zone), demonstrated a significant association with hybrid zones studied since 1970, prior to Bonferoni correction. Indeed, 22.4% of the hybrid zones mapped in this study overlapped, at least in part, with these two suture zones and 49.1% of the hybrid zones that overlapped with Remington's suture zones did so with suture zones 1 or 4. Both of these suture zones were considered to be major by Remington, who postulated that suture zone 1 occurred as a result of an anthropogenic disruption of forested areas 200 or more years ago. Remington believed that this disruption allowed closely related species pairs that were adapted to “shrubby field edges” or “open woods” and that were previously separated by dense forest to form secondary contact. Hewitt (2000) offered an alternative explanation for suture zone 1. Noting that this suture zone coincides with the maximum southern extent of ice sheets in this region of North America, he postulated that the suture zone is an area where northern taxa, which rapidly expanded in range following the retreat of the ice, obstruct the advance of taxa from the south.

Remington (1968) provided two potential explanations for the occurrence of suture zone 4. The first focused on the possible expansion of eastern biota as European settlers planted trees and thereby modified the landscape of the plains at

the foot of the Rockies. The second postulated that the climate following the Wisconsin Glaciation was sufficiently cold until the recent period to prevent western species from colonizing higher elevations in the mountains. Once the climate warmed, the western species were able to colonize the eastern slopes by way of low mountain passes, where they met the eastern species and began to hybridize. Given the support for the occurrence of suture zones 1 and 4 reported here, further studies of the factors that might explain their origins are warranted.

Interestingly, suture zone 2 of Remington, which has attracted much attention in recent years and which Hewitt (2000) again attributed to northern species blocking the expansion of southern species, was not supported in our analysis (although clustering analysis did identify one small hotspot directly south of this suture zone; Fig. 2). One explanation for the lack of support is that most of the hybrid zone studies carried out in the vicinity of suture zone 2 since 1970 have concentrated on aquatic species (Avise et al. 1987; Avise 2000) and thus have been excluded from our analysis.

Why did our survey of hybrid zones in Canada and the United States provide results so different from those reported by Remington? First, it is important to note that our dataset is quite distinct from the dataset considered by Remington. Of the 117 hybrid zones mapped in our study, only 21 were included in Remington's (1968) dataset. Twenty of these hybrid zones were reported as “known” by Remington, while one (*Bufo americanus*–*Bufo hemiophrys*) was reported as “suspected.” Thus, the datasets are sufficiently different that some discrepancies in patterns are not surprising. However,

these are not small discrepancies; they are great enough to suggest that many of Remington's suture zones do not exist.

A second possible explanation for the disparity in results is that the suture zones drawn by Remington were exaggerated in size. In delineating his suture zones, Remington (1968) mapped areas of hybrid zone clustering and then extended these areas along parts of the landscape that exhibited a similar environment. For example, Remington's suture zone 4 was drawn to encompass the entire junction of the Great Plains and the eastern foothills of the Rocky Mountains. Our hotspots are much smaller than Remington's suture zones, a finding that suggests that the extrapolations of suture zone area carried out by Remington may have been inappropriate and that Canadian and U.S. suture zones are smaller in size than those he drew. Alternatively, and perhaps more likely, the small size of our hotspots and the small size of many of the hybrid zones that were mapped as part of this study may reflect limited geographic sampling of hybrid zones. Greater sampling efforts would undoubtedly expand the size of many hybrid zones and perhaps enlarge the amount of overlap between recently studied hybrid zones and Remington's suture zones. We emphasize the tentative nature of the explanations provided above and the importance of reevaluating them as other hybrid zones are mapped in Canada and the United States especially in light of the difference in sample sizes between this study (117 hybrid zones) and that of Remington (almost 400 known and suspected hybrid zones).

This brings us to a larger question, not whether Remington's suture zones are real, but whether the phenomenon of suture zones is real. Suture zones are predicted to occur based on the following considerations. First, many species experience the environment in much the same way, therefore barriers to dispersal, whether biotic or physical, will affect many species simultaneously, and an elimination of those barriers will allow closely related species that were formerly isolated to make contact and hybridize in the same area. An example of such a barrier is a mountain chain, which might be impassable to species adapted to warm climates during some periods, but that might be crossed by these species, especially through low passes, during other, warmer, periods (Hewitt 1996, 1999). Second, major climatic events, such as the onset of an ice age, will impact many species in the same way, forcing them into shared refugia (Hewitt 2000). As the climate warms and the ice retreats, close relatives from many different taxonomic groups will emerge from these refugia, make contact, and hybridize in the same area (Hewitt 1996, 2000). This scenario assumes that dispersal rates of close relatives coming out of different refugia are similar. Alternatively, taxa that are better adapted to cold conditions may live in the area directly adjacent to glaciers and may expand their ranges as the ice retreats, thereby blocking range expansion of related taxa from the south (Hewitt 2000). Factors that mitigate the formation of suture zones include differences in dispersal rates among vicariants emerging from refugia (Endler 1982), individualized responses to climate change and to environmental parameters by different species (Webb and Bartlein 1992; Hewitt 1996), and movement of hybrid zones after formation based on differences in abundance of the hybridizing taxa (Barton and Hewitt 1981; Bar-

ton and Gale 1993) or based on changes in the environment that differentially affect disparate taxa (Endler 1977).

North America has experienced dramatic changes in climate over the course of the past 18,000 years (Webb and Bartlein 1992). At the beginning of this period the climate warmed and ice sheets that covered vast areas of the continent began to shrink in size. In response, animals and plants previously limited to refuges at various spots on the continent expanded their ranges (Schwert 1992; Webb and Bartlein 1992). This range expansion was reversed during a period of cooling that took place 11,000–10,000 years ago, known as the Younger Dryas chronozone. It was not until 6000 years ago that plant distributions began to resemble those seen today (Webb and Bartlein 1992). Given the relatively short time interval since the North American climate stabilized and the potential for hybrid zones to be stable over extended time periods (Barton and Hewitt 1981; Barton and Gale 1993), the occurrence of terrestrial suture zones seems likely.

Indeed, the clustering analysis carried out in the present study identified 23 areas of hybrid zone clustering in Canada and the United States (Fig. 2). The locations of many of these clusters are consistent with ideas put forth by Hewitt (1996, 1999, 2000) concerning suture zone formation. In particular, seven of the largest hybrid zone clusters we identified (Fig. 2) are located along North American mountain chains (the Appalachian Mountains, Rocky Mountains, Sierra Nevada, and Cascade Range), while another occurs in the Great Lakes region of North America near the maximum southern extent of the Laurentide ice sheet (Fig. 2).

Remington's (1968) work on suture zones did not initially receive an enthusiastic reception from evolutionary biologists, but has slowly gained acceptance among some phylogeographers and hybrid-zone researchers. Evidence from contemporary studies of hybrid zones analyzed herein indicates that evolutionary biologists should proceed cautiously in embracing Remington's suture zones. While there are good reasons to expect hybrid zones to cluster and there is empirical evidence supporting clustering, the suture zones identified by Remington do not correspond well to clusters we identified by mapping recently studied hybrid zones. Whether better correspondence would be found with a larger dataset awaits further investigation.

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