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A Review of *Dendroctonus frontalis* Zimmermann Systematics

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Abstract

The systematic history of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, is reviewed. Morphological, biological, karyological, and molecular data clearly define and diagnose the species limits of *D. frontalis*. More complete phylogenetic analysis and characterization of population genetic variation will further clarify the evolutionary history of the *D. frontalis*.

1.1. TAXONOMIC HISTORY

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is one of the most important bark beetle pests in the United States. As a consequence of its economic impact, this species has been the subject of intensive taxonomic study. The original description (Zimmermann 1868) was brief and based on merely a few specimens limited to Southeastern United States, and it would be another 120 years before the species concept of *D. frontalis* was solidified. The taxonomy of *D. frontalis* has often fluctuated because morphological character states such as body size, and abundance and size of punctures and setae vary geographically and often overlap with closely related species. Collection of hundreds of *Dendroctonus* specimens during the early 1900s in the Western United States and Mexico allowed for the first comprehensive revision of the genus. *Dendroctonus frontalis* was first synonymized with *D. brevicomis* LeConte (Dietz 1890). However, Hopkins (1902, 1909) resurrected *D. frontalis* based on the study of a larger series of specimens and diagnosed *D. frontalis* by the presence of long setae on the elytral declivity. Two species, *D. arizonicus* Hopkins and *D. mexicanus* Hopkins, were described for specimens from the Southwestern United States and Mexico, respectively (Hopkins 1905, 1909). Wood (1963) completed a second large revision of the genus. He was systematically more conservative than Hopkins and synonymized *D. arizonicus* and *D. mexicanus* with *D. frontalis* based on the gradation of anatomical characters among southeastern, southwestern, and Mexican populations. Years later, several studies re-examined the validity of *Dendroctonus* species based on new morphological (i.e., male genitalia), ecological, and karyological data (Vité and others 1974, 1975; Wood 1974, 1982b). As a result, *D. mexicanus* was resurrected (Wood 1974) and a new species, *D. vitei*, was described for Guatemalan specimens of *D. frontalis* (Wood 1974). Thus Wood (1982b) defined *D. frontalis* as a small species occurring in Southeastern United States, Arizona, and Honduras (at elevations below 1,000 m) and having a flatter female frons with finer punctation than *D. mexicanus*.

1.2. BIOSYSTEMATICS

The extensive biosystematic study of the *D. frontalis* species complex (*D. frontalis*, *D. brevicomis*, *D. mexicanus*, *D. vitei* Wood, *D. approximatus* Dietz, and *D. adjunctus* Blandford) redefined the species limits of *D. frontalis* (Lanier and others 1988). This study extensively examined intra- and interspecific variation of male genitalia, body size, external morphology, karyology, and fertility. Diagnostic characters were found for the closely related sympatric species *D. frontalis*, *D. mexicanus*, and *D. vitei*.

Male genitalia were taxonomically informative for this species complex. Examination of nearly 260 individuals representing many populations for each species revealed major interspecific differences in the seminal rod structure allowing for indisputable diagnosis of male specimens (Figure 21 in Lanier and others 1988). Generally, little intraspecific variation was observed. Some *D. frontalis* individuals from Guatemala, Honduras, Mexico, and Arizona possessed a relatively longer seminal rod process; however, this character was not diagnostic for these populations.

Pronotal width varies considerably within species, but the mean pronotal width measured from a series *D. frontalis* specimens was significantly different from other sympatric *Dendroctonus* species (Table 5 in Lanier and others 1988). Nonetheless, size and external morphology were not consistently associated with seminal rod shape in the *D. frontalis* complex. The size ranges of *D. frontalis*, *D. mexicanus*, and *D. vitei* overlap substantially, and external morphology, specifically the size and density of setation on the elytral declivity, correctly identified only 75 percent of a series of *D. frontalis* and *D. mexicanus* specimens. However, *D. frontalis* was confidently distinguished from *D. vitei* when an additional character, the lighter hue of the elytra relative to the pronotum and head in *D. frontalis*, was also considered.

Karyology also demonstrated diagnostic characters for *D. frontalis* (Figure 17 in Lanier and others 1988). Meiotic metaphase I cells in males had a karyotypic formula of seven pairs of autosomes and a parachute-shaped sex bivalent chromosome. The only observed intraspecific variation was meiotic abnormalities in one individual. Morphologically similar species *D. mexicanus* and *D. brevicomis* had a meiotic karyotypic formula of five pairs of autosomes and a parachute-shaped sex bivalent chromosome, although some variation in the sex chromosome was observed for *D. brevicomis*.

Breeding experiments tested intra- and interspecific fertility among *D. frontalis* individuals from 16 populations taken from the Southeastern United States, Arizona, and Mexico, *D. mexicanus*, *D. brevicomis*, and *D. vitei* (Lanier and others 1988, Vité and others 1974). Intraspecific fertility among individuals from different populations was similar to individuals from the same population. However, female F1 with one parent from a Mexico population had a low hatchability of laid eggs, whereas males from these crosses produced fertile offspring. These hybrids did not exhibit morphological irregularities that would preclude interbreeding between these populations. Interspecific fertility tests demonstrated that most pairings produced either no eggs or sterile eggs (Lanier and others 1988, Vité and others 1974). Interspecific pairings were also uncommon; that is, males were resistant to join heterospecific females, and often males had to be forced into the females' nuptial chambers (Lanier and others 1988).

This study of Lanier and others (1988) provided much evidence for the taxonomic limits of *D. frontalis*. It also demonstrated that individuals from disjunct populations were capable of interbreeding and that pre- and post-zygotic barriers exist among sympatric species, of the *D. frontalis* species complex (Figure 1.1). Thus *D. frontalis* is currently defined as the smallest species in the *D. frontalis* species complex that possesses a seminal rod with a dorsal process and rounded ventral bulb, short and long setae on strial interspaces 1-3 of the elytral declivity (Figures 1.2 and 1.3), a meiotic formula of 7AA + Xyp, and a range that includes Southeastern United States, the Southern Rocky Mountains of the United States, Mexico (coastal facing slopes, 1300-1800 m), and Central America (at elevations between 900-1300 m) (Figure 1.1).

1.3. MOLECULAR PHYLOGENETICS

1.3.1. Intraspecific Variation

Intraspecific genetic variation has been investigated for *D. frontalis,* although these studies are mostly limited to electrophoretic investigations and to merely a few populations. Electrophoretic analysis of six enzyme loci and five populations (Virginia, Georgia, Texas, Arizona, and Mexico) provided the most geographically extensive survey of genetic variation among *D. frontalis* populations to date

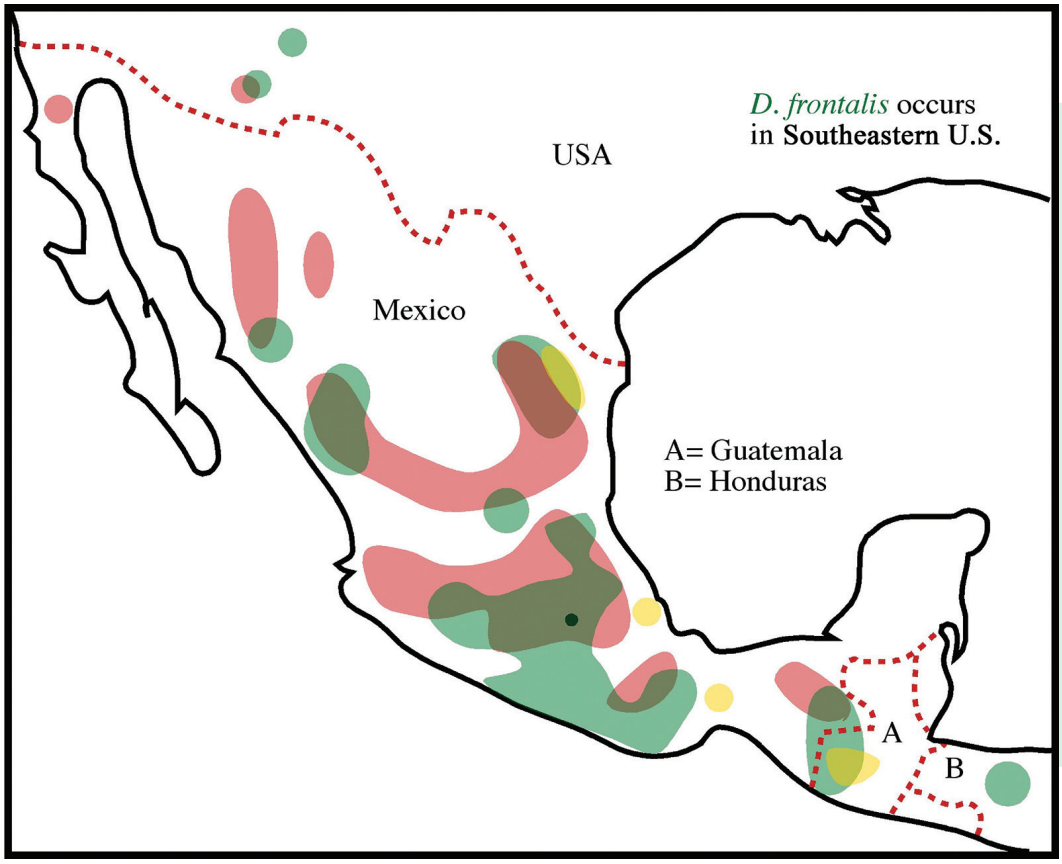

Figure 1.1—Approximate distribution of related species *D. frontalis* (green), *D. mexicanus* (red), and *D. vitei* (yellow) in the United States, Mexico, and Central America. *Dendroctonus frontalis* primarily occurs in Mexico on coastal facing slopes (1300-1800 m) and in Central America (900-1300 m); *D. mexicanus* occurs in Mexico in semiarid forests (1800-2500 m); and *D. vitei* occurs in Mexico on coastal facing slopes (1000-1500 m) and in Central America (less than 2500 m). (redrawn from Salinas-Moreno and others 2004, Lanier and others 1988)

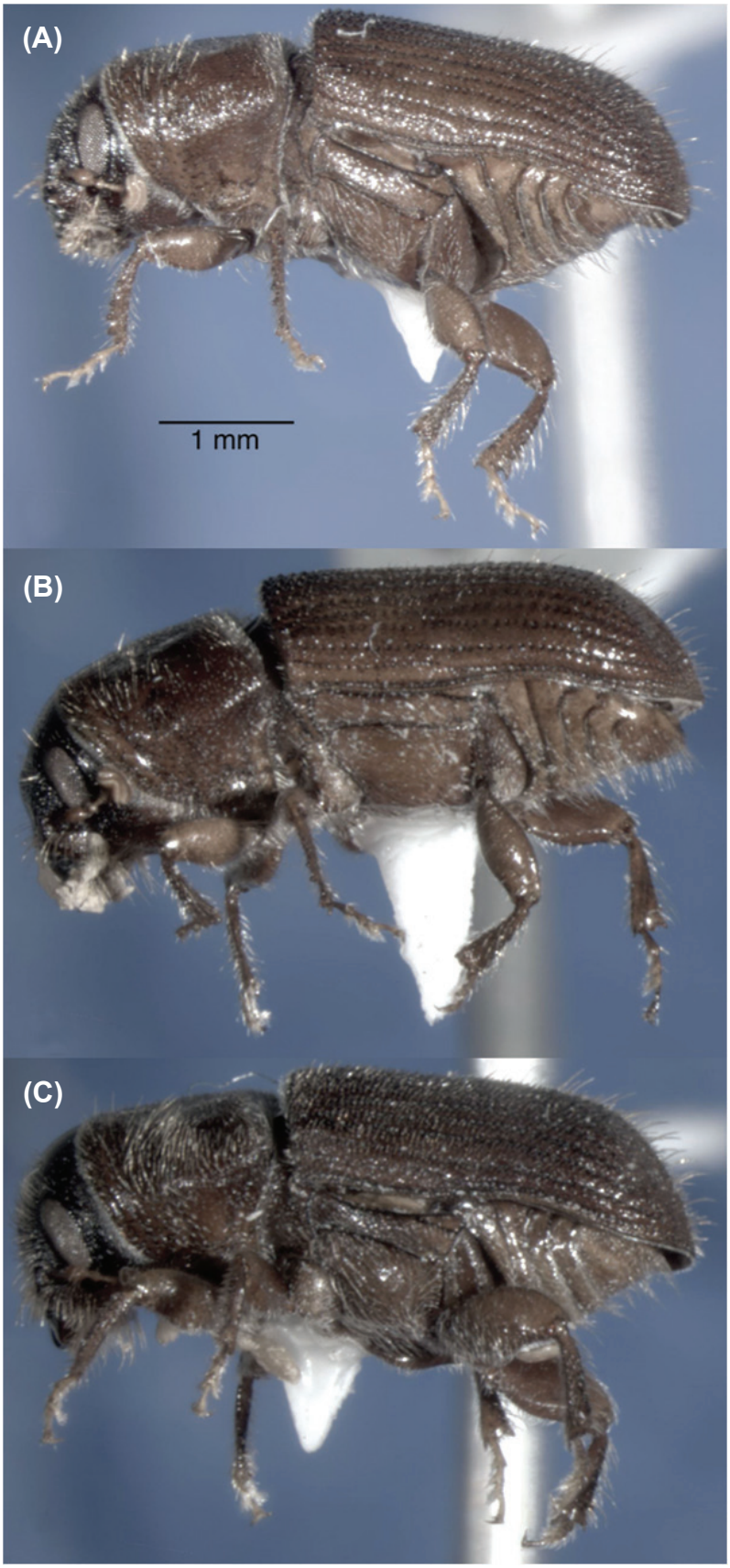

Figure 1.2—Lateral view of three related *Dendroctonus* species, (A) *D. frontalis*, (B) *D. mexicanus*, and (C) *D. vitei*. (photograph by A.I. Cognato)

(Anderson and others 1979). The frequencies of alleles varied across populations and were generally in Hardy-Weinberg proportion, which suggested that factors such as non-random mating, selection, migration, and flawed sampling were not issues for this study. Significant differences in allele frequencies were observed between eastern and western populations. The *D. frontalis* individuals from Mexico and Arizona differed genetically both from each other and from Texas, Georgia, and Virginia beetles, suggesting a historical separation of these three populations. The significant difference of allele frequencies between eastern and western populations was confirmed by another study that examined the genetic variation among individuals in Virginia, North Carolina, Georgia, Louisiana, Texas, and Arizona (Namkoong and others 1979). Allele heterogeneity was observed among these populations and was confirmed by a subsequent study (Roberds and others 1987).

While isozymes allow for a coarse assessment of genetic variation, microsatellites and nucleotide variation of specific genes allows for inferences of population structure on a smaller geographic scale (Avise 2004). Microsatellite loci have been characterized for *D. frontalis* (Schrey and others 2007). The allelic variation of these loci showed no population structure among six localities in Mississippi, suggesting that *D. frontalis* throughout this State represented a cohesive genetic unit (Schrey and others 2008). However, heterogeneity likely exists for disjunct populations separated by greater distance.

Intraspecific nucleotide variation for specific genes is not well characterized for *D. frontalis*. Kelley and Farrell (1998) included three individuals from Texas and Michoacan, Mexico, in their phylogenetic analysis of *Dendroctonus* based on mitochondrial cytochrome oxidase I (COI) DNA sequence. They reported that these sequences exhibited less than 1 percent difference. Given the limited sample size, it is premature to characterize *D. frontalis* as having low COI nucleotide diversity because more extensive studies have revealed much intraspecific COI DNA variation (>4 percent) for other *Dendroctonus* species (Cognato 2006, Cognato and others 2005, Kelley and others 1999, Maroja and others 2007).

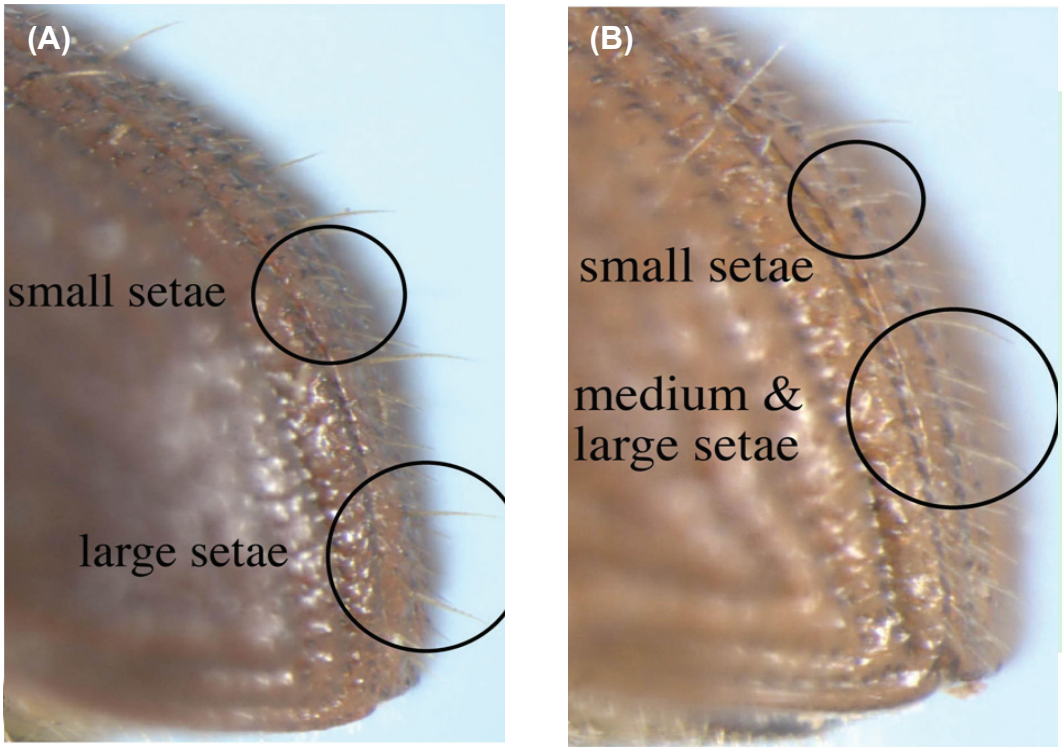

Figure 1.3—Oblique angle of the elytral declivity of (A) *D. frontalis* and (B) *D. mexicanus*. *Dendroctonus frontalis* is diagnosed by short and long setae on strial interspaces 1-3 of the elytral declivity as compared to *D. mexicanus*, which is diagnosed by short, medium, and long setae on strial interspaces 1-3 of the elytral declivity. *D. vitei* is diagnosed by larger mean size and darker coloration. (photograph by Lanier and others 1988)

1.3.2. Interspecific Variation

Electrophoretic data provided the first phylogenetic evidence for the relationship of *D. frontalis* with congeners. Wagner distance analysis of the allele frequencies of 18 gene loci revealed a relationship between *D. frontalis* and *D. brevicomis* (Bentz and Stock 1986) as predicted by morphological similarity (Wood 1963). A Nei distance of 0.675 between these species suggested that they were not closely related. Kelley and Farrell (1998) provided the first comprehensive phylogeny based on mitochondrial COI DNA nucleotides that included most valid *Dendroctonus* species. One most parsimonious tree revealed a sister relationship between *D. frontalis* and *D. vitei*, and *D. mexicanus* was basal to these species. However, the authors suggested that the relationship between *D. frontalis* and *D. vitei* might have been an artifact of the incomplete sequence of *D. vitei,* and suggested a possible sister relationship between *D. frontalis* and *D. mexicanus* that is consistent with morphological data. The *D. frontalis* species complex as defined by Lanier and others (1988) was monophyletic.

Dendroctonus frontalis has also been included in higher-level phylogenetic analyses of scolytines (Sequeira and Farrell 2001, Sequeira and others 2000). These studies used various single copy nuclear and ribosomal genes to reconstruct, in part, phylogenies of eight *Dendroctonus* species, including members of the *D. frontalis* species complex. The phylogenies resulting from these separate gene analyses differed in the arrangement of some species. Notably, the author of this chapter conducted a parsimony analysis including 4,684 nucleotides from five genes (small nuclear ribosomal subunit 18S, large nuclear ribosomal subunit 28S, elongation factor-1alpha, enolase, and COI) for eight *Dendroctonus* species including *D. frontalis* (for GenBank numbers see Sequeira and Farrell 2001, Sequeira and others 2000). An exhaustive tree search using default settings in PAUP* (Phylogenetic Analysis Using Parsimony [*and other methods]) version 4 (Swofford 2002) resulted in one most parsimonious tree (Figure 1.4). High bootstrap values were found for all clades within the tree (Figure 1.4). A close relationship between *D. frontalis* and *D. mexicanus* was recovered, and relationships of the remaining species were similar to those that were predicted by biological data (Lanier and others 1988).

1.4. CONCLUSION

We have a good understanding of the state of *D. frontalis* systematics. The species is concretely defined by morphological and molecular data. Future systematic research on

D. frontalis would best focus on phylogenetics and population genetics. A phylogenetic analysis using the above nucleotide data and morphological characters for all *Dendroctonus* species, especially *D. vitei,* would firmly fix the relationship of *D. frontalis* among the other species. A detailed examination of intraspecific genetic variation would allow for inference of contemporary gene flow and the evolutionary processes that shaped the biology and ecology of *D. frontalis*.

1.5. ACKNOWLEDGMENTS

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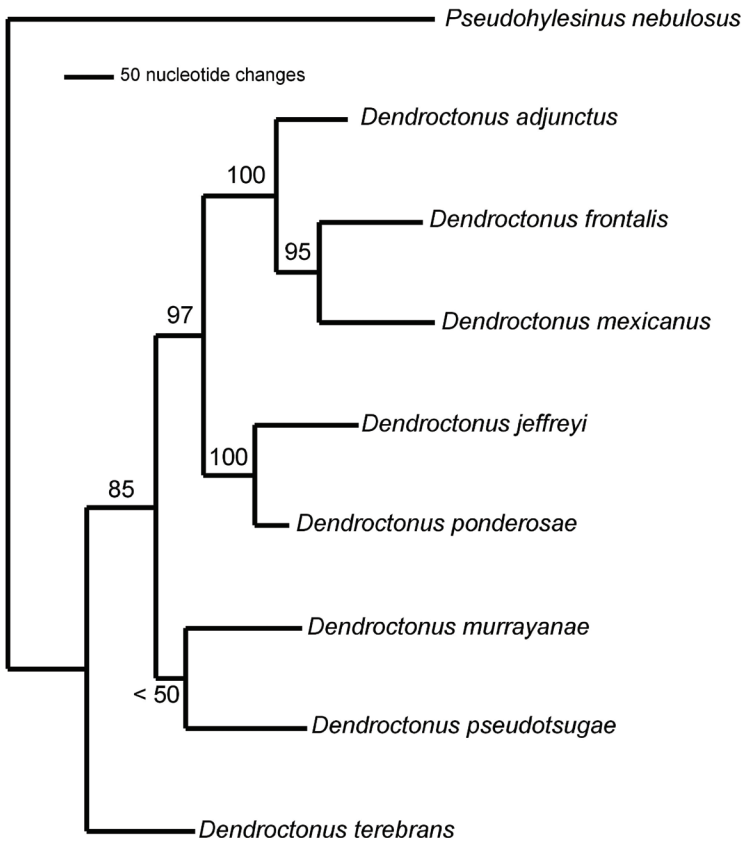

Figure 1.4—Molecular phylogen of *Dendroctonus* species reconstructed with 401 parsimony-informative characters derived from 4,684 nucleotides from 18S ribosomal subunit (1666 bp), 28S ribosomal subunit (684 bp), elongation factor-1alpha (865 bp), enolase (423 bp), and COI (1046 bp). An exhaustive search recovered one most parsimonious tree. Bootstrap values calculated with 1,000 pseudo-replicates are given at the branches, and branch lengths are equal to number of character state changes.